

Volume 6, Number 8

June 1983
ISSN 0007-1056

BRITISH JOURNAL OF HERPETOLOGY

Published by
The British Herpetological Society

BRITISH JOURNAL OF HERPETOLOGY

Volume 6, Number 8 June 1983

CONTENTS

DEGANI, G. Oxygen consumption rate of <i>Salamandra salamandra</i> (L.) from different habitats	281
MEEK, R. Body temperatures of two species of desert amphibians, <i>Rana perezii</i> and <i>Bufo mauritanicus</i>	284
BUSTARD, H. R. and SINGH, L. A. K. Movement of wild gharial, <i>Gavialis gangeticus</i> (Gmelin) in the River Mahanadi, Orissa (India)	287
GITTINS, S. P. Diurnal activity of the common toad (<i>Bufo bufo</i>) during the breeding migration to a pond in mid-Wales	292
BEEBEE, T. J. C. Factors influencing the growth and survival of natterjack toad (<i>Bufo calamita</i>) tadpoles in captivity	294
COOKE, A. S. Estimating numbers of natterjack tadpoles (<i>Bufo calamita</i>)	299
GRIFFITHS, R. A. Ontogenetic changes in phototaxis in the smooth newt, <i>Triturus vulgaris</i> (L.)	301
HOUSE, S. M. and SPELLERBERG, I. F. Comparison of <i>Lacerta agilis</i> habitats in Britain and Europe	305
QUAYLE, A. Notes on the diet of Erhard's wall lizard, <i>Podarcis erhardii</i>	309
VICKERS, B. R. Balearic <i>Emys orbicularis</i> (short note)	310
SPAWLS, S. A new <i>Psammophis</i> from northern Ghana	311
BOOK REVIEW	313
ANNOUNCEMENTS	314

British Journal of Herpetology is published by the British Herpetological Society and edited on behalf of the Society by R. A. Avery.

The Journal is published twice a year and is issued free to members. Applications to purchase copies and/or for details of membership should be made to the Hon. Secretary, British Herpetological Society, c/o The Zoological Society of London, Regent's Park, London NW1.

Instructions to authors are printed inside the back cover; contributions should be addressed to the editor, Dr R. A. Avery, Department of Zoology, The University, Bristol BS8 1UG.

British Journal of Herpetology is indexed in *Current Contents: Agriculture, Biology and Environmental Sciences*.

The Editor is grateful to the following people who kindly reviewed manuscripts during 1982: A. Arak, T. J. C. Beebee, A. d'A. Bellairs, D. Bird, A. S. Cooke, K. F. Corbett, R. A. Dutton, S. P. Gittins, T. R. Halliday, B. Hughes, L. C. Kelleway, M. R. K. Lambert, M. A. Linley, C. J. McCarthy, J. Ryder, A. Salvador, I. F. Spellerberg, K. D. Wells.



WORLD CONGRESS OF HERPETOLOGY

By recent action of the officers and official representatives of the major national and international herpetological societies, an international committee has been established to plan the first World Congress of Herpetology. The congress will be held in 3-5 years at a site yet to be selected. The Planning Committee consists of:

Donald G. Broadley (Zimbabwe)	Toshijiro Kawamura (Japan)
Harold G. Cogger (Australia)	Michael R. K. Lambert (U.K.)
J. C. Daniel (India)	Hubert Saint Girons (France)
Ilya S. Darevsky (U.S.S.R.)	P. E. Vanzolini (Brazil)
Marinus S. Hoogmoed (Netherlands)	David B. Wake (U.S.A.)
Kraig Adler (U.S.A.), <i>Secretary-General</i>	

The congress will be organized to include a wide range of topics, to appeal to all persons interested in the scientific study of amphibians and reptiles. The committee currently is setting guidelines for operation, including the establishment of a larger and broadly representative International Herpetological Committee to provide a self-perpetuating mechanism for future congresses.

The Planning Committee solicits comments from the herpetological community on all aspects, in particular the choice of a convenient site and content of the congress. Potential hosts for the congress are also invited to communicate. Further announcements will be published in this journal.

Address comments or questions to any member of the Planning Committee or to the Secretary-General: Professor Kraig Adler, Cornell University, Section of Neurobiology and Behavior, Seeley G. Mudd Hall, Ithaca, New York 14853, U.S.A.

OXYGEN CONSUMPTION RATES OF *SALAMANDRA SALAMANDRA* (L.) FROM DIFFERENT HABITATS

GAD DEGANI

*Department of Biology, Technion, Haifa, Israel**

(Received 28 February 1982)

SUMMARY

Oxygen consumption was measured during winter and summer in *Salamandra salamandra* from three different habitats, one moist and the others semi-arid. Oxygen consumption rates of all salamander populations were higher in winter than in summer. Weight specific oxygen consumption was lower in salamanders from semi-arid habitats than in salamanders from the moist habitat. This difference is related to differences in the body size of these populations. The effect of body size on metabolic rate was greater in winter than in summer. Q_{10} values for both groups were lower in summer than in winter; this may be an adaptation for reduced activity when food is unavailable.

INTRODUCTION

Salamandra salamandra is found throughout Europe, Israel and North Africa (Eiselt, 1958; Degani, 1979). In Israel, it is found in semi-arid habitats on Mt Carmel and Central Galilee where water is available in ponds, streams and springs only in winter, and in a moist habitat, Tel Dan, where water is available during the entire year (Degani & Mendelssohn, 1979). In the semi-arid habitats where summer temperatures are high and humidity is low (Degani & Warburg, 1978), salamanders would be in danger of dehydration if they were active in summer as they are in temperate climates. In these habitats, however, they retreat underground and remain inactive for several months. A low Q_{10} during this period would evidently be advantageous but, in all amphibia, high ambient temperatures tend to raise the metabolic rate but sometimes the Q_{10} is lower at high temperatures (Fitzpatrick, Bristol & Stokes, 1972). In the moist habitat studied this problem is less severe and salamanders there are active and breed at all seasons.

Adult salamanders in Israel are larger than those from most of the temperate habitats (Degani, 1979) and in Israel those from semi-arid habitats are larger than those from the moist habitat (Degani, 1979). The larger body size is a positive factor in maintaining a balanced water economy (Warburg & Degani, 1979). It is known that there is an inverse correlation between the body size of a species and its weight-specific metabolic

rate (Feder, 1976). It might be expected that a similar relation holds within a species.

To better understand how salamanders survive a long period of inactivity during the dry hot summer, we compared oxygen consumption in summer and winter of salamanders from semi-arid habitats with that of salamanders from a moist habitat, where they do not experience a long dry period.

MATERIALS AND METHODS

Adult *S. salamandra* (60–90 g) were collected in Galilee and Carmel (semi-arid habitats) and (18–40 g) from Tel Dan (moist habitat). Juveniles from Galilee weighing between 8–12 g, were raised from larvae collected from Gush Halav Pond (see Degani & Mendelssohn, 1979) and were studied in the second year after metamorphosis. All salamanders were kept without food at an acclimation temperature of $16 \pm 0.5^\circ\text{C}$ for 21 days, 12 hr of light, 12 hr of dark before the oxygen consumption measurements. The metabolic rates were measured from 9:00 a.m. to 3:00 p.m. with the animals at rest. Three salamanders from the same population were placed in individual metabolic chambers which were connected to each other by plastic pipes. The three metabolic chambers were placed within temperature controlled cabinets. Air flow to the metabolic chambers was measured (48 ml/min), the air was dried over silica gel and percentage of O_2 in the air entering and leaving the metabolic chamber was determined by a Paramagnetic O_2 Analyzer (Beckman Model G_2), at several temperatures: 16, 20, 25 and 30°C . The salamanders were kept at the experimental temperature for 2 hours before measurements were taken.

RESULTS

Oxygen consumption rates of salamanders from different localities and seasons at various experimental temperatures are shown in Table I. Mean metabolic rates at all temperatures were higher in all the salamander populations in winter than in summer, but significant differences were found mostly at temperatures between $25\text{--}35^\circ\text{C}$. Oxygen consumption rate was higher in the Tel Dan salamanders than in the semi-arid populations (Galilee and Carmel; Table I) and the difference was significant at most of the experimental temperatures. No significant difference of

* Present address: Galilee Technological Centre, Kiryat Shmona 10200, Israel.

TABLE I. Rates of oxygen consumption of *Salamandra salamandra* from different habitats under four experimental temperatures during two seasons (acclimation temperature 16°C)

Experimental temperature °C	N	$\mu\text{l O}_2 \text{g}^{-1}\text{h}^{-1}(\bar{x} \pm \text{SD})$		P (t-tests)	
		summer	winter		
Galilee					
16	10	15.03 ± 2.95	14	18.37 ± 3.29	< 0.05
20	9	16.48 ± 2.74	12	33.20 ± 13.70	< 0.01
25	10	24.84 ± 5.68	13	50.95 ± 12.53	< 0.001
30	8	39.60 ± 3.36	14	74.81 ± 15.20	< 0.001
Carmel					
16	8	17.55 ± 5.37	10	20.48 ± 7.05	> 0.1
20	9	23.41 ± 6.53	15	31.70 ± 15.12	> 0.1
25	9	29.15 ± 5.23	12	44.28 ± 9.48	< 0.001
30	9	35.4 ± 5.43	16	65.70 ± 11.14	< 0.001
Dan					
16	10	21.51 ± 3.40	12	22.96 ± 9.09	> 0.1
20	11	28.65 ± 4.38	15	38.71 ± 9.61	< 0.001
25	10	37.13 ± 8.10	14	59.81 ± 7.61	< 0.001
30	12	54.45 ± 10.92	24	137 ± 45.90	< 0.001
Galilee (Juveniles)					
16	14	41.76 ± 12.65	9	60.19 ± 4.43	< 0.001
20	12	66.81 ± 24.02	9	83.46 ± 18.03	> 0.1
25	13	85.79 ± 16.49	9	114.00 ± 7.99	< 0.001
30	8	126.14 ± 27.82	9	210.60 ± 12.04	< 0.001

TABLE II. The relationship of metabolism (MR: $\mu\text{l O}_2 \text{h}^{-1}$) and body weight (W: grams) of *Salamandra salamandra* from Galilee under different temperatures

Experimental temperature °C		N	r	P
Summer				
16	MR = 56.4W ^{0.41}	24	0.77	< 0.01
20	MR = 183.83W ^{0.20}	21	9.63	< 0.05
25	MR = 117.57W ^{0.45}	23	0.83	< 0.001
30	MR = 271.54W ^{0.28}	16	0.91	< 0.001
Winter				
16	MR = 10.01W ^{0.86}	23	0.99	< 0.001
20	MR = 22.57W ^{0.70}	21	0.95	< 0.001
25	MR = 53.85W ^{0.59}	21	0.99	< 0.001
30	MR = 95.03W ^{0.53}	21	0.98	< 0.001

TABLE III. Comparison of Q_{10} of *S. salamandra* from different habitats during summer and winter

Locality	Mean $Q_{10} \pm \text{SD}$ at experimental temperature		
	16–20°C	20–25°C	25–30°C
Summer			
Galilee (adult)	1.59 ± 0.25	2.12 ± 0.50	1.81 ± 0.48
Carmel (adult)	2.28 ± 0.88	1.67 ± 0.51	1.49 ± 0.16
Dan (adult)	2.04 ± 0.66	1.76 ± 0.28	1.99 ± 0.47
Galilee (juvenile)	3.70 ± 1.41	2.23 ± 0.45	3.05 ± 1.53
Winter			
Galilee (adult)	3.42 ± 1.52	2.90 ± 1.23	3.42 ± 1.41
Carmel (adult)	3.18 ± 1.16	2.76 ± 1.61	2.87 ± 0.53
Dan (adult)	4.16 ± 2.58	3.33 ± 1.45	5.51 ± 2.41
Galilee (juvenile)	2.59 ± 1.10	3.37 ± 1.52	2.60 ± 1.08

oxygen consumption rate was found between salamanders from Galilee and Carmel populations. Oxygen consumption of juvenile salamanders (Galilee) was

significantly higher than that of adult salamanders from all populations (t-test: $P < 0.05$).

Relationships between body size and metabolic rate are shown in Table II. Probability values in the Table show the significance of differences between measurements and an equation $\ln MR = b \ln W + \ln a$ evaluated from $t = r\sqrt{(n-2)/(1-r^2)}$ with $(n-2)$ degrees of freedom. Slopes were higher in winter than in summer at all experimental temperatures but the difference was significant only at 25–30°C (t-test: $P < 0.001$). Moreover the slopes were higher at lower temperatures than at higher temperatures and the differences were significant (t-tests: $P < 0.05$) between all temperatures in summer and most of the temperatures in winter.

There were no significant differences between Q_{10} of salamanders from different populations. In all adult salamanders, however, Q_{10} was higher in winter than in summer (t-tests: $P < 0.05$. See Table III).

DISCUSSION

Salamanders in the semi-arid habitats studied have adapted their metabolism to the climatic conditions in several ways. Of these, this study deals with larger body size and seasonal variation in the temperature dependence of the metabolic rate. The parameters connecting body size to metabolic rate at different temperatures were found, in this intra-species study, to be essentially the same as those found in inter-species studies (Feder, 1976; Whitford & Hutchison, 1967). This is true, however, only in the wet winter season. In summer, the influence of body size on metabolic rate is less, as may be seen from the lower exponents.

The rise of metabolic rate with temperature (Q_{10}) was also found to be dependent on the season. Over the same temperature range, the Q_{10} was lower in summer than in winter. No significant difference in Q_{10} was

found between the various populations. The lower O_2 consumption rates of salamanders from semi-arid habitats may be accounted for by their larger body size.

All these factors may be correlated to the life cycle of the salamander (Degani & Warburg, 1972; Degani & Mendelssohn, 1980). In the semi-arid habitats studied, salamanders are active mainly in winter, and breed only in the early winter. In the moist habitat, the breeding period extends into spring and even into summer. Salamanders in the semi-arid locations then must endure a long dry period without food. The larger body size of salamanders in these habitats together with the seasonal variation in Q_{10} lead to a lowering of the metabolic rate, which enables them to live through the summer. This is in agreement with the conclusions of Noble (1931), Vernberg (1952) and Dunlap (1969, 1971), but they found the higher resting metabolic rate in spring and the lower rate at the beginning of the winter.

ACKNOWLEDGEMENTS

I wish to thank Professor A. Shkolnik and Professor H. Mendelssohn for their help and advice, and Gideon Barch for his help in preparing this paper for publication.

REFERENCES

- Degani, G. (1979). Morphological and biochemical differences between *Salamandra salamandra* (L.) populations in Israel. *Israel Journal of Zoology* **28**, 54–55.
- Degani, G. & Mendelssohn, H. (1979). The food of *Salamandra salamandra* (L.) tadpoles in Israel in different habitats. *Israel Ecological Society* 1979, 19c–45c.
- Degani, G. & Mendelssohn, H. (1980). Seasonal activity of adult and juvenile *Salamandra salamandra* (L.) at the southern limit of their distribution. *British Journal of Herpetology* **6**, 79–81.
- Degani, G. & Warburg, M. R. (1978). Population structure and seasonal activity of adult *Salamandra salamandra* (L.) (Amphibia, Urodela) in Israel. *Journal of Herpetology* **12**, 437–444.
- Dunlap, D. G. (1969). Influence of temperature and duration of acclimation, time of day, sex and body weight on metabolic rate in the hylid frog *Acris crepitans*. *Comparative Biochemistry and Physiology* **31**, 555–570.
- Dunlap, D. G. (1971). Acute measured metabolic rate—temperature curves in the cricket frog, *Acris crepitans*. *Comparative Biochemistry and Physiology* **38A**, 1–16.
- Eiselt, J. (1958). Der Feuersalamander *Salamandra salamandra* (L.). Beitrag zu einer taxonomischen synthese. *Abhandlungen und Berichte aus dem Museum für Naturkunde und Vorgeschichte in Magdeburg* **10**, 77–154.
- Feder, M. E. (1976). Oxygen consumption and body temperature in neotropical and temperate zone lungless salamanders (Amphibia: Plethodontidae). *Journal of Comparative Physiology* **110**, 197–208.
- Fitzpatrick, L. C. (1971). Influence of sex and reproductive condition on metabolic rate in the Allegheny Mountain salamander *Desmognathus ochrophaeus*. *Comparative Biochemistry and Physiology* **40A**, 603–608.
- Fitzpatrick, L. C. (1973). Influence of seasonal temperature on the energy budget and metabolic rates of the northern two-lined salamander *Eurycea bislineata bislineata*. *Comparative Biochemistry and Physiology* **45A**, 807–818.
- Fitzpatrick, L. C., Bristol, J. R. & Stokes, R. M. (1972). Thermal acclimation and metabolic rates in the dusky salamander *Desmognathus fuscus*. *Comparative Biochemistry and Physiology* **41A**, 89–96.
- Knapp, W. (1974). Die jahreszeitliche steuerung der Atmung in Abhängigkeit von Akklimations temperature und Experimental temperature bei *Triturus alpestris* Laur. und *Salamandra atra* Laur. (Amphibia). *Oecologia (Berlin)* **15**, 353–374.
- Noble, G. K. (1931). *The Biology of the Amphibia*. New York: McGraw-Hill.
- Ultsch, G. R. (1974). Gas exchange and metabolism in Sirenidae (Amphibia, Caudata). I. Oxygen consumption of submerged sirenids as a function of body size and respiratory surface area. *Comparative Biochemistry and Physiology* **47A**, 485–498.
- Warburg, M. R. & Degani, G. (1979). Evaporative water loss and uptake in juvenile and adult *Salamandra salamandra* (L.) (Amphibia, Urodela). *Comparative Biochemistry and Physiology* **62A**, 1071–1075.
- Vernberg, J. (1952). The oxygen consumption of two species of salamanders at different seasons of the year. *Physiological Zoology* **25**, 243–249.
- Whitford, W. G. & Hutchison, V. H. (1967). Body size and metabolic rate in salamanders. *Physiological Zoology* **40**, 127–133.

BODY TEMPERATURES OF TWO SPECIES OF DESERT AMPHIBIANS, *RANA PEREZI* AND *BUFO MAURITANICUS*

R. MEEK

561 Coal Road, Leeds 14

(Received 29 January 1982)

SUMMARY

Measurements were made in the field on the body temperatures of two species of anuran amphibians, *Rana perezi* and *Bufo mauritanicus*, in a desert region of southern Morocco. Both species were found to employ heliothermy to elevate their body temperatures above air and water temperature.

INTRODUCTION

Amphibians are ectothermic and rely on behavioural mechanisms to regulate their body temperature. Many species of anuran amphibians are heliothermic and through basking and conduction are able to raise their body temperature to levels that may be similar to those attained by certain species of reptilian heliotherms (for reviews see Brattstrom, 1963, 1979). However, the permeability of the amphibian integument and the excretion of nitrogenous wastes in the form of urea imposes severe water balance problems for these animals when they inhabit dry environments and thus in these regions heliothermy may be restricted to those species or populations that live in the vicinity of permanent water. This paper reports on observations on the body temperatures of two species of anuran amphibians: *Rana perezi* and *Bufo mauritanicus* which were found in a habitat consisting of a series of natural and man-made bodies of water in a desert region in Southern Morocco.

Brattstrom (1970) has drawn attention to the fact that body temperature data are conspicuously lacking for even the commonest amphibians from continents other than the Americas and there are indeed few such data available on species from the Mediterranean region. Under field conditions Busack (1978) found maximum body temperatures of 25°C in *Alytes obstetricans* and 16°C in *Salamandra salamandra* in Spain. These however fell below the body temperatures recorded for these species in a laboratory study by Strübing (1954).

METHODS, MATERIALS AND STUDY AREA

Field observations were carried out from late May through to mid-June 1980. Data on the temperature of both the animals and the environment were recorded with mercury bulb thermometers and a Whitley digital

thermometer. The Whitley digital thermometer was battery operated and consisted of a silicon sensor probe combined with LSI CMOS circuitry. This thermometer had a temperature range of –50 to +150°C with an error of $\pm 0.5^\circ\text{C}$. The ambient air temperatures at the sites were recorded with the bulbs shaded; sand temperatures by inserting the bulbs approximately 8 mm into the sand. The water temperature was measured at depths of 10–15 cm. Body temperatures in both species were taken orally when the animals were out of water. To minimize the effects of heat transference, body temperatures were recorded as quickly as possible. A total of 55 body temperature readings on *R. perezi* and 40 on *B. mauritanicus* were taken. All *R. perezi* were caught with nets that had been constructed with adjustable handle lengths, which made it possible to capture animals at distances up to 3.5 m. All *B. mauritanicus* were caught by hand.

Rana perezi were studied at an irrigation channel running from southeast to northwest; *Bufo mauritanicus* at a small pond that lay 30 m from the channel. The area surrounding the site was mostly “reg” or stony desert which was typically barren with the only major plant life being patches of dense growth of succulents (*Euphorbia* sp.). The climate of the region is arid; the most extreme daily air temperatures occur during the months of August and September when maxima between 44–47°C may be experienced.

RESULTS

Rana perezi. Basking in *R. perezi* was observed at all times of day. Some of the frogs basked in open patches with no shade, but others were in partly shaded sites. All of the body temperature data recorded were under conditions of clear skies between 11:00–16:30 hr. During the time that data were gathered the relative humidity at distances of 3 m from the water averaged at 45% and never exceeded 48%. Sand temperatures ranged from 45°C to 55°C. Body temperatures for *R. perezi* in relation to air (T_A) and water (T_W) temperatures are shown in Fig. 1. A range of body temperatures from 24.5–32°C ($\bar{x} = 28.4^\circ\text{C}$, $n = 55$) were recorded. Generally they were found to be higher between 11:30–13:30 hr; after this time they showed a general decrease. As would be expected from the extremely high levels recorded, all frogs had body temperatures below that of sand temperatures, but all except one individual had body temperatures in excess

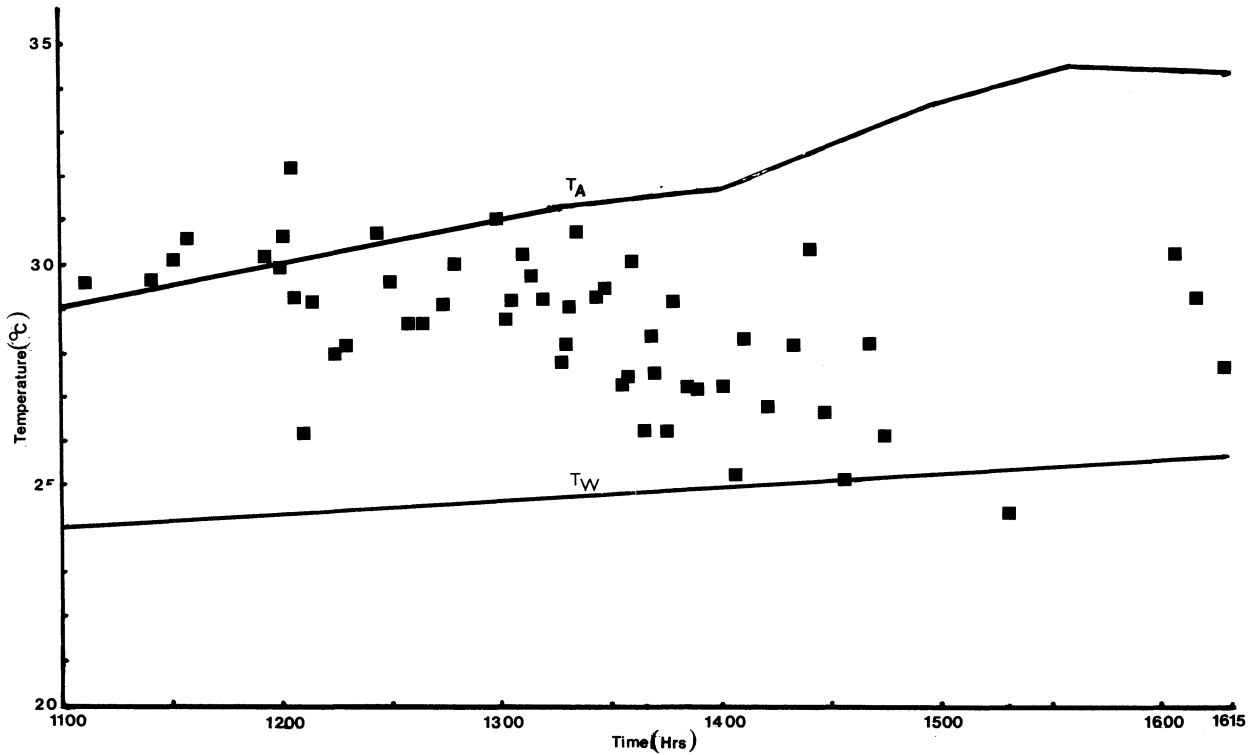


FIG. 1. Graph of body temperature against time of day for *Rana perezi* in relation to change in air temperature (T_A) and water temperature (T_W). Mean body temperature ± 1.96 SD = $28.45 \pm 3.14^\circ\text{C}$ ($N = 55$).

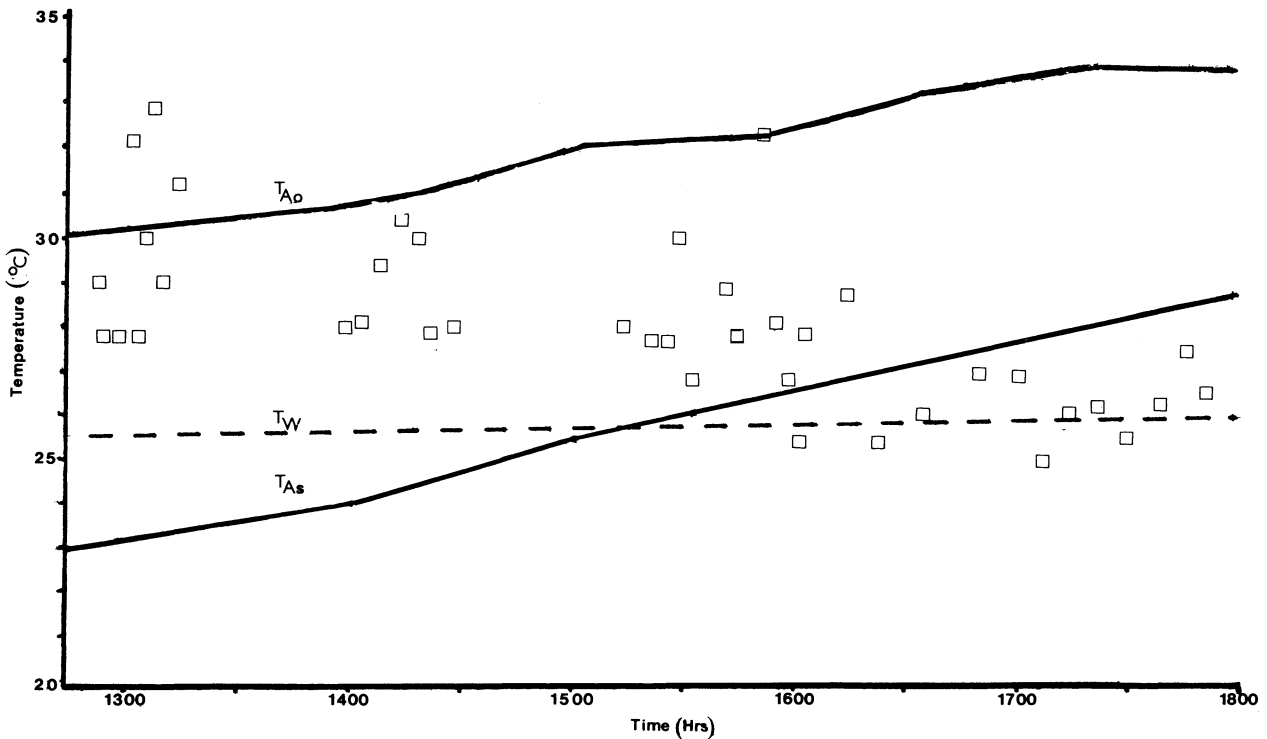


FIG. 2. Graph of body temperature against time of day for *Bufo mauritanicus* in relation to changes in air temperature in unshaded areas (T_{A0}), air temperature in shaded areas (T_{As}) and water temperature in the pools (T_W). Mean body temperature ± 1.96 SD = $28.15 \pm 3.79^\circ\text{C}$ ($N = 40$).

of water temperature (98.2%) with 16.3% of body temperatures exceeding air temperature. As the day progressed however the relationship between body temperature and air temperature altered. For example, no frog after 12:30 hrs was found to have a body temperature in excess of air temperature although one

animal, at 12:55 hrs, had a body temperature equal to air temperature.

Bufo mauritanicus—Body temperatures in *B. mauritanicus* were recorded between 12:30 and 18:00 hr. In contrast to the area inhabited by *R. perezi*, this study site had abundant shaded areas in the form of

trees (*Eucalyptus sp.*) and crevices in the rocks, therefore a wider range of environmental parameters were recorded. The highest temperatures were those of the sand in the open areas which ranged from 45–55°C, but fluctuated around 30°C in the shade. The relative humidity in exposed sites was 45% but increased to 76% in the area surrounding the pool.

Basking on the sand in open unshaded areas was observed in only three *B. mauritanicus* and this was for only brief periods in each case. The data in Fig. 2 show the relationship between *B. mauritanicus* body temperatures and environmental temperatures. A range of body temperatures from 25–33°C ($\bar{x} = 28.1$, $n = 40$) were recorded. Generally they were higher between 12:30–15:30 hr after which the toads tended to retire to cooler sites. Ten percent of the toads had body temperatures higher than air temperatures in open areas while 60% had body temperatures in excess of air temperature in the shade. The majority (90%) had body temperatures equal to or higher than water temperature. The data recorded from 12:00 hr onwards show that after this time no animal had a body temperature in excess of air temperature in unshaded areas. The three animals found basking on the sand in the open area had body temperatures of 30, 32.3 and 33°C.

DISCUSSION

The observations on the behaviour and body temperatures of *R. perezii* and *B. mauritanicus* indicate that they regulate their body temperature by shuttling between sunlit and shaded areas or by retreating into water and are thus able to maintain body temperature to within a range of approximately 8°C. The ability to reduce body temperature may be increased as a result of the substantial amounts of evaporative cooling that take place as a result of the permeability of the amphibian integument (Mellanby, 1941, Cloudsley-Thompson, 1974). In a laboratory study of the water relations of *B. mauritanicus*, Cloudsley-Thompson (1974) measured the rate of evaporative water loss and compared it to evaporative losses in *B. regularis*. He found that at high air temperatures the losses were higher in *B. mauritanicus* but that this enabled *B. mauritanicus* to maintain lower body temperatures. The conclusions were that an ability to maintain low body temperatures may be more useful in dry environments than an ability to conserve body water since neither species demonstrated an ability to survive for long in a dry atmosphere. Evaporative cooling and a constant water supply is probably the major contributing factor in allowing these amphibians to remain abroad even during periods when because of high temperatures,

most of the reptile species on the study area (e.g. *Eumeces*, *Sphenops* and *Tarentola*) retire underground or to shaded areas.

The maximum voluntary temperature of 32°C found for *R. perezii* and 33°C for *B. mauritanicus* compares with the maximum recorded for ranids of 34.7°C and bufonids of 33.7°C (Brattstrom, 1963), temperatures which fall just below the maximum recorded for amphibians of 34.8°C in *Acris crepitans* (Fitch, 1956, reviewed in Brattstrom, 1963). These observations on basking behaviour and body temperatures support the view of Brattstrom (1963) that heliothermy is possible in anurans while they are in association with permanent water. Clearly this effectively limits the problems of dehydration that they would encounter even while employing heliothermy in a region with high daily temperatures and low humidity levels.

ACKNOWLEDGEMENTS

Ken Umpleby and Helen Meek assisted with the field work. For equipment used in the field I thank the University of Leeds, Paul Walton of Don Whitley Scientific Ltd and Michael Dixon (who constructed the catching equipment).

REFERENCES

- Brattstrom, B. H. (1963). A preliminary review of the thermal requirements of amphibians. *Ecology* **44**, 238–255.
- Brattstrom, B. H. (1970). Amphibia. In *Comparative physiology of thermoregulation. I. Invertebrates and non-mammalian vertebrates*, 135–166. Whitton, G. C. (Ed.) New York & London: Academic Press.
- Brattstrom, B. H. (1979). Amphibian temperature regulation studies in the field and laboratory. *American Zoologist* **19**, 345–356.
- Busack, S. D. (1978). Body temperatures and live weights of five Spanish amphibians and reptiles. *Journal of Herpetology* **12**, 256–258.
- Cloudsley-Thompson, J. L. (1974). Water relations of the African toad, *Bufo mauritanicus*. *British Journal of Herpetology* **5**, 425–426.
- Fitch, H. S. (1956). Temperature responses in free-living amphibians and reptiles of north eastern Kansas. *University of Kansas. Publications of the Museum of Natural History* **8**, 417–476.
- Mellanby, K. (1941). The body temperature of the frog. *Journal of Experimental Biology* **18**, 55–61.
- Strübing, H. (1954). Über Vorzugstemperaturen von Amphibien. *Zeitschrift für Morphologie und Ökologie der Tiere* **43**, 357–386.

MOVEMENT OF WILD GHARIAL, *GAVIALIS GANGETICUS* (GMELIN) IN THE RIVER MAHANADI, ORISSA (INDIA)

H. R. BUSTARD* AND L. A. K. SINGH

Central Crocodile Breeding and Management Training Institute, Rajendranagar Road, Hyderabad 500 264, India

(Received 11 January 1982)

SUMMARY

Four adult gharial in the Mahanadi River made long range movements up to 44.4 km, although their home ranges were considered to have been very much smaller than this.

INTRODUCTION

A study of the movements of wild adult gharial was carried out in the Mahanadi River, Orissa, between 1 August 1975 and 31 January 1976 as part of a study of the conservation requirements of the species. In 1974 a detailed study of gharial biology was an essential prerequisite for the elaboration of an effective plan for the future survival of the gharial since as pointed out by Bustard (1970), it is not possible to plan the conservation of a species whose ecology has not been studied. In Orissa the remnant gharial population of the State was resident in and around Satkoshia Gorge in trans-Mahanadi. This area was recommended for a sanctuary by the senior author as being one of the best remaining sites in the Indian range of the species (FAO, 1974). However, without knowledge of the movements of the remaining gharial it was not possible to delineate biological boundaries of the proposed sanctuary.

METHODS

Water-borne gharial guards were posted during 1975 as part of the gharial protection programme (FAO, 1974, 1975). These guards were local fishermen with an intimate knowledge of the Gorge and its surroundings who maintained a daily watch over the last four adult gharial remaining in the gorge. The four gharial comprised two of each sex. Sex is easily recognizable in gharial due to the presence of an enlarged protuberance, the "ghara" (Hindi = pot) at the tip of the upper portion of the snout in mature males, that is absent in females. The two individuals of each sex were readily recognizable from size differences and other individually diagnostic features like colour. The males measured approximately 6.6 and 5.5 m in total length and the females approximately 4.6 and 3.6 m. Since the

adult gharial are extremely shy, spoor and pugmarks provided reliable evidence of the presence or recent presence of an individual nearby. From plaster casts of pugmarks it was also possible to individually distinguish the animals on most occasions. In all cases where the pugmarks could not be allocated to one of the four individuals with certainty, that particular record was discounted.

For an easy reference the river was divided into a series of locations numbered with reference to the distance from the foot of the gorge. All confirmed sightings were recorded in relation to these numbers. The numbers of locations downstream from the foot of the gorge are preceded by a negative (–) sign (Fig. 1). The numbers for places which are on the right bank of the river, when reviewed facing upstream, are followed by an asterisk (*). Changes in water level are denoted by (–) or (+) signs when there is a respective fall or rise from the previous level (*i.e.* this has no relation to the datum). Changes in water levels of less than 35 cm, considered minor, have been included in the "no change" category (Table IV).

A meteorological station was maintained at the Gharial Research and Conservation Unit located on the banks of the Mahanadi, within the gorge near Tikerpada village. Temperature and rainfall data presented below (Table I) were recorded here. Water level records (Table I) were also maintained twice daily at the same site.

STUDY AREA

Satkoshia Gorge is a narrow, 22 km (Oriya sat kosh = 14 miles) long stretch of the Mahanadi, flanked on

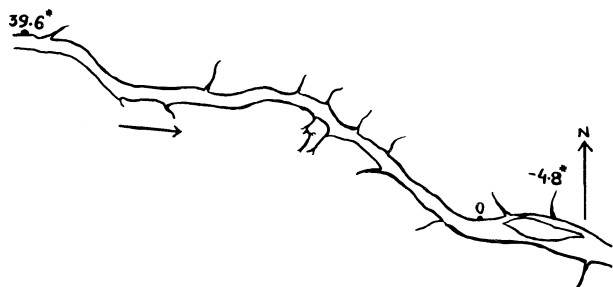


FIG. 1. The Mahanadi River with main tributaries in the study area. "0" marks the foot of the gorge. 39.6* is the point upstream from 0 to which the large male and female gharials moved (see text). –4.8* is 4.8 km downstream from 0.

* Present address: Airlie Brae, Alyth, Perth PH11 8AX, UK.

either banks with high hills rising to over 700 m which fan out at either end. Technically speaking, the area is not strictly a gorge in that the hills do not fall vertically into the river. The river passes between the hills which serve to constrict it, resulting in deeper water, greater

rate of flow during the monsoon, and the retention of deep pools during the dry season.

During summer the depth of water in the gorge measures over 10 m at places, increasing by about 14 m during the monsoon. The flow of water in the gorge has a speed of about 30 cm/sec during summer and about 4 m/sec during high flood. The water flow is influenced by Hirakud Dam, about 210 km upstream from the Unit.

Three well-defined seasons are experienced in this part of Orissa. The rainy season lasts from the third week of June to October, the winter from the middle of October to the middle of February, and the summer from the middle of February to mid-June. The rainfall is mainly derived from the South-West monsoon. The annual rainfall averages approximately 1000 mm. The climate is influenced by its inland situation within the State, by the location between hills and by the abundant forest cover. The first of these results in hot summers and cool winter months, the second restricts sunshine within the gorge to between 09:30 and 15:30 hr during the winter, and the last ameliorates extremes and results in more humid conditions. Screen temperatures vary between 5.0 to 49.3°C. Days are usually humid. Relative humidity varies from 0% to 100% at different times of the day and during different seasons.

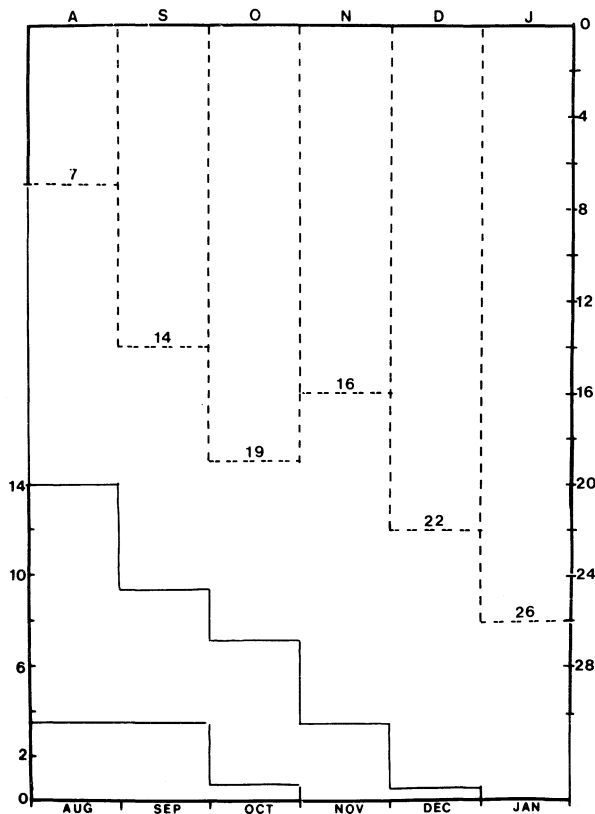


FIG. 2. Number of sightings in the River Mahanadi (dotted bars—scale on right) of the 5.4 m male gharial in relation to monthly maximum and minimum water levels (solid line—scale in m on left).

RESULTS

The 184 days of study cover the period from mid-monsoon to the low water levels of late winter. The following water levels are measured against a lean season datum point. At the start of the study on 1 August 1975 water level was 5.08 m above datum; the highest floods were recorded on 22 August (+13.94 m) and by 31 January 1976 water levels had virtually reached the low season datum, being +0.14 m.

TABLE I. Gharial sightings in relation to climatic conditions: temperature (°C) and rainfall (mm) and water level height (m) above datum. Percentages given in parenthesis are in relation to total sightings for that particular individual (see Table 3)

Data	Aug. 1975	Sept. 1975	Oct. 1975	Nov. 1975	Dec. 1975	Jan. 1975
Number of days sighted						
1. Small male	7 (6.7)	14 (13.4)	19 (18.2)	16 (15.3)	22 (21.1)	26 (25.0)
2. Large male	10 (37.0)	8 (29.6)	5 (18.5)	2 (7.4)	2 (7.4)	0 (0)
3. Small female	0 (0)	3 (15.7)	6 (31.5)	2 (10.5)	4 (21.0)	4 (21.0)
4. Large female	1 (20.0)	4 (80.0)	0 (0)	0 (0)	Remained near 38.4+	
Total sightings	18	29	30	20	28	30
Water level						
1. Maximum	13.94	9.35	7.20	3.53	0.59	0.22
2. Minimum	3.52	3.45	0.79	0.08	0	0
Rainfall	352	345	79	8	0	0
Screen temperature						
1. Maximum	39.5	36.5	36.25	32.5	33.5	31.25
2. Minimum	23.5	23.25	21.5	9.5	5.5	5.0

TABLE II. Gharial movements in relation to water level changes. Percentages given in parenthesis are in relation to total sightings for that particular individual (see Table III)

Movement	5.4 m male	6.6 m male	3.6 m female	4.6 m female	Total movements
1. Upstream with					
(a) Increase in water level	1 (0.9)	2 (7.4)	—	—	3
(b) Decrease in water level	10 (9.6)	7 (29.6)	2 (10.5)	2 (40.0)	21
(c) No change in water level	27 (25.9)	2 (7.4)	4 (21.0)	—	33
2. Downstream with					
(a) Increase in water level	3 (2.8)	4 (14.8)	—	—	7
(b) Decrease in water level	4 (3.7)	1 (3.7)	—	—	5
(c) No change in water level	24 (23.0)	4 (14.8)	8 (42.0)	—	36

TABLE III. Movements of four wild gharial in Satkoshia Gorge (distances in km)

	5.4 m male	6.6 m male	3.6 m female	4.6 m female
1. No. of days sighted	104	27	19	5
2. Percent days sighted*	67	17.4	12.2	3.0
3. Intervals (in days) between sightings	1-10	1-44	1-20	1-75
4. No. of places sighted	22	16	10	4
5. No. of sightings at different places:				
(a) 1 sighting at:	7 places	9 places	5 places	3 places
(b) 2 sightings at:	2 places	5 places	4 places	—
(c) 3 sightings at:	2 places	—	—	1 place
(d) 4 sightings at:	3 places	2 places	—	—
(e) 5 sightings at:	1 place	—	—	—
(f) 6-10 sightings at:	4 places	—	1 place	—
(g) 11-15 sightings at:	1 place	—	—	—
(h) 16-20 sightings at:	—	—	—	—
(i) 21-25 sightings at:	2 places	—	—	—
6. Maximum distance moved in km (all are upstream)				
(a) 28.8	(a) 28.8	(a) 44.4	(a) 22.8	43.2
in 110 days	in 110 days	in 131 days	in 24 days	in 3.5 months
(b) 27.2	(b) 27.2	(b) 20.8	—	—
in 96 days	in 96 days	in 5 days	—	—
(c) 26.4	(c) 26.4	—	—	—
in 22 days	in 22 days	—	—	—

* In relation to total sightings (155).

SEASONAL VARIATIONS IN SIGHTINGS

Data on sightings in relation to water level and climatic conditions are presented in Table I. As can be seen from the Table, total sightings of the four individuals taken together were closely similar in September, October, December and January. However, there is considerable variation in the incidence of sighting individual gharial. For instance, maximum sightings of the large male occurred during August when sightings of the others were minimal. The lower incidence of sightings in August (Table I) may have been due to high flood conditions making sightings more difficult (Fig. 2) and in part due to much more circumscribed movements of the patrolling canoes. The cause of reduced sightings in November is not known but could perhaps be due to increased activity by fishermen.

Table II shows movements and their orientation (upstream or downstream) in relation to changes in water levels. As is shown in the Table, most movements took place without any corresponding change in water level. The only exception to this was a tendency to move upstream with decrease in water levels.

MOVEMENTS

Movement data are presented in Figs 3 and 4 and summarized in Table III, which sets out information on 155 sightings of the four individuals. All four gharial moved very considerable distances in the river. During the study, both the large male and the large female moved similar maximum distances of 44.4 and 43.2 km respectively. The 5.4 m male and 3.6 m female moved lesser but also approximately similar distances of 28.8 and 22.8 km respectively.

Males contributed the bulk of the records—84% of the 155 sightings. This is explicable on the basis that the females were noticeably shyer than the males. In both

cases the larger individuals were also recorded much less than the smaller individuals which accounted for only 20.1% and 20.8% of the sightings of male and female sex groups respectively. Sixty-seven percent of the total sightings were recorded on the small (5.4 m) male.

Short-term movement data are presented in Table IV. These data indicate rapid movements in the river comparable to a man walking briskly along the bank and also that considerable distances may be covered in the course of a single day. The 5.4 m male was sighted regularly, and was seen in every month.

On 13 occasions it was seen twice in a day and on two occasions three times in one day. Excepting only two instances, it was always detected between 1.6 and 20.8* (a distance of 19.2 km). The exceptions are: once downstream to -6.4* when the water level was +10.1 m and once upstream to 22.4 when the water level was +34 cm. Hence it is considered that the home range of this male included a 19.2 km stretch of the river.

Out of 27 records made for the 6.6 m male, eight were between 1.6 and 9.6*, 17 were upstream of 14.4, one was as -4.8* and one at 13.2. This indicates a home range of 12.8 km (1.6 to 14.4).

One of the 19 recordings made on the 3.6 m female, 15 were between 4.0 and 6.8*, two at 14.4, one at 18.0 and one at -4.8*, indicating a home range of 10.4 km (+4 to +14.4).

The 4.6 m female was sighted near -4.8* to 6.8 for five times, after which it moved upstream and remained near 38.4*. This female is considered to have had a home range of 11.6 km (-4.8 to +6.8) and to have subsequently shifted this to the area around 38.4.

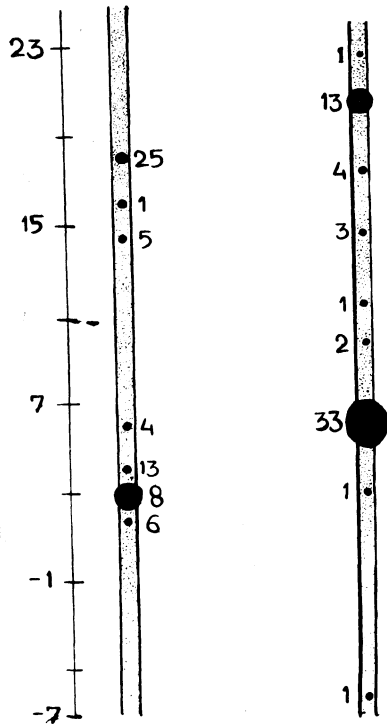


FIG. 3. Movement of the small male gharial. Size of the points accords to the area covered. Numbers beside the points show the number of sightings. Numbers on the scale refer to the distance from the foot of the gorge.

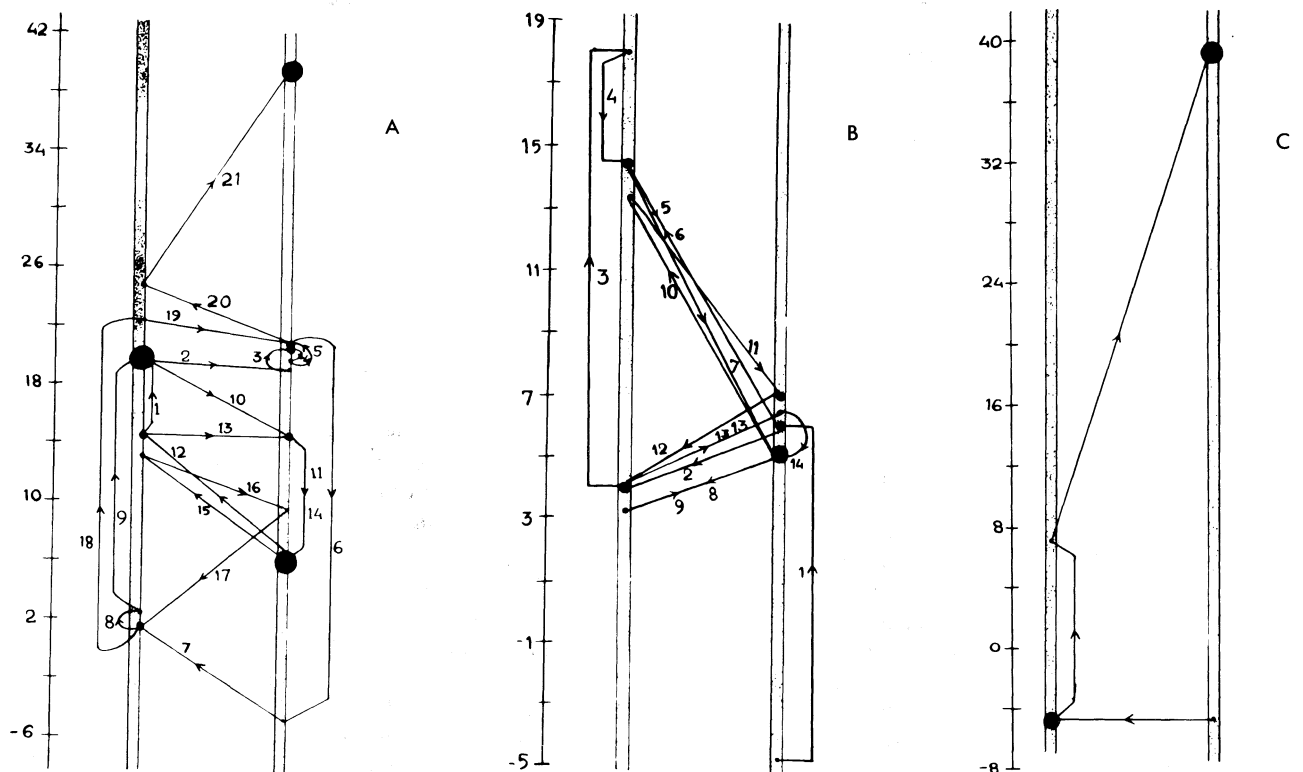


FIG. 4. Movements of the large male (A), small female (B) and large female (C). Each dot shows the place visited. The scale shows the distance from the foot of the gorge. Size of dot accords to the area covered. Lines joining the dots are imaginary; they join consecutive sightings. Numbers beside the lines show the sequence of movements.

TABLE 4. Short term movements in the gharial (distances in km)

Time interval	5.4 m male	6.6 m male	3.6 m female	4.6 m female
1. In 30 minutes	3.6 up	—	—	—
2. In 2 hours	11.98 up	—	—	—
3. In 1 day	11.98 up	—	3.58 up	—
	6.78 up	—	—	—
	10.4 up	—	—	—
4. In 2 days	12.8 up	8.4 down	—	—
	16.4 down	—	—	—
5. In 3 days	—	17.76 up	8.4 up	—
6. In 4 days	—	25.28 down	—	—

The stretch of the Gorge between 4.0 (*) and 6.8 (*) appears to have been favoured by all four gharial. During 1975 and 1976 eggs were collected near 5.2* and 6.0* respectively. This zone, therefore, appears to be their breeding ground.

During the flood gharial are often seen in side streams.

DISCUSSION

The extent of movements recorded for gharial in the present study are much greater than anticipated. However, the areas considered to represent the home ranges are more modest. It is suggested that these extensive movements may have occurred in the absence of other gharial in the river. Male gharial are territorial (Bustard & Maharana, in press) and would be expected to restrict movements of other males in the river. Similar considerations may also be applicable to females. Habitat disturbance may also have played a role. Gharial were observed to leave favoured areas where nylon gill nets were used.

Limited data on movements of two mugger crocodiles (*Crocodylus palustris*) inhabiting Satkoshia Gorge do not indicate any long range movements (Singh, in preparation). Over a twenty month period these two animals moved a maximum distance of only 10.7 km.

Long range movements of gharial necessitate the inclusion of long stretches of the river within sanctuaries created and managed for conservation purposes.

Movements of gharial into side streams during floods

may be associated with similar movements of their fish prey. During high floods fish and gharial enter small side streams probably to avoid the force of water flow in the main river.

ACKNOWLEDGEMENTS

The senior author thanks UNDP/FAO for support. The work was carried out when the junior author was in receipt of a Research Fellowship from the State Government of Orissa (Forest Department). We acknowledge support from our respective organizations and from the Government of India. We particularly want to thank the gharial guards, the late Raja Behera and Prafulla Behera who assisted in the collection of the basic data.

REFERENCES

- Bustard, H. R. (1970). *Australian Lizards*. Sydney & London: Collins.
- Bustard, H. R. & Maharana, S. (in press). Fatal male-male conflict in the gharial (*Gavialis gangeticus*, Gmelin) (Reptilia, Crocodylia).
- FAO. (1974). *India: a preliminary survey of the prospects for crocodile farming (based on the work of H. R. Bustard)*. Rome: UNDP/FAO, reference FO:IND/71/033.
- FAO. (1975). *Gharial and crocodile conservation management. Interim Report, Crocodile Farming Project, India (based on the work of H. R. Bustard)*. UNDP/FAO, reference FO:IND/71/033.

DIURNAL ACTIVITY OF THE COMMON TOAD (*BUFO BUFO*) DURING THE BREEDING MIGRATION TO A POND IN MID-WALES

S. P. GITTINS

Department of Applied Biology, UWIST, King Edward VII Avenue, Cardiff CF1 3NU

(Received 30 September 1982)

SUMMARY

Although the migration of common toads to the breeding pond is mainly nocturnal, 28% of females and 8% of males moved into traps during daylight. The peak of activity occurred early in the night and the decline in activity throughout the night can be explained to a large extent by the fall in air temperature.

INTRODUCTION

Although it is a matter of common knowledge that toads (*Bufo bufo*) are nocturnal (Smith, 1973), and that the migration to the breeding site takes place mainly at night (Moore, 1954; Heusser, 1969), few data have been presented to support this fact. Therefore, during the course of an investigation of the migration of amphibians to a pond in mid-Wales (Gittins, 1983; Harrison, Gittins & Slater, 1983), the opportunity was taken to record the diel activity pattern of the numbers of toads arriving at the pond.

METHODS

Llysdinam Pond, Newbridge-on-Wye (SO 009 586) has a surface area of just under 900 m² and a mean depth of 0.6 m (Fig. 1). For a further description of the pond and the surrounding area see Gittins (1983). The pond was completely encircled by a clear polythene barrier, 203 m long, 30 cm high and buried to a depth of 5 cm. Pitfall traps consisting of plastic buckets, 22 cm in diameter and 22 cm in depth, were sunk on each side of the barrier at approximately 15 m intervals (Fig. 1). Toads migrating into or out of the pond encountered the barrier, turned and moved parallel with the polythene sheeting until they fell into one of the pitfall traps. Individuals showed little tendency to climb or burrow under the barrier. The captured toads were collected during circuits of the pond made at 2 hr intervals throughout the day and night, and once recorded, individuals were released on the opposite side of the barrier to that on which they were captured. Data for this study were collected over 11 complete days from 20 March 1982 to 1 April 1982, and during this period all captures occurred while the toads were entering the pond. Air temperature was recorded continuously at a site adjacent to the pond.

RESULTS

The daily patterns of the number of male and female toads arriving at the barrier are shown in Fig. 2. During the study period it became dark at approximately 19:00 hr and light at approximately 05:00 hr, and it is clear from Fig. 2 that the majority of movement took place at night. However, 28% of females and 8% of males were captured during the day-time (06:00–18:00 hr) showing that toads are willing to move during day-light. The difference in the number of males and females active during the day-time was significant ($\chi^2 = 13.64$, $P < 0.001$), although the significance test is not strictly valid as the expected frequency for females fell below 5. It does suggest, however, that there may be sexual differences in toads in their degree of activity during daylight.

The peak of activity of both sexes falls in the early part of the night, between 18:00–22:00 hrs for males and 20:00–22:00 hr for females. This peak is even more pronounced than the graph suggests because the 18:00–20:00 hr collection represents only one hour of darkness. The decline in numbers throughout the night follows closely the fall in the average air temperature (Fig. 2), and the large sample for male toads was used to test this relationship. A multiple regression of the numbers captured in a two-hour period against temperature and time since sunset was significant ($R^2 = 0.346$, $F_{2,63} = 16.69$, $P < 0.001$; temperature $t = 4.88$, $P < 0.001$; time $t = 2.02$, $P < 0.05$), and shows clearly that temperature is more important in determining the number of toads active than time since sunset. However, both variables explain only 35% of the variability in the number of toads moving at different times of the night, so other factors need to be identified.

DISCUSSION

The findings of this study, that toads migrate to the breeding site mainly at night, confirms earlier casual observations in a quantitative way. Rather unexpectedly, however, it was found that 28% of females and 8% of males were moving during day-light, showing clearly that darkness itself is not essential for migration to take place.

It has been suggested that toads move at night to avoid predation, but at the present time there is little evidence to show that diurnal predators are any more

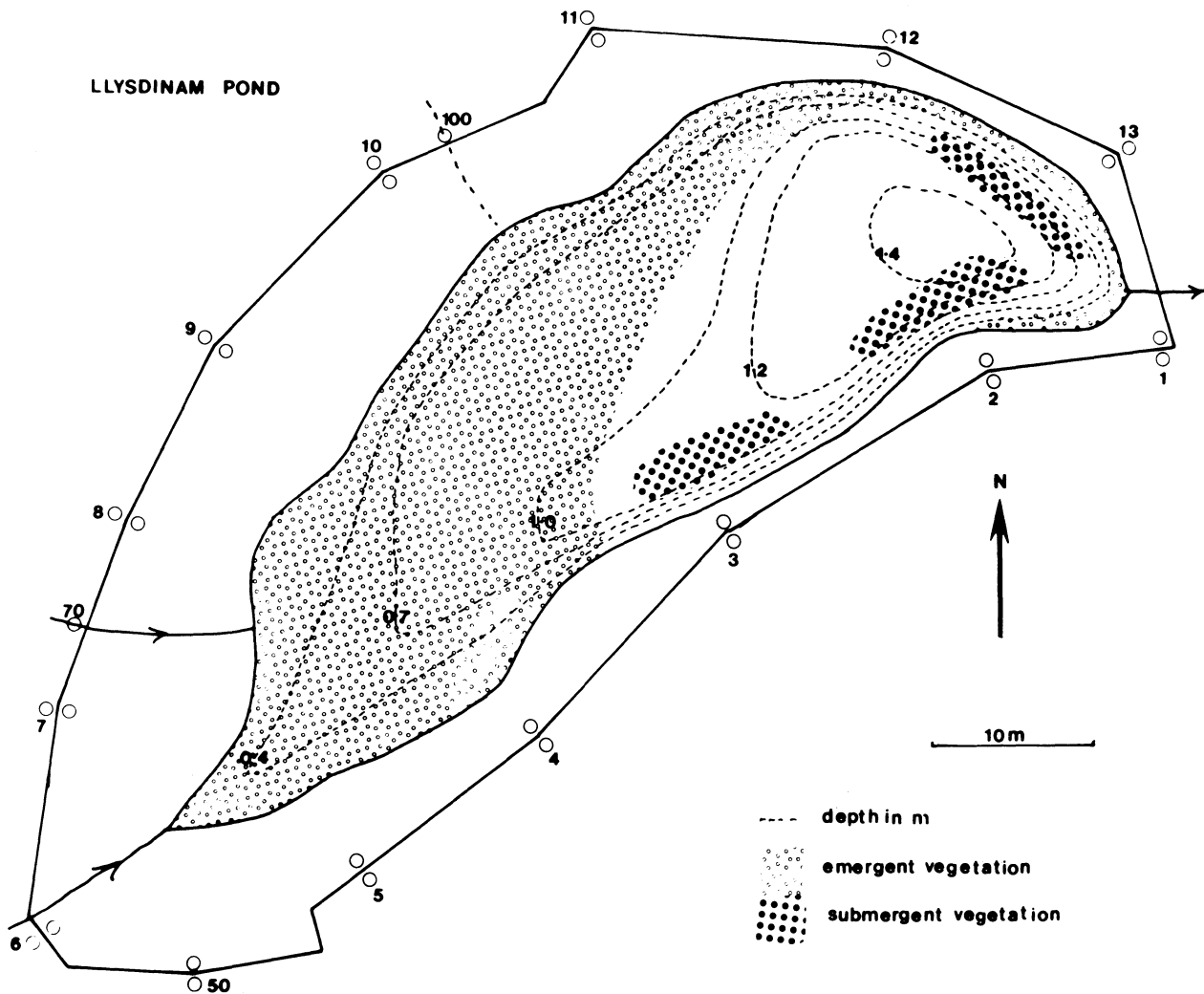


FIG. 1. Llysdydin Pond showing the barrier and pitfall-trap system.

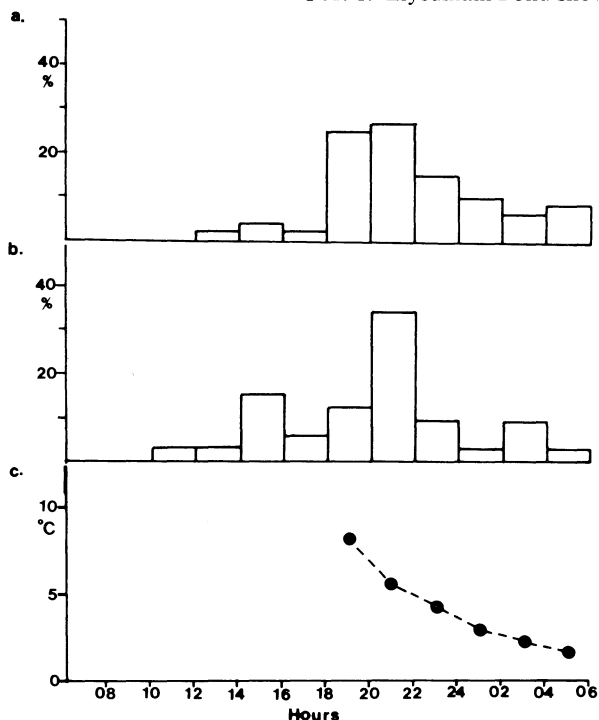


FIG. 2. Daily pattern of the number of toads arriving at the breeding site. (a) Males, $n = 332$. (b) Females, $n = 32$. (c) Average air temperature mid-way through the two-hour period.

effective at catching toads than nocturnal predators. Perhaps a more likely explanation is that the toads are reducing the risk of desiccation by moving at night, as relative humidity is much higher than during the day. Travelling to the breeding site at night, however, poses a problem, as temperatures at that time often fall to freezing and toads, being cold blooded are inactive at these low temperatures (Gittins, Parker & Slater, 1980; Wisniewski, Paull & Slater, 1981). It seems then that there is normally only a short period of the day when relative humidity is high and temperatures are above the critical for movement. These conditions are met only during the early part of the night and this is when the peak of toad movement occurred.

ACKNOWLEDGEMENTS

I would like to thank the Llysdydin Charitable Trust for facilities provided and the following UWIST Applied Biology 2nd year students for their assistance in recording amphibians at the barrier: K. Banks, D. Davis, J. Dixon, D. Lane, A. Longley, A. Jones, C. Plested, M. Pritchard and W. Wint. Helpful comments on an earlier draft of this paper were made by Professor R. W. Edwards and Mr J. D. Harrison.

REFERENCES

- Gittins, S. P., Parker, A. G. & Slater, F. M. (1980). Population characteristics of the Common Toad (*Bufo bufo*) visiting a breeding site in mid-Wales. *Journal of Animal Ecology* **49**, 161–173.
- Gittins, S. P. (1983). The breeding migration of the Common Toad (*Bufo bufo*) to a pond in mid-Wales. *Journal of Zoology* **199**, 555–562.
- Harrison, J. D., Gittins, S. P. & Slater, F. M. (in press). The breeding migration of smooth and palmate newts (*Triturus vulgaris* and *T. helveticus*) at a pond in mid-Wales. *Journal of Zoology* **199**, 249–258.
- Heusser, H. (1969). *The ecology and life history of the European Common Toad Bufo bufo (L.). An abstract of a five-year study.* Zurich: Offset-Druckerei der Zentralstelle der Studentenschaft.
- Moore, H. J. (1954). Some observations on the migration of the toad (*Bufo bufo bufo* (L.)). *British Journal of Herpetology* **1**, 194–224.
- Smith, M. (1973). *The British Amphibians and Reptiles.* 5th Edition London: Collins.
- Wisniewski, P. J., Paull, L. M. & Slater, F. M. (1981). The effects of temperature on the breeding migration and spawning of the Common Toad (*Bufo bufo*). *British Journal of Herpetology* **6**, 119–121.

BRITISH JOURNAL OF HERPETOLOGY. Vol. 6, pp. 294–299 (1983)

FACTORS INFLUENCING THE GROWTH AND SURVIVAL OF NATTERJACK TOAD (*BUFO CALAMITA*) TADPOLES IN CAPTIVITY

TREVOR J. C. BEEBEE

School of Biology, University of Sussex, Brighton BN1 9QG

(Received 13 September 1982)

SUMMARY

Natterjack larvae were grown from spawn to metamorphosed toadlets under a variety of controlled conditions in the laboratory. The following observations were made:

(1) Natterjack tadpoles required less food than those of common toads (*Bufo bufo*) to complete development and responded differently to food shortage.

(2) Natterjack development proceeded best at around 25°C. Lower temperatures delayed the rate of development while higher ones caused mortality just after hatching.

(3) Organic material in pondwater from a heathland site had no direct adverse effects on natterjack development though it may increase susceptibility to anoxia under certain circumstances.

(4) There was no direct developmental requirement for any inorganic ions and metamorphic success was high even in distilled water.

INTRODUCTION

The natterjack toad (*Bufo calamita*) is an endangered and protected species in Britain (Beebee, 1976, 1977). Largely for this reason there is considerable interest in understanding how the success of the species may be modulated by environmental influences and in particular the effects of such influences on larval development. A major problem has been the especially

severe declines of natterjacks on lowland heaths, the reasons for which are not clearly known but are suspected to lie at least partly in deteriorating breeding site conditions. Some possible factors affecting larval development and survival are amenable to test in the laboratory, and the study reported here was carried out to try and ascertain the relative likely importance of a number of such variables in the field.

MATERIALS AND METHODS

All experiments used spawn from heathland natterjacks less than 24 hr after deposition. Sections containing 10 eggs were cut out with scissors and grown up in tanks with 2 l of medium. This medium was changed at least once every week. Numbers surviving in each tank were recorded at weekly intervals, and random batches of five tadpoles from each measured (beak-tail tip). Larvae were scored as successful to metamorphosis and removed for release on appearance of the third limb (Beebee & Beebee, 1978). For conservation reasons each experimental situation was in a single tank without duplication.

FOOD REQUIREMENTS

These experiments were carried out outside during the first year of study, tanks being placed in sunny positions and covered to prevent dust and rain entry. Common toad and natterjack studies were carried out at the respective spawning times and were therefore not

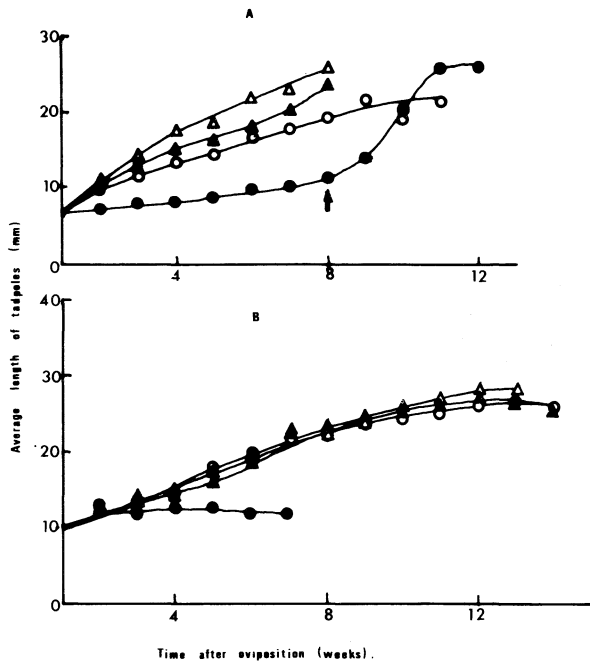


FIG. 1. Effects of food supply on growth rates of *Bufo calamita* and *B. bufo* larvae. Tadpoles were reared in the presence of varying amounts of rabbit pellet food; *Bufo calamita* in Fig. A, and *B. bufo* in Fig. B. ●, No food added; ○, 60 mg per week for first 3 weeks post hatch, 120 mg/week thereafter; ▲, 120 mg/week for 3 weeks, then 240 mg/week; △, 240 mg/week for 3 weeks then 480 mg/week. Arrow indicates point at which feeding of survivor commenced.

synchronous. Commercially available pellet food (for rabbits) was used in these and all other experiments; addition of material was once or twice weekly (see Figure legends). A single large pellet weighed about 240 mg. Growth was unusually slow in all tanks due to the prevailing cool weather conditions in spring 1981.

TEMPERATURE REQUIREMENTS

Tanks with spawn were placed in water baths (equilibrated at the appropriate temperature) for the duration of the experiment. Food was given *ad libitum* on the basis of the first year study data, *i.e.* 240 mg/week for the first 2 weeks and 480 mg/week thereafter. This and all subsequent experiments were carried out in the second year of study.

EFFECTS OF ORGANIC COMPOUNDS

Twenty litre batches of water from a heathland pond of high organic content (*Q* in Beebe *et al.*, 1982) were collected and filtered through glass sinters to remove debris. The water was stored in sealed containers at 4°C prior to use, and absorbance at 260 nm measured to determine the concentrations of organic compounds (Beebe *et al.*, 1982). This water was used in growth trials, either alone or after dilution (see Table legend), otherwise in standard 2 l tanks at ambient temperatures and with excess food as described above.

EFFECTS OF INORGANIC IONS

Distilled water was the basis for all growth media, which were prepared fresh every week from stock solutions of "Minimal Medium" (= 10 g/l NaHCO₃, 5 g/l MgCl₂, diluted 1/1000 in tanks), "Ca" (= 10 g/l CaCl₂ diluted 1/1000 or 1/10 000 in tanks) and "K" (= 10 g/l KCl, diluted 1/2000 or 1/10 000 in tanks). Stock solutions were stored at -20°C and thawed out each week prior to use. Food was always in excess and temperature ambient.

RESULTS

FOOD REQUIREMENTS

Bufo calamita and *B. bufo* larvae responded differently to food stress (Fig. 1). In both cases, as might be expected, excess food (480 mg/week at start) caused rapid and complete mortality presumably due to anoxia induced by bacterial growth. However, reducing the amount of food resulted in no change of growth rate in *B. bufo* while in *B. calamita* growth and metamorphosis times were clearly proportional to food availability. These results for the natterjack were statistically significant; at week 5, tadpoles given at 60/120 mg/week regime were smaller than those on the 120/240 mg/week regime ($t = 3.16$, d.f. = 8, $P < 0.01$) which were in turn smaller than those on the 240/480 mg/week regime ($t = 1.95$, d.f. = 8, $P < 0.05$). The reason why *B. bufo* tadpoles were able to maintain constant growth rates is shown in Fig. 2. Early mortality reduced the numbers of common toad larvae to those sustainable by the amount of food

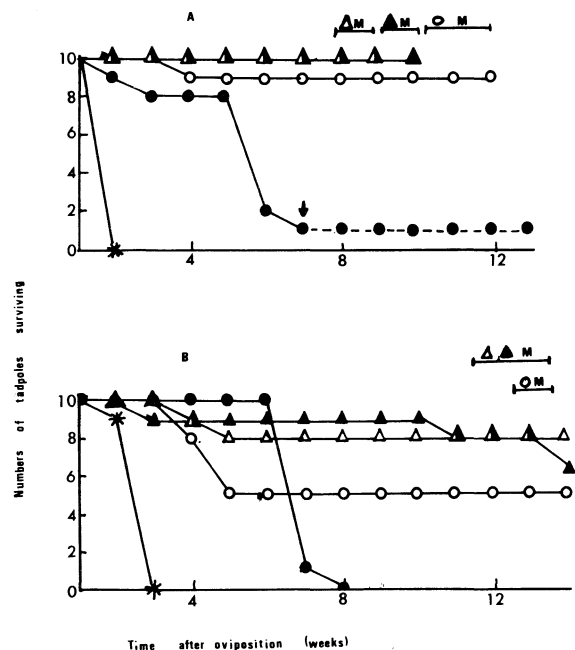


FIG. 2. Effects of food supply on survival of *Bufo calamita* and *B. bufo* larvae. Conditions for the experiment are described in the legend to Fig. 1. In addition, * = effect of feeding at 480 mg/week at start. — indicates times over which metamorphosis occurred. A, *Bufo calamita*; B, *B. bufo*.

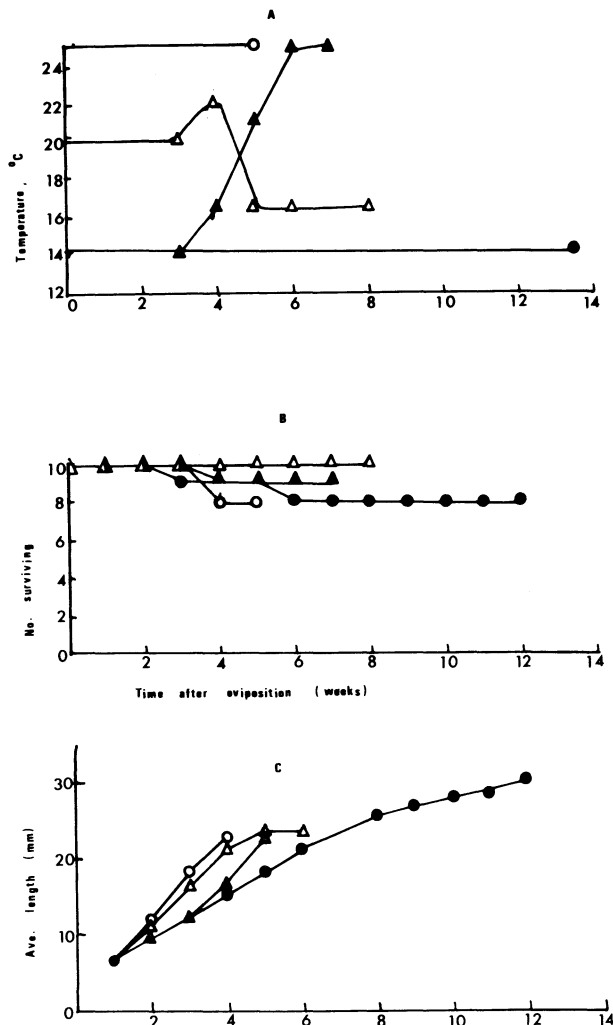


FIG. 3. Effect of temperature on growth and survival of *Bufo calamita* larvae. A: temperature regimes employed. ●, Constant around 14°C; ○, Constant around 25°C; ▲, 3 weeks at 14°C followed by progressive rise to 25°C; △, 3 weeks at 20°C, brief increase to 22°C and then a drop to stabilize at 16.5°C. B: Survival under the various regimes; symbols as in (A). C: Growth rates under the various regimes; symbols as in (A).

given. No comparable mortality was seen with natterjacks. Much less food sufficed to produce a natterjack toadlet (a minimum of about 120 mg (total) over 10 weeks for each tadpole) compared with a common toad one (min. 250 mg over 12 weeks). Growth rates of surviving common toad tadpoles were relatively invariant, averaging about 1.5 mm/week irrespective of food (apart from those completely starved) and all metamorphosis occurred within the same two-week period. Natterjack tadpoles, on the other hand, grew at rates varying between 1.9–2.7 mm/week depending on food supply. Metamorphosis time averaged 10 weeks with minimal food but only 7.5 weeks with maximal food.

In the complete absence of added food tadpoles of both species could survive many weeks without much growth. A single natterjack survivor after 6 weeks of starvation was rescued with food and then grew rapidly and metamorphosed normally (Fig. 1). Starved tad-

poles remained motionless for most of the time and were certainly much less active than their growing siblings, but showed no other behavioural or physical abnormalities.

TEMPERATURE EFFECTS

Temperature had a dramatic effect on natterjack tadpole growth rates and also on time of metamorphosis (Fig. 3). Spawn developed successfully to the hatching stage at 30° and 35°C, but at both these temperatures total mortality followed the rapid hatch (accomplished within 18–24 hours). Tadpoles exposed to the other four temperature regimes exhibited little mortality and even at a constant 14°C metamorphosis eventually occurred. In this instance the tadpoles grew much larger than in the other tanks, averaging 30.4 mm just prior to metamorphosis compared with the more usual 24–25 mm. Larvae maintained at 25°C grew very rapidly (averaging 5.3 mm/week) and metamorphosed 28–32 days after the eggs were laid. A “warm spring + cold summer” regime, shifting down from 20/22°C to 16.5°C after 5 weeks, produced rapid initial growth rates but metamorphosis later than a converse “cold spring + warm summer” 14 → 25°C shift. Small temperature differences had significant effects; thus after 3 weeks tadpoles at 25°C were significantly larger (av. 18.3 mm) than those at 20°C (av. 16.5 mm) ($t = 5.69$, d.f. = 8, $P < 0.0005$). More dramatically, shifting one group from 14° to 16.5°C resulted in a significantly different average size, compared with those left at 14°C, after only one week (16.9 mm *vs.* 15.7 mm, $t = 2.4$, d.f. = 8, $P < 0.025$).

EFFECTS OF ORGANIC COMPOUNDS

The presence of mixed organic solutes, mainly humic (fulvic) acids (Beebee *et al.*, 1982) had no detectable effect on rate of development or survival of natterjack tadpoles at least up to 700 mg/l (Table 1). However, in an unillustrated experiment high mortality was observed at 700 mg/l organics, and somewhat less at 350 mg/l, on a warm night following addition of food. Such mortality was not seen in control tanks. The deaths may have been due to cooperative effects of food and organic solutes in reducing oxygen levels in the water, but the observation was not investigated further.

EFFECTS OF INORGANIC IONS

Experiments varying the amounts of inorganic ions in the tadpole tanks are reported in Table II. A number of features are notable. Firstly, growth rates in the 7 days immediately following hatch (7–14 in the Table) were significantly slower in all tanks based with distilled water compared with those containing tapwater +/- organics (shown in Table I) ($t = 7.16$, d.f. = 53, $P < 0.0005$). This growth “pause” was however fully made up by day 21, by which time there were no significant differences between Table I and Table II. Secondly, survival in distilled water was lower than in the other cases, though still 70%, and this was probably not a chance effect. Growth rates were much more

TABLE I. Effects of organic solutes on development of *Bufo calamita* larvae. Filtered pondwater containing about 700 mg/l organic compounds was either used directly or diluted with equal volumes of distilled water or tapwater. A tank with tapwater was used as a control. Hatch in all cases was on days 6/7, and metamorphosis was completed within 6 weeks of spawn deposition. For all size data, SD are given in brackets. All M = All metamorphosed. N = Number surviving; S = average size (mm)

Time (days after oviposition)	Conditions							
	Tapwater		700 mg/l organics		350 mg/l organics + tapwater		350 mg/l organics + dist. water	
	N	S	N	S	N	S	N	S
0	10	—	10	—	10	—	10	—
7	10	6.5(0)	10	6.5(0)	10	6.5(0)	10	6.5(0)
14	10	11.9(0.4)	10	12.2(0.8)	10	11.8(0.6)	10	12.2(0.3)
21	10	18.3(1.2)	9	18.9(1.7)	10	17.8(1.6)	10	18.5(1.9)
28	10	22.8(0.9)	9	23.1(1.2)	10	24.1(1.4)	10	24.2(1.1)
40	9	All M	9	All M	10	All M	10	All M

TABLE II. Effects of inorganic ions on development of *Bufo calamita* larvae. Minimal medium (MM) produced concentrations of: Na⁺ = 2.7 mg/l; Mg²⁺ = 0.6 mg/l. K⁺ was present at 0, 0.5 or 2.5 mg/l and Ca²⁺ at 0, 0.3 or 3.3 mg/l. Distilled water and tapwater (Table I) controls were carried out simultaneously. Other details and abbreviations are as described in Table I

Time (days after oviposition)	Conditions											
	Distilled water		MM only		MM + K ^{2.5}		MM + K ^{2.5} + Ca ^{0.3}		MM + K ^{0.5} + Ca ^{3.3}		MM + Ca ^{3.3} + K ^{2.5}	
	N	S	N	S	N	S	N	S	N	S	N	S
0	10	—	10	—	10	—	10	—	10	—	10	—
7	10	6.5(0)	10	6.5(0)	10	6.5(0)	10	6.5(0)	10	6.5(0)	10	6.5(0)
14	10	9.2(0.9)	10	10.6(1.1)	10	11.2(0.3)	10	10.5(1.2)	10	10.7(1.0)	10	10.9(0.4)
21	9	17.0(4.2)	10	18.0(0.6)	10	18.1(0.6)	9	18.5(1.0)	10	18.6(1.0)	10	18.7(0.3)
28	7	24.2(0.8)	10	23.6(1.7)	10	23.5(1.6)	9	23.6(0.9)	10	23.2(1.1)	10	23.8(0.8)
40	7	All M	10	All M	8	All M	8	All M	8	All M	10	All M

variable in the early stages prior to the main mortality (see SD on day 21) than were those in other tanks. Growth of tadpoles in distilled water between days 7–14 was slowest of all, significantly slower than the other distilled-water based experiments containing added ions ($t = 4.11$, d.f. = 33, $P = < 0.0005$). However, the main point is that survival was quite high in all cases and the presence of various concentrations, or the absence, of K⁺ and Ca²⁺, made no detectable difference to growth rates or metamorphic success. A slightly higher level of mortality in tanks containing K⁺, manifest immediately before metamorphosis, was noted although the significance of this is not clear.

DISCUSSION

The experiments on food requirements lead to a number of points. Firstly, the data should be useful to those rearing natterjack tadpoles in captivity as is regularly done for conservation purposes (Beebee & Beebee, 1978). It is now possible to select a food ration which will support optimal growth rates without risk of pollution, providing water changes are made regularly. This amounts to one large rabbit pellet per 10 tadpoles per week for the first 3 weeks after hatch, and two pellets per week thereafter. Secondly, the different responses of *Bufo calamita* and *B. bufo* larvae indicate that different forms of selection may have operated on the two species. Common toad tadpoles can react to food stress with reduced growth rates if food is in excess but of poor nutritional value (Scorgie, 1980) but

when amounts of food are limiting, as in the present study, inter-tadpole competition becomes severe and mortality results even earlier than in tanks with completely starved tadpoles. This is probably because when no food at all is present all the tadpoles behave differently, resting for most of the time and conserving their limited reserves. With only a little food, all the tadpoles become active in searching but only some are sufficiently successful. The mortality was not apparent with natterjack tadpoles, which reacted to food stress by a general reduction in growth rates (*i.e.* similar to common toad larvae with excess poor foodstuffs). This could be advantageous to a species with a protracted spawning season and thus a wide range of tadpole sizes normally present in ponds during the spring; an ability to grow slowly in competition with larger tadpoles for limited food is clearly required if any but the earliest spawnings are to be productive of toadlets. Common toads, in which spawning is usually much more synchronous, do not have this problem and selection pressures at this stage of life may well be different. These experiments also confirm the postulate of Kadel (1975) that natterjack tadpoles require relatively little food to support development in comparison with other types such as common toads, and also show that natterjack tadpoles, unlike those of common toads, can respond to food excess by increasing their growth rates. It seems that tadpoles of both species (Scorgie, 1980) can recover and develop normally when refed after an extensive period of starvation. Finally, the variable growth rate response of natterjack tadpoles to food availability may be useful in the field in assessing

reasons for poor metamorphic success at breeding sites. Slow growth relative to near-by comparable ponds could therefore indicate a food limitation, providing temperature conditions are known to be adequate. Another proviso is that secretions from larger tadpoles, of the same or other species, may also have inhibitory effects on growth and the possibility of this being responsible would also have to be taken into account.

There is now evidence that hypoxia constitutes the physiological trigger for amphibian embryo hatch (Petranka *et al.*, 1982). Deaths of large numbers of embryos well prior to hatch is sometimes seen in the field in late (June) spawn, but the results of this study suggest that this phenomenon is unlikely to be temperature-related, since even at 35°C there were no losses prior to hatch. This temperature is rarely attained in the vicinity of natterjack spawn in Britain even in June (personal observations). Although natterjack tadpoles kept at 14°C (a temperature much lower than normally predominant in ponds used by this species and more typical of agricultural ponds in summer) eventually metamorphosed it cannot be presumed that temperature effects are unimportant in the wild. Longer developmental periods involve longer exposure to aquatic predators and there is increasing evidence that this factor is crucial to recruitment rates (B. Banks in preparation). Natterjacks are adapted to develop fast at high temperatures, partly no doubt to minimize such exposure, and in this regard it appears that cool springs and warm summers (the normal situation) will be more favourable than the converse in which metamorphosis is more delayed. The results support the notion that events of metamorphosis itself are particularly temperature-sensitive (Beebee & Beebee, 1978). Another result of late metamorphosis from cold ponds would be that toadlets have a shorter time to feed and gain weight before their first hibernation, with unknown consequences for survival. Ponds with regions regularly attaining temperatures in the 20–25°C, perhaps up towards 30°C range should be good ones for natterjacks and in Britain this means relatively shallow water (generally ≤ 20 cm) fully exposed to the sun. Very cold ponds (10°C or less) would certainly be lethal directly (Mathias, 1971). Although other circumstances may generate unusually large natterjack tadpoles (such as growth at low densities with abundant food), any observations of large (>25 mm) larvae in a pond suspected to be cool could be treated as corroborative evidence and thus provide a useful diagnostic measurement in the field.

Organic compounds, at least in heathland waters, probably have little bearing on natterjack development and this is supported by observations with caged tadpoles in the ponds (B. Banks, in preparation). Higher concentrations than those tested here rarely occur, and circumstances leading to anoxia are unlikely to arise in the wild. These data should not however be extrapolated to infer that organic solutes are never important and qualitative differences, including a greater variety of organics, in more eutrophic ponds may produce different results.

The ability of natterjacks to develop quite successfully in distilled water was surprising. Such mortality as

was observed can probably be attributed to pH effects alone, since distilled water is unbuffered and due to dissolved carbon dioxide has a pH of around 5.5 (Beebee & Griffin, 1977). Growth and survival was clearly independent of the presence of any inorganic ions, but there is evidence from the field that natterjacks do select more (but not excessively) eutrophic pools when a choice is available (Strijbosch, 1979; Beebee *et al.*, 1982) and larvae certainly fare better in such pools. The field observations also tend to discount the significance of slight pre-metamorphic mortality in the presence of potassium seen in the laboratory. Field and laboratory observations may be reconciled by the indirect effects of inorganic ions in increasing the primary productivity of freshwaters, notably the growth of algae as postulated by Savage (1961) in relation to frog *Rana temporaria* breeding sites. Natterjack larvae were able to grow in the laboratory because food was provided for them, but such oligotrophic conditions in the wild would result in severe shortage of natural food organisms.

These experiments suggest that studies of natterjack larval food in the wild, together with other factors likely to exert major influences on survival (notably predators) would be the next logical step, and such work is currently under way.

ACKNOWLEDGEMENTS

I thank Brian Banks for his assistance with some aspects of this work, which was carried out under license and on behalf of the Conservation Committee of the British Herpetological Society.

REFERENCES

- Beebee, T. J. C. (1976). The natterjack toad *Bufo calamita* in the British Isles: a study of past and present status. *British Journal of Herpetology* **5**, 515–521.
- Beebee, T. J. C. (1977). Environmental change as a cause of natterjack toad *Bufo calamita* declines in Britain. *Biological Conservation* **16**, 107–134.
- Beebee, T. J. C. & Beebee M. L. (1978). A quantitative study of metamorphosis in the natterjack toad *Bufo calamita*. *British Journal of Herpetology* **5**, 689–693.
- Beebee, T. J. C., Bolwell, S., Buckley, J., Corbett, K. F., Griffin, J. R., Preston, M. & Webster, J. (1982). Observation and conservation of a relict population of the natterjack toad *Bufo calamita* (Laurenti) in southern England over the period 1972–1981. *Amphibia-Reptilia* **3**, 33–52.
- Beebee, T. J. C. & Griffin, J. R. (1977). A preliminary investigation into natterjack toad *Bufo calamita* breeding site characteristics in Britain. *Journal of Zoology, London* **181**, 341–350.
- Kadel, K. (1975). Field studies on the survival rate of natterjack larvae (*Bufo calamita*, Laur.). *Revue Suisse de Zoologie* **82**, 237–244.
- Mathias, J. H. (1971). *The comparative ecologies of two species of amphibia* (*Bufo bufo* and *Bufo calamita*) on the Ainsdale sand dunes national nature reserve. University of Manchester: Ph.D thesis.
- Petranka, J. W., Just, J. J. & Crawford, E. C. (1982). Hatching of amphibian embryos: the physiological trigger. *Science, N.Y.* **217**, 257–259.

Savage, R. M. (1961). *The ecology and life history of the common frog*. London: Pitman.

Scorgie, H. R. A. (1980). Growth and development of tadpoles of the common toad *Bufo bufo* Linnaeus on

different foods. *British Journal of Herpetology* **6**, 41–43.

Srijbosch, H. (1979). Habitat selection by amphibians during their aquatic phase. *Oikos* **33**, 363–372.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 299–300

ESTIMATING NUMBERS OF NATTERJACK TADPOLES (*BUFO CALAMITA*)

A. S. COOKE

Nature Conservancy Council, P.O. Box 6, Godwin House, Huntingdon

(Received 12 November 1982)

SUMMARY

The accuracy of two methods of estimating tadpole numbers was tested with a known number of tadpoles in an artificial pond. Both methods, simple counting and mark-recapture involving dyeing with neutral red, were found to be satisfactory for certain situations.

INTRODUCTION

The natterjack (*Bufo calamita*) is the rarest amphibian native to Britain. Over the last few years there has been much effort expended on conserving this species, coupled with monitoring and research. Each year, Nature Conservancy Council co-ordinates a programme to ensure that attempts are made to assess the reproductive success in each site. Coverage devoted to individual sites varies from single brief visits to intensive full-time research projects. Some observers report on numbers of tadpoles present in their sites. Several techniques are available for estimating tadpole numbers. This paper reports some observations on two such techniques: mark-recapture involving neutral red dye, and simple counting.

Mark-recapture methods for estimating numbers of tadpoles of various ranid species have been used by Herreid & Kinney (1966), Wijnands (1972), Guttman & Creasey (1973) and Cooke (1978), with neutral red as the marking dye. One of the requirements of the marking process is that it should not harm the tadpoles. Treatment with 250 ppm neutral red for 1 min produced a red colour in tadpoles of the common frog (*Rana temporaria*) which lasted for 20 hr or more (Cooke, 1978); no detrimental effects were noted following this treatment regime. Treatment for longer gave a more lasting colour, but led to behavioural changes and perhaps to mortality (Cooke, 1978). The same treatment conditions are also suitable for tadpoles of the smooth newt (*Triturus vulgaris*), but tadpoles of the common toad (*Bufo bufo*) retain the dye much less satisfactorily (unpublished observations). A marking

technique for natterjack tadpoles could prove especially useful in small sites where there is likely to be rapid mixing of marked and unmarked tadpoles but in which poor visibility, perhaps because of plant growth or turbidity, precludes simple counting.

Counting tadpoles could be expected to be achieved fairly accurately in some small open sites. As tadpoles will burrow into fine silt, only sites on a hard substrate can be studied with confidence in this manner. In order to overcome the problem of miscounting moving tadpoles, the entire cohort could be netted and counted individually. But this operation might involve considerable disturbance and can only be attempted under licence. It seemed worthwhile, therefore, obtaining information on the ability of an observer to count accurately numbers of tadpoles in a controlled site with easy visibility, to which known numbers had been added.

METHODS

A pond of dimensions 2 m × 3 m × 6.5 cm deep was constructed using a stone-coloured vinyl liner. Tap water was added and allowed 12 days to "age" and become non-toxic, before 700 natterjack tadpoles were added, giving a density of about 120/m². Typically, these tadpoles were 12–13 mm in total length and their hind legs were beginning to develop (stages 25, 26; Witschi, 1956). The tadpoles originated from spawn laid at Saltfleetby Theddlethorpe National Nature Reserve. They were being held as part of the Nature Conservancy Council's intensive rearing programme and were released back at the site the day after this trial ended. In the artificial pond, tadpoles were fed on rabbit pellets and sausage meat. In addition, they evidently fed on natural food, spending considerable time grazing at the vinyl surface or congregating around drowned invertebrates. Day-time maximum water temperatures ranged from 22 to 30°C, while night-time minima were 9–15°C. After nine days, when the trial was terminated, 694 tadpoles (99% survival) were taken from

TABLE I. Details of counts and estimates of tadpoles present in the pond

Day	No. handled and counted	No. estimated with neutral red Mean \pm SD	No. estimated by counting free-swimming tadpoles		
			No. of Counts	Mean \pm SD	Range
0	700	742 \pm 158	6	675 \pm 38	654–752
1			6	733 \pm 58	649–806
2			6	715 \pm 56	660–791
6			6	680 \pm 36	638–716
9	694		6	648 \pm 60	545–725
		All counts:	30	690 \pm 56	545–806

the pond: mostly 16–18 mm, stage 27. Thus, losses were insignificant and will not have affected the estimates.

On day 0, 1–2 hr after the tadpoles had been introduced to the pool, a sample of 100 was caught and dyed for 1 min in 500 ml of freshly-prepared 250 ppm neutral red. These tadpoles were washed, released back into the pool and watched while they mixed with the unmarked tadpoles. Later, after the recapture operation, ten red tadpoles were removed and kept in a bucket for nine days to monitor survival and development; these were replaced in the pool by ten unmarked tadpoles.

To facilitate counting, bamboo canes were laid across the top of the pond to divide it into four equal sections. Rapid counts were made of tadpoles in the pond on days 0, 1, 2, 6 and 9. In view of the continuous movement of the tadpoles, it was thought better to make a series of rapid counts using a hand counter rather than fewer, slower counts. On each day, 6 counts were made, each taking about 4 min (count rate 150–200 tadpoles/min).

RESULTS

Two hours after the release of the dyed tadpoles, a sample was recaptured: out of 141 caught, 19 were red, giving an estimated total \pm SD of 742 \pm 158. The 10 red tadpoles kept in the bucket all survived for nine days and showed no adverse effects. Rate of loss of the red colour varied between tadpoles; thus 16 hr after being dyed, some were still noticeably red while others showed no trace of having been dyed.

Information on the counts is given in Table I. Although individual counts occasionally differed by >100 from the 700 introduced, none of the daily means differed by as much as one SD from the number present. By day 9, an algal bloom in the pool had reduced visibility substantially, and this was probably reflected by the lower mean estimate. Of course it was only on day 9, when all the tadpoles were removed and counted, that the fact that losses had been negligible was confirmed.

DISCUSSION

Simple counting gave estimates which did not differ significantly from the number known to be present. At sites where it is applicable, this technique is attractive

as it involves no disturbance. Counting may be especially appropriate in artificial rearing pools such as the one described here.

Neutral red dyeing would seem to be satisfactory for small sites or perhaps for discrete aggregations of tadpoles in sites with poor visibility. The recapture should be made within two hours or so. Complete mixing of marked and unmarked tadpoles plus the recapture session must take place before the red dye fades. In some large sites, the colour may fade before mixing is achieved, and this topic requires further study. This uncertainty concerning mixing could be overcome by temporarily confining aggregations of tadpoles by barriers (e.g. plastic sheeting) and working within these barriers. Some thought should be given to numbers of tadpoles dyed and recaptured. One has to balance the need for an accurate estimate (i.e. minimizing the SD compared with the total estimate) with the desire to cause as little disturbance as possible. The dyeing operation causes more disturbance than recatching. If about 10% of the total tadpoles are dyed and 20% later recaptured, the SD should be roughly 20% of the total estimate. Of course, in the type of situation for which dyeing is being recommended, it is likely that any preliminary guess at numbers may be wildly inaccurate, but it would seem to be a reasonable rule to aim to dye at least 5% of the tadpoles believed to be present. Failure to do so may lead to a very low recapture of red tadpoles and to a SD half as large as the total estimate.

ACKNOWLEDGEMENTS

I thank Steven Cooke for help in the field and I am grateful to Dr Trevor Beebee and Brian Banks for discussions about the techniques and the manuscript.

REFERENCES

- Cooke, A. S. (1978). Neutral red dye as a marker for tadpoles. *British Journal of Herpetology* **5**, 701–705.
- Guttman, S. I. & Creasey, W. (1973). Staining as a technique for marking tadpoles. *Journal of Herpetology* **7**, 388.
- Herreid, C. F. & Kinney, S. (1966). Survival of Alaskan Woodfrog (*Rana sylvatica*) larvae. *Ecology* **47**, 1039–1041.
- Wijnands, H. E. J. (1972). Mortality of *Rana temporaria* and *Rana arvalis* larvae. *Netherlands Journal of Zoology* **22**, 224–225.
- Witschi, E. (1956). *Development of vertebrates*. Philadelphia: Saunders.

ONTOGENETIC CHANGES IN PHOTOTAXIS IN THE SMOOTH NEWT, *TRITURUS VULGARIS* (L.)

R. A. GRIFFITHS

Department of Zoology, Birkbeck College, London WC1E 7HX

(Received 12 October 1982)

SUMMARY

The phototactic behaviour of *Triturus vulgaris* at different stages of development was monitored throughout the light and dark (dim) phases of a LD 12:12 cycle. During subjective day-time small larvae with hind limbs not yet fully developed displayed a weak photopositive response which became reversed towards the time of metamorphosis. It is postulated that photonegativity by larger larvae and newly metamorphosed newts is of adaptive value in that it is concerned with concealment from predators. During the postmetamorphic period, however, newts became increasingly photopositive and this behaviour was probably associated with the adoption of a crepuscular diel activity rhythm. Under the dim subjective night-time intensity the pattern was less clear, but immature and adult newts retained the photopositive response. There appeared to be little variation in the response to ambient light intensity during the light and dark phases of the diel cycle.

INTRODUCTION

The orientation of amphibians to a light stimulus is a behaviour of strong adaptive significance, and may be associated with microhabitat selection, predator avoidance and feeding and thermoregulatory behaviour. Adult *Ambystoma* spp. are generally nocturnal and photonegative, but the behaviour of the larvae varies both inter- and intraspecifically, and can be correlated with local environmental conditions. Anderson (1972), for example, found that large larvae of the montane *A. macrodactylum sigillatum* were positively phototactic whereas those of the lowland subspecies *A. m. croceum* responded negatively. Marangio (1975) observed photopositive *A. opacum* larvae to reverse their response to light on the completion of hind limb development. According to De Neff and Sever (1977), however, all larval stages of *A. tigrinum* are positively phototactic, but a reversal in orientation takes place in newly metamorphosed individuals. No comparable studies on ontogenetic changes in phototaxis have yet been conducted on European urodeles. Czeloth (1931) and Himstedt (1967), however, demonstrated that adult *Triturus* spp. may orientate towards dark stimuli, but Muntz (1963) found *T. vulgaris* to be photopositive, displaying a peak response to blue light. The retina of

T. vulgaris consists predominantly of cones (Möller, 1951; Himstedt & Fischerleitner, 1975) and the species is generally less nocturnal than other closely related urodeles (Himstedt, 1971).

The ecology of the larvae of *T. vulgaris* has been described by Avery (1971) and Bell & Lawton (1975), and the ontogeny of feeding behaviour discussed by Himstedt (1967). According to Himstedt (1971), the larvae of smooth newts display high overall activity, but are more diurnal than adults, although the rhythm is not very pronounced.

The object of the present study, then, was to investigate ontogenetic changes in the phototactic behaviour of *T. vulgaris* in larval and metamorphosed stages. In order to determine and account for any diel changes in the response to light, the animals were entrained to a LD 12:12 cycle and observation made throughout both light and dark (*i.e.* dimly lit) phases.

MATERIALS AND METHODS

Although previous studies of phototactic behaviour have frequently been conducted using groups of animals, all newts used in the current survey were tested individually. Metamorphosed newts tend to aggregate when kept in groups and consequently phototaxis may be masked by a thigmotactic response. Similarly, factors such as schooling, cannibalism and growth inhibition of small larvae by large larvae (*e.g.* see Rose, 1960; Wassersug & Hessler, 1971; Degani, Goldenberg & Warburg, 1980) may affect phototaxis in groups of larval amphibians.

Newts were grouped according to stage of development as follows:

Small larvae: larvae with a snout-vent length of 6.5 mm or less.

Intermediate larvae: larvae with a snout-vent length of between 6.5 and 14.0 mm. This group consisted of premetamorphic larvae with fully developed hind limbs.

Large metamorphosing larvae: larvae of 14.0 mm snout-vent length or over. These consisted of large larvae about to reach, or already having reached, metamorphic climax, which displayed evidence of gill and tail fin atrophy.

Newly metamorphosed newts: Newts which had completed metamorphosis and emerged on to land, but measuring up to 25 mm snout-vent length.

Immature newts: Terrestrial newts measuring between 25 mm and 35 mm snout-vent length and sexually immature.

Adult newts: Terrestrial, sexually mature newts measuring at least 35 mm snout-vent length.

The results obtained from any newt at a stage of development which did not conform to the respective size group above were rejected from the results (e.g. those larvae which underwent precocious metamorphosis at a small size). Adult and immature *T. vulgaris* were collected from the vicinity of local ponds and fed on earthworms in the laboratory. Newly metamorphosed and larval newts were collected as eggs or larvae and raised to the required stage of development on a commercial nutrient suspension and *Daphnia*. No feeding took place on test days. Adult, immature and newly metamorphosed newts were all tested using standard choice chamber apparatus measuring 200 mm diameter by 35 mm deep, one half of which was darkened with a black cover. A uniformly moist substrate of damp foam covered by filter paper was used for terrestrial stages. Larvae were tested in glass covered plastic dishes measuring 90 mm in diameter with a 20 mm depth of water. Over one half of each dish was placed a black cover, which had a partition extending down to just above the water surface to prevent any areas of intermediate intensity between light and dark sections.

Experiments were conducted using a cabinet (800 mm × 600 mm × 500 mm) equipped with a series of 10 mm diameter observation holes. Lighting during the photophase (i.e. subjective day-time) was provided by a series of white fluorescent tubes which yielded an intensity of 800 lux at choice chamber level on the uncovered side. Light intensity on the covered (i.e. darkened) half was approximately 0.5 lux. During the dimly lit phase (i.e. subjective night-time) lighting was by two further tubes which were foil covered save for a 5 mm wide slit running the length of each. These gave an intensity of 6 lux on the uncovered half of the chambers and 0 lux in the covered area. All light measurements were made using an EEL photoelectric photometer. Air temperature inside the cabinet was 25°

± 2°C. Visual contact between experimental animals was prevented by cardboard partitions.

Experimental procedure was the same for all stages of development. Newts were placed in their respective choice chambers under LD 12:12 (800 lux:6 lux) for several days. Observations were then made on their selected positions at hourly intervals for the duration of the light phase, which was from 08:00–20:00 hr (i.e. 12 observations per animal). The experiment was then repeated under reversed LD and observations were made throughout the dark (dim) phase. In this way, any circadian or diel rhythm in the phototactic response could be taken into account.

RESULTS

During the light phase (800 lux) the smallest larvae were slightly photopositive but tended to become increasingly photonegative as hind limbs were developed (Table I, Fig. 1). Negative phototaxis was maintained through metamorphosis but immature and adult newts were strongly photopositive. Under the dim, subjective night-time intensity of 6 lux the responses of larvae were less significant but clear positive phototaxis was observed in immature and adult newts. The distribution of phototactic responses across the LD cycle was fairly uniform in all six stages (Fig. 1) and there was little evidence of any diel variation in the response i.e. newts appear to be equally responsive to ambient photic conditions at different times of subjective day or night.

DISCUSSION

The phototactic behaviour of ambystomid salamanders appears to differ from that of *T. vulgaris* in a number of respects. Photopositivity in larval *Ambystoma* spp. has been associated with thermoregulation and the need to increase the rate of development by seeking warm areas of water and is characteristic of species inhabiting cool, montane regions or pools which are

TABLE I. Summary of phototactic responses of *T. vulgaris*. Ratios in the first row of each table represent *no. newts on light (uncovered) half of chamber: no. newts on dark (covered) half of chamber*, with sample sizes indicated in parentheses (intermediate positions were scored according to the position of the head). The second row represents the same ratio expressed as a percentage for easier comparison of results. Original scores were tested for deviation from a 1:1 result using χ^2 , assuming 1 d.f.

Light phase (800 lux)	Small larvae	Intermediate larvae	Large larvae	Newly metamorphosed newts	Immature newts	Adult newts
No. ⊕:No. ⊖	106:76 (15)	319:377 (58)	114:222 (28)	65:103 (14)	69:27 (8)	69:27 (8)
% ⊕:% ⊖	58:42	46:54	34:66	39:61	72:28	72:28
χ^2	4.36	4.83	34.71	8.60	18.38	18.38
<i>P</i>	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> < 0.001	<i>P</i> < 0.01	<i>P</i> < 0.001	<i>P</i> < 0.001
	slightly ⊕	slightly ⊖	strongly ⊖	⊖	strongly ⊕	strongly ⊕
Dark phase (6 lux)						
No. ⊕:No. ⊖	31:41 (6)	217:167 (32)	63:93 (13)	49:47 (8)	61:35 (8)	65:31 (8)
% ⊕:% ⊖	43:57	57:43	40:60	51:49	64:36	68:32
χ^2	1.39	6.51	5.77	0.02	7.04	12.04
<i>P</i>	<i>P</i> > 0.05	<i>P</i> < 0.05	<i>P</i> < 0.05	<i>P</i> > 0.05	<i>P</i> < 0.01	<i>P</i> < 0.001
	not significant	slightly ⊕	slightly ⊖	not significant	⊕	strongly ⊕

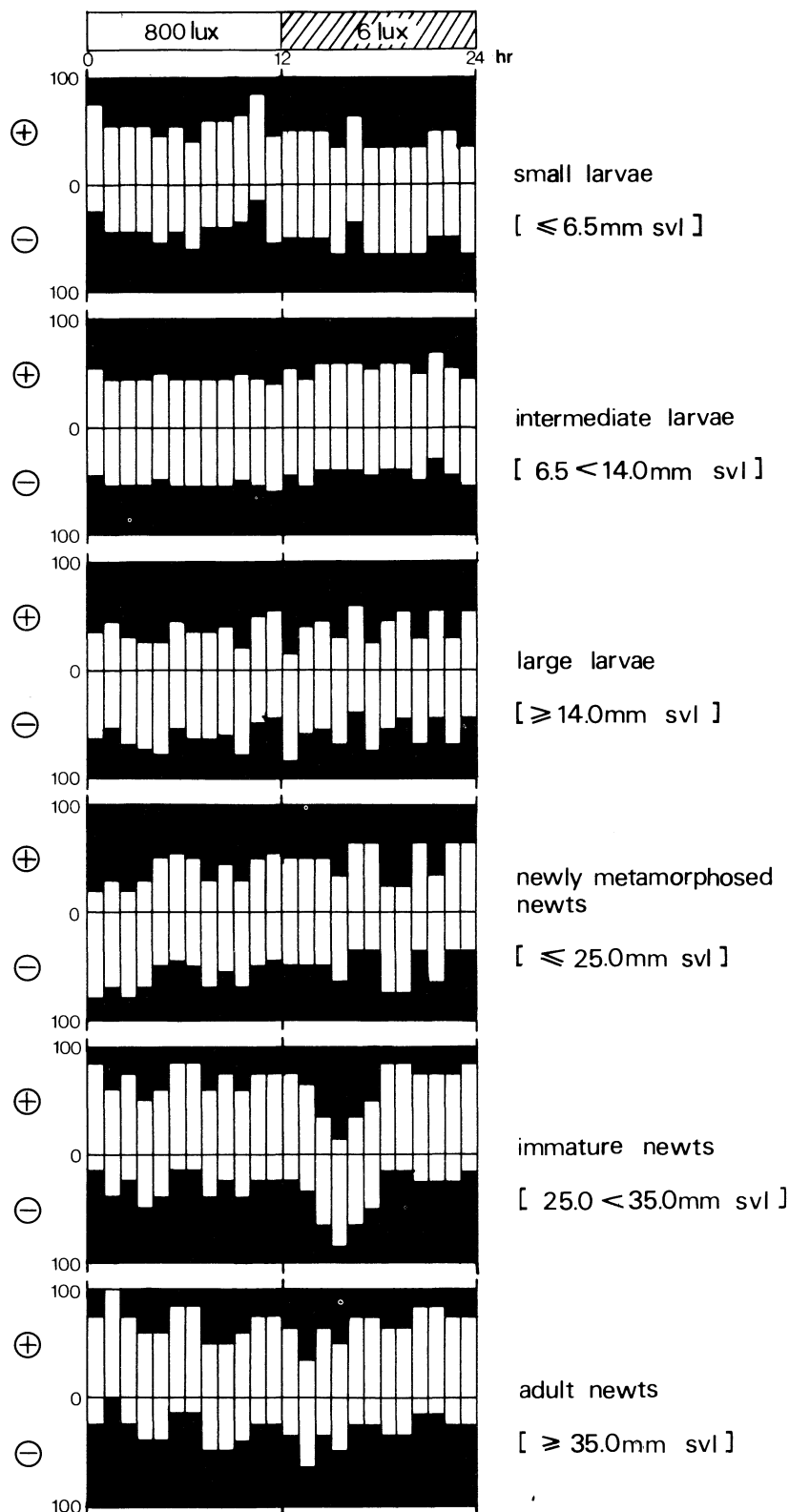


FIG. 1. Distribution of responses to ambient light conditions across a diel cycle. Photoperiod is indicated in the bar at the top of the figure. Number of photopositive and photonegative scores were summated separately for each hour of the LD cycle and each expressed as a percentage of the total number of responses. Sample sizes are given in Table I. Responses are indicated by % ⊕ photopositive, and ⊖ photonegative.

subject to desiccation (Anderson, 1972; Marangio, 1975; De Neff & Sever, 1977). Conversely, the photonegative response of *A. m. croceum* larvae was

correlated with the obviation of a thermoregulatory response due to the mild temperatures prevailing in its lowland habitat (Anderson, 1972). Positive phototaxis

by amphibian larvae carries with it an increased risk of exposure to predators, and may be selected for in populations where predation pressure is low. As the larvae of *T. vulgaris* tend to be mainly photonegative, however, there would appear to be little selection for a behavioural mechanism to increase development and metamorphosis. Furthermore, the larvae undergo a protracted developmental period, usually lasting several weeks, and are frequently observed to overwinter in permanent bodies of water. Bell & Lawton (1975) observed three distinct larval cohorts in *T. vulgaris*. The middle cohort, with larvae metamorphosing about mid-July, was the largest, whereas the late cohort either metamorphosed in September or overwintered and emerged from water the following spring. The same authors further pointed out that smooth newt larvae lead an essentially immobile existence until a total length of 14–18 mm is reached and the hind limbs appear, when they become active predators. Indeed, Bell & Lawton (1975) observed a marked inflection in the survival curve when larvae reached this stage of development and postulated that this transition to active hunting increased the chances of larvae being predated. It would seem advantageous therefore for larvae at this stage to display increased photonegativity and hunt amongst the darker regions of the pond and thereby minimize the effective increase in exposure to predators. The present study indicates that larvae at this stage of development (*i.e.* >6.5 mm snout-vent length, hind limbs fully developed) did display a greater degree of negative phototaxis than at earlier stages under 800 lux. Under 6 lux the results were more variable, but the largest larval stage (≥ 14.0 mm snout-vent length) displayed the greatest preference for darkness. Although phototaxis *per se* may depend upon ambient temperature conditions, it seems likely that this behaviour in *T. vulgaris* plays little part in aiding orientation to warmer waters in order to accelerate development, and the predominantly photonegative behaviour of larvae probably serves a predator avoidance function.

Newly metamorphosed newts are particularly prone to predators and must seek a dark, moist refuge soon after emergence. Himstedt (1971) observed a degeneration of the diel rhythm of activity during metamorphosis, a new rhythm appearing some weeks after emergence onto land. The photopositive response of immature and adult newts are less easily explained but are probably a function of the light intensities employed in the experiment. In their account of phototactic responses of frogs and toads, Jaeger & Hailman (1973) pointed out that the dichotomous terms “photopositive” and “photonegative” as described by Fraenkel & Gunn (1961), are artefacts of experimental technique when applied to the Anura, and postulated an “optimum ambient intensity” (frequently outside the limited range of intensities provided in the laboratory) at which a modal response occurs. Furthermore these authors put forward a relationship between daily activity period and phototactic behaviour—although photonegative species are predominantly nocturnal, photopositive species include both diurnal and nocturnal forms. As *T. vulgaris* is an essentially crepuscular amphibian (Himstedt, 1971; Dolmen,

1976; Griffiths, in press), this species’ optimum ambient intensity most probably falls during the periods of twilight experienced during early morning and evening. The maximum intensity of about 800 lux provided in the present laboratory study is close to measurements of illuminance made under field conditions during these periods (natural light intensity may reach 50 000 lux in the middle of the day and is consequently difficult to simulate in laboratory conditions). The response of adult newts to 6 lux was less significant than that to 800 lux indicating that the latter intensity is closer to the hypothetical optimum.

Although the responses to the subjective night-time intensity of 6 lux were generally less marked than those to the higher, day-time intensity, there did not appear to be any marked variation during the hours of day or night. Jaeger & Hailman (1973) found that light and dark acclimation had a slight effect on phototaxis but the responses of frogs and toads tested at different times of the diel cycle did not show any significant divergence.

Changes in the phototactic response during metamorphosis may be connected with the conversion of visual pigments in the retina that is thought to occur at this time. Studies on the spectral sensitivity of different stages of *Triturus* spp. suggest that whereas rods of larvae contain vitamin A₂ pigments (porphyropsins), metamorphosed and terrestrial adult newts possess vitamin A₁ pigments (rhodopsins). Adult newts are thought to reconvert retinal A₁ to A₂ pigments on return to water, and hence their spectral sensitivity is similar to that of larvae (Himstedt, 1973; Grüsser-Cornehls & Himstedt, 1976).

In *T. vulgaris* then, phototactic behaviour varies according to stage of development, but in the natural situation it may be that populations from extreme environments (*e.g.* those described by Dolmen, 1980) differ in their behaviour to those inhabiting more temperate regions, and in this respect, a study of the effect of temperature on phototaxis might prove worthwhile. It is also probable that in amphibian communities differences in the response to light may play a role in niche utilization of an interspecific basis.

ACKNOWLEDGEMENTS

I would like to thank Professor J. L. Cloudsley-Thompson for reviewing the manuscript and Miss Katherine Beech for typing it. The work was carried out whilst in receipt of a SERC research studentship.

REFERENCES

- Anderson, J. D. (1972). Phototactic behaviour of larvae and adults of two subspecies of *Ambystoma macrodactylum*. *Herpetologica* **28**, 222–226.
- Avery, R. A. (1971). The ecology of newt tadpoles: food consumption, assimilation efficiency and growth. *Freshwater Biology* **1**, 129–134.
- Bell, G. & Lawton, J. H. (1975). The ecology of the eggs and larvae of the smooth newt (*Triturus vulgaris* (Linn.)). *Journal of Animal Ecology* **44**, 393–423.

- Czeloth, H. (1931). Untersuchungen über die Raumorientierung von Triton. *Zeitschrift für Vergleichende Physiologie* **13**, 74–163.
- Degani, G., Goldenberg, S. & Warburg, M. R. (1980). Cannibalistic phenomena in *Salamandra salamandra* larvae in certain water bodies and under experimental conditions. *Hydrobiologia* **75**, 123–128.
- De Neff, S. J. & Sever, D. M. (1977). Ontogenetic changes in phototactic behaviour of *Ambystoma tigrinum tigrinum* (Amphibia: Urodela). *Proceedings of the Indiana Academy of Sciences* **86**, 478–481.
- Dolmen, D. (1976). Diel rhythm of *Triturus vulgaris*. In *Proceedings of the 1st Nordic Symposium on Herpetology. Norwegian Journal of Zoology* **24**, 234.
- Dolmen, D. (1980). Distribution and habitat of the smooth newt, *Triturus vulgaris* (L.), and the warty newt, *T. cristatus* (Laurenti) in Norway. *Proceedings of the European Herpetological Symposium, Oxford 1980*, 127–139.
- Fraenkel, G. S. & Gunn, D. L. (1961). *The orientation of animals: kineses, taxes and compass reactions*. New York: Dover.
- Griffiths, R. A. Circadian activity patterns in the Amphibia. *Proceedings of the International Herpetological Congress, Oxford* (in press).
- Grüsser-Cornehls, U. & Himstedt, W. (1976). The urodele visual system. In *The amphibian visual system—a multidisciplinary approach* 203–266, Fite, K. V. (Ed.). New York: Academic Press.
- Himstedt, W. (1967). Experimentelle Analyse der optischen Sinnesleistungen im Beutefangverhalten der einheimischen Urodelen. *Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **73**, 281–320.
- Himstedt, W. (1971). Die Tagesperiodik von Salamandriden. *Oecologia (Berlin)* **8**, 194–208.
- Himstedt, W. (1973). Die spektrale Empfindlichkeit von Urodelen in Abhängigkeit von Metamorphose, Jahreszeit und Lebensraum. *Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **77**, 246–274.
- Himstedt, W. & Fischerleitner, E. (1975). Die Antworten von Retinaneuronen auf Farbreize bei Urodelen. *Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **79**, 128–147.
- Jaeger, R. G. & Hailman, J. P. (1973). Effects of intensity on the phototactic responses of adult anuran amphibians: a comparative survey. *Zeitschrift für Tierpsychologie* **33**, 352–407.
- Marangio, M. S. (1975). Phototaxis in larvae and adults of the marbled salamander, *Ambystoma opacum*. *Journal of Herpetology* **9**, 293–297.
- Möller, A. (1951). Die Struktur des Auges bei Urodelen verschiedener Körpergröße. *Zoologische Jahrbücher-Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **62**, 138–182.
- Muntz, W. R. (1963). Phototaxis and green rods in urodeles. *Nature* **199**, 620.
- Rose, S. M. (1960). A feedback mechanism of growth control in tadpoles. *Ecology* **41**, 188–199.
- Wassersug, R. & Hessler, C. M. (1971). Tadpole behaviour: aggregation in larval *Xenopus laevis*. *Animal Behaviour* **19**, 386–389.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 305–308 (1983)

COMPARISON OF *LACERTA AGILIS* HABITATS IN BRITAIN AND EUROPE

S. M. HOUSE* AND I. F. SPELLERBERG

Biology Department, The University, Southampton SO9 5NH

(Received 22 November 1982)

SUMMARY

A questionnaire was circulated to several European herpetologists and a large amount of original and unpublished information was obtained on details of the habitat of the Sand Lizard (*L. agilis*).

Throughout Europe, *L. agilis* inhabits a variety of environments including open woodland, scrub, dwarf shrub associations, grasslands and dune habitats. Two common features were open but diverse vegetation structure and open areas of soil for egg incubation.

* Present address: *The Research School of Pacific Studies, Australian National University, Canberra, Australia. N.B. Please address all correspondence to the second author.*

In the North West of its range (England, Sweden and The Netherlands), *L. agilis* seems to be restricted to areas with a sandy substratum but any loose, well-drained soil is suitable in central Europe.

A comparison between Continental and Southern England habitat *L. agilis* features suggests that this species is more specialized (in terms of habitat ecology) in England.

INTRODUCTION

The known geographical range of the Sand Lizard, *Lacerta agilis* L., extends from northwest and southern England (two disjunct populations), across southern Sweden, Denmark, the Baltic Soviet Republic, The

Netherlands, Belgium and France. It is found throughout the whole of middle Europe, north of the Alps, where it is known up to 1800 m, and in eastern Europe, the Balkans and west and middle Siberia (Arnold & Burton, 1978).

The English populations are considered to be relict distributions, although more recent declines are due to habitat changes rather than climatic deterioration (British Herpetological Society, 1973).

Characteristics of the Sand Lizard habitat in southern England have been described by Corbett & Tamarind (1979) and Spellerberg & House (1980), and in northwest England by Jackson (1979). These studies demonstrate that, in England, viable *L. agilis* populations are associated with two important habitat features; a shrubby mosaic of vegetation cover broken by frequent plant/ground interfaces, and areas of bare sandy substrate in which the eggs are incubated (House & Spellerberg, 1980). The investigation reported here was designed to gather new information and compare data collected from *L. agilis* habitats in continental Europe with that known from English habitats. In view of the changing status of *L. agilis* in Europe, it is important to be able to assess habitat quality for the conservation of this species throughout its range.

References to *L. agilis* habitat in the published literature are few. Rollinat (1934) describes typical habitat in France as sandy locations along hedgerows and forest margins, but the species is now extinct from many of the localities he names (Rosselot & Saint Girons, pers. comm.). Glandt (1976) describes West German lizard habitats in greater detail, with reference to the suitability of the sites for locally sympatric species *L. agilis* and *L. vivipara* Jacq. Bund (1964) discusses habitat types for *L. agilis* in The Netherlands, naming a variety of natural and manmade features. More recently, a report was made on a coastal *L. agilis* population in The Netherlands (van Leeuwen & van der Holf, 1976). A monograph on *L. agilis* published in Moscow includes a chapter on the distribution and habitat of the species in the U.S.S.R. (Jablokov, 1976).

METHODS

A questionnaire was circulated to herpetologists in Europe, inviting them to participate in a *L. agilis* habitat survey. The circulation established contact with persons having an active interest in the species and they were able to give detailed information. The questionnaire consisted of an introductory letter explaining the purpose of the survey; a survey sheet in English; a translation sheet with relevant words and phrases translated into either Dutch, French, German or Russian; and a sheet of explanatory notes with examples. Much of the information provided here comes from translation of original reports and publications. This being the case, difficulties were encountered in the translation of ecological terms. To avoid misinterpretation, technical terms have been translated so as to give the most reliable interpretation of the original material.

RESULTS

The response to the questionnaire survey was mixed and included the following categories: no answer, answer but no information, answer with suggestions for alternative contacts, answers with general information, answers with detailed information. A description of *L. agilis* habitats for several European countries is summarized below, using the most informative questionnaire results in conjunction with information available in the literature. Full details may be found in Spellerberg & House (1980).

SOUTHERN ENGLAND

A description of English *L. agilis* habitat types is given in House & Spellerberg (1983). Results from an intensive three-year research programme suggests that *L. agilis* is associated with heathland communities and their derivatives or vegetation similar in structure and morphology, such as mixed grass species interdispersed with shrubs and open ground. Plant species richness bore no relationship to the selected habitat whereas structural diversity was found to be an important component of the lizard's habitat.

U.S.S.R.

A monograph describing *L. agilis* habitats in the U.S.S.R. has been mentioned (Jablokov, 1976). A translation of the list of habitat types has been undertaken and the *L. agilis* habitat distribution can be summarized as follows.

In natural landscapes of woodland forest and forest steppe, lizards were found in a number of habitats including forest margins, wet meadows, borders of bogs and around swamps, and in areas of natural rock falls. In semi-desert and mountainous areas, lizards were found in fewer habitats such as forest "islands", secondary scrub thickets, meadows and rocky outcrops. Anthropomorphic or cultural landscapes seem to provide a larger number of suitable habitats. These included cereal fields, small gardens, vineyards, parks, roadsides, plantations, churchyards, railway embankments and industrial wasteland.

FEDERAL REPUBLIC OF GERMANY

Information obtained suggests that *L. agilis* was formerly classified as common and widespread in Germany but is now found sporadically and occasionally throughout large areas of its range (Honnegar, 1977). Glandt (1976) describes seven population habitats distributed between inland dune areas on the lower Rhine terrace and large forest areas on the main Rhine terrace. Glandt (1979) explores the habitat requirements of *L. agilis* and *L. vivipara* in more detail by scoring the number of populations of each species specifically associated with different substratum and vegetation characteristics over a range of landscape types. He concludes that *L. agilis* requires a loose, well drained substratum combined with a plant cover described as sparse to moderately thick. The Common Lizard (*L. vivipara*) on the other hand, is associated

with habitats with dense vegetation covering a broad spectrum of ecotypes, generally at the moist end of the scale. Details of habitat characteristics supplied by Glandt may be found in Spellerberg & House (1980).

THE NETHERLANDS

L. agilis is found only on sandy soils in The Netherlands (Bund, 1964). Suitable habitat types fall into three categories: (i) inland heathlands subject to a variety of management practices; (ii) coastal dune systems; (iii) man-made habitats. Inland heaths cover a variety of geobotanical formations including drifting dunes subject to erosion and stabilization processes. Permanent open tracts of heath are formed on glacial sand ridges and are subject to management practices such as burning, grazing and afforestation. Grasses are a more important component of the vegetation structure than in the heathland formations of southern England. Topographic relief is generally slight. Coastal dune habitats lie on a calcareous substrate and consist of a series of steep-sided dune ridges and slacks carrying a variable representation of shrubs (*Crataegus monogyna*, *Salix repens*) and grasses (*Calamagrostis*). Man-made habitats include railway embankments and road cuttings in rural areas.

DENMARK

L. agilis is relatively common along the west coast of Jutland and the north coast of Zealand, and locally common on the islands except Bornholm. There are several populations in the east of the country. Many of the island populations are threatened by intensive afforestation with conifers. Typical habitats are generally open coastal areas with low or sparse vegetation on dunes, heathlands or abandoned gravel workings.

FRANCE

The distribution of *L. agilis* in France is very fragmented, the species being more common in the north, east and centre of the country. Outside these areas the precise distribution of *L. agilis* is not known. The greater concentrations of populations tend to be in central and eastern parts of the country (Rosselot, pers. comm.). It is generally assumed that *L. agilis* is a continental species compared with *L. vivipara* and *Podarcis muralis* which are more widespread and locally abundant in coastal areas. Confusion between *L. agilis* and *L. viridis* makes accurate recording difficult, particularly in the southwest of the country. Some large populations of *L. agilis* are known in Alsace and the French Pyrenees (Rosselot & Cheylan, pers. comm.). It is considered by Saint-Girons (pers. comm.) to be a species found on high ground, occurring in large populations up to 1800 m and most abundant between 1400 m and 1800 m. The following vertical zonation has been noted: *L. vivipara*—plains/low ground to low hills; *L. agilis*—low hills to mountain foothills; *L. viridis*—low to high mountains (Saint-Girons, pers. comm.). A Sand Lizard habitat in the French Pyrenees is described as being dwarf shrub

cover with localized patches of bare ground, generally on relatively undisturbed slopes. It is also known from low, flat marshland in the Brennes district of central France, particularly in hedges, along roadsides and in meadows. In these latter habitats the species tend to be widespread but not abundant.

SWEDEN

In Sweden *L. agilis* is found as far north as lat. 61°N (West Varmland, Mora and West Sweden). It is more common in southern and eastern areas such as Scania and Smaland. It is abundant on the island of Ven off the south coast and is sparsely distributed around Gothenburg and eastern areas. The species inhabits sandy areas throughout much of its range in Sweden. Different habitat types have been described by Andren & Nilson (1979). The most common habitats are moving sand dunes and old sand pits partly overgrown with tussock grasses and herbs. The species is also found amongst grassland communities and on exposed slopes on rocky ground.

YUGOSLAVIA

The details of one *L. agilis* site in western Yugoslavia and described by Soti (pers. comm.) were obtained. In this case, the habitat was a mixed grass community on very basic soils.

ROMANIA

The distribution of *L. agilis* is central and widespread in mountainous ground, often in forested areas.

CZECHOSLOVAKIA

L. agilis is still common in non-cultivated regions of Czechoslovakia, from low lying areas to approximately 500 m above sea level. In Slovakia it reaches 1500 m. It was reported that *L. agilis* is one of the most common reptiles in the country.

DISCUSSION

Both on the continent and in England the habitat of *L. agilis* is formed structurally by low shrubby vegetation with frequently occurring patches of bare ground, litter or bryophyte cover. The implications of this structural diversity of invertebrate abundance, thermoregulatory behaviour, incubation requirements and cover are discussed in Spellerberg & House (1980) and House & Spellerberg (1980). Comparative studies on the habitat of *L. vivipara*, a smaller viviparous species (Glandt, 1979; Spellerberg & House, 1980) suggest that the latter species is more often associated with less structurally diverse and less well drained habitats.

The vegetation cover in *L. agilis* habitat in continental Europe varies from sparse to fairly dense with open areas. The degree of tolerance to invasion by tall scrub may be expected to decrease towards the

climatically less favourable edge of the species ranges, for instance in southern England. However, House and Spellerberg (1983) show that a certain amount of scrub invasion can enhance certain microclimatic conditions in favour of basking and egg incubation requirements, providing the habitat structure is both topographically and vegetationally diverse. Invasion by tall, dense shrubs and trees would not be tolerated as well on sites of little topographical relief, either in England or on the continent. The low relief areas described by Glandt as becoming overgrown support very small numbers of adult lizards.

In Europe it appears that *L. agilis* requires a dry, loose substratum for egg incubation but not necessarily a sandy soil. In the more maritime climate of England and the west coasts of Sweden and The Netherlands, the species' requirements may be more specialized, the optimal heating and drainage conditions being provided by very sandy soils (House & Spellerberg, 1980).

In southern England, the heathland formation represents an ideal habitat structure for *L. agilis* and in a condition managed along traditional lines this provides natural open areas suitable for basking and egg incubation. On the continent, manmade landscapes other than heathland provide the same structural features but have often been produced under different management regimes so that grasses and mixed shrub species sometimes replace the Callunetum structure (Noirfalise & Vanesse, 1977). The "natural" habitats relatively unmodified by anthropogenic trends tend, both in England and on the continent, to be open coastal or mountainous locations where substratum instability and/or exposure to harsh environmental factors preclude the extensive growth of tall shrub and tree species. The common occurrence of *L. agilis* in abandoned gravel workings and railway cuttings is due to a historical migration into these areas from surrounding populations soon after human disuse of the sites. Subsequent land use changes of the hinterland often isolate a population in what is only temporarily an optimum habitat until management intervenes. The same is true of pockets of *L. agilis* populations in afforested areas of England and on the continent.

In conclusion, it is suggested that *L. agilis* requires a structurally diverse habitat both in England and on the continent. In cooler, more moist areas, however, those topographic and biotic features that improve the opportunities for egg incubation and thermoregulation, become major influences in the lizards' habitat.

ACKNOWLEDGEMENTS

The authors thank the following for kindly providing information on habitat features in Europe. E. Wedekinch (Denmark), Dr E. A. Fromhold, D. Glandt (Federal Republic of Germany), C. Andren, G. Nilson

(Sweden), J. P. Soti (Yugoslavia), Professor I. S. Darevskij (U.S.S.R.), Dr I. Baran (Turkey), B. Rossetot, M. Cheylan, Dr H. Saint Girons (France), Drs A. H. P. Stumpel, J. and B. van Leeuwen (The Netherlands), Dr Z. Rocek (Czechoslovakia).

REFERENCES

- Andren, C. & Nilson, G. (1979). Sandodlan *Lacerta agilis* vid sin nordgrans i Sverige. *Fauna och Flora* **74**, 133–140.
- Arnold, E. N. & Burton, J. A. (1978). *A field guide to the reptiles and amphibians of Europe*. London: Collins.
- British Herpetological Society. (1973). The conservation of British amphibians and reptiles—a policy. *British Journal of Herpetology* **4**, 339–341.
- Bund, C. F. van de. (1964). *De verspreiding van de reptilien en amfibieën in Nederland*. s'Gravenhage: Vierde Herpetografisch verslag "Lacerta".
- Corbett, K. F. & Tamarind, D. L. (1979). Conservation of the sand lizard, *Lacerta agilis* by habitat management. *British Journal of Herpetology* **5**, 799–823.
- Glandt, D. (1976). Ökologische Beobachtungen an nieder-rheinischen *Lacerta*—Populationen *Lacerta agilis* und *Lacerta vivipara*. *Salamandra* **12**, 127–139.
- Glandt, D. (1979). Beitrag zur Habitat—Ökologie von Zauneidechse (*Lacerta agilis*) und Waldeidechse (*Lacerta vivipara*) in nordwestdeutschen Tiefland, nebst Hinweisen zur Sicherung von Zauneidechsen—Beständen. *Salamandra* **15**, 13–20.
- House, S. M. & Spellerberg, I. F. (1980). Ecological factors determining the selection of egg incubation sites by *Lacerta agilis* in southern England. *Proceedings of the European Herpetological Symposium, Oxford, 1980*, 41–54.
- House, S. M. & Spellerberg, I. F. (1983). Ecological conservation of the sand lizard (*Lacerta agilis* L.) habitat in southern England. *Journal of Applied Ecology* **20**, 417–438.
- Honegger, R. (1977). Unknown, unloved, threatened. *Naturopa* **27**, 13–18.
- Jackson, H. C. (1979). The decline of the sand lizard, *Lacerta agilis* L. population on the sand dunes of the Merseyside coast, England. *Biological Conservation* **16**, 177–193.
- Jablokov, A. (1976). *Pritkaja Jascherica*. Moscow: Government Publishing House "Nauka".
- Leuwen, B. H. van & van de Hoef, J. C. M. (1976). *Onderzoek Naar de Oecologie und populatie dynamica van de Zundagedis (Lacerta agilis L.) in de Duinen van Oostvoorne*. Unpublished manuscript: report to Rijk-instituut voor Natuurbeheer, Leersum.
- Noirfalise, A. & Vanesse, R. (1977). *Heathland conservation*. Brussels: Council of Europe "Nature and Environment" series no. 12.
- Rollinat, R. (1934). *La vie des Reptiles de la France centrale*. Paris: Delagrave.
- Spellerberg, I. F. & House, S. M. (1980). *An analysis of the sand lizard habitat in southern England*. Southampton University: unpublished report.

NOTES ON THE DIET OF ERHARD'S WALL LIZARD, *PODARCIS ERHARDII*

ANDREW QUAYLE*

Department of Zoology, The University, Manchester M13 9PL

(Received 19 May 1982)

INTRODUCTION

The diets of free-living lacertid lizards have been recorded by numerous authors. It is well known that *Podarcis* species are primarily insectivorous, but there has been no account of the diet of Erhard's wall lizard, *Podarcis erhardii*. This paper records the diet of individuals on the island of Ios, in the southern Aegean Sea, determined by faecal analysis.

MATERIALS AND METHODS

Thirteen wall lizards were collected on drystone walls near the island's harbour between 21 and 27 Sept. 1980. The lizards, consisting of six females and seven males, were kept in clean plastic boxes to facilitate the collection of faecal pellets. When the digestive tracts of the lizards were judged to be empty, they were released.

Faecal pellets were collected and stored in 70% ethanol. They were analysed in England by dissecting our fragments for identification under 10× or 20× magnification. This is most easily performed in a Petri dish with some ethanol (Quayle, in preparation). By dissecting out and identifying the numerous chitinous fragments contained in the faeces one can discover the minimum number and arthropod group of the prey that have been devoured.

RESULTS

The results are given in Table I, which shows the total numbers of each prey category recovered from the 13 lizards. The Table also gives the data as per-

TABLE I. Diet of *Podarcis erhardii*

Arthropod group	Minimum number	Percentage
Formicoidea	58	78
Coleoptera	5	7
Hemiptera	5	7
Orthoptera	2	3
Scorpionida	2	3
Diptera	1	1
Araneae	1	1

* Present address: 54 Joyce Street, Manchester M10 8HA.

tages, calculated as

$$\frac{\text{number of prey of a given group in all lizards}}{\text{total number of prey items in all lizards}} \times 100$$

The percentages have been rounded off to the nearest whole number.

DISCUSSION

Ants (Formicoidea) predominate in the diet of *P. erhardii* on Ios, forming 78% of the total. It may be argued that the small physical size of these insects makes the result a misleading figure. However, many of the fragments comprised the entire head of an ant. Many of them were from the large soldier castes and were as much as 2 mm in width. In spite of this, it is probably correct to assume that the contribution to the diet by groups other than Formicoidea may be somewhat greater than the percentage suggests.

Ants also appear to predominate in the diets of other lacertid lizard species on islands (*P. sicula* on Vivaro di Nerano, near Naples—Ouboter, 1981; *Lacerta dugesii* on islands in the Madeiran archipelago—and Salvage Islands—Sadek, 1981). They form a relatively insignificant fraction, however, of the diets of *Podarcis* and *Lacerta* from mainland habitats (e.g. Angelov, Tomov & Gruev, 1966; Avery, 1966; Itamies & Koskela, 1971; Kabisch & Engelmann, 1969; Koponen & Hietakancas, 1972).

The presence of portions of two small scorpions in the sample suggests that *P. erhardii* performs at least some of its foraging underneath stones: the lizard is diurnal, while scorpions are nocturnal but were fairly common amongst the stones of the walls in the lizards' habitat. It seems reasonable to assume that, with the high surface temperatures attained at this time of the year, the majority of invertebrate prey will take refuge in the shade. At the time of the study it was noted that invertebrates, with the exception of Diptera, were not conspicuous.

ACKNOWLEDGEMENTS

My thanks are due to the following people: Miss J. K. Strogen, for her assistance in catching the lizards; Dr D. W. Yalden, for his criticism and advice regarding the work, which formed part of a final year thesis for an honours degree in Zoology at Manchester University.

REFERENCES

- Angelov, P., Tomov, V. & Gruev, B. (1966). Researches on the food of some species of lizards in Bulgaria. *Nauchni Trudove. Vissih Pedagogicheskii Institut, Plovdiv* **4**, 99–106 (in Russian).
- Avery, R. A. (1966). Food and feeding habits of the Common lizard (*Lacerta vivipara*) in the west of England. *Journal of Zoology, London* **149**, 115–121.
- Itamies, J. & Koskela, P. (1971). Diet of the common lizard (*Lacerta vivipara* Jacq.). *Aquilo serie Zoologica* **11**, 37–43.
- Kabisch, K. & Engelmann, W.-E. (1969). Zur Nahrung von *Lacerta muralis* (Laurenti) in Ostbulgarien. *Zoologische Abhandlungen Staatliches Museum für Tierkunde in Dresden* **30**, 89–92.
- Koponen, S. & Hietakancas, H. (1972). Food of the common lizard (*Lacerta vivipara* Jacquin) on a peat bog in southwestern Finland. *Annales Zoologici Fennici* **9**, 191–192.
- Ouboter, P. E. (1981). The ecology of the island-lizard *Podarcis sicula salfii*: correlation of microdistribution with vegetation coverage, thermal environment and food size. *Amphibia-Reptilia* **2**, 243–257.
- Sadek, R. A. (1981). The diet of the Madeiran lizard *Lacerta dugesii*. *Zoological Journal of the Linnean Society* **73**, 313–341.

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, p. 310 (1983)

HISTORY OF *EMYS ORBICULARIS* ON MENORCA (SHORT NOTE)

B. R. VICKERS

Protecfauna SA, Son Cifre de Baix, Apartado 178, Manacor, Mallorca

(Received 15 January 1982)

I was interested to read the letter in *British Journal of Herpetology* on the capture of *Emys orbicularis* on Menorca (Dutton, 1981), but am surprised that the author states that the terrapin had not previously been recorded on the island. The existence of *E. orbicularis* on Menorca was mentioned by Barceló y Combis (1876); earlier undated references also exist. The terrapin was frequently named in Balearic literature until around the turn of the century, when it seems to disappear as many failures in early records were found (e.g. Salvador, 1890, mentions how *E. orbicularis* were exported from Menorca to Barcelona on mainland Spain for the manufacture of motor oil). Field work to prove the existence of the species was not undertaken until fairly recently.

Colom Casanovas (1978) failed to give any reference to other than Mallorcan *E. orbicularis*, whose range at present includes the Albufera marsh at Alcudia and two streams in the eastern sector of the island; while Arnold, Burton & Oviden (1978) leave the Balearic Islands completely outside this terrapin's distribution. Publications of limited distribution such as those of the Natural History Society of the Balearics and INCAFO (1978) however do mention *E. orbicularis* in the "Es Grao" marsh, north of the Shangri-la urbanization on Menorca, and the "Barranco de Algendar" on the southwest coast, which shelters the terrapin in many of its streams.

I have no records of *E. orbicularis* on Ibiza, but this

does not mean that it is absent; certainly it occurs on the other major islands, but in decreasing numbers. Several terrapin-inhabited streams on Mallorca have, or are, losing their water to agriculture and roadways that divert it for other uses. In view of the lack of knowledge of these insular populations of terrapins (the possibility that there are island varieties or subspecies still exists) and the threat under which they now live, work on them from the scientific and conservation sides would seem fully justified.

REFERENCES

- Arnold, E. N., Burton, J. A. & Oviden, D. W. (1978). *A field guide to the reptiles and amphibians of Britain and Europe*. London: Collins.
- Barceló y Combis, F. (1876). *Nuevos apuntes para la fauna Balear. Catálogo de reptiles observados en las Islas Baleares*. Palms de Mallorca: Gelabert.
- Colom Casanovas, G. (1978). *Biogeografía de las Baleares*. Palma de Mallorca: Instituto de Estudios Balearicos, C.S.I.C.
- Dutton, R. A. (1981). *Emys orbicularis* on Menorca. *British Journal of Herpetology* **6**, 143.
- INCAFO. (1978). *Guía ecológica de las Baleares*. Madrid: Pub. Omnia.
- Salvador, Archduque Luis (1890). *La isla de Menorca*. Mallorca: La Caixa (Spanish translation from German).

A NEW *PSAMMOPHIS* FROM NORTHERN GHANA

STEPHEN SPAWLS

35 Woodland Rise, London N10

(Received 5 May 1982)

SUMMARY

A new species of *Psammophis* (Colubridae) from Wa, northern Ghana, is described. A brief discussion of its habits and the significance of its occurrence are included.

INTRODUCTION

On 20 January 1980 the author collected a small snake at Wa in the Upper Region, northern Ghana. The morphology, lepidosis and distinct maxillary dentition of this snake, examined according to Boulenger (1896) and Bogert (1940), indicate that it belongs to the genus *Psammophis*. Further examination shows that it is distinctly different from the other known *Psammophis*, and represents a hitherto undescribed species.

Psammophis leucogaster sp. nov.

Holotype: British Museum (Natural History) number BM 1980:261. A male, collected by the author at 4.30 p.m. on 20 January 1980. The snake had fallen into a concrete pit on the campus of Wa Secondary School, 2 km south-east of Wa town (10° 03' N, 2° 29' W). The species is named in respect of its uniformly white ventral surface. *Diagnosis*: A small *Psammophis*, differing from other known members of the genus by possession of the following combination of characters: 7 Supralabials, 17 midbody scale rows, a single anterior temporal scale, an entire anal scale and an unmarked ventral surface.

DESCRIPTION OF THE HOLOTYPE

Dimensions (in mm): Overall length 504 when measured dead on bench, snout-vent length 355, tail 149 (see remarks on tail length under lepidosis), length of head 15.1 from snout tip to level of first ventral, maximum width of head 5.7, diameter of eye 2.7.

Lepidosis: Rostral broader than deep, visible from above. Internasals shorter than the prefrontals. Nostril pierced between 2 nasals, without a well-defined posterior prolongation. Loreal $2\frac{1}{2}$ times as long as deep. One preocular, not in contact with the frontal. Two postoculars (right side), 3 postoculars (left side). Temporals 1 + 2. Supralabials 7, 3rd and 4th entering orbit. Nine infralabials (left side), 7 infralabials (right side), those corresponding to numbers 3–4–5 on the left side fused into a single scale on the right side. Second infralabial on the right side larger than its fellow on the left side. Three infralabials in contact with the anterior

sublinguals on the left side, 2 infralabials in contact with the anterior sublinguals on the right side. Anterior sublinguals shorter than the posterior. Dorsal scales smooth, in 17–17–15 rows. 162 ventrals (count according to Dowling (1951) but numerically equal to traditional count in this case). Anal entire. 89 subcaudals. The terminal spike is only two-thirds of the length of the preceding subcaudal, which according to Broadley (1977) indicates that a small portion of the tail is missing.

Dentition: Maxillary teeth clumped with spaces between: 4–3–2–2. The three teeth in the second clump are enlarged, the last two teeth are grooved fangs.

Colour: (in life) A fine yellow vertebral stripe one scale wide is bordered on either side by a light brown stripe three scales deep. This stripe is bordered with black on its lower margin. Below this is a fawn stripe four scales deep. On its lower edge the fawn darkens abruptly to brown. The lowest dorsal scale row has the upper half brown and the lower half ivory white. Each dorsal scale, save the lowest row on each side, is covered in very fine black stippling. The scales of the lowest dorsal row are stippled on the upper half. The ventrals are an immaculate ivory white. The head is yellow-grey posteriorly, blending to fawn anteriorly, the fawn narrowing forward of the level of the eyes to a stripe running down the centre of the snout. This stripe is edged with black, the outer edges of the prefrontals and internasals are brown. Along the side of the head and neck are a series of brown blotches, some bordered with black. The chin, throat and supralabials are immaculate ivory white.

HABITS

The specimen was kept in captivity from 20 January 1980 until 22 May 1980. During this time it showed a diurnal pattern of activity, becoming active between approximately 9 a.m. and 5 p.m. During the night it usually took cover beneath a flat piece of tile. Although several branches were provided in the cage, the specimen spent most time on the ground and was rarely observed climbing. The specimen was offered and accepted the following species as food; Lizards—*Ptyodactylus hasselquistii*, *Hemidactylus brookii*, *Mabuya quinquetaeniata*; Frogs—*Ptychadena maccarthiensis*, *Ptychadena longirostris*. Most food items were observed and seized as soon as they moved. Only small food items (less than 80 mm length) were offered, as when captured the specimen had a large open wound on its neck.

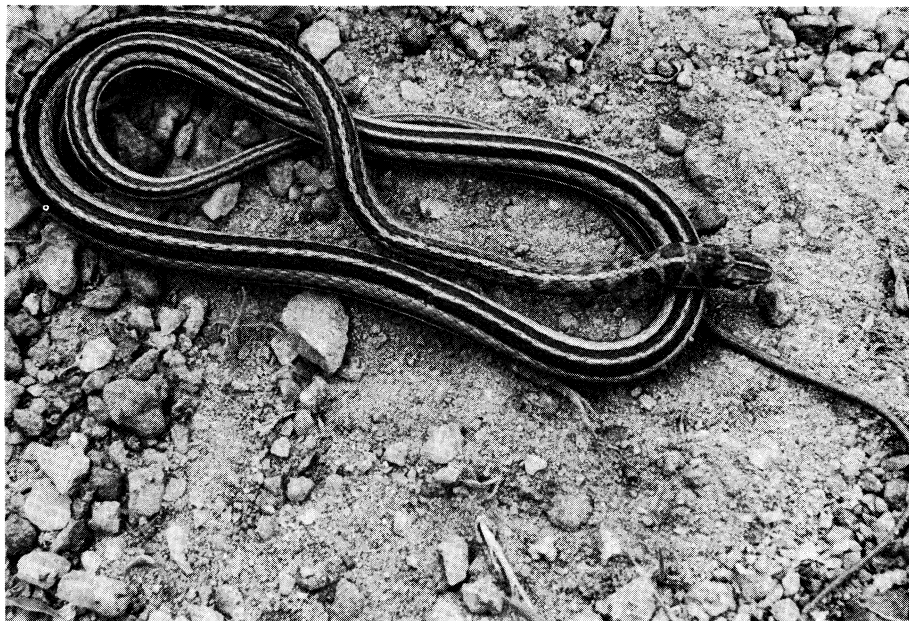


FIG. 1. Photograph of the holotype of *Psammophis leucogaster*. Total length = 504 mm.

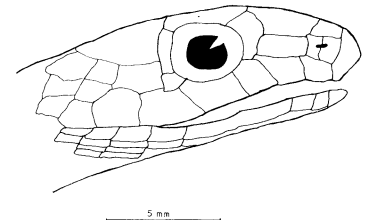


FIG. 2. Right side of head of *Psammophis leucogaster*.

DISCUSSION

RELATIONSHIP WITH LOCAL SPECIES

Other species of *Psammophis* known from northern Ghana include *Psammophis phillipsii*, *P. sibilans* and *P. elegans* (Hughes & Barry, 1969, Papenfuss, 1969). Specimens of these three species have been collected by the author within 50 m of the exact collection locality of the holotype of *P. leucogaster*. In addition, *Psammophis rukwae* may possibly occur in the area, as it is known from Senegal (Böhme, 1978). However, these four species differ from *P. leucogaster* in that they all usually possess some sort of ventral marking (*P. leucogaster* has none), eight or more supralabials and two anterior temporals.

HABITAT

The vegetation of the Wa area is described by Keay (1959) under the heading "Woodland, savannah and steppe", and under the sub-heading "Northern areas, with abundant *Isobertinia doka* and *I. dalzieli*". This vegetation type occurs in a wide band from Guinea eastwards across Africa to the Sudan, with few natural barriers, and it seems surprising that species found in such a widespread habitat has not been recorded previously. However, this vegetation type is rarely closer than 500 km to the sea, which would place it beyond the reach of many early collectors. Of interest in comparison is the existence of a small *Psammophis*, *P. pulcher*, in eastern Africa. This snake occurs in two widespread vegetation types and yet is known from only a handful of specimens (Drewes & Spawls, 1973).

ACKNOWLEDGEMENTS

The preparation of this paper would have been impossible without the assistance of Stephen Cooke, my field officer in Accra, to him I am grateful. My thanks are also due to Barry Hughes, of the Department of Zoology, University of Ghana, who not only

kindly read the text of this paper and passed valuable comment upon it, but also allowed me the use of his extensive library and access to the University of Ghana reptile collection. I would also like to thank Miss A. G. C. Grandison, Colin McCarthy and Barry Clarke of the Herpetological section of the British Museum (Natural History) for allowing me to research there. I am also grateful to Dr Donald Broadley of the National Museum, Bulawayo, Zimbabwe, for his comments on the specimen, to my brother-in-law Adrian Marlowe for his help with the photographic work, and to the staff and pupils of Wa Secondary School, especially Mr Jakalia Abdulai, Mahama Seidu Pelp, Alexander Suglo and Richard Azeikho, for their assistance with my field work.

REFERENCES

- Bogert, C. M. (1940). Herpetological results of the Vernay-Angola expedition, with notes on African reptiles in other collections. I. Snakes, including an arrangement of the African Colubridae. *Bulletin of the American Museum of Natural History* **77**, 1-107.
- Böhme, W. (1978). Zur Herpetofaunistik des Senegal. *Bonner Zoologische Beiträge* **29**, 360-417.
- Boulenger, G. A. (1896). *Catalogue of the snakes in the British Museum (Natural History)*, volume 3. London: British Museum (Natural History).
- Broadley, D. G. (1977). A review of the genus *Psammophis* in southern Africa (Serpentes, Colubridae). *Arnoldia, Rhodesia* **8**, 1-29.
- Dowling, H. G. (1951). A proposed standard system of counting ventral scales in snakes. *British Journal of Herpetology* **1**, 97-99.
- Drewes, R. C. & Spawls, S. (1973). The occurrence of the colubrid snake *Psammophis pulcher* in Kenya. *Herpetologica* **29**, 306-307.
- Hughes, B. & Barry, D. H. (1969). The snakes of Ghana, a checklist and key. *Bulléin de l'Institut Fondamental d'Afrique Noire* **31**, 1004-1041.
- Keay, R. J. W. (1959). *Vegetation map of Africa*. Oxford: University Press.
- Papenfuss, T. J. (1969). Preliminary analysis of the reptiles of arid central West Africa. *Wasmann Journal of Biology* **27**, 249-325.

BOOK REVIEW

BIOLOGY OF THE REPTILIA, Volume 12. *Physiology C, Physiological Ecology*. Edited by Carl Gans and F. Harvey Pough (1982). xv + 536 pp. London, New York, Paris, San Diego, San Francisco, Sao Paulo, Sydney, Tokyo, Toronto: Academic Press. £52.00.

Over the last few decades, it has become increasingly apparent that reptiles, birds, and mammals demonstrate different and quite distinctive approaches to the physiological problems posed by life on land. No longer are reptiles to be regarded as evolutionary "stepping stones" between fishes and amphibians on the one hand, and birds and mammals on the other. Investigation of physiological ecology has proved to be an especially fruitful approach to the study of their adaptations and diversity. Many aspects of the biology of reptiles reflect their ectothermy; low resting metabolic rates are accompanied by limited aerobic power input during activity and occasional reliance upon anaerobic metabolism, so that "sit-and-wait predation" is advantageous. Some species are extremely selective and specialize on rare prey items, their low food requirements and small size enabling them to exploit narrow niche breadths and to endure the dense packing of individuals. Others move about steadily in "search-capture cycles" with a low level of activity interspersed by short dashes. But the prey is seldom chased by sustained effort: surprise and crypsis appear to predominate.

Not only is the physiological ecology of reptiles a comparatively new area of research but, rather than following patterns set by studies on other taxa, it has included many key developments in the field. This is made abundantly clear by the superb volume under review, in which only a small proportion of the references appeared before 1965. The first part is devoted to temperature regulation (with chapters by F. H. Pough and Carl Gans, Raymond B. Huey, R. A. Avery, George A. Bartholomew, Bruce J. Firth and J. Scott Turner, and C. Richard Tracy), the second to water relations (with chapters by John E. Minnich, H. B. Lillywhite and P. F. A. Maderson, William J. Mautz, and Kenneth A. Nagy). It is not possible in a brief review, to render justice to such a galaxy of talent or to such a wealth of interesting topics. All I can do is to

illustrate some of the intellectually exciting problems discussed. These include the functions of sun basking, the physiological control of rate of change in body temperature, endogenous heat production, the effects of gaping by crocodylians, evaporative cooling in tortoises, voluntary hypothermia and circadian rhythms in thermoregulation, the acquisition and utilization of water, the function of the reptile bladder, patterns of evaporative water loss and water fluxes in free-living reptiles.

These examples have been selected on the basis of the present writer's subjective interests. For others, more mathematically and theoretically inclined, Richard Tracy's chapter on biophysical modelling, that on skin structure and permeability by H. B. Lillywhite and P. F. A. Maderson, and the one on patterns of evaporative water loss by William Mautz will be of special interest. Most British readers would probably opt for Roger Avery's brilliant review of field studies of body temperatures and thermoregulation, and George Bartholomew's inspired account of the physiological control of body temperature. Of the various authors, only R. A. Avery is British and Bruce Firth Australian, the remainder all work in the U.S.A. Although many other distinguished herpetologists from these countries and elsewhere might well have collaborated in this book, the proportions selected by the Editors are probably fairly representative of the amounts and degree of research interest currently devoted to reptile biology throughout the world. Like all the volumes in the series *Biology of the Reptilia*, this is written by zoologists for zoologists. With its emphasis on field observations, however, it should have a wider readership than most of the others, and appeal more to general herpetologists who will be able readily to check the significance of their personal observations. It would be mistaken to suppose that exciting new discoveries can be made only by professional biologists—indeed, the debt owed to amateur naturalists is widely recognized. They should not allow themselves to be deterred from the benefits of consulting this encyclopaedic work of reference.

J. L. CLOUDSLEY-THOMPSON

ANNOUNCEMENTS

HERPETOFAUNA TRANSLOCATIONS IN BRITAIN—A POLICY

Statement from the Conservation Committee of the British Herpetological Society

(Received 17 September 1982)

INTRODUCTION

The movement of animals for release into the wild has become an increasingly controversial topic in recent years. A working party under the auspices of the Nature Conservancy Council recently looked into the matter in Britain, ultimately producing a report (*Wildlife Introductions into Great Britain*) laying down guidelines for future policy. Only a few of the recommendations made have been, and seem likely in the future to be, implemented largely because of the costs involved. Furthermore, this necessarily general review could not address itself to the problems posed by specific groups such as the herpetofauna. The Wildlife and Countryside Act of 1981 also addresses the problem, and any translocations of species not native to Britain, as well as native species on the protected list, now require a license from the Nature Conservancy Council.

The Conservation Committee of the British Herpetological Society has been involved with the translocation of amphibians and reptiles for more than a decade, and has already published a preliminary dissertation on the topic (*British Journal of Herpetology* 4, 339–341). However, in view of the recent developments the Committee decided that it was appropriate to reconsider the subject in more detail and has after due deliberations produced the Policy described below. This Policy has been submitted to the Nature Conservancy Council for comment.

DEFINITIONS

In general it is no doubt sensible to stay within the broad definitions laid down in the recent NCC publication *Wildlife Introductions to Great Britain*. However, due to the types of operation likely to be carried out with herpetofauna and also for other reasons (see below) we suggest the following:

Introduction. This for all practical purposes should relate to the release of species not generally accepted as being part of the British fauna in post glacial times.

Translocation. It would seem logical if all movement and release of the 12 indigenous British species other than that covered by restocking (see below) could be placed under this category. This would avoid trying to make distinctions between introduction and reintroduction within Britain, a difficult procedure for several reasons.

(i) Introduction would be poorly defined, not

immediately distinguishing between truly alien and British species.

(ii) Resolution of previous records is often poor, and accurate distinction between what is an "introduction" and what is a "reintroduction" at neighbouring sites would not be possible (e.g. on adjacent blocks of heathland).

(iii) Historical records extend only over a very short, and hence arbitrary period of time during which distribution may in any case not have been typical of the post glacial era.

(iv) Recording for creatures such as amphibians and reptiles has always been poor, and it is virtually certain that even within recent times sites have been lost without ever having been recorded. For example, should a single unverified natterjack record from a Cornish dune system cause it to be defined as a "reintroduction" site or an "introduction" site? The term "translocation" overcomes this difficulty.

(v) Since the methodology employed to establish new colonies will be essentially the same whether the species existed at a site in the past or not, distinction between introduction and reintroduction is in any case a pedantic one assuming an overall strategy is agreed (see later).

(vi) It is arguable that all movements of British species to sites within the U.K. could be classified as "reintroductions" since movement of animals across national boundaries to any site within the receiving country in which they were once extant is so designated by the Berne Convention (to which the U.K. is a signatory and has now ratified). Using the term "translocation" in the present context would obviate this difficulty, leaving "reintroduction", like "introduction", free for use in a solely international context. Since the U.K. has not lost any herpetofauna within post glacial times so far as we know, reintroductions on the basis of this definition need not be further considered.

Restocking. Release of animals of a species into an area in which it is already present.

INTRODUCTIONS

REASONS AND JUSTIFICATION

(i) General interest as experimental activity, e.g. in garden ponds.

(ii) Enrichment of the British fauna, otherwise poor

in reptiles and amphibians compared with mainland Europe.

- (iii) For commercial purposes, *e.g.* frog's legs.

POLICY

(i) Introduction of non-European species should generally be prohibited, since these are the most likely to compete destructively with native forms and have the least predictable consequences.

(ii) Introduction of some European forms should be discouraged on genetic grounds, since they can cross-breed with native species and produce sterile or low-fertility hybrids, *e.g.* *Triturus marmoratus*, *T. cristatus* subspecies other than the type form, *Bufo viridis*.

(iii) Introduction of some European forms should be acceptable, since many coexist with our own on the mainland and are probably absent from Britain only either (a) by accident, because they did not reach here before the English Channel opened up, or (b) because the climate is much less than optimal, in which case dramatic colonization is unlikely. Known acceptables are *Rana esculenta*, *R. lessonae*, *Rana ridibunda*, *Hyla arborea*, *Alytes obstetricans*, *Bombina bombina*, *B. variegata*, *Triturus alpestris*, *Salamandra salamandra*, *Emys orbicularis*, *Podarcis muralis*.

(iv) Introduction of European forms on neither of these lists should only be permitted subject to consultation with NCC and BHS.

TRANSLOCATIONS

REASONS AND JUSTIFICATION

(i) The primary purpose of translocations is to assist with the conservation of the endangered British species; nationally *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca*, and regionally *Triturus cristatus*.

(ii) The aim is to compensate as far as practicable for recent losses in species abundance and distribution, and should involve

- (a) Attempting to maintain the recent historical distribution.
- (b) Extending distribution to unrecorded or poorly-recorded areas where this seems reasonable (see later). This is especially important where there could be major significance for the long term future of a species; for example, establishing viable sand lizard colonies in dunes in southwest England would be a safeguard against continuing heathland losses (the latter being a much more endangered habitat) as well as a compensation for losses on Merseyside dunes.

(iii) The loss of populations from otherwise doomed sites (*e.g.* those facing imminent development) is seen as an unacceptable waste of resources which should instead be used for translocation purposes.

(iv) The value of nature reserves is enhanced by their particular use as translocation sites wherever suitable (see later).

(v) Translocation can be a valuable experimental tool for investigating various aspects of the ecology of a species.

POLICY

(i) The following broad objectives should be considered:

Sand lizard: (a) Should have recent distribution on heathland in southern England maintained, *e.g.* by translocations to Thursley, Dur Hill, Witley etc.

(b) Should be extended to dune systems in southern England and South Wales as part of long-term safeguard, *e.g.* Braunton, Penhale.

Smooth snake: (a) Recent distribution on southern heathlands should be maintained, perhaps by translocations to *e.g.* Thursley, Ambersham.

Natterjack: (a) Repopulation of heathland sites in England should be attempted, *e.g.* Cannock, Studland, Thursley, Roydon.

(b) Extensions of dune range should be attempted in East Anglia, Wales and southwest England, *e.g.* Holme, Newborough, Braunton.

Crested newt: (a) Encouragement for garden pond stocking should be given.

(ii) The following criteria should be used to judge the suitability of a potential translocation site:

(a) The species should be absent, *i.e.* current survey negative and no previous reliable records for at least ten years.

(b) The habitat should be judged suitable as far as it is possible to ascertain with current knowledge.

(c) The area should fall within the climatic range of the species.

(d) There should be adequate site safeguard, *e.g.* at least SSSI and preferably private or nature reserve and necessarily have low public pressure.

(e) The needs of other rare species on the release site must be fully considered.

(f) Account must be taken of potential predators and competitors.

(iii) All translocation work should be done, and the criteria agreed, in consultation between all conservation bodies involved.

(iv) The precise methods employed, *i.e.* use of adults, immature, larvae or eggs; numbers; time of year; sustenance of effort etc. will be based on current experience and will be refined in the light of increasing data.

(v) Monitoring requirements will be necessary and require discussion, but efforts for proven and reliable methods (*e.g.* sand lizard translocations on heathland) should be less than those needed for unproven ones.

RESTOCKING

REASONS AND JUSTIFICATION

(i) Extreme decline and senility/low fertility problems can sometimes lead to a situation in which the population is unlikely to recover as a result of habitat management alone (*e.g.* natterjacks in Hampshire). Restocking can then be an essential aid.

POLICY

(i) Ebbing populations should be revived by habitat management alone wherever possible.

(ii) Animals which happen to become available (*e.g.* from doomed sites) should not be added to extant colonies since the existing population will already be filling the niche space available.

(iii) Sites at which the population is deemed to have reached a precariously low ebb can be restocked using animals reared in captivity but hailing from the same population that is already present on the site, unless circumstances render this impossible (*e.g.* the population is already so small that abstraction for captive rearing is not feasible).

(iv) The status of such sites should be agreed with NCC and BHS.

(v) Methods used should be dictated by the current level of knowledge, as for translocations.

CONCLUDING REMARKS

Several facets of this Policy have already been actively and successfully pursued by the Conservation

NEW BATRACHOLOGICAL SOCIETY AND JOURNAL

On 6 November 1982 the *Société Batrachologique de France* (*Société pour l'Étude et la Protection des Amphibiens*) was founded in Paris. The purpose of this society will be to contribute to our knowledge of Amphibians, to preserve the species and their habitats, and to further communication between batrachologists. It is probably the first scientific society in the World to be specifically devoted to batrachology. The study of Amphibians has long been included in herpetology, but Amphibians are only distantly related to Reptiles and they require a specific discipline. Membership of the SBF is open worldwide to anyone interested in Amphibians. Applications for membership should be sent to the General Secretary at the address below.

The SBF is publishing a new quarterly journal, *Alytes*, which is open to all kinds of papers dealing with Amphibians. The Co-Editors are Alain Dubois and Jean-Jacques Morère, and the Editorial Board presently consist of Jean-Louis Amiet (Yaoundé), Michail Fischberg (Genève), Benedetto Lanza (Firenze), Raymond Laurent (Tucumán) and Madeleine Paillette (Brunoy). Manuscripts should be in English or in French and should be sent in triplicate to the Co-Editors. If you wish to receive the journal in 1983 please place an order with the General Secretary and credit the following bank account:

Société Batrachologique de France
Banque Nationale de Paris, Agence Assas,
Bank Account no. 748056/37,
(30004 01697 00000748056 37)

Committee of the British Herpetological Society. Thus, numerous sand lizard translocations extending back more than ten years have nearly *all* resulted in the establishment of new colonies on heathlands in SW and SE England, and even an early experiment on the dunes of a Hebridean island has proved successful with this species. Crested newts have been established in a variety of garden ponds, as of course have the other common native amphibian species. Work with the natterjack has been the least successful so far; early projects on heathland in Surrey and Dorset in the early 1970s all failed, but experiments started over the past few years, in the light of more ecological information, look promising at the present time. Translocations are only one aspect of conservation work, and usually a minor one, but there is no doubt about their value when circumstances are favourable.

with the sum of FRF 35. Please do not send cheques directly to the Treasurer.

Alain Dubois,
General Secretary of the SBF,
Laboratoire des Reptiles et Amphibiens,
Muséum National d'Histoire Naturelle,
25 rue Cuvier,
75005 Paris,
France.

MEETING

Joint meeting of the Herpetologists' League and the Society for the Study of Amphibians and Reptiles, University of Utah, Salt Lake City, 7–12 August 1983. For further information write to John M. Legler, Department of Biology, University of Utah, Salt Lake City, UT 84112, U.S.A.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The Commission gives six months notice of the possible use of its plenary powers in the following case, published in the *Bulletin of Zoological Nomenclature* **40**, part 1 (29 March 1983), and would welcome comments and advice on it from interested zoologists. Correspondence should be addressed to the Secretary as soon as possible.

Case no. 2373 UROPLAT—as the stem of family-group names in Amphibia and Insecta (Coleoptera): proposals to remove the homonymy.