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NOTES ON THE HERPETOFAUNA OF KASHMIR AND LADAKH

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SUMMARY

During two journeys to Kashmir and Ladakh in June–July 1976 and August 1977 the following species were collected: *Bufo latastii latastii*, *Cyrtodactylus stoliczkai*, *Agama himalayana*, *Phrynocephalus theobaldi*, *Scincella himalayana* and *Scincella ladacensis*. The habitats examined range from 2600 to 4200 m. *Bufo l. latastii* was found in the semiarid region near Dras in Ladakh and in the moist area of Naranag in Kashmir. *Cyrtodactylus stoliczkai* was discovered at rocky places in Ladakh. *Agama himalayana* in Ladakh ecologically replaces *A. tuberculata* from the more southern and eastern parts of the Himalayas. Both species can be distinguished easily from each other by a number of distinct characters. *Phrynocephalus theobaldi* is a true desert animal; a number of behavioural pecularities and morphological characters are noted. *Scincella himalayana* is the most common reptile in the Kashmir mountains, it ascends up to 4200 m and more. It is generally viviparous (mainly 2–3 embryos), although a population from Gulmarg southwest of Srinagar seems to be oviparous. *Scincella ladacensis* in Ladakh was found on places covered with a combination of sparse bushes, some grass and stones, often in the surrounding of human settlements. The systematic relationships and characteristic differences between *S. sikkimensis*, *S. himalayana* and *S. ladacensis* are noted and discussed.

INTRODUCTION

During two journeys in June–July 1976 and August 1977 I visited Kashmir and Ladakh. Because I was travelling with a group of non-herpetologists, the observations on the herpetofauna of the areas visited are somewhat fragmentary and do not cover all the amphibians and reptiles that might be expected. But since all previous reports from the region are very incomplete, any new observations on the herpetofauna of Kashmir and Ladakh are important and useful contributions to our knowledge of the fauna of that remote area.

Early reports on the herpetofauna of Kashmir and Ladakh were given by Zugmayer (1909) and Brongersma (1935). The results of investigations on amphibians and reptiles in the northwestern frontier area of India were finally summed up in the *"Fauna of British India, Amphibians and Reptiles"* by Smith (1931, 1935, 1943). Recently Murthy & Sharma (1976) have published a short paper on amphibians and snakes from Jammu and Kashmir, concentrating on the district of Poonch, 70 miles southwest of Srinagar.

During my visit I collected the following species: *Bufo latastii latastii* (Hemmer, Schmidtler & Boehme, 1977), *Cyrtodactylus stoliczkai*, *Agama himalayana*, *Phyrynocephalus theobaldi*, *Scincella himalayana* and *Scincella ladacensis*.

AREA OF STUDY

The area of study was partly situated in the rather moist Himalayas north of Srinagar, which are densely covered with forest and grassland vegetation, and partly in the completely dry, desertlike area of Ladakh itself. There were great differences in the various habitats. The meadows and open, sunny places in the mountain forests of Kashmir with mainly firs, pinetrees and birchtrees and the open pastures in the altitudes above the timberline (around 3000 m) were preferred by *Scincella himalayana*. The species *Cyrtodactylus stoliczkai* and *Phrynocephalus theobaldi*, however, could only be found in the desert of Ladakh itself, especially in the upper Indus valley. *Agama himalayana* and *Scincella ladacensis* also live in the semiarid transitional zone between the Zoji pass and Dras, as they do in the rocky, extremely dry region of central Ladakh. There *Agama himalayana* prefers rocks and stone walls, whereas *Scincella ladacensis* lives in the neighbourhood of irrigated, arable land. The

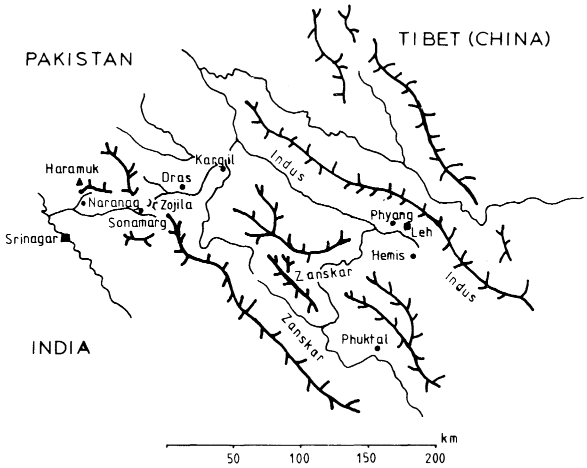

FIG. 1. Map of Kashmir and Ladakh showing the main places of investigation.

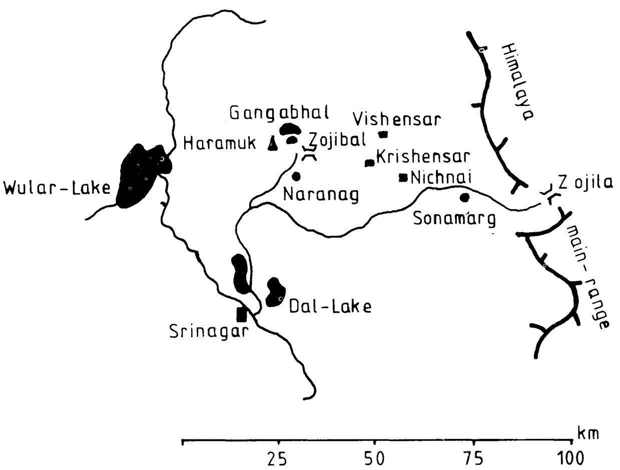

FIG. 2. Detailed map of the Haramuk mountain area in Kashmir.

distribution of both these species ends abruptly in the region of the Zoji La; on the Kashmir side of this pass only *Scincella himalayana* and *Agama tuberculata* are found. Although *Bufo l. latastii* is quite resistant to dry conditions and exists all over the arid habitats of its central Asiatic distribution, it is usually found not too far from water. I discovered it in wet habitats in the forest area of Naranag (2600 m) below the Haramuk mountains and along a small creek containing several rivulets running through irrigated meadows and fields of a village near Dras. It is noteworthy that the vast district of Zanskar in southern Ladakh seems to lack amphibians and reptiles in most places. During our journey through this region, we only saw one population of *Agama himalayana* which was on a mountain ridge near Phuktal in a side valley of the Lungnak river.

The altitudes of the area visited in Kashmir ranged from 2600 m in Naranag, 2700 m in Sonamarg, 3500 m at the timberline near Nichnai, the high altitude pastures in the Haramuk region at 3400–3900 m up to the highest passes crossed, such as Krishensar Pass 4100 m, Vishensar Pass 4150 m and Zojibal Pass 4100 m. The highest summits in that region reach approximately 5200 m. In Ladakh the altitudes were: Dras 3200 m, Kargil 2700 m, Leh 3500 m, Phyang Ghompa 3600 m, Hemis 3700 m and Phuktal 4100 m; here the mountain tops range between 6000 and something above 7000 m.

MATERIAL AND RESULTS

Bufo latastii latastii BOULENGER, 1882

n = 6: ZSMH 463/76, 4 ♂♂, oasis near Dras, Ladakh, 3200 m, 30.6.1976; ZSMH 464/76, 2 sad, Naranag, Kashmir, 2600 m, 16.7.1976; all coll. Gruber.

In the evening of 30 June I heard trilling calls from a small creek which irrigated the neighbouring fields of a village near Dras. They resembled the calls of the European green toad (*Bufo viridis*) and using a torch I discovered several "green toads" in the water. These could be found only after dark as they hid during the day-time. It appeared that the spawning period was already nearly over for no females could be found and several tadpoles were observed in the water. Vegetation was scarce in the surrounding area with only some bushes and willows growing on the edge of the irrigated sections, but the environment contained many stones and big rocks. All six toads were collected alive and placed at the disposal of W. Boehme, H. Hemmer and J. F. Schmidtler (1977) for taxonomic study. They discovered that these green toads belong to the subspecies *Bufo latastii latastii* Boulenger, 1882.

Cyrtodactylus stoliczkai (STEINDACHNER, 1869)

n = 14: ZSMH 119/77, 1 juv, Kargil, Ladakh, 2750 m, 12.8.1977; ZSMH 121/77, 1 ♀, Saspool, Ladakh, 3100 m, 16.8.1977; ZSMH 45/77 and 149/77, 2 ♂♂, 5 ♀♀, 3 juv, Phyang Ghompa, Ladakh, 3600 m, 5.7.1976 and 19.8.1977; ZSMH 46/77 and 124/77, 2 ♀♀, Hemis, Ladakh, 3700 m, 6.7.1976 and 17.8.1977; all coll. Gruber.

Cyrtodactylus stoliczkai was first described by Steindachner (1869) from Karoo, north of Dras in Ladakh. Later it was recorded from Yarkand (Anderson, 1872), from Chitral (Ingoldby, 1922) and from central Ladakh itself (Leh, Brongersma, 1935; Lamayuru, Zugmayer, 1909). My specimens were found in rocky habitats below Phyang Ghompa near Leh and in the surroundings of Hemis Ghompa (first recorded in the upper Indus valley). One specimen was encountered sitting in a small hole of a willow tree. The Ladakh desert geckos seem to prefer bare, dry habitats in the non-irrigated areas without or with very sparse vegetation. They seem to avoid the direct neighbourhood of human settlements like *Cyrtodactylus kotschyi* (Beutler & Gruber, 1977).

Cyrtodactylus stoliczkai is similar to *C. kotschyi* (Steindachner, 1870) in size, shape, pholidosis and colour pattern. The colour of the back is grey, with an irregular pattern of seven or eight transverse bands, especially distinct in juvenile animals. The dark colour is produced by black tubercles and scales. The dark transverse bands are continued on the unregenerated tail. There are irregular dark speckles on the upper surface of the head. The tubercles of the back are flat, round and smooth, without prominent points or keels. There are only a few weak tubercles on the thighs. The males seem to lack preanal pores. Two postanal tubercles are present and there are two rows of prominent tubercles on either side of the unregenerated tail. Behind each pair of these tuberles the tail is narrowed forming distinct segments. Obvious "segmentation" is restricted to the first third of the tail. The scales underneath the tail are cycloidal. Zugmayer (1909) reports that the regenerated tail of *Cyrtodactylus stoliczkai* is often extremely thickened at the base, but I found only two specimens in which this was so.

Agama himalayana (STEINDACHNER, 1869)

n = 16: ZSMH 47/77, 2 ♂♂, Leh, Ladakh, 3700 m, 4.7.1976; ZSMH 48/77 and 151/77, 5 ♂♂, 3 ♀♀, 3 juv, Hemis, Ladakh, 3700 m, 7.7.1976 and 17.8.1977; ZSMH 49/77, 1 juv, near Kargil, Ladakh, 3200 m, 1.7.1976; ZSMH 126/77, 1 juv, between Dras and Zojila pass, Ladakh, 3200 m, 20.8.1977; ZSMH

150/77, 1 juv, near Phuktal, Zanskar Ladakh, 4100 m, 6.8.1977; all coll. Gruber.

Whereas *Agama tuberculata* is the most common and widely distributed agamid lizard in the moist areas of the Himalayas from Kashmir eastward to Nepal, it is replaced in similar habitats in Ladakh by *Agama himalayana*. This species usually occurs on stone-walls along roads and in the neighbourhood of human settlements, or in ruins like the ancient palace above Leh. Human activities in the form of buildings and cultivations may have exerted a great influence on the recent distribution pattern of *Agama himalayana*. The species is found also in the semiarid transitional zone between Zojila pass and Dras and in the desertlike landscapes of true Ladakh from Kargil on to the upper Indus valley. Where it exists, it is quite common, sitting in the bright sunlight with great numbers of different age and size, on every stone wall or rock. The altitude range which this agamid lizard covers reaches up to more than 4000 m above Hemis in Ladakh and near Phuktal in Zanskar.

Agama himalayana shows close relationships to *A. tuberculata*, but it can be distinguished by a number of distinct differences listed below in comparison with a population from Nepal:

A. himalayana	*A. tuberculata*
1. shape rather slender	shape strong and robust
2. enlarged dorsal scales smooth	enlarged dorsal scales keeled
3. no enlarged scales on the flanks	enlarged, tuberclelike scales on the flanks
4. males without an elongated patch of callous scales on on the middle of belly	males with elongated patch of callous scales on the middle of belly
5. scales on tail continuously arranged, without separated segments; scales rather spiny	scales on tail arranged in separate segments, 4–5 scale whorls in each; scales less spiny (characters less distinct in specimens from Kashmir or Kulu valley)
6. colour of strip of enlarged dorsal scales distinctly brighter than colour of back	colour of strip of enlarged dorsal scales not distinctly brighter than colour of back
7. young animals with rusty red patches on sides of neck	young animals without red patches on sides of neck
8. belly dark grey	belly light grey to yellowish

In addition to this comparison it is noteworthy that breeding adult males of *A. tuberculata* show a steel-blue colour on the shoulders, upper arms and thighs, whereas the males of *A. himalayana* do not have such striking coloration.

Phrynocephalus theobaldi BLYTH, 1863

n = 6: ZSMH 452/76 and 125/77, 3 ♂♂, 2 ♀♀, 1 juv, Phyang Ghompa, Indus valley, Ladakh, 3600 m, 5.7.1976 and 18.8.1977; coll. Gruber.

These small, strange looking animals show remarkable features in their behavioural pattern. They prefer sitting exposed on a stone or a rise in the ground, watching their surroundings attentively. As soon as danger or a rival approaches they rise on their legs and hold their tail curled above the back like the tail of a Pomeranian dog. Then, becoming more and more excited, they wave their tail or beat it violently forward and backwards. When they try to escape they run away fast on high stalking limbs.

The habitat where *Phrynocephalus theobaldi* was collected is extremely arid, covered with alternating sand and stones and almost without any vegetation. This agamid lizard is said to be viviparous; Zugmayer (1909) found embryos in an advanced state of development and newborn young in the month of August.

The tip of the tail is intensely black below in the males of *Phrynocephalus theobaldi*. Both sexes may have elongated black patches in the middle of the belly varying in size and intensity of colour, but sometimes these are missing. The two specimens caught on the 5 July 1976 showed these black patches, but the four specimens obtained on 18 August 1977 did not have any dark colouring on their bellies. It might be that these dark patches are seasonal (Smith, 1935). The life colour of the back is ochre-brown like sand, with 5–6 cross-bands of irregular, dark blotches which extend to the upper surface of the tail (8–12). One single specimen was uniform ochre-brown without any pattern of cross-bands or blotches. The pineal foramen is clearly visible. The belly is light coloured without spots or blotches; one specimen had an orange-red throat and anterior thorax. In the adults, the head and body lengths (snout to vent) were 42, 43, 45, 46, 48 mm and the lengths of tail were 49, 51, 53, 58, 61 mm.

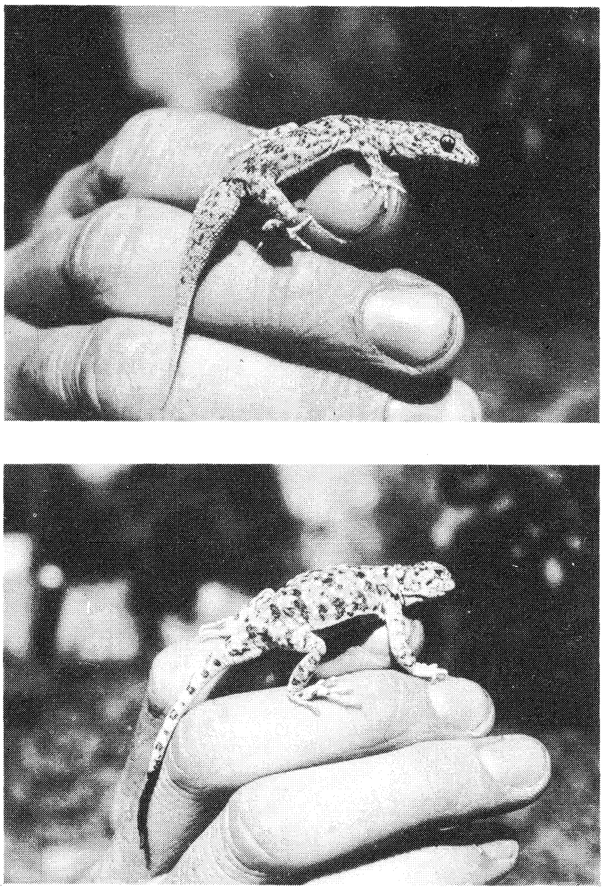

FIG. 3. *Above*: *Cyrtodactylus stoliczkai*, adult male. *Below*: *Phrynocephalus theobaldi*, adult male.

Scincella himalayana (GUENTHER, 1864)

n = 74: all from Kashmir; ZSMH 128/77, 3 ♂♂, 2 ♀♀, Sonamarg, 2700 m, 20.8.1977; ZSMH 50/77, 1 ♂, above Sonamarg, 2900 m, 10.7.1976; ZSMH 51/77, 1 ♀, Nichnai pass, Haramuk mountains, 3800 m, 11.7.1976; ZSMH 52/77, 2 ♂♂, 4 ♀♀, Nichnai above Sonamarg, 3400 m 10.7.1976; ZSMH 53/77, 5 ♂♂, 1 ♀, Vishensar pass, 3800–4100 m, 12.7.1976; ZSMH 54/77, 2 ♀♀, between Vishensar and Gadsar, 3400 m, 12.7.1976; ZSMH 55/77, 3 ♂♂, 9 ♀♀, Gadsar 3400–3600m, 12.7.1976; ZSMH 56/77, 3 ♂♂, 11 ♀♀, Gangabhal below Haramuk, 3600 m, 15.7.1976; ZSMH 57/77, 2 ♂♂, 8 ♀♀, Between Gangabhal and Naranag, 3200–3300 m, 16.7.1976; all coll. Gruber.

ZSMH 154/77, 3 ♂♂, 4 ♀♀, Sonamarg, 2700 m, 15.6.1977; ZSMH 155/77, 1 ♂, Vishensar, 3600 m 6.1977; ZSMH 157/77, 1♀, Nichnai, 3500 m, 6.1977; ZSMH 158/77, 1 ♂, 1 ♀, Tanmarg, 30 km west of Srinagar, 2100 m, 8.6.1977; ZSMH 159/77, 2 ♂♂, 4 ♀♀, Gulmarg, 2700 m, 10.6.1977; all coll. Schmidtler.

By far the most common reptile of the Kashmir highlands at altitudes between 2700 and 4500 m is *Scincella himalayana*. Within this range the region with the highest population density extends from 3000 to 3800 m. Here *S. himalayana* lives in the stony borders along the tracks, on rocky slopes with alpine vegetation and on meadows with quite long-growing grass, where it often hides in the burrows of mice.

The ecological requirements of this species seem to be similar to those of the lizard *Lacerta vivipara* in the European Alps. Like *L. vivipara*, *Scincella himalayana* lives in high altitude habitats, uses every glimmer of sun to raise its temperature, hibernates for at least 5–6 months and is usually viviparous. Out of 41 females collected in June and July, 17 specimens contained 2–3 embryos (1 ♀ had 1 embryo, 3 ♀♀ had 4 embryos). Three other females each gave birth to two or three young after having been brought back to Europe and kept in cages. In the oviducts of 16 further females I counted five or six very small eggs, which may indicate that only half of the eggs originally implanted undergo full embryonic development. The situation in the small series (*n* = 6) caught at Gulmarg in the mountains about 40 km southwest of Srinagar, however, is rather puzzling. The four pregnant females out of this series contained 1–4 eggs without any sign of a pigmented embryo; this population therefore seems to be oviparous.

Scincella ladacensis (GUENTHER, 1864)

n = 23: all from Ladakh; ZSMH 120/77, 2 ♀♀, 1 juv, Suru valley, 3300 m, 14.8.1977; ZSMH 122/77, 5 ♂♂, 4 ♀♀, 4 juv, Bhodkarbu between the passes Namikala and Fatula, 3200 m. 15.8.1977; ZSMH 123/77, 1 ♀, Hemis, 3700 m, 17.8.1977; ZSMH 127/77, 3 ♂♂, 1 ♀, 2 juv, between Dras and Zojila, 3200 m, 20.8.1977.

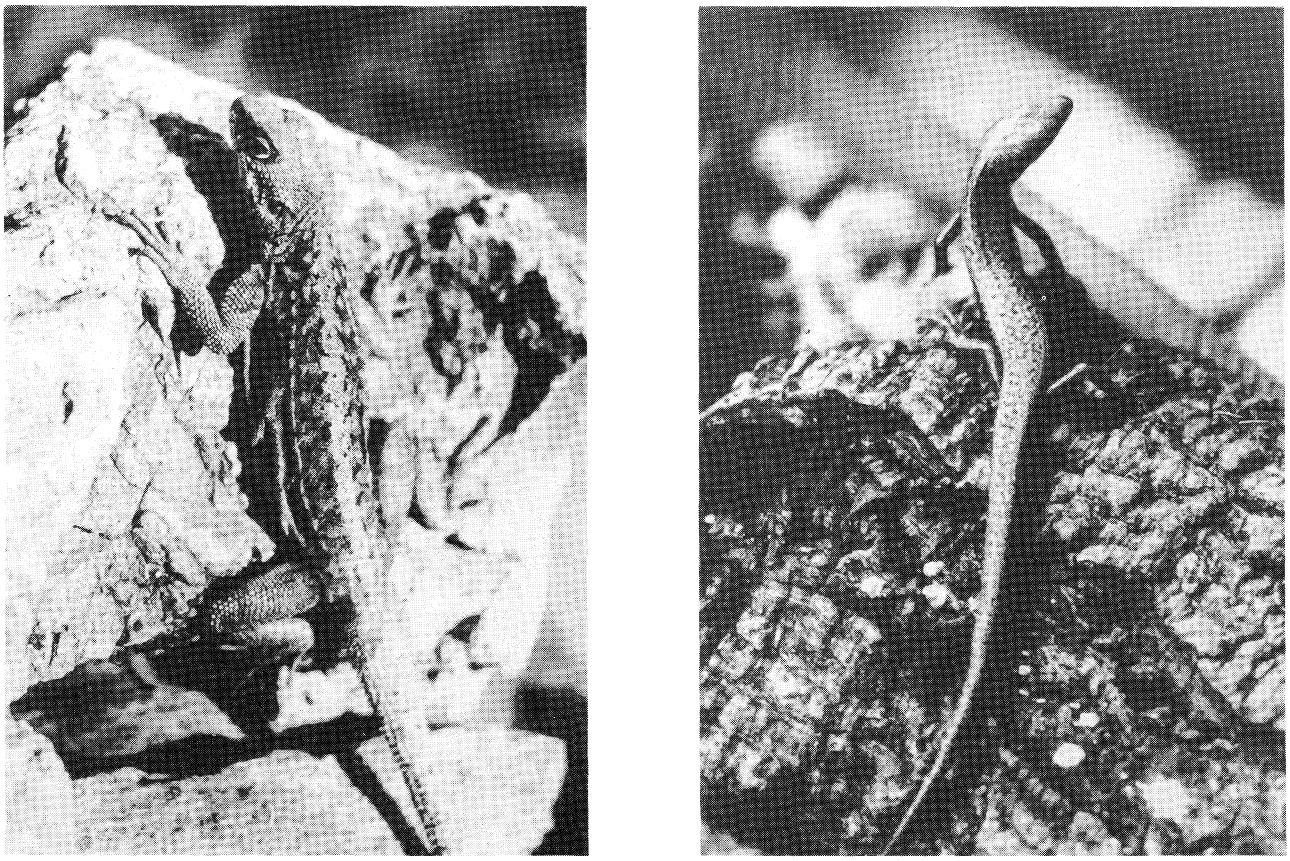

FIG. 4. *Left*: *Agama himalayana*, adult male. *Right*: *Scincella ladacensis*

The 23 specimens of *Scincella ladacensis*, obtained from different places in Ladakh during the journey in 1977, show similar habitat preferences. In Bhodkarbu and Hemis they live at the borders of cultivated land around human settlements. These areas are partly covered with sparse bushes and grass vegetation and partly with rock-rubble. In the Suru valley and at places along the road between Dras and Zojila I discovered the skinks in a similar combination of bushes, grass and stones. Within the vegetation and underneath the stones there are many places where they can hide. At all localities investigated, except Hemis, these skinks were quite common. Many small, young specimens were observed, born obviously in the same year. Although none of my collected females was pregnant, this species seems to be viviparous, as is indicated by some specimens, containing 2–3 embryos, from the British Museum (Natural History).

Scincella ladacensis can be distinguished from its next relatives *S. himalayana* and *S. sikkimensis* by a larger number of scales around the midbody (32–38), a larger number of lamellae underneath the 4th toe (19–24), a more slender habitus and longer hind- and forelimbs. There is very little brown on the back, which is mostly grey or olive with a silvery tinge.

RELATIONS OF CHARACTERS OF HIMALAYAN *Scincella*

The systematic relationship of the three forms of *Scincella* inhabiting the Himalayas (*S. sikkimensis*, *S. himalayana*, *S. ladacensis*) causes difficulties. Smith (1935) writes about the genus *Leiolopisma* (= *Scincella* Mittleman, 1950; Greer, 1974): "the determination of the species grouped under this genus is often extremely puzzling. Two forms that in one area seem quite distinct, in another area appear to intergrade. They are, perhaps, species in the making, and until we have a more exact conception of what a species is they will continue to confound us." This is exactly the case with *S. sikkimensis, S. himalayana* and *S. ladacensis*. The differences known so far between these three species are listed as follows:

	S. sikkimensis	*S. himalayana*	*S. ladacensis*
1.	22–24 scales around midbody	26–30 scales around midbody	32–38 scales around midbody
2.	15–17 lamellae underneath the 4th toe	14–20 lamellae underneath the 4th toe	19–24 lamellae underneath the 4th toe
3.	prefrontals in contact with one another	prefrontals usually separated from one another	prefrontals often widely separated from one another
4.	Ear-opening small, smaller than the palpebral disc; no projecting lobules	ear-opening big, nearly as big as eye-opening; 2–3 projecting lobules	ear-opening medium and with distinct projecting lobules
5.	build rather slender	build mostly robust	build slender
6.	adpressed limbs do not meet or just reach to the wrist	adpressed limbs do not meet or just overlap	adpressed limbs reach to wrist or elbow
7.	colour of the back bronze-brown	colour of the back olive-brown to olive green or greyish	colour of the back silvery grey to greyish olive
8.	belly pale bluish or whitish	belly dark or red, scales edged with black	belly bluish or greyish, scales sometimes edged with darker grey
9.	oviparous, 3–6 eggs, rarely 2 or 8	generally viviparous, 2–3 embryos, rarely 1 or 4	presumably viviparous

It is uncertain whether viviparity is obligatory, because a population from central Nepal (*S. sikkimensis* or a hybrid population of *himalayana* and *sikkimensis*), occurring in altitudes between 2000 and 3000 m, lays eggs. Oviparity, however, is also observed in a population from Gulmarg southwest of Srinagar.

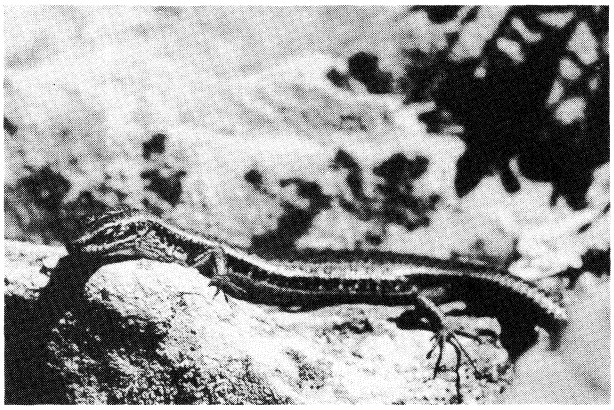

FIG. 5. *Scincella himalayana* sunbasking.

Living specimens in the population from the Haramuk region in Kashmir have a pale olive-grey to olive-greenish back sprinkled with diffusely scattered dark spots, whereas in living specimens from Ghorepani in central Nepal (Annapurna range) it is a bronze brown colour with a dark vertebral stripe. The bellies of the former are red or have scales edged with black, the bellies of the latter are uniform whitish-blue. Comparison of the Haramuk population with the data given in literature (Boulenger, 1890; Minton, 1966; Smith, 1935; Zugmayer, 1909) confirms that this population is a true *Scincella himalayana* (Guenther, 1864), very like the nominate form, and that it is quite different from *Scincella ladacensis* (Guenther, 1864). However, things are less clear in other populations from Kashmir, as from Tanmarg and Gulmarg or from the close vicinity of Sonamarg. The majority of specimens from Sonamarg (2700–3300 m), Tanmarg (2100 m) and from a site above Naranag (3200–3300 m), all places situated at lower elevations, possess a dark vertebral stripe and uniform, light whitish-blue belly-scales. Four of the six specimens from Gulmarg, the largest of all *Scincella* material under investigation (58–66 mm), carry a pair of distinct, light coloured parietal stripes and lack the dark vertebral stripe. Final interpretation is actually not possible unless more material and more comprehensive studies on these scincid lizards in the Kashmir mountains becomes available.

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LOCAL MIGRATION, RHEOTAXIS, AND PHILOPATRY BY *TRITURUS VULGARIS* WITHIN A LOCALITY IN CENTRAL NORWAY

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(*Received* 22 *April* 1980)

SUMMARY

Specimens of *Triturus vulgaris* (L.) were marked and later recaptured at a locality in central Norway. Movements of aquatic *T. vulgaris* showed a mean range of about 35 m within a system of drainage ditches, the females being more vagile than the males. A certain part of the ditches was preferred during the reproductive period. After breeding the newts once again dispersed. Aquatic newts were usually positively rheotactic in the breeding season, but were seemingly indifferent later on in the year. When adult aquatic specimens of *T. vulgaris* were forcibly removed from the site of capture to another part of the ditch system, they usually found their way back. Terrestrial newts were found to be very philopatric, usually hiding under the same stone (or nearby) for weeks and months on end, and even in the following year, only a few metres away from the water's edge. Dispersal is considered to be mainly carried out by juveniles, by aquatic adults moving along water-courses, and by terrestrial newts which lose their way *en-route* to their home breeding pond.

INTRODUCTION

Most authors agree that newts (*Triturus* spp.) rarely move far from the pond in which they breed, but few have ever mentioned just how far the animals move about *within* the pond (Gauss, 1961). In connection with investigations on the diel activity of newts carried out at Vasseljemoen, Malvik near Trondheim in central Norway (Dolmen, 1976a, b) a number of *Triturus*

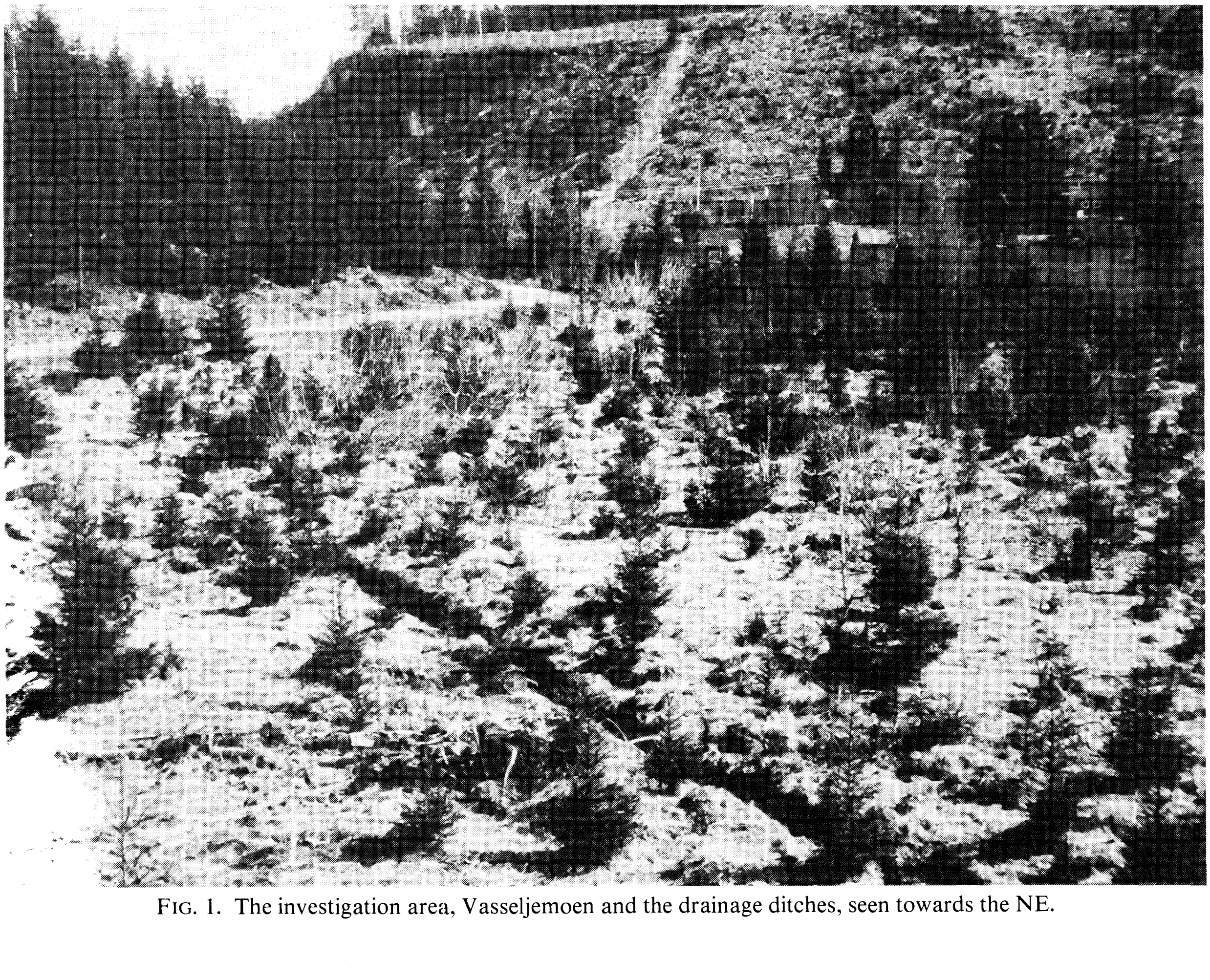

FIG. 1. The investigation area, Vasseljemoen and the drainage ditches, seen towards the NE.

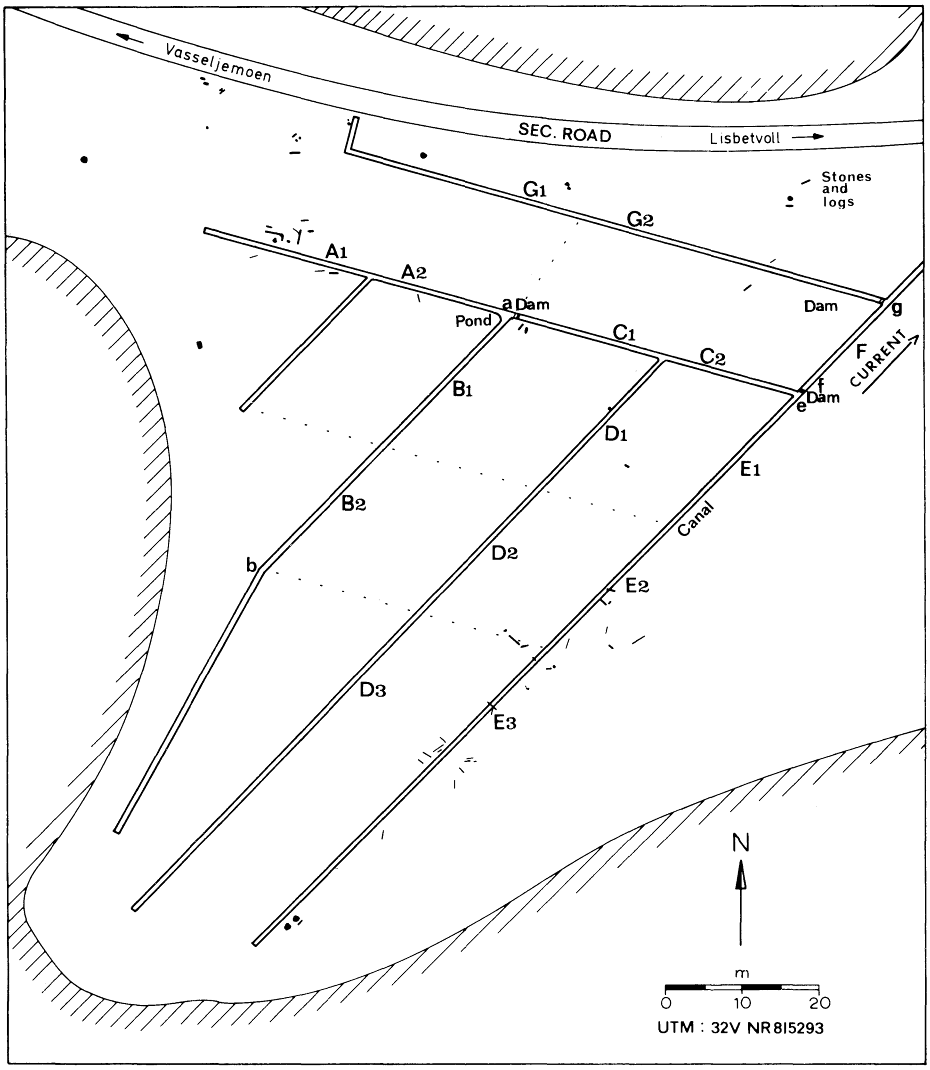

FIG. 2. The stagnant water system of drainage ditches at Vasseljemoen, showing the central pond and the three dams (*a*, *f*, *g*). Suitable hiding-places for terrestrial newts (logs and stones) can be seen along the banks of the ditches. In the eastern canal the water is more or less slow-running. Hatched areas indicate hills and forest.

vulgaris (L.) were individually marked by toe-clipping. Some of the newts were recaptured one or more times, thus providing the opportunity to follow their movements from week to week.

During these investigations *T. vulgaris* seemed to show a positive rheotaxis, at least early on in the summer; some specimens were occasionally observed swimming up against the streamflow, which is relatively strong, north of the dam across the (eastern) canal (Fig. 2). On one occasion 12 specimens were found to have gathered under the dam, seemingly being unable to either force the waterfall or to climb the dam wall.

Few previous experiments have been made on orientation, homing ability or philopatry in *Triturus* species. A limited homing ability has been suggested (Cummings, 1910, 1912; Czeloth, 1931; see also Smith, 1964). Frazer (1973) states that examination of a newt population beneath marked stones shows that they vary from day to day; this, however, seemed not to be true for the population at Vasseljemoen.

The present investigation was therefore also intended to yield an answer to the question of the degree of philopatry/vagility and homing ability found in aquatic and terrestrial newts, and also to test their rheotactic response, thus enabling a better understanding of their dispersal ability to be gained.

DESCRIPTION OF THE LOCALITY

The investigation area (Fig. 1), a drainage system at Vasseljemoen, consists of two main ditches, filled with stagnant water, each 50–60 m in length, and running approximately east–west to join a collection canal in the east, running southwest–northeast, with slowly-flowing water. The water depth is 20–30 cm. Three minor ditches, also running southwest–northeast, drain into the southern main ditch (Fig. 2). The surrounding country is a newly afforested, relatively open and sunny area, occasionally grazed by sheep or cattle. A fuller description of the area is given by Dolmen (1976b). In order to maintain a certain water-level, and also to prevent or delay any drying-out of these ditches, a central dam/pond and two additional, more peripheral, dams, were specially dug for these investigations.

METHODS

The newts were marked according to a code resembling that described by Davis (1962) and Twitty (1966). The toe-clipping did not seem to have any deleterious effects on the animals. Individual movements could thus be followed from week to week. The ability of newts to regenerate limbs is great, but some newts were still easily recognisable more than a year after being toe-clipped. For more long-term investigations, however, the use of belly pattern for identifying individual newts is preferable and necessary (see Edelstam, 1954; Hagström, 1973).

Searches for newts were made, not only in the ditches, but also on dry land between and around them, up to a distance of about 40 m from the ditches.

In 1974 and 1975 captures/recaptures were mostly made at one to two-week intervals throughout May, June and July; in 1976 an interval of two to four weeks was used, and in 1977 weekly captures/recaptures were made in May and June. In a few cases further captures/recaptures were made after an interval of only one or at most a few days. During the four consecutive study years the following numbers of newts were marked: 1974: 117, 1975: 428, 1976: 35, 1977: 244; of these 168 were recaptured.

In 1977, 35 of the marked, aquatic newts were carried away from their different original localities, and immediately after capture, released in another part of the ditch system (Table 4), in order to test their homing ability. The transport was made along a more or less complicated track, in an open, non-transparent, plastic bucket (10 l) filled with water. Thirteen of the newts were recaptured.

An introductory rheotaxis experiment was carried out, on 8 June 1978, in a nearby brook without any connection to the draining ditch system, and situated southwest of the ditches. The streamflow direction of the brook was northwest.

The next experiments, however, were carried out in the slowly-running water (10 cm/sec at the surface) of the eastern canal, midway between *f* and *g* (Fig. 2); the newts were collected from ditch G, and the movements made as described previously for the homing experiment. The newts were released on the bottom of the canal, with equal distances to both banks, with their heads facing towards the right or left bank (alternately), and their bodies perpendicular to the streamflow. When altering the animals' position in relation to the current they were always turned in a vertical plane perpendicular to the axis of the streamflow, so that they had no reason to make any compensatory, horizontal, head-movements (see Cummings, 1912) when choosing their moving direction. The newts were then free to choose between going up- or downstream, or straight ahead to the bank. In some experiments the animals were placed with their heads facing the streamflow, or downstream. The newts' choice of direction indicated either positive or negative rheotaxis, or indifference. The experiments took place during the main courtship season, in the early part of June and also at the end of their aquatic phase at the beginning of July.

RESULTS

MOVEMENTS AND MIGRATIONS

Data on the movements of aquatic *T. vulgaris* within the ditches are given in Table I. The newts often moved considerable distances, and most of them were recaptured at new localities from time to time. The distances, as measured along the ditches, should be regarded as minimum values. Maps showing some of these movements are given by Dolmen (1976b). The difference in

TABLE I. Movements of aquatic *Triturus vulgaris* (in m) during the same year, as observed at Vasseljemoen. Distances are measured along the ditches, from one edge of the range covered to the other

Sex	Number of animals recaptured	Mean range	SD	Maximum range	Number of recaptures	Number of observations of stationary animals
Males	62	32	36.5	116	76	16
Females	40	37	32.0	123	50	4

TABLE II. Number of *Triturus vulgaris* recaptured during their aquatic life, in different parts of the ditch system. Symbols refer to ditch parts (see Fig. 2)

Recaptures:	A(1 + 2)	B(1 + 2)	b	C(1 + 2)	D(2 + 3)	E1	E2	E3	G1	G2
Original captures										
A(1 + 2)	59	2	2	2	5	2	1	1	—	—
B2	—	1	—	—	—	—	—	—	—	—
b	3	—	8	—	—	—	1	—	—	—
C1	—	—	—	1	2	—	—	—	1	—
C2	2	—	—	2	1	1	—	1	—	—
D1	—	—	—	—	1	—	1	—	—	—
D3	—	—	—	1	7	—	1	—	—	—
E1	—	—	—	—	—	2	—	—	—	—
E(2 + 3)	1	—	—	2	—	—	1	—	—	—
G1	1	—	—	—	—	—	—	—	6	8
G2	—	—	—	—	—	—	—	—	3	3

range generally covered by males and females was not found to be statistically significant ($P > 0.05$; *t*-test). Some aquatic males, however, seemed to remain stationary (± 1 m), and the difference in relative number of stationary males and stationary females was significant ($P < 0.05$; χ^2 test).

From Table II it seems clear that the ditches A–B (limited by a dam) definitely had the largest number of newts, and also the highest number of recaptures. Compared to the C–D–E ditch system, which is twice the size of A–B (accordingly the difficulty of recapturing newts is doubled, and therefore also the number is doubled in the calculation), the A–B ditch has a much higher density of *T. vulgaris*, as calculated from the number of newts recaptured in the same ditch system ($P < 0.02$; χ^2 test). Also compared to the ditch G, which is about the same size as the A–B ditch system, the latter is superior ($P < 0.001$).

In many cases, aquatic individuals of *T. vulgaris* must have travelled overland to reach their new sites in another ditch (Table II). The shortest distance some of these animals would have covered is 14 m, or more, over bare soil, grass and moss. They *might*, on the other hand, have followed the ditches, involving a considerable distance and the need to surmount at least three or two dams, respectively. Such dams were, however, surmounted by other newts, viz. by at least 13 males and 9 females.

THE RHEOTAXIS EXPERIMENT

It was found that in the relatively strong current of the brook, all (10) animals always swam upstream; in slowly-running water, in the same brook, the newts crept on a few occasions onto dry land, but usually they went upstream.

The rheotaxis results from the canal for *T. vulgaris* are given in Table III. On 9 and 11 June, when the newts were released with their bodies pointing perpendicularly to the streamflow, they almost exclusively went upstream, *i.e.* they showed a positive rheotactic response ($P < 0.01$, χ^2 test; $P < 0.01$, Wilcoxon's two-tailed matched-pairs signed-ranks test—used when only up- and down-movements are considered). They never went downstream, and only a few times straight ahead to the bank of the stream. When placed facing in the direction of the streamflow the newts usually went downstream ($P < 0.001$; $P < 0.01$), but some turned round and went upstream. Familiar odours (see Grant, Anderson & Twitty, 1968) can be ruled out as a guiding factor (see under Methods).

TABLE IV. Homing ability of aquatic *Triturus vulgaris* in the ditch system; + indicates correct return, ° not recaptured, — wrong direction chosen. Other symbols refer to ditch parts (see Fig. 2)

Transported: Originally captured	Ee	Ff	Fg
A + B	5+ 11° 1–	2+ 5°	
D2	2+ 1°		
G			1+ 5° 2–

About four weeks later, on 5 July, the newts showed no obvious tendency to go in either direction, no matter what their starting position was, except in the first experiment, where the upstream response was better than the downstream response, when the animals were placed perpendicularly to the streamflow ($P < 0.02$; χ^2 test).

HOMING

Most of the newts recaptured in 1977, after having been transported up to 70–80 m away from their "home" ditch area, found their way back (Table IV). If we suggest that homing ability does not exist in *T. vulgaris*, and that the chance of being recaptured in the home area, compared to another area, is 1 : 1 (in reality it would be much less), the positive homing result was not by chance ($P \approx 0.05$; χ^2 test). It must also be mentioned, that of the three "non-homing" newts, one was recaptured very near to its home area, the other two had moved upstream and ended up in the A ditch. The percentage of recaptures in the homing experiment was even greater than usual, being 37% compared with 20% in the capture/recapture investigations.

TABLE III. Direction of movement of 15 *Triturus vulgaris* (7 males, 8 females) on three different dates, when released with their heads pointing in different directions in relation to the streamflow. Data for 10 trials with each individual, in each direction

Date	Position of body in relation to the streamflow (on release)	Number of newts	Number of trials per individual	Number of responses: up	Number of responses: to the bank	Number of responses: down	Main direction of movement
June 9	perpendicular	6	10	57	3	0	upstream
June 9	down	6	10	6	21	33	—
June 11	perpendicular	5	10	46	4	0	upstream
June 11	down	5	10	16	7	27	—
June 9 + 11	perpendicular						upstream
June 9 + 11	down						downstream
July 5	perpendicular	4	10	16	19	5	—
July 5	down	4	10	14	7	19	—
July 5	up	4	10	15	18	7	—

PHILOPATRY

Out of 117 *T. vulgaris* marked in the first year, 12 with markings still visible were recaptured during the next. Eight of the newts were captured on land in one year and in the water again during the next, in a nearby ditch, or further away. Two terrestrial specimens (L, W, Fig. 3) were recaptured under the same stone or log as in the previous year.

On land both males and females of *T. vulgaris* show a pronounced degree of philopatry. Every individual which was recaptured at least once (23 specimens) within the same year was observed less than 7.5 m from the original site of capture. Usually they were found in the same hiding-place ($P < 0.01$; χ^2 test). These newts were never observed outside the regular hiding-places marked on the map (Fig. 3). In addition to these 24 places, a number of potential hiding-places were examined, of which 42, only occasionally, were visited by (other) newts (Fig. 2).

Two males (L and W, Fig. 3) are especially interesting, since they were both recaptured in the spring at the same hiding-place that they occupied when captured the previous summer. The hiding-places in question are situated on small patches of dry ground, rising above the wet surrounding terrain, and offering the possibility of digging down into the soil, *i.e.* "islands" of mosses, heather and stone-strewn, sandy, bare soil. The newt W actually shared its hiding-place with hundreds of small black ants (*Formica lemani* Bondroit) in an ants' nest built under a flat stone.

DISTRIBUTION ON LAND

Of the 65 more or less permanent terrestrial hiding-places for newts around the ditches at Vasseljemoen, 51 were situated less than 5 m from a ditch, and only seven were situated more than 10 m away, the maximum distance being 17.5 m (east of the southern main ditch: A).

DISCUSSION

AQUATIC MIGRATIONS AND HABITAT PREFERENCE

The present investigations support the view that aquatic *T. vulgaris* maintain a home range, at least for a period of time, since the numbers of aquatic males at a significantly higher frequency were recaptured exac-

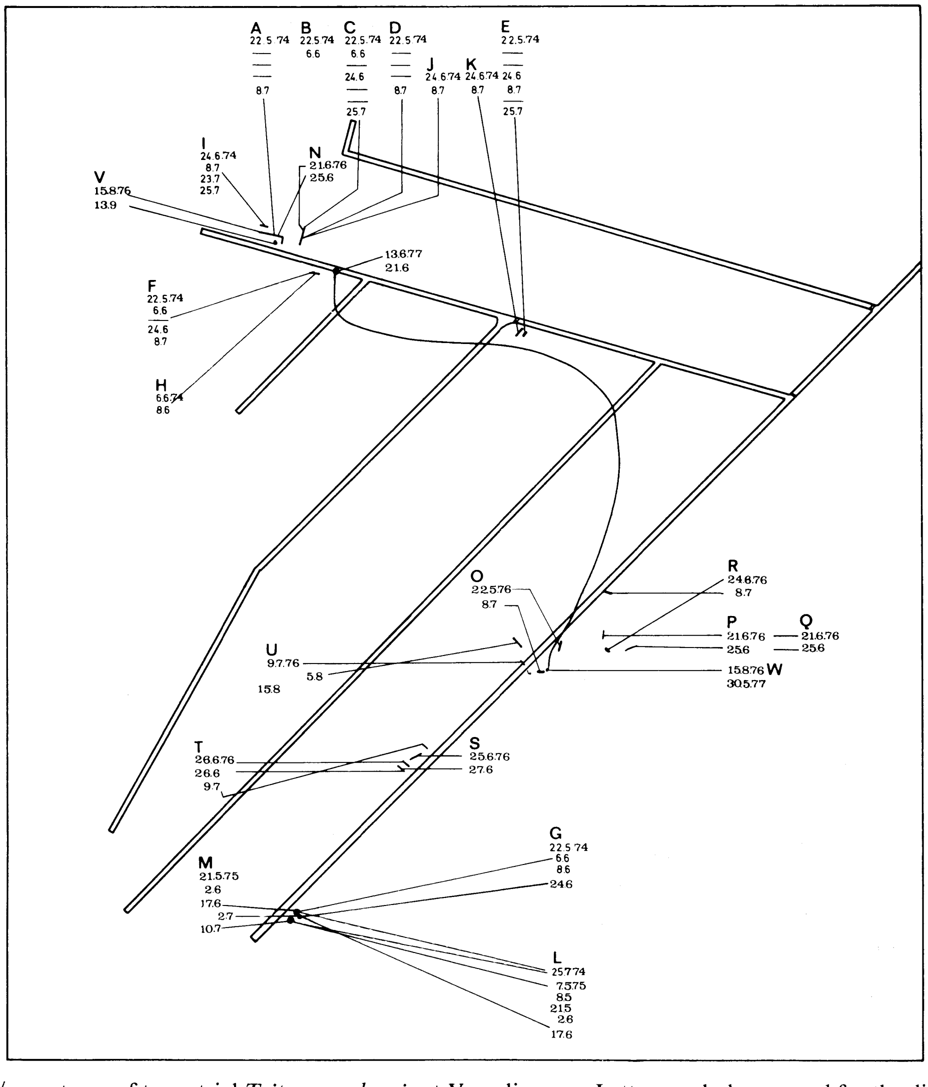

FIG. 3. Captures/recaptures of terrestrial *Triturus vulgaris* at Vasseljemoen. Letter symbols are used for the different specimens. Horizontal lines between dates of captures/recaptures indicate absence of the specimen in question.

tly at their place of capture, compared to the females. This seems to be contrary to observations made by Halliday (1977). According to Gause (1961), however, *Triturus* males maintain "territories", marked by pheromones, and "fights" between males may occur (see also Curry-Lindahl, 1963). What is called "fight", however, is in reality no more than a territorial optical signalling, a male to male fanning display, and much like the courtship display shown before a female. As also stated by Halliday (1975), aggression does not exist in the behaviour of newts.

The stationary ("territorial") males are known usually to enter the pond earlier than the more vagile females (Steward, 1969), and thus the females, on their wandering and lookout for suitable egglaying sites may be caught up by one or several males. This might be of importance for the fertilisation of a maximum number of eggs. According to Smith (1964), a female, once she has been inseminated, will not take up more spermatophores until those eggs ready to be fertilised have been laid. After that she is prepared to mate again. A second mating is probably necessary, even though the number of spermatozoa contained in one spermatophore is far in excess of the number of eggs produced by a female. Polyspermy, however, is known to occur in the newts, and in that way the excess may be disposed of.

The highest density of newts was found in ditch A. Also judging from the biotope itself, the ditch west of the pond should be the most favourable one for newts during the breeding period. This area of stagnant water readily warms up in spring, and there is little influx of snow melt-water. Although the ditches are not very deep, they are usually full of water in May and June. Moreover, the surroundings are very open and sunny, and there is an abundance of aquatic vegetation (mainly *Carex rostrata* and Bryophyta). This ditch part is also where the other newt species, *T. cristatus* (Laurenti), has been observed most frequently, and where frogs (*Rana temporaria* L.) lay their first eggs.

Most of the newts are found exclusively in this part of the ditch. Others, however, spend the first few weeks (May) of their aquatic phase in this area and later (in June) move on to other ditches; movements of more than 120 m were recorded. Similar movements, of more than 100 m have been recorded for *T. cristatus* from the eastern to the western part.

The ditch E, for example, is very poor for newts to breed in, being full of cold slowly-running water. Nevertheless, terrestrial newts are as frequently found in the vicinity of the eastern canal as of the western ditches. It would thus appear that a breeding migration occurs to the more "ideal" western part of the ditch system from areas near by and further away, and back again later in the summer, probably following the same route. Shoop (1965, 1968) found that specimens of the American salamander *Ambystoma maculatum* entered and left their pond at approximately the same point.

T. vulgaris is shown not to be exclusively aquatic during the breeding season. Both males and females can cross land bridges and move 10 m or more over more or less dry-land. This is in agreement with the statement by Smith (1964) and Steward (1969) that aquatic *T. vulgaris* may often leave the water for a few hours during the night, to wander on land along the banks. Hagström (1979) also found that some newts may visit a pond for more than one (short) period in any one year.

RHEOTAXIS

The tendency to move either up- or downstream is dependent on such external factors as initial position of the animal, and the presence or absence of barriers, such as dams. At Vasseljemoen, in spring, the eastern canal may serve to direct newts arriving from the north, and to a limited extent also those coming from the south, up into the main ditch and thus into the most suitable breeding area.

The newts, when placed in the stream, even before the current took hold of their tails, turned their heads against the streamflow. The current is perceived by the lateral-line organs (see *e.g.* Smith, 1964). The orientation against the stream is a tropotactic response (Heymer, 1977), and this also explains why newts placed facing downstream usually went ahead with the streamflow, in that the stimuli on both sides of the animal then became equal in strength.

A few *T. cristatus* were also tested for rheotactic response on 11 June 1978 (Dolmen, unpublished); a positive rheotaxis was found. Steinmann (1914) also showed experimentally, using a rotating disk, that both adults and larvae of *T. cristatus* and *T. alpestris* are positively rheotactic.

In nature, the positive rheotaxis in *Triturus*, early in the season, should lead mature animals, which might happen to come in contact with a brook, up into the nearest pond or lake for breeding. Positive rheotaxis may be common in newts and salamanders, as in fish, even though many species usually live in stagnant water, and should be an ethological/ecological parallel to the upstream flight observed in the adults of many insects, which compensates for drift in the stream-living juvenile stages (see *e.g.* Müller, 1974). Salamander drift is also described by Stoneburner (1978) for premetamorphic *Eurycea bislineata*; post-metamorphic salamanders, and individuals about to undergo metamorphosis, did not appear in the stream drift.

HOMING

Evidently most aquatic *T. vulgaris* were capable of finding their way "home" when forcibly moved out from their previous area. Most of the newts transported experimentally at Vasseljemoen were taken from the western part of the ditch system; their orientation may have been due to the smell of other newts living under favourable conditions, or to a gradient in other biological or chemical components in the water. It also might have been due to many right–left choices, according to the habitat itself, which gradually became more and more well known (farotaxis or mnemotaxis, Heymer, 1977), since other newts also found their way back to their former sites in other, less favourable, parts of the ditch system.

Long-distance homing experiments, such as those of Twitty (1959, 1966), have not yet been tried with *Triturus*. Smells emitted by certain water plants (Czeloth, 1931; Noble, 1954; Twitty, 1959, 1966) or humidity gradients (Cochran, 1961) may probably represent guiding factors in newt orientation (see also Savage, 1961). Celestial and magnetic cues have also been shown to play an important role in the orientation of American salamanders (see *e.g.* Landreth & Ferguson, 1967; Taylor, 1972; Phillips & Adler, 1978).

At Vasseljemoen, as in Cummings' (1912) investigations, terrestrial newts were only observed a few meters away from open-water, usually less than five. This fact agrees with the findings of Bell (1977). To a limited degree Cummings' newts also showed some homing ability: the orientation to and from the breeding-pond in *T. cristatus* and *T. helveticus* was due to a shift from positive (in spring) to negative (in summer) geotaxis (see also Czeloth, 1931).

PHILOPATRY

On land, *T. vulgaris* is definitely philopatric. One, or sometimes a few, permanent hiding/dwelling-places are usually used throughout the year, perhaps also in subsequent years. The newts mostly hunt for food at night (in reality twilight, see Dolmen, 1976a, b), and not far away from their hiding-places. This contrasts with Frazer's (1973) information, that examination of the newt populations under marked stones show that they vary from day to day. Newts, however, are easily disturbed, and will soon leave their original hiding-places after mechanical disturbance, as well as unfavourable changes in illumination and humidity.

Other species of Salamandridae have also been investigated with similar results. Joly (1963, 1968) followed the movements and migrations of *Salamandra salamandra* in France, and found this species to be fairly philopatric, the home range being on average about 68 m^2. Some animals stayed for at least seven years within the limits of their domain, and the homing ability of salamanders displaced by 300 m or more from their bases, was proven in general. Feldmann (1974) found that *S. salamandra* showed a high degree of philopatry as regards its hibernation site.

DISPERSAL

Some of the newts in any particular population are almost certainly less philopatric than the rest. Wanderings away from the pond will help to prevent overcrowding, and also ensure dispersal of the animals. The juveniles are thought to be more vagile than the adult newts and to be the agents of dispersal, as also postulated by Bell (1977), who points out that terrestrial adults of *T. vulgaris* settle down within a few meters of the breeding pond. Because of this, a relatively high degree of vagility in juvenile newts has a survival value, since juvenile newts are readily eaten by the adults.

Adult aquatic newts may also be responsible for dispersal of the species to some extent, since they not only follow streams and ditches for long distances, but can also surmount land "barriers". Because the terrestrial adult newts are philopatric and do not move far away from their breeding pond, it is mostly those of them that get "lost" which are thought to be responsible for species dispersal, usually downhill to new localities in spring, according to Cummings (1912).

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ASPECTS OF THE FIELD BIOLOGY OF A POPULATION OF HERMANN'S TORTOISE (*TESTUDO HERMANNI*) IN SOUTHERN YUGOSLAVIA

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SUMMARY

A population of Hermann's tortoise, *Testudo hermanni* Gmelin, was studied in its scrubland habitat in Montenegro, Southern Yugoslavia. The relative abundance of *T. hermanni* was recorded in relation to other reptile species. The body temperatures of active tortoises between 11.00 and 16.00 hr ranged from 21.5°C to 34°C (mean = 30.2°C). From the measurements of length (m) and body mass (kg) of 43 tortoises an allometric equation defining the relationship between the two has been produced. Females grow larger than males and in tortoises above 200 g the sex ratio is 1:1. Eighty-one per cent, of the tortoises exceeded 300 g. While tortoises in captivity accept a wide range of fruit and vegetables, 90% of the food plant species of wild ones were of the subfamily Papilionidae (Family Leguminosae). Tortoises were most commonly observed feeding after 15.00 hr. The supracaudal plate of the carapace was divided in 88% of those tortoises investigated. Shell abnormalities and carapacial and limb injuries were found in 4% of those tortoises investigated.

INTRODUCTION

The habits of *Testudo hermanni* under natural conditions are poorly documented, the only published field work until the present report being that by Chelazzi & Francisci (1979) who investigated homing behaviour in this species in Central Italy. Most of the present knowledge of *T. hermanni* is from captive animals (*e.g.* Krische, 1967; Noel-Hume & Noel-Hume, 1970).

A survey of wild *Testudo* populations has been carried out by Lambert (1969). His work on *Testudo graeca* populations in Morocco indicated a total of five million animals giving a mean density of 30/km^2. However, in a further survey Lambert (1979) suggested the possibility of the net effect of collecting of *Testudo* in Morocco to have resulted in the populations being reduced by as much as 86% over the 80 years or so of collecting. Honnegger (1974) reported that in Yugoslavia, where the present study was conducted, between 300 000 and 400 000 *Testudo hermanni* are exported annually.

The present paper is an account of a preliminary study of a population of *Testudo hermanni* in Yugoslavia carried out by the authors over a seven day period during the Spring of 1978.

METHODS AND MATERIALS

A population of Hermann's tortoise was located during mid-May in a scrub area of approximately 2 km^2 in Montenegro in Southern Yugoslavia, close to the Albanian border. The tortoises were collected in the field and records taken of carapace lengths (measured as a straight line from the nuchal to the supracaudal scute) and weights of a sample of the population. Weights were determined using a spring balance that had a range from 0–2 kg. However, some of the smaller animals were weighed with a Johnson 12A scale which was more sensitive at low weights. Body temperatures were measured by inserting a mercury-bulb thermometer into the cloaca. This procedure was carried out as quickly as possible once the animals had been located in order to reduce any affect of capture on body temperature. The behaviour and location of the tortoises immediately prior to recording their temperature was noted. A total of 38 readings were taken on male, female and juveniles. Air temperatures were recorded approximately 30 cm above the ground with the thermometer shaded. To record soil temperatures the thermometer was inserted 8 mm into the soil.

Plant species being consumed by the tortoises were collected and later identified. Since controversy exists on the condition of the supracaudal plate in *T. hermanni* the condition of this element in some of the animals was investigated. The terminology for plate identification is taken mainly from Romer (1968). The sex of captured individuals was noted. This was determined by the condition of the plastron which in males is concave, while females have a more flattish appearance. Confirmation of the sexes was further sought in the position of the cloaca on the tail, and the comparative lengths of the tails which in males is known to be longer (Arnold, Burton & Ovenden, 1978). These latter diagnostic features were used to determine sex in juveniles.

RESULTS

BEHAVIOUR AND HABITAT

The study area was typical scrub country in that there was a wide variety of plant communities which although fairly dense in places were frequently interupted by pathways and clearings (Fig. 1). The north, south and eastern end of the scrub was bordered by steep mountains—the Dinaric Alps, which arose abruptly

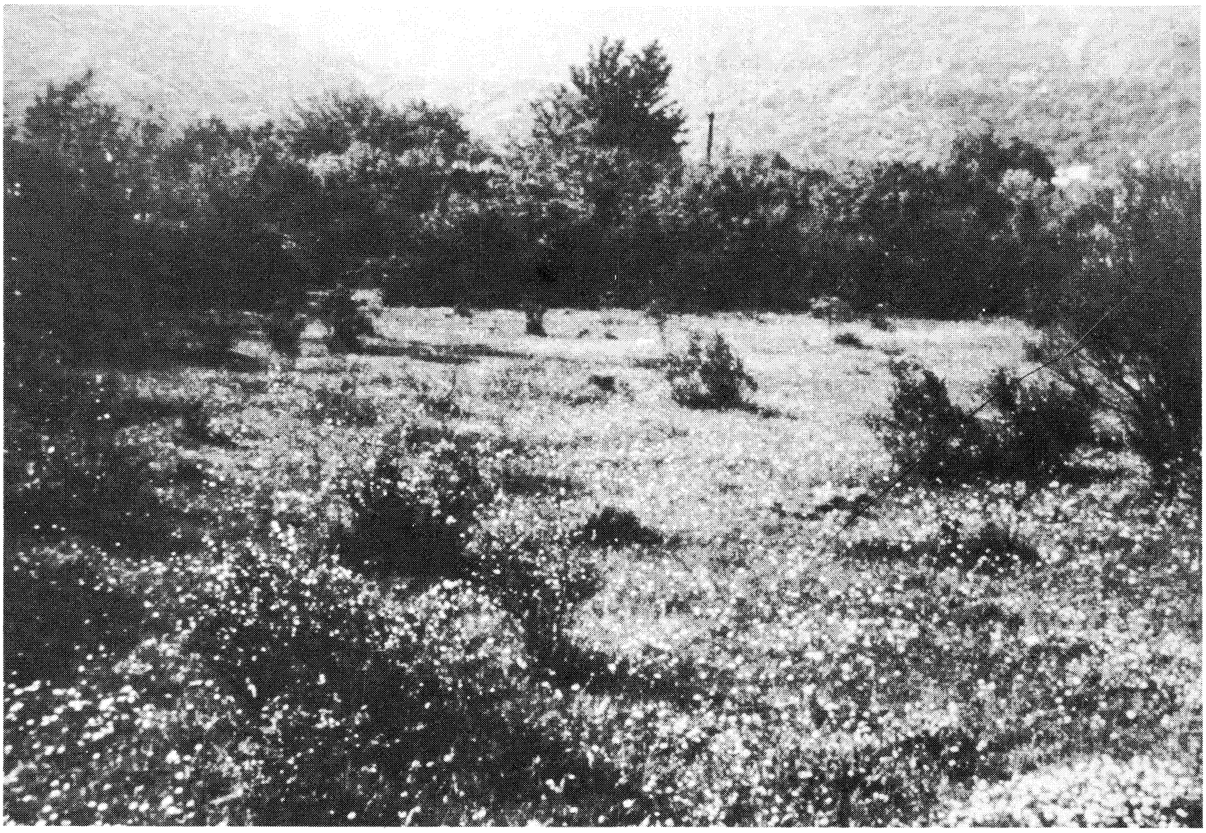

FIG. 1. View of north east end of the study area showing typical scrub type habitat and surrounding hills.

from its limits. The coastline of the Adriatic sea and the main Adriatic highway determined the western limits. The climate of the region is warm temperate with July and August the warmest months of the year when averages of 25–26°C are reached (Landsberg, 1977). Maximum daily temperatures recorded during our study were 25°C (substrate) and 26°C (air). During the winter the reptiles enter a dormant state as the temperatures occasionally drop below 0°C. The area has a January isotherm of 7.8°C. In July and August an average of 370–380 hr per month of clear skies are experienced (Landsberg, 1977).

During the warmer months precipitation reaches a peak through April and May with average falls of around 60 mm for each month (Landsberg, 1977). In our study area we found a single very deep pond which probably has a good depth of water all the year round, although in July and August many of the other water courses apparently dry up.

Figure 1 shows a typical part of the study site; densely bushed areas and open grass-covered clearings can be clearly seen. At night the tortoises retire into the thick grass beneath the bushes and well-defined resting sites were observed. Chelazzi & Francisci (1979) have recorded, however, that these nightly resting spots are not used exclusively by any one animal. During the day the tortoises move into the clearings to feed and thermoregulate. Well worn pathways through the thick grass were common. These ran through both clear and densely bushed areas and appear to be a result of tortoise movements, suggesting that the reptiles may follow set daily routines. Indeed it is often a simple matter to locate a tortoise by following one of these pathways.

The tortoises share this habitat with a variety of other reptiles. A list of these and their relative abundance in the scrub is shown in Table I. Two species of mammal, a feral cat (*Felis domesticus*) and a hedgehog (*Erinaceus europaeus*) were also found in the area, but these did not appear to the particularly common—only one of each species was sighted.

BODY TEMPERATURES

Body temperatures were recorded on days when there was little or no cloud cover; thus the availability of solar radiation to the tortoises on such days was good. On the days that we recorded our data, soil temperatures always exceeded air temperatures (shaded). The readings were taken when the reptiles were most commonly seen, between 11.00–16.00 hr.

The data presented in Fig. 2 show that body temperatures are essentially unrelated to changes in air and substrate temperatures for this part of the day. The highest body temperatures were recorded between 13.00–14.30 hr in both males and females. After this period body temperatures showed a decrease although environmental temperatures continued to increase. The graph shows that in all instances body temperatures exceeded air temperatures and that in all cases but two, they exceeded substrate temperatures. The difference between body temperature and substrate temperature—the closest variable, could be as much as

TABLE I. Relative abundance of *Testudo hermanni* and associated herpetofauna estimated from sightings or captures. Also shown are specific locations of each species in the study area and types of habitat

	No.	Location	Habitat
Testudo hermanni	⩾125	All areas	Open areas and under bushes
Emys orbicularis	⩾15	Central and eastern section	Confined to ditches
Lacerta viridis	>50	All sections except western	Open areas using bushes for cover
Anguis fragilis	3	Southern section	Under stones; one specimen regurgitated by *Coluber gemonensis*
Ophisaurus apodus	>20	Central, eastern and southern section	Open clearings and in bushes
Coluber gemonensis	5	All areas	Found active usually in clearings
Elaphe longissima	2	Eastern section	Adult located in tree, juvenile while crossing clearing

10°C. Body temperatures of *T. hermanni* ranged from 21.5–34°C (mean = 30.2 C).

Records of body temperatures in relation to specific location of the animals at the time the readings were taken showed that some tortoises, although in the shade, had a range of body temperatures from 21.5°C to 32.5°C (n = 7). The mean body temperature of 30.2°C found in *T. hermanni* closely approximates that found in other chelonia (*e.g.* Gatten, 1974; Brattstrom, 1965; Fitch, 1956; Legler, 1960).

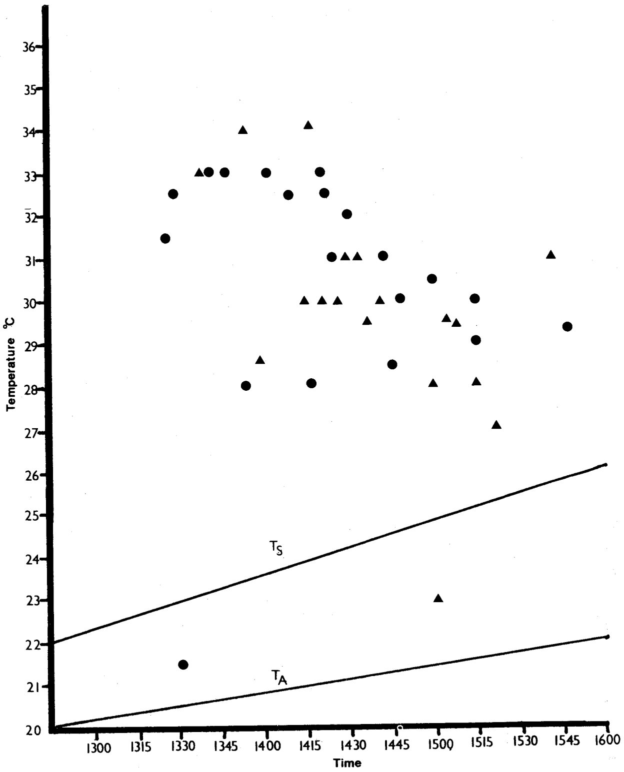

FIG. 2. Scatter diagram of *Testudo hermanni* body temperatures plotted against air (T_A) and soil (T_S) temperatures. Mean = 30.20°C (n = 38). 95% confidence limits ± 5.16°C. Males = ▲, females = ●.

BODY MASS/CARAPACE LENGTH

From the field measurements of body mass and carapace length for our *T. hermanni* population, an allometric equation was obtained by least squares regression after transformation to logarithms. Student's *t*-test was used to assign 95% confidence limits to the exponent (Bailey, 1959).

This gave

$$\text{Carapace length} = 0.29 \times \cancel{\frac{0.35 \pm 0.14}{\text{body mass}}} \quad \text{body mass}^{0.35 \pm 0.14}$$

$$(r = 0.99 \quad n = 43)$$

where r is the correlation coefficient and n the number of individuals.

Figure 3 is a graph of these data plotted on logarithmic co-ordinates. The points fall very nearly on a straight line and the allometric equation which defines this line can be used to predict an animal's mass from its carapace length or vice versa.

POPULATION CHARACTERISTICS

Figure 3 shows the maximum and minimum sized tortoises recorded in the population. This shows that adult females are the largest members of the community, the largest male being 200 g lighter than the largest female. Our records of the sexes of 39 tortoises weighing in excess of 200 g indicate a 1:1 sex ratio. The four animals below this weight shown in Fig. 3 took several days to locate. These and five smaller tortoises that appeared to be the previous season's hatchlings (Fig. 4) were all that we managed to collect that fell below this size. Tortoises weighing more than 300 g were the most abundant and formed 81% of collected animals.

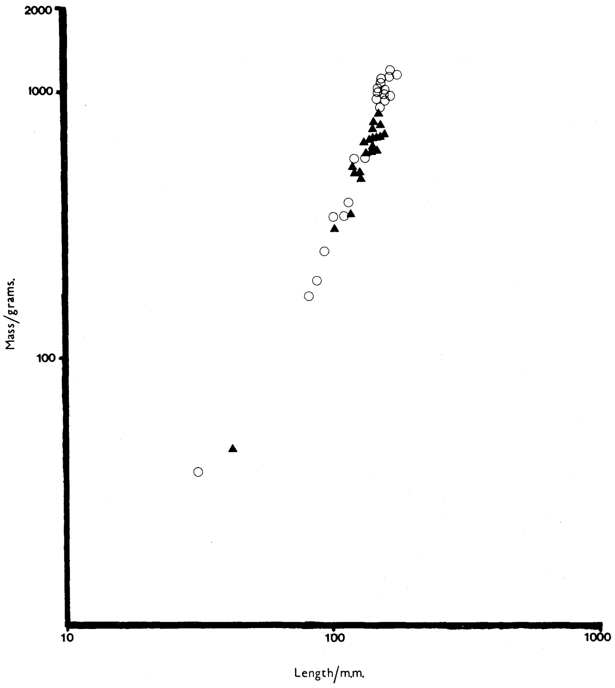

FIG. 3. A graph on logarithmic co-ordinates showing body mass plotted against carapace length in a sample of *Testudo hermanni*: ($n = 43$). Males = ▲, females = ○.

FOOD PREFERENCE

Although *T. hermanni* appears to feed on a wide variety of plant material we discovered that one particular group, belonging to the family Leguminosae, formed the bulk of plant material eaten. These were mainly of the subfamily Papilionoidea (beans, clovers, lupines etc.), and these formed in the region of 90% of specimens that we collected. To a lesser extent, other types were taken. These were from the families Ranuncalaceae (buttercups etc.) which was 7% of the sample, and the Graminea (grasses) 3%. We were unable to identify one further specimen that we collected.

The tortoises were most commonly seen feeding in the late afternoon (15.00 hr onwards) although feeding was observed less frequently during other times of the day, mainly around 11.00 hr. Although there were several growing areas in the scrub (approximately 9 m^2 in each area) run by the local people for growing vegetables, we never at any time saw tortoises on these sites, despite the fact that some of the vegetables grown were similar to those offered to and accepted by captive animals (see Noel-Hume & Noel-Hume, 1970).

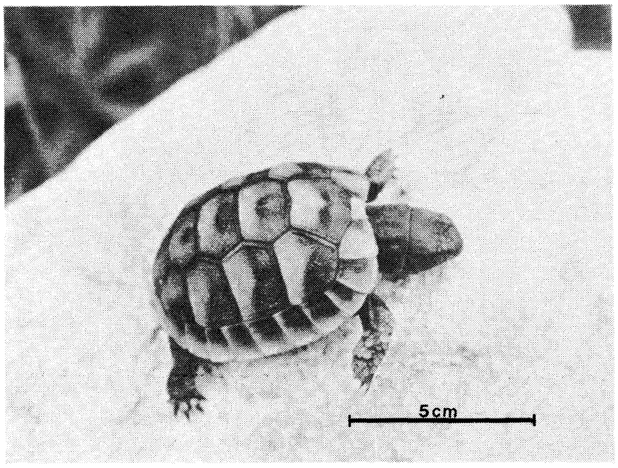

FIG. 4. Juvenile *Testudo hermanni* of less than one year in age (see text for discussion on tortoises of this size range).

TABLE II. Condition of the supracaudal plate in a sample of *Testudo hermanni* of different sex and age groups ($n = 43$)

	Males	Females	Juveniles	Total
Divided	14	21	3	38
Single	1	3	1	5
Single/divided Ventrally	1	3	1	5

CARAPACE CHARACTERISTICS

Supracaudal condition

Lambert (1977) and Hellmich (1962) state that *T. hermanni* is differentiated from *T. greaca* in having a divided supracaudal (pygal). Noel-Hume & Noel-Hume (1970) claim that the supracaudal is divided only in the male *T. hermanni*. Our data shown in Table II indicate that a divided supracaudal is not a definitive feature of *T. hermanni*, although such a condition was found to exist in 88% of the animals we investigated. We did, however, find that in the remaining 12% of tortoises exhibiting the single supracaudal dorsally, these were subsequently found to have a division when viewed ventrally. In addition, the data in Table II show that females also exhibit a divided supracaudal.

Shell abnormalities and injuries

Our observations on the physical condition of wild tortoises indicated that serious injuries to the shells or limbs of the animals were not particularly common. Of a total of 58 animals examined only 4% could be classed as having a serious deformity. The majority of these deformities involves the carapace (2.5%), the remainder the limbs and plastron. The tortoise in Fig. 5 was the most extreme example of those that we found. Here the front right limb had been severed at least 50% up the length of the humerus. This tortoise also showed an abnormality of the first and second peripheral plates which lie just above the absent limb. Other somewhat less serious cases were: (i) peripheral plates, the right number 9 and 10 virtually absent; damage also to the

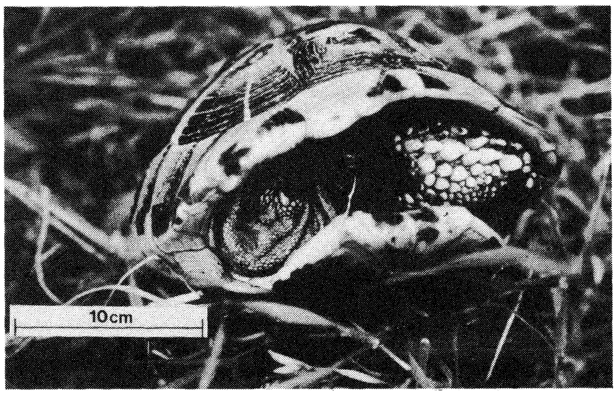

FIG. 5. Tortoise with part of the front right limb absent.

postneural and both the 4th pleurals, (ii) indentation on the carapace involving 2nd and 3rd neurals and 3rd pleural; indentation is sufficiently deep to reveal bony elements that underlie dorsal scutes, (iii) abnormally shaped carapace in a yearling tortoise. Here the peak height of the carapace was reached in the left pleural plates giving the animal an unbalanced appearance, (iv) indentations on plastron involving mainly right humeral, right femoral and right abdominal scutes.

DISCUSSION

HABITAT

The effect of climate on the distribution and ecology of reptiles has long been known. Nevertheless, the intrinsic relationship that exists between reptiles and their environment is often obscure and difficult to determine without a detailed analysis of the biological requirements of the animals in the field. Our records of the associate herpetofauna of *T. hermanni* show that several comparable-sized species were present in the study site. The importance of these in the lives of *T. hermanni* is unclear at present. Two of the forms recorded—*Elaphe longissima* and *Ophisaurus apodus*—approach *T. hermanni* in size. Under natural conditions these are both known to consume eggs (Petzold, 1975; Street, 1979) and it is possible that they may play a role in preying on the eggs of tortoises. The most common and active snake in the study site appeared to be *Coluber gemonensis* but whether this much smaller reptile plays a part in the ecology of *T. hermanni* is difficult to say at present. In addition, the two species of mammal—a feral cat and a hedgehog which were also recorded from the area could also have some effect on the eggs and juvenile tortoises.

BODY TEMPERATURES

Our records of body temperatures in relation to specific location of the tortoises at the time the readings were taken, indicate that *T. hermanni* is a shuttling heliotherm regulating its body temperature by moving between sunlit and shaded areas. This is suggested by the fact that some tortoises, although in the shade, had body temperatures higher than either air or substrate temperatures, suggesting that they had recently been basking or active but had moved to shade either to effect a reduction in temperature or to resist a further temperature increase.

BODY MASS/CARAPACE LENGTHS

Grubb (1971) has shown the relationship between body mass and carapace length in the giant Aldabra tortoise (*Geochelone gigantea*) but did not quantify the relationship. Using his graph we estimate that

$$\text{Carapace length} \propto \cancel{\frac{0.36}{\text{body mass}}}\ \text{body mass}^{0.76}$$

The two body mass exponents appear to be similar, but it must be noted that they are derived from tortoises at very different size ranges; our largest animal measured was 1.3 kg, whereas Grubb measured animals up to 100 kg.

POPULATION CHARACTERISTICS

The data in Fig. 3 show several breaks in the slope as a result of our inability to locate animals at appropriate size levels. At present we are uncertain as to why these gaps should occur. It may be that the data point clusters represent different age groups within the population and that each cluster of animals has an age grouping within only a few years of one another. The scarcity of yearling tortoises is of particular interest. This could be a function of behavioural differences between these and the larger animals, although it could also be a problem of the smaller tortoises being more difficult to locate (see Fig. 4). It is of interest to note however that Stubbs (personal communication) also found tortoises of this size difficult to locate.

SHELL ABNORMALITIES AND INJURIES

The general condition of the shell in the tortoise population appeared to be good with serious injuries somewhat uncommon. The condition of the tortoise shown in Fig. 5, which we considered to be the most serious found, was probably a result of embryonic faults. Some of the other tortoises may have sustained damage by falling off the drystone walls that were to be found in the scrub. Tortoises were on several occasions found walking along these. Other hazards could be in the form of birds of prey which Mattison (personal communication) when visiting the same site some years earlier, observed perched on the carapace of the tortoises. Chelazzi & Francisci (1979) found the horny scutes of *T. hermanni* in the faeces of the fox *Vulpes vulpes* and they also mention that several animals showed scars resulting from attacks by this predator. Rodents, although not seen in the area, may have been responsible for some of the injuries by gnawing at the shells either when the animals are in winter dormancy or during the night when they are inactive. In some areas it is possible that tortoises are injured by agricultural machinery but in our study site we did not observe any such machinery in use, nor, due to the very small size of the growing areas, would we expect any to be used.

ACKNOWLEDGEMENTS

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AN ENCLOSURE DESIGN ALLOWING QUANTIFICATION OF DISPERSAL IN LIZARD POPULATION STUDIES

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SUMMARY

Dispersing common lizards were trapped in pitfall traps buried along both sides of an enclosure that fenced the study area. Local movements across the fence comprised about half of the captures made. An estimated 25% of the movements were not recorded by the traps. Less than 10% of the emigrants were detected by searching the surroundings of the plot. Use of the method described resulted in a tenfold increase of the accuracy of the emigration estimates compared to estimates obtained by searching the surroundings of the area.

INTRODUCTION

Dispersal is not often measured in population studies especially in lizards. The paucity of investigations of dispersal processes in lizard populations is well illustrated in a recent review of the dynamics of squamate populations (Turner, 1977), in which no special attention to dispersive movements could be given. This is unfortunate but not surprising since dispersal is undoubtedly very difficult to investigate. For this reason investigators usually assume dispersal to be negligible, or that immigration and emigration rates are equal. Although studies of dispersal are laborious and often difficult, they may provide important insight in the dynamics of population structure and in components of life history strategies (Horn, 1978).

In lizard population studies, estimates of dispersal may be obtained by intensive search for marked individuals beyond the margins of the study area (Tinkle, 1967; Ballinger, 1973). This method is however extremely laborious and therefore often impracticable. Attempts to estimate dispersal in lizard population studies are therefore rarely made (Turner, 1977).

In a population study of the common lizard, *Lacerta vivipara*, we initially attempted to quantify dispersal by an intensive capture–recapture programme both within and beyond the margins of the study plot. In addition to being very time consuming, the method proved to be unsuccessful since we could show that the observed emigration rate underestimated the actual dispersal rate (Bauwens & Verheyen, 1980). Although a rather high number of lizards marked within the plot were subsequently recaptured outside the study area, the majority, if not all of them, were animals whose home ranges were located on both sides of the margins of the plot. Lizards considered as dispersers were only occasionally captured, probably because the majority of them moved to areas that were not visited by us. Intensive search in a larger area would possibly reveal more dispersal, but was impracticable within the time available. In order to overcome this problem, we designed an enclosure allowing quantification of dispersal. The reliability of the estimates obtained by this method is discussed here.

MATERIALS AND METHODS

A population of common lizards, *Lacerta vivipara*, was studied in a 52 m × 36 m study plot located in the Belgian national nature reserve "de Kalmthoutse heide" (Kalmthout (51°25′N, 4°25′E), Province of Antwerp, Belgium).

The vegetation of the study area is characteristic of moist heathland. Dominant plants are cross-leaved heath (*Erica tetralix*), purple moor-grass (*Molinia caerulea*) and bog asphodel (*Narthecium ossifragum*). A part of the study site is flooded temporarily (Fig. 1). Birch (*Betula pendula*) and pine (*Pinus sylvestris*) stand isolated and form small bushes. A long side of the plot borders on a sand dune. On the lee-side the dune is overgrown by birch and some pine (Fig. 1). The top and the weather-side of the dune form a zone of bare sand of about 50 m wide which acts as a natural barrier for the lizards.

Lizards were captured by hand. We gave each lizard a unique and permanent mark by toe-clipping. A corresponding colour mark was painted on its back, allowing future identification by sighting.

Three age classes could readily be distinguished in the field: juveniles (young born during the current activity season), subadults (lizards born during the preceding activity season) and adults (animals being at least in their third activity season).

Within the study plot, lizards were captured and/or identified by sightings daily, weather permitting, from March through to October. A 30 m wide zone surrounding the plot was visited weekly from March to June and daily from July to September 1979.

During the winter of 1978–79 an enclosure was placed at 5 m distance from the margins of the study area (Fig. 1). The enclosure was constructed of aluminium sheets (2.5 m × 0.6 m × 0.8 mm) and supported by wooden stakes which extended about 20

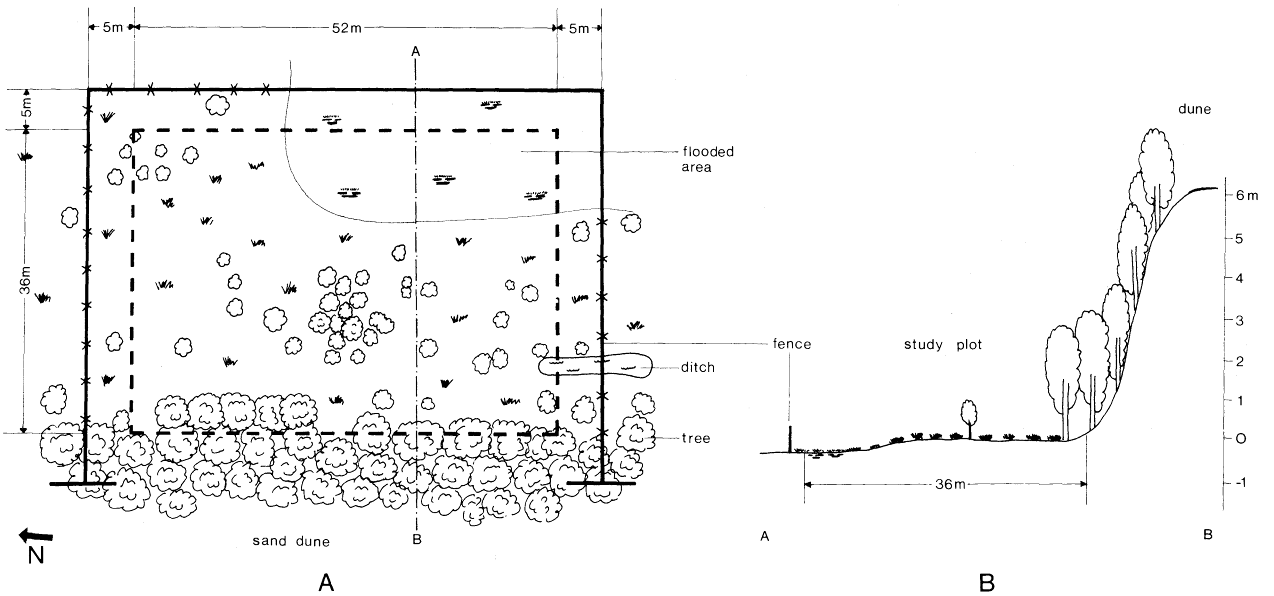

FIG. 1. (a) Map of the study area showing boundaries of the plot (dashed line), location of the enclosure (solid line) and characteristics of the vegetation. The position of the pitfall traps along the fence is indicated by crosses (a persisting high water table prevented burying of traps in the flooded area). (b) Cross section of the study area through the line A–B.

cm aboveground (see also Medica, Hoddenbach & Lannom, 1971). The metal sheets were placed in the ground to a depth of about 15 cm and extended 45 cm aboveground. Approximately every 4 m a gap of about 35 cm wide was left in the fence. On both sides of every gap we placed a plastic box (45 cm x 15 cm x 15 cm) as a pitfall (Fig. 2). Previous tests indicated that the lizards could not escape from these traps. Within the traps we placed small boxes of white plastic as a shelter against possible avian predators and to allow the lizards to thermoregulate. Preliminary tests demonstrated predation by nocturnal carabid beetles (mainly *Carabus clathratus* and *C. violaceus*) on the lizards in pitfalls. To avoid such artificial predation, traps were removed at night and during periods of abscence, and the gaps were closed so that dispersal was prevented. The 19 pairs of pitfall traps were examined at least twice daily.

Lizards attempting to enter the plot were trapped in one of the outer boxes, toe-clipped and placed within the study area. Lizards trapped in an inner box were identified and placed outside the study area.

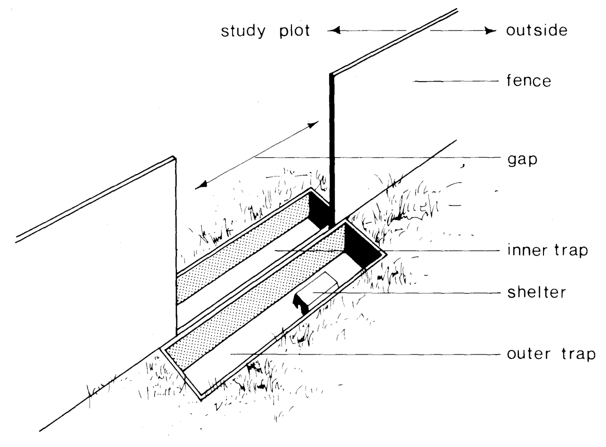

FIG. 2. Detail of the enclosure which allows trapping of dispersing lizards.

The gaps in the fence are perhaps not a necessary device for the method. Gaps were left to allow possible directional orientation toward visible objects such as trees, forest-edges and other objects in the landscape.

Lizard movements across the enclosure traps were classified into five categories (according to definitions of Caughley, 1977):

(i) dispersal: one way in- or outward movements of lizards which were not known to have occupied a home range near the margins of the plot before and after the movement.
(ii) non-permanent migration: in- or outward movement followed, after an interval of at least one month, by a movement in the reverse direction. During their temporary presence or absence in the plot, these lizards did not occupy a home range near the margins of the plot. This category includes movements from an animal's summer home range toward its hibernation site and vice versa.
(iii) nomadism: movements of lizards which enter and subsequently leave the plot, within an interval of one month, at localities (traps) that are at least 30 m apart.
(iv) local movements: movements across the fence of animals which occupied a home range near or at both sides of the enclosure.
(v) unclassifiable movements: movements that, due to a lack of information before and after it, could not be assigned to one of the former categories.

RESULTS AND DISCUSSION

In order to provide accurate estimates of dispersal, the method described here must meet two major requirements. Firstly, only dispersing or migrating animals should be trapped in the enclosure-traps, or

TABLE I. Number of animals trapped and number of captures made during 1979 in the enclosure traps. Movements of lizards across the fence were classified into five categories according to the capture–recapture history of the individual animals (see text for definitions)

	Number of animals trapped	Number of captures
Dispersal	52 (27%)	52 (19%)
Non-permanent migration	21 (11%)	28 (10%)
Nomadism	13 (8%)	20 (7%)
Local movements	69 (36%)	139 (51%)
Unclassifiable*	33 (17%)	33 (12%)
Total	191	272

* Includes three animals killed in the traps by carabid beetles.

one should be able to distinguish between dispersive and local movements. Secondly, all dispersing and migrating lizards should be trapped in the boxes.

It is obvious from the data shown in Table I that not only dispersing or migrating animals are trapped in the enclosure-boxes. About half of the captures relate to local movements. This may not be surprising since the enclosure acts as a drift fence on lizards with home ranges near or along both sides of it. Since these animals are captured repeatedly as they move back and forth across the gaps in the fence and/or at both sides of the enclosure, they are distinguishable from migrating animals. Omission of these movements reduces, to a large degree, the bias that would result if we would estimate dispersal by counting the number of animals trapped in the pitfall traps. However, it remains possible that a number of local movements were erroneously considered as dispersive because the lizards involved were missed when we inspected the surroundings of the study plot or died shortly after they crossed the fence. This would result in an overestimate of the actual dispersal rate. Since our capture–recapture programme was very intensive (about 40% of the minimum number of lizards alive in the plot were captured daily) it is likely that the resulting bias is small.

In spite of repeated attempts to prevent lizards leaving or entering the enclosure via routes other than by the traps, some lizards were known to escape through the enclosure wall. Estimates of the number of these "escapes" can be made more accurately for the process of immigration than for emigration because animals moving into the study area will usually be detected while the reverse is not necessarily true. Adult lizards which avoided the pitfall traps could be recognized since all resident adults and subadults were marked during 1978 (Bauwens & Verheyen, 1980). Since only a fraction of the juveniles present during 1978 were marked, we could not always distinguish between resident subadults (the juveniles of the preceding activity season) and subadults avoiding the pitfall traps during 1979. For the subadult age-class, an indirect method had to be used. Figure 3 shows the cumulative number of marked and unmarked subadults captured in the study area during 1979. By the end of May we had captured all surviving marked subadults, whereas the curve for unmarked lizards only levels off by the end of June. We estimate the minimum and maximum number of clandestine immigrants in this age-class as the number of unmarked lizards captured respectively from July and June onwards. These figures were compared to the actual number of immigrants trapped in the enclosure boxes (Table II). Table II also shows the minimum number of illegal local movements across the fence. These could be detected by analysing the successive capture localities of the individual lizards. According to the data in Table II we estimate that approximately 25% of the movements across the enclosure were uncontrolled. Assuming that this figure also applies for movements out of the plot, it is possible to correct the obtained estimates for emigration rate. Nevertheless, the number of "escapes" remains high and some elaboration is needed here. Repeated attempts to prevent the lizards from escaping by stopping

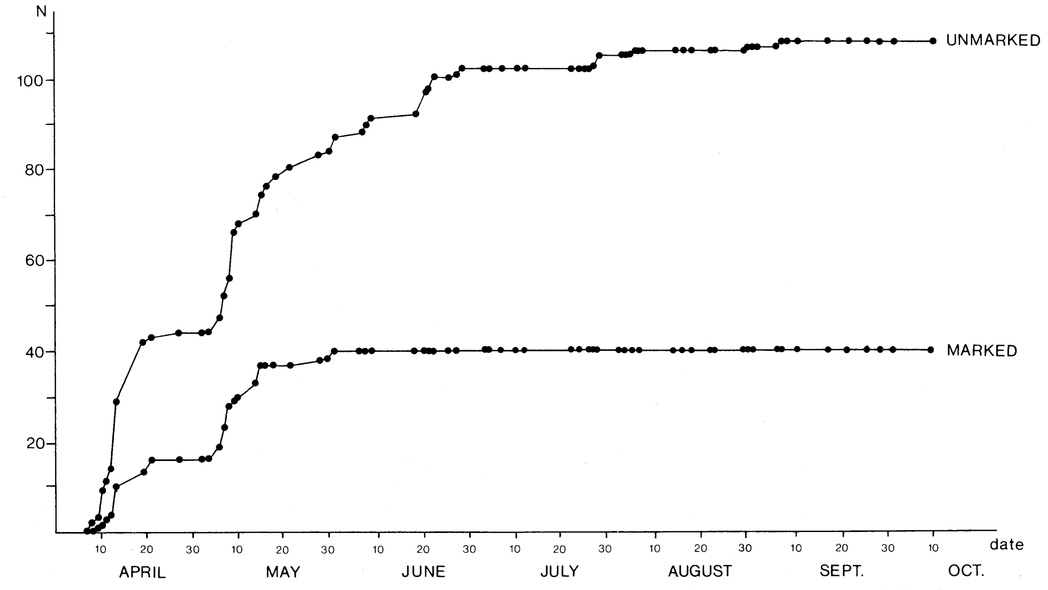

FIG. 3. Cumulative number of different subadults trapped during 1979 within the study plot. Distinction was made between subadults that were marked during 1978 (as juveniles) and unmarked subadults.

TABLE II. Number of captures made in the enclosure traps and estimated number of uncontrolled movements across the fence assigned to the processes of immigration and travelling within a home range

	Number of captures made	Estimated (minimum and maximum) number of "escapes"	% "Escapes" (minimum and maximum) of total number
immigration*	47	7–22	13–32
local movements	141	33	19

* Includes dispersive, migrating and nomadic movements.

up small crevices at both sides and under the metal sheets as well as by joining the sheets tightly were unsuccessful. As the possibility existed that lizards could get through the gaps without actually falling into the pitfalls by climbing over the joined side-walls of both traps, we placed a plate between the pitfalls that extended about 7 cm above them. This modification did not completely prevent "escapes". Hence, we suppose that the alternative ways still remaining which were used by the lizards to cross the enclosure include small crevices and perhaps burrows of small mammals that remained undetected by us. In building a similar enclosure, care should thus be taken to place the metal sheets as deep as possible and to make every attempt to stop up all visible crevices.

Since we also visited the surroundings of the study plot, we compared the estimates of emigration rate obtained by both the enclosure- and the search-method. Of 41 animals that were known to have left the plot during the processes of dispersal, non-permanent emigration or nomadism, 5 were recaptured in the surroundings of the area. Taking into account that an estimated 25% of the actual number of dispersing lizards avoid the pitfalls (none of which was recaptured out of the area), less than 10% of the emigrants were detected out of the plot. In view of these findings, it is not surprising that we underestimated the actual emigration rate during 1978 when only the search method was employed.

Although a rather high number of movements across the enclosure were uncontrolled, the method described seems to provide estimates of dispersal rate which are less biased compared to estimates obtained by searching beyond the boundaries of an unfenced area. In addition, the timing of dispersal can be determined exactly and the occurrence of nomadic movements can be demonstrated. We therefore conclude that the enclosure method is currently the most accurate and least time consuming for use in lizard population studies.

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THE ADAPTATION OF *SALAMANDRA SALAMANDRA* (L.) FROM DIFFERENT HABITATS TO TERRESTRIAL LIFE

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SUMMARY

Salamandra salamandra (L.) shows high tolerance to water loss. The salamanders from semiarid habitats (Galilee and Carmel) can survive long periods of water loss (15 days) as compared to those of Tel Dan (8 days).

The plasma concentration of the mountain populations (Galilee and Carmel) was higher than the plasma osmolarity of the Tel Dan populations during dehydration at 5% RH and 25°C, and after a long period of dehydration (1.5 months). On soil, however, no significant difference was observed.

The urine concentration was hypo-osmotic as compared to plasma in hydrated salamanders and isosmotic in dehydrated salamanders.

The increase in proportion of urea was higher than that of the other components.

The mechanism of this increase in plasma concentration is clarified.

INTRODUCTION

Salamandra salamandra is found throughout Europe, reaching the limit of its southern distribution in Israel and North Africa (Eisalt, 1958). After metamorphosis salamanders are terrestrial and live in different habitats. In Israel three isolated localities of *S. salamandra* populations are found (Degani & Warburg, 1978; Degani, 1979): (i) on Mt. Carmel, (ii) in Western and central Galilee, where some of the ponds and streams are dry in summer, and (iii) on Tel Dan, around the Dan stream, where water is available throughout the entire year (Degani & Mendelsshon, 1979). Most terrestrial amphibians appear to show adaptive changes in tolerance to high percentage of water loss. The ability to generate and tolerate very high body fluid concentration is highly adaptive during prolonged dry periods. However, the range of change in body fluid during dehydration has been studied only in the urodele *Ambystoma tigrinum* (Delson & Whifford, 1973). Moreover, there is no information available regarding the comparison between the body fluids among species during short and long periods of dehydration of salamanders from different habitats. There is also no information available about the limits of water loss and the changes of body fluids of *S. salamandra*.

MATERIALS AND METHODS

Adult salamanders were collected from Carmel, Galilee and Tel Dan, as described previously by Degani & Warburg (1978). Salamanders from the Galilee and Carmel populations weighed 40–120 g and those from Tel Dan weighed 20–50 g. The animals were kept at 16 ± 0·5°C, as described previously by Warburg & Degani (1979). The upper limit to withstanding water loss was determined at 0–5% RH and 25°C until the salamanders lost their coordination. In this situation it is possible to hydrate back to normal condition. The rate of rehydration was described previously by Warburg & Degani (1979). There were two rates of dehydration. Fast dehydration was conducted in dessicators over dry silica gel (0–5% RH) at 25°C. The first group of five salamanders from the three populations were dehydrated to 10% body weight, the second group to 15% body weight and the third group to 20% body weight. One group of salamanders was not dehydrated. Slow dehydration was conducted on soil at room temperature, 20 ± 5°C for 1·5 months. The salamanders from the three populations lost more than 30% of their initial body weight before samples were taken.

Blood and urine samples were taken from each experimental group. The blood samples were taken by cardiac puncture with a 1 ml syringe which had previously been washed with lithium heparin. Urine was collected by a cannula from the bladder. The blood samples were immediately centrifuged for 10 min at 3000 r.p.m. The plasma was transferred to small tubes and analysed immediately, or frozen for later analysis. Plasma and urine osmolality were determined using osmometer (Fiske Automatic Osmometer, Model 130). The Na and K content of plasma and urine were determined by atomic absorption spectrophotometry, and Cl using a radiometer chloride titrator. The concentration of urea was determined by using an enzymatic colorimetric method (Med. Chem. Inc. Bun. Test Cat. No. 700).

RESULTS

The salamanders from Galilee and Carmel reached their water loss limit after 15 days, having lost 39% body weight. However, salamanders from the Tel Dan populations reached their water loss limit after 8 days, having lost 37% of their body weight (Fig. 1). The

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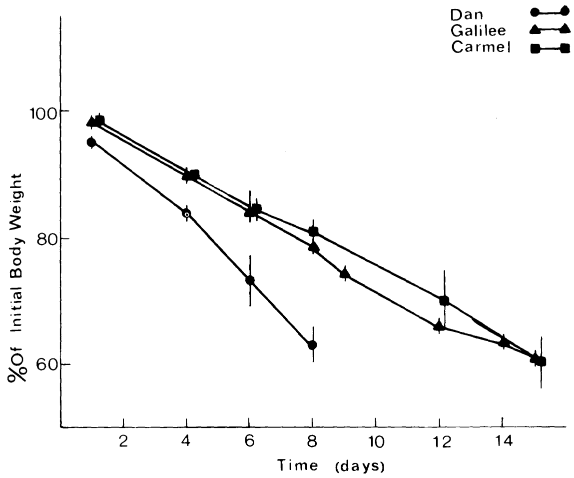

FIG. 1. Duration of water loss tolerance in salamanders from different localities.

plasma concentration of *S. salamandra* increased during dehydration. The plasma osmolality of the Galilee and Carmel salamanders was higher than that of the Tel Dan population, but the difference was not significant in all the dehydrated groups (Table I). The maximum plasma concentration of salamanders from the Galilee population was 768 mOsm/kg; from the Carmel population 700 mOsm/kg and from the Tel Dan population 655 mOsm/kg. The plasma concentration of the salamanders from the Galilee populations was higher (636 ± 103 mOsm/kg) than the other populations after long dehydration on the soil, but the difference was not significant (Table II).

TABLE I. Plasma concentration and plasma constituents in salamanders during progressive dehydration ($n \geqslant 5$)

	Plasma osmolality	Concentration in % of plasma osmolality			
Locality	mOsm/kg ± SD	Na	Cl	Urea	K
		Fully hydrated			
Galil	239 ± 7	42	34	7	2
Carmel	238 ± 14	45	36	8	2
Dan	235 ± 24	41	35	5	2
		Dehydrated to 90% body wt.			
Galil	326 ± 21	48	27	15	2
Carmel	288 ± 16	46	34	15	2
Dan	281 ± 8	39	34	21	1
		Dehydrated to 85% body wt.			
Galil	381 ± 65	58	39	20	4
Carmel	342 ± 14	45	36	10	2
Dan	303 ± 22	50	34	22	1
		Dehydrated to 80% body wt.			
Galil	427 ± 69	53	27	20	2
Carmel	373 ± 34	47	37	28	2
Dan	351 ± 20	48	33	26	1

Plasma constituents in the fully-hydrated salamanders were mainly Na and Cl. During dehydration the proportion of urea increased as compared to Na and Cl (Table I). Moreover, after long dehydration on the soil, the plasma urea concentration was similar to the Na and Cl concentration. The plasma Na concentration of the Galilee population was higher than that of the others (Tables I, II).

The plasma concentration was hyperosmotic as compared to urine concentration in the control group, and reached a near isosmotic condition during dehydration. There was no significant differences in the urine concentration of the three populations during dehydration. The urine consisted mostly of urea and Na (Table III).

DISCUSSION

S. salamandra showed a marked adaptation to survival in semiarid habitats, as compared with other urodeles (Table IV). Moreover, the salamanders from semiarid habitats (Galilee and Carmel) survived dehydration for longer periods than salamanders from moist habitats (Tel Dan). The low survival of salamanders from moist habitats can be explained by the high rate of dehydration of salamanders from the Tel Dan population. Warburg & Degani (1979) found that the rate of water loss of juvenile *S. salamandra* was higher than in adults. The adult salamanders from the Galilee and Carmel populations are significantly larger than the salamanders from the Tel Dan populations (Degani, 1979). The relationship of size to water loss is shown in the water turnover of salamanders from Tel Dan, which was higher than that of salamanders from semiarid habitats (Degani and Shkolnik, 1979).

The plasma concentration of *S. salamandra* from semiarid habitats in the Galilee population reached 768 mOsm/kg. This is higher than available data on urodeles (Table V). Resistance to high plasma concentration after long periods of dehydration on soil was found in this study and also described for *A. tigrinum*, 550 ± 75 mOsm/kg (Delson & Whitford, 1973).

A comparison between plasma concentrations of different populations of the species *Salamandra*

TABLE II. Plasma concentration and constituents in salamanders after 1.5 months of dehydration on soil

% Dehydration	Osmolality mOsm/kg ± SD	Na mM	Cl mM	Urea mM
	Galilee ($n = 5$)			
34 ± 8	636 ± 104	267 ± 55	194 ± 59	223 ± 77
	Carmel ($n = 4$)			
32 ± 7	65 ± 70	230 ± 61	166 ± 8	187 ± 47
	Dan ($n = 4$)			
33 ± 5	574 ± 85	253 ± 64	179 ± 25	125 ± 42
Total	597 ± 84	251 ± 56	183 ± 41	190 ± 70

TABLE III. Urine concentration and urine constituents in salamanders during progressive dehydration ($n = 5$)

Locality	Osmolality mOsm/kg ± SD	Na ± SD mM	Cl ± SD mM	Urea ± SD mM	K ± SD mM
			Fully hydrated		
Galilee	84 ± 15	14 ± 6	5 ± 2	29 ± 22	11 ± 6
Carmel	94 ± 47	22 ± 14	2 ± 2	27 ± 4	2 ± 2
Dan	99 ± 31	29 ± 14	9 ± 7	9 ± 9	6 ± 4
			Dehydrated to 90% body wt.		
Galilee	279 ± 13	62 ± 44	5 ± 4	58 ± 39	21 ± 1
Carmel	181 ± 27	25 ± 3	4 ± 2	45 ± 29	6 ± 1
Dan	205 ± 56	50 ± 32	3 ± 1	45 ± 18	26 ± 30
			Dehydrated to 85% body wt.		
Galilee	303 ± 15	105 ± 23	3 ± 3	77 ± 10	23 ± 14
Carmel	310 ± 5	70 ± 42	20 ± 12	70 ± 23	32 ± 10
Dan	299 ± 36	50 ± 21	4 ± 3	109 ± 13	32 ± 24
			Dehydrated to 80% body wt.		
Galilee	332 ± 20	118 ± 17	9 ± 1	105 ± 6	44 ± 6
Carmel	349 ± 19	119 ± 18	23 ± 2	105 ± 28	41 ± 7
Dan	334 ± 30	70 ± 29	4 ± 3	138 ± 14	48 ± 46

TABLE IV. Maximum water loss (% body weight) in various Urodeles

Species	maximum water loss % body wt.	Habitat
Notophthalmus viridescens	27	aquatic[a]
N. viridescens	35	terrestrial[a]
Plethodon cinereus	34 ± 1	terrestrial[b]
P. hoffmani	26 ± 1	terrestrial[b]
Ambystoma opacum	30	terrestrial (semi-arid)[c]
Desmognathus fuscus	22	semi-aquatic, moist soil[c]
D. monticolus	19	mountain streams[c]
P. jordani	24	terrestrial[c]
Pseudotriton ruber	18	aquatic and terrestrial[c]
Salamandra salamandra (Galilee)	39	terrestrial (semi-arid)[d]
S. salamandra (Carmel)	39	terrestrial (semi-arid)[d]
S. salamandra (Dan)	37	terrestrial (moist)[d]
A. tigrinum	45	terrestrial (arid)[e]

[a] Walter & Greenwald, 1977; [b] Brown, Hastings & Fyre, 1977; [c] Spight, 1968; [d] this study; [e] Alvarado, 1972.

TABLE V. Plasma concentration in Urodeles

	Osmolality mOsm/kg	Na mM	Cl mM	Urea mM	K mM
Ambystoma tigrinum normal condition[a]					
	205 ± 5			10 ± 4	
Long dehydration on soil[a]					
	550 ± 75			220 ± 99	
A. mexicanum normal condition[b]					
	216 ± 16	94 ± 4	85 ± 2		3 ± 0.5
A. gracile normal condition[c]					
	197 ± 3	104 ± 2	82 ± 1		8 ± 1
Salamandra salamandra (Galilee) normal condition[d]					
	239 ± 7	101 ± 24	80 ± 3	17 ± 2	5 ± 2
Salamandra salamandra (Galilee) 34% dehydration on soil[d]					
	636 ± 104	267 ± 104	194 ± 59	223 ± 77	9 ± 7
S. salamandra (Tel Dan) normal conditions[d]					
	235 ± 24	97 ± 21	83 ± 6	11 ± 3	6 ± 13
S. salamandra (Tel Dan) 33% dehydration on soil[d]					
	574 ± 85	238 ± 71	179 ± 25	196 ± 17	1 ± 1

[a] Delson & Withford, 1973; [b] Alverado, 1972; [c] Alverado & Dietz, 1970; [d] this study.

salamandra was studied for the first time in urodeles in this work. It has been found from this study that the high plasma concentration in the mountain populations explains their adaptation to semiarid habitats. The increase of plasma concentration during dehydration can be explained by the following factors: the secretion of urine is reduced or stopped during dehydration. After salamanders lost more than 10% of their body weight, secretion of urine was not recorded. Na is actively reabsorbed from the bladder and Cl passes with it (Whitting & Brown, 1977). These factors explain the high plasma concentration of Na and Cl in comparison with urine in the fully-hydrated salamander. Moreover, the plasma Na concentration of the Galilee population was higher than that of the other populations after fast dehydration. It is possible that the adaptation of the Galilee and Carmel population is through reabsorption of Na, resulting in increase in the plasma concentration and resistence to high Na concentration in plasma. Licht, Feder & Bledse (1975) and Jones & Hillman (1978) found that the terrestrial plethodontid salamanders have a high rate of survival in sea water. Plasma and urine urea increase significantly, possibly because the urea continues to be created as the body fluid decreases. Plasma urea was higher after slow dehydration when compared with short periods of water loss. Delson & Withford (1973) observed the same phenomenon in *A. tigrinum*.

S. salamandra, therefore, shows good adaptation to a high concentration of plasma, helping it to survive dehydration. The difference between the populations of the same species from different habitats (*i.e.* semiarid or moist) was found throughout the entire experiment.

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NEW LOCALITY RECORDS FOR REPTILES IN FRANCE

D. J. STREET

(*Received* 1 *November* 1976)

During the course of numerous visits made to France for the purpose of observing reptiles, I have on several occasions found species in localities from where, so far as I have been able to ascertain, they have not previously been reported.

On 11 May 1976 I found four male slow worms (*Anguis fragilis*) in the Camargue region. Weber & Hoffmann (1970) do not include the species in their checklist of reptiles for this area. All four specimens were lying together under a large paper sack, three of them being entangled in a cluster, together with a young viperine snake (*Natrix maura*). The locality concerned was situated between the Petit Rhône and the D 38 road, approximately 7 km northwest of the town of Saintes Maries. A further point of interest is that two of the slow worms were of the blue-spotted form. Smith (1973) refers to a specimen of this variety from Fontainebleau, but remarks that it has not been recorded from elsewhere in France.

In his paper concerning the wall lizards of the Atlantic region, Klemmer (1964) stated that the island of Noirmoutier did not appear to have been investigated with regard to its wall lizard population. Neither Angel (1946) nor Fretey (1975) make any reference to the reptiles of this island. On 8 September 1969 I made a brief excursion there, and during the course of a few hours I found large numbers of wall lizards. These were similar to those found on the nearby island of Yeu which I also visited, and thus appear to belong to the subspecies known as *Podarcis muralis oyensis*, described by Blanchard in 1891 (Fig. 1). According to Klemmer, one characteristic feature of this subspecies is its red belly. However all the specimens I examined from Noirmoutier and Yeu (both males and females) possessed a cream or yellow belly. Klemmer has since suggested (in litt.) that the reddish coloration may be a seasonal factor, associated with springtime. The green lizard (*Lacerta viridis*) was, I found, quite a common species on Noirmoutier.

Although Fretey (1975) remarks that the occurrence

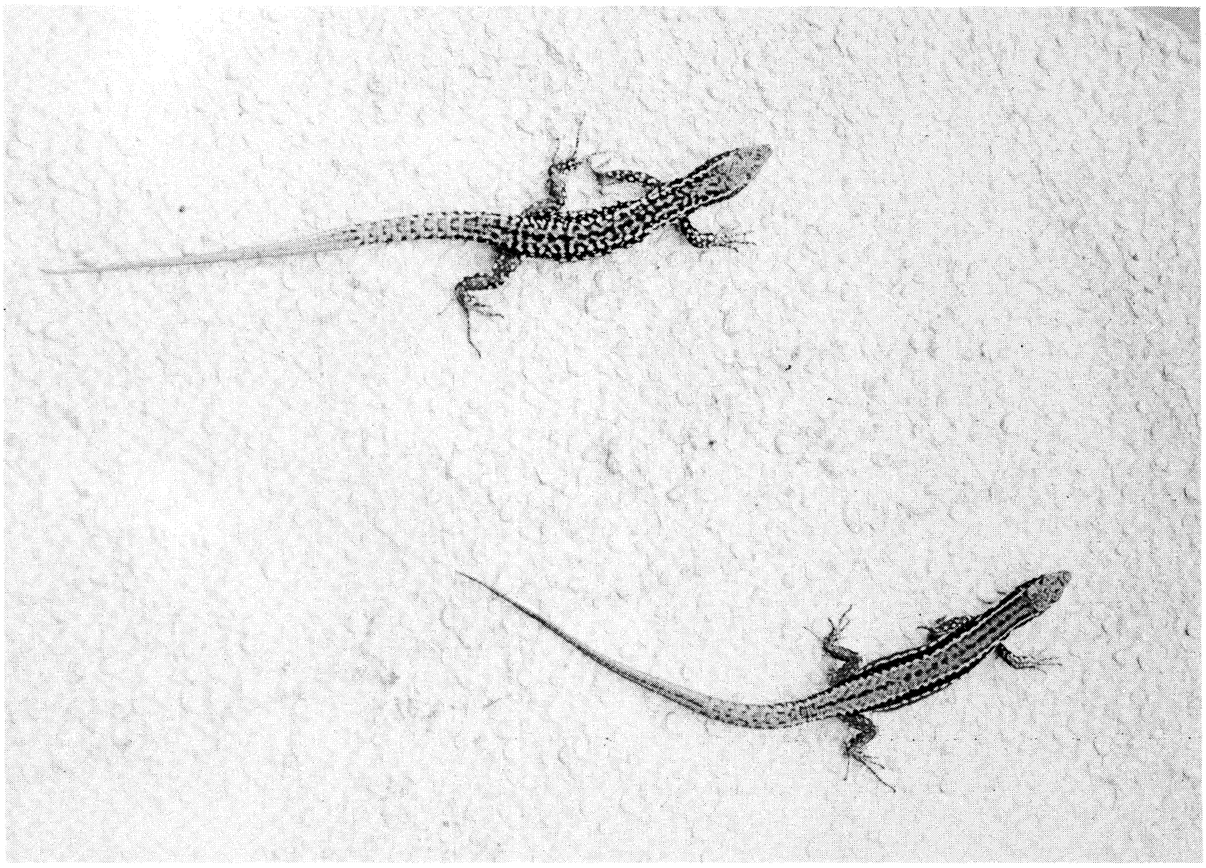

FIG. 1. A pair of wall lizards (*Podarcis muralis oyensis*) from the island of Noirmoutier (photograph by courtesy of Eric Hosking FRPS).

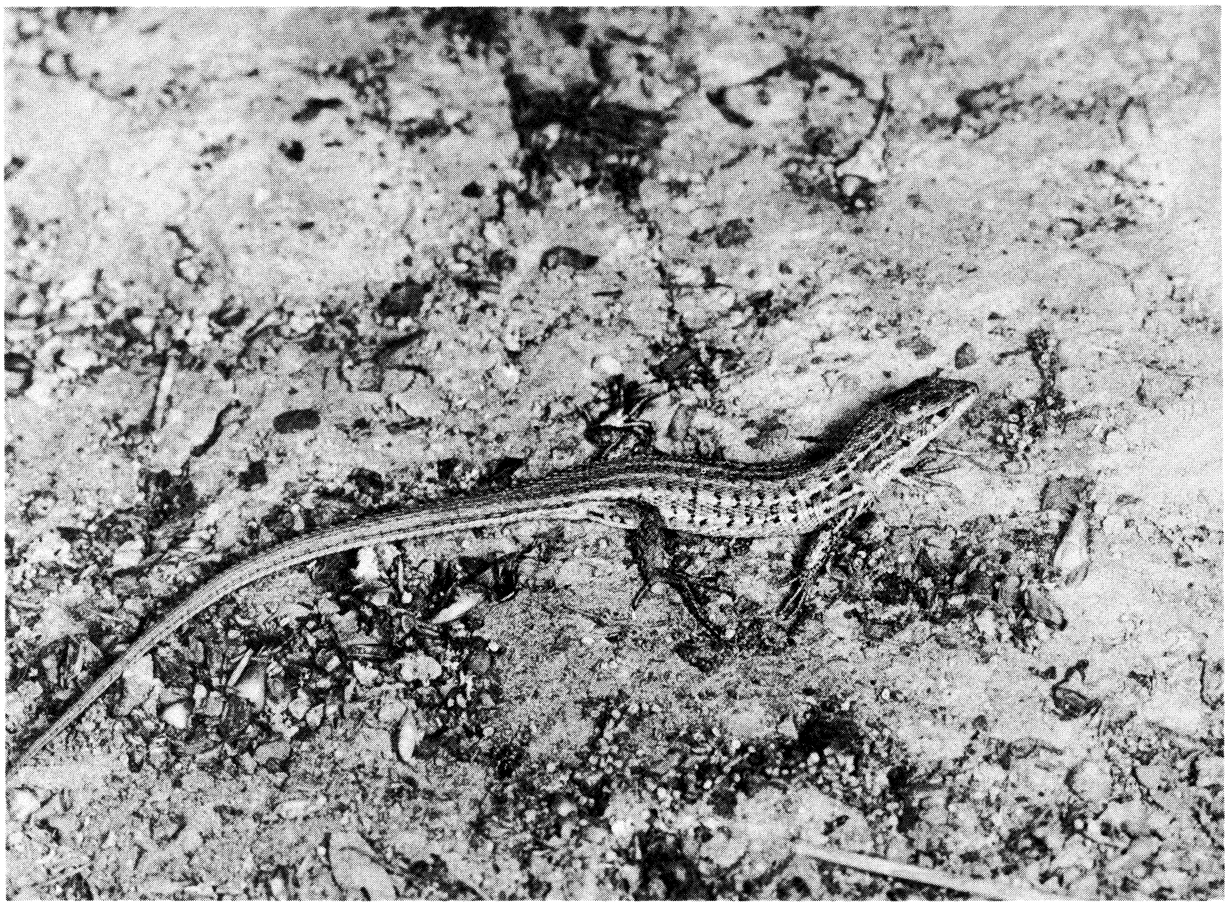

FIG. 2. Spanish sand racer (*Psammodromus hispanicus*) from the Bouches du Rhone region (photograph by courtesy of Eric Hosking FRPS).

of the Algerian sand racer (*Psammodromus algirus*) is uncertain in the département of Hérault, I observed a single specimen basking on 2 May 1971, to the west of the village of Les Matelles, north of Montpellier. Its smaller congener, the Spanish sand racer (*Psammodromus hispanicus*) is also present in Hérault, as well as in the adjoining département of Bouches-du-Rhône, where it is found in the regions of Marseilles and Cassis (Angel, 1946; Fretey, 1975). In June 1962, and again in May 1976, I found this species to be fairly common in the rocky scrubland area, situated between Miramas and the village of Cornillon and also in the département of Bouches-du-Rhône (Fig. 2).

Lataste (1876) refers to the European pond tortoise (*Emys orbicularis*) as being either rare or absent from the Atlantic département of Charente-Maritime. Fretey (1975) however reports it from the localities of Royan and Marennes. On 21 May 1976, after much searching in the vicinity of stagnant irrigation canals, I observed a single adult specimen to the north of the village of St. Augustin. This area is situated between the two localities mentioned by Fretey.

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THE OCCURRENCE OF NEUSTOPHAGIA AMONG PODOCNEMINE TURTLES

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Belkin & Gans (1968) described an inertial feeding mechanism for the ingestion of fine particulate matter from the water's surface. They termed this behaviour neustophagia and noted its occurrence as part of the feeding repertoire of the podocnemine turtle *Podocnemis unifilis* as well as the emydine *Chrysemys picta*. The closely related *Podocnemis expansa* was not observed to feed by neustophagia. Legler (1976) described neustophagia as occurring in an Australian chelid, *Emydura* sp., though the observed behaviour differed markedly from the inertial mechanism originally described by Belkin and Gans. Briefly, inertial neustophagia is a coordinated feeding mechanism whereby the turtle opens its jaws at the water's surface, keeping the mandibular tomial edge 1–2 mm below and parallel to the surface, at the same time that rapid and maximal hyoidal pharyngeal expansion is taking place, thus creating a gravitational inertial sucking force that allows only surface water with fine particulate matter to flow into the wide open pharynx. Particulate matter from a considerable radius is thereby drawn into the mouth. When no more water can be taken in, pharyngeal contraction occurs against nearly-closed jaws, thus forcing the excess water out and retaining the ingested particulate matter through a process of filtration.

We have observed all eight species of turtles of the subfamily Podocneminae (Testudines: Pleurodira) in captivity. Neustophagia is a routine component of the feeding behaviour repertoire of *Podocnemis unifilis* and *P. vogli*, and an occasional occurrence in juvenile *P. erythrocephala* and *P. expansa*. It does not appear to occur in *P. lewyana*, *P. sextuberculata*, *Peltocephalus tracaxa* or *Erymnochelys madagascariensis*.

Our observations are as follows:

(i) Two subadult specimens of *P. vogli* were kept in a 55 gallon aquarium for six months with a variety of chelid turtles. The water was kept at about 28°C and cleaned by a continuously operating power filter. The animals were fed a variety of chunk-sized foods, mainly beef and fish, and also ate lettuce leaves which floated on the surface. During this time no episodes of neustophagia were observed. Neustophagia was first observed immediately after the water in the tank was changed, and the filter was not in operation. With a still water surface, a film of fine particulate food matter formed on the surface, whereupon one of the *P. vogli* fed by neustophagia for approximately one hour. The mechanism was exactly as described by Belkin & Gans (1968). Flow currents on the surface distinctly converged on the open mouth, and particulate matter from a large distance around the mouth flowed into it. Neustophagia ceased shortly after the power filter was turned on and the surface became turbulent.

(ii) The same two *P. vogli* plus a juvenile housed under the same conditions were fed fruit. The power filter was operating at a low level and the water was free of surface currents. After eating the chopped fruit, a film of particulate matter remained on the water surface. One of the subadults and the juvenile proceeded to feed by neustophagia over the next half hour.

(iii) Of the other podocnemine turtles in this collection, neustophagia has been briefly observed in two juvenile *P. unifilis*, but never in two subadult *P. lewyana*, two juvenile *P. sextuberculata*, two juvenile *P. erythrocephala*, two adult and one juvenile *Peltocephalus tracaxa* and one adult *Erymnochelys madagascariensis*.

(iv) Several observations of neustophagia have been made in the collection of F. Medem, which is housed in Villavicencio, Colombia in large outdoor pools through which there is only a very slow water flow. When pellets of dog food were fed to several podocnemines in a large pool, a film of particulate matter developed on the surface. Several juvenile *P. vogli*, *P. unifilis*, *P. expansa* and *P. erythrocephala* fed by means of neustophagia, with the *P. vogli* exhibiting the most prolonged episodes. Juvenile *P. lewyana*, *P. sextuberculata* and *Peltocephalus tracaxa* did not feed from the surface. In a larger pool where several adult turtles are kept, specimens of *P. vogli* and *P. unifilis* are the only species noted to have fed by neustophagia. This behaviour was regularly observed at times when there was heavy algae colonization on the water surface. Adult *P. erythrocephala*, *P. expansa*, *P. sextuberculata*, *P. lewyana* and *Peltocephalus tracaxa* were not observed to feed by neustophagia. Specific attempts at inducing neustophagia in adult *P. lewyana* were unsuccessful, despite providing a surface film of particulate food to evidently hungry animals.

The observations reported here indicate that neustophagia occurs in slow moving or stagnant bodies of water in which a film of particulate matter has a chance to accumulate on the surface. Within the subfamily of podocnemine turtles two species, *P. vogli* and *P. unifilis*, exhibit this behaviour regularly. These two species often occur in lagoons, oxbow lakes, and other such slow moving waters. Two species within the subfamily, *P. expansa* and *P. erythrocephala*, exhibit neustophagia as juveniles, but apparently not as adults. This may be related to choice of ecological niche, in that juveniles tend to inhabit areas of stiller water than that occupied by adults. However, virtually nothing is known of the niches occupied by juveniles of these or any other podocnemine species. Three species within the subfamily, *P. lewyana*, *P. sextuberculata* and *Peltocephalus tracaxa*, do not feed by neustophagia at all. *P. lewyana* inhabits mainly large fast-water rivers, and *P. sextuberculata* and *P. tracaxa* are primarily bottom-feeders. The final species in the subfamily, *Erymnochelys madagascariensis*, does not appear to exhibit neustophagia, but only one adult has been observed and no data is available on choice of habitat.

Belkin & Gans (1968) point out that inertial neustophagia is a specialized modification of the general pharyngeal expansile feeding mechanism of pleurodire turtles, with the primary behavioural component in *Podocnemis* being the coordinated ability to hold the mandible open at the water's surface during pharyngeal expansion. Interestingly, only two species of podocnemine turtles have perfected the technique and two others appear to display it only as juveniles. Though Legler (1976) described "neustophagia" in the pleurodiran chelid turtle *Emydura* sp., this behaviour was simply one of striking and biting at small particles on the water surface. No component of inertial feeding was observed. We have never observed neustophagia in any species of pleurodiran chelid turtle, with observations having been made in captivity on the following: *Chelodina longicollis, C. novaeguineae, C. siebenrocki, C. parkeri, Elseya novaeguineae, Emydura subglobosa, Chelus fimbriatus, Hydromedusa tectifera, Phrynops dahli, P. gibbus, P. hilarii, P. geoffroanus, P. tuberosus, P. nasutus, P. wermuthi, P. vanderhaegei, Platemys platycephala, P. radiolata* and *P. spixii.*

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LETTERS TO THE EDITOR

HISTORICAL ASPECTS OF BRITISH HERPETOFAUNA DISTRIBUTION

(Editorial note: the second, third and fourth letters under this heading were submitted by invitation).

The recent discussion concerning the development of historical and present distributions of the rare British herpetofauna (Beebee, 1978, 1980; Yalden, 1980a, 1980b) deals with problems which may well be impossible to finally solve, as pointed out by the participants. Reasoned speculations already yield explanations which differ in certain details, while new evidence which may be presented in the future will no doubt act to modify these and other suggestions, as in any scientific enquiry. However, several points have been raised which should not go unquestioned.

For example, Beebee (1978) argues that isolated populations (of *Lacerta agilis* and *Bufo calamita*) are unlikely to have survived for several thousand years without local extinction, and then offers this as circumstantial evidence that there must have been more widely distributed populations during warmer periods so that geneflow could continue between populations that are now widely separated. While there can be little doubt that warmer periods would favour these species, assuming that suitable habitats were available, "chance" factors cannot be introduced to show that local extinction would be an inevitable consequence in the absence of a more widespread distribution, the particular examples being the populations of the northwest dunes. Unless populations are exceedingly small, chance seems to have little to do with survival. Either enough individuals are fitted to survive prevailing conditions that the population is self-maintaining, or otherwise, when there is a decline to extinction. Selection pressures are particularly intense on the edges of distribution ranges, resulting in extension or retraction of range as conditions become more or less suitable. In this way it is conceivable that northernmost populations would disappear or become more restricted in range as climate became less favourable, but in such cases the relevant factors are identifiable and measureable. They may be difficult to identify and their effects may be extremely complex, but they are not "chance" factors.

Yalden (1980b) presents convincing evidence that the northwest dunes have had a characteristic fauna and flora for a long time. However, his suggestion, that the rare species of the British herpetofauna may be absent from dune systems in southwest England because a rising sea level destroyed previously existing dune habitats and therefore any occurring populations, is not valid. Dune-building processes rely principally on a source of sand, and wind, so a rising sea level may destroy dunes, but others develop at higher elevations in a more or less continuous process. Populations then simply move up with their preferred habitat; they are not destroyed.

Whether our rare reptiles and amphibians arrived in Britain soon after the end of the last glaciation or at a later date is certainly a difficult problem. However, it is questionable whether a period warm enough to favour thermophilous animals, occurring 9000–10 000 years ago, would lead to their extension northwards in advance of tree species, as suggested by Yalden (1980a). This may have been so for certain beetles, but surely these highly mobile animals have rates of dispersal far higher than small ground-dwelling toads or lizards. Wind-blown tree seeds can also rapidly travel long distances, so any warming trend would be expected to lead rapidly to a northward movement of forest certainly no slower than that of ectothermic quadrupeds, and likely a good deal faster.

The British populations of *Coronella austraica*, *Lacerta agilis* and *Bufo calamita* represent the, now isolated, northwestern part of the entire European populations. Any discussion seeking to understand past and present British distributions must also consider the mainland populations. Thus it is well known that the habitats of these animals in Britain are specific and restricted, whereas in mainland Europe the same species are found in a wider variety of habitats. During previous warmer periods then, it seems reasonable to consider that these animals occupied a greater diversity of habitats in Britain, as they do now in mainland Europe, and it is probably not necessary to search for previously existing heaths and dunes when plotting dispersal routes. Man's alteration of the landscape has produced a variety of habitats which did not previously exist, and removal of forest cover has been a significant factor in the history of, for example, the European herpetofauna. Nevertheless, these animals were present before European agriculture, so forest clearance is not a pre-requisite of herpetofaunal existence, nor range extension.

Yalden (1980b) underestimates the significance of seemingly "modest" temperature changes. The first half of this century saw an increase of 0.5°C in the average water temperature in the western English Channel (Maddock & Swann, 1977). More recently a slight cooling trend has been noted—these apparently slight changes of average annual temperature are believed to be linked with extensive range alterations of a wide variety of marine organism. By comparison, increases of average summer temperatures of 1.5°C are considerable and likely to be of far more significance in the thermal biology of our herpetofauna than Yalden believes.

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I think that Walters has failed to appreciate the nature and the abundance of the geological evidence. Firstly, as he says, sand dunes require a continuous supply of sand, implying wide beaches. A change in relative sea level in S.W. England from – 20 m at 9500 years BP to –5 m at 6500 years BP implies to me too rapid a rate of change for the successful accretion of dunes, during that period at least (see Fig. 8.7a of West, 1977). Secondly, the notion that thermophilous beetles may have spread north ahead of the vegetation (due, incidentally, to Coope *e.g.* 1977, and certainly not to Yalden, 1980) seems to me to be well founded. Not all beetles can fly, and it is not at all clear to me that they should disperse faster than ectothermic quadrupeds. More important, not all trees have wind-blown seeds and travel long distances rapidly. While birch and pine perhaps fall in that category, hazel and oak most assuredly do not. The data from palynology show, certainly, that birch appears first, but pine and hazel appear about synchronously, though one is wind-dispersed and the other not. Similarly, elm (wind dispersed) and oak appear about synchronously and alder (wind dispersed?) is rather later. The relative timings seem to have more to do with the known ecological tolerances (birch occurs furthest north, and is a pioneer species) and generation times than with the mode of dispersal. The evidence recently published by Osborne (1980) suggests that a "cold" beetle fauna at 10 000 years BP was replaced by a warm temperate fauna within about 50 years, with birch present in another 500 years, and full deciduous woodland present in, again, another 500 years, that is by about 9000 BP. The latter date corroborates the date of 9000 years BP (7000 BC) suggested by the palynologists (see, *e.g.*, West 1977) for the rise of deciduous woodland pollens (hazel, oak, elm etc.) which might be considered as the start of the period when a closed forest canopy developed. There seems, then, to have been a period of 500–1000 years when the climate was as warm as now, but open vegetation conditions would have allowed open-ground animals (beetles or reptiles) to spread. It seems that some molluscs also spread somewhat ahead of the trees; Kerney, Preece & Turner (1980), studying mollusc faunas from the Folkestone area, backed by pollen analysis and radio-carbon dates, show a tundra fauna and compatable flora of pollen zone III type rapidly replaced by a temperate mollusc fauna ("Group A species") in pollen zone IV; the first appearance of woodland ("Group B species") coincides with pollen zone V (pine/hazel) and their replacement of Group A species, suggesting complete woodland cover, in pollen zone VI. The radio-carbon dates suggests at least 1000 years from the first appearance of temperate (Group A) molluscs to the first appearance of oak, elm, and alder pollens, and possibly a further 750 years before closed woodland cover developed.

In short, the mollusc evidence corroborates the beetle evidence; there was a long period of temperate conditions during which the vegetation cover was open, and animal species were evidently spreading faster than trees. If the molluscs could so spread, reptiles and amphibians surely could.

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I am convinced that Walters is wrong to dismiss chance effects in the way he does: much recent debate about island biogeography and the value of nature reserves has highlighted the fact that small areas of habitat in "oceans" of unsuitable terrain will gradually become impoverished with regard to species diversity, essentially through chance effects. For example with the natterjack it is easy to envisage a situation where a small area of dune with only one or two breeding pools might dry out long enough to exterminate the species, whereas a larger area with many pools is much more likely to maintain at least one or two and avert extinction in dry periods.

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It seems there is little argument between Dr Beebee and myself—only over the definition of "chance". It is clear in his example what the causes of decline and/or extinction might be, while it is probably the case that in small fragmented areas of suitable habitat different combinations of factors act to bring about the same end result of decline. Nevertheless I would prefer to attempt to identify such factors rather than assign them all under the term "chance", a term which perhaps is best used referring to genetic effects in very small populations, where the random manifestation of a severely reduced genepool might well result in a population weighted with individuals which are unfavourably suited for surviving the prevailing conditions.

Dr. Yalden has responded with some interesting material concerning relative northern expansion rates of the British post-glacial fauna and flora. Further information will no doubt finally allow a concensus, though the lack of herpetological remains will, I suspect, allow this area to remain open for speculation and interpretation.

G. J. Walters

AMPHIBIAN GROWTH RATES

My own observations over the last 10 years or so in this area agree with the conclusion of Beebee (1980) that if spawn of the common frog *Rana temporaria* is introduced into a suitable new site, then frogs return to breed for the first time two years later. As Dr Beebee intimated, this does not mean that all animals attain sexual maturity in two years. Neither does it necessarily imply that two years is the norm for frogs in a stable established population (see the comments of Hagstrom (1979) on populations of smooth newts *Triturus vulgaris* in Sweden).

Two methods for determining growth rates of amphibians are (1) to monitor the progress of unmarked individuals in cohorts of assumed age, (2) to follow marked individuals. As an example of the first technique, A. A. Bell (personal communication) caught and measured a sample of 12 adult male natterjacks *Bufo calamita* from among the population at Redrocks on the Wirral during June 1980. As no recruitment had been observed to this colony during 1975, 1976 or 1978, but had been considerable in 1977, it was very probable that each of these natterjacks was three years old. Mean length was 52 mm (range 47–59 mm).

I have been studying changes in lengths and weight of a small population of common frogs breeding in two pools in my garden in Ramsey in Cambridgeshire. Spawn was first introduced in 1978. Froglets emerged and were seen throughout the autumn. These were the first frogs I had seen within 1 km of my garden during the five years I had lived there. Frogs of sub–adult size were seen in 1979, and frogs bred for the first time in 1980. During the spawning season in February 1980 and after spawning during May, 13 separate mature males were caught, weighed, measured and marked individually by toe-clipping. It seems reasonable to assume that these frogs originated from the spawn in 1978 and were therefore two years old in 1980. Eight of these frogs were recaptured during spawning in March 1981. Mean weights and lengths are given in Table I. For frogs captured during the two spawning seasons, average weight and length were significantly greater for the three year olds than for the two year olds (Table I; weight: $t_{18} = 3.93$, $P < 0.001$; length: $t_{18} = 5.31$, $P < 0.001$). For the seven individuals captured during both spawning seasons, the mean percentage increases in weight and length were 38% and 12% respectively (Table II). The greatest percentage increase in weight of 72% was recorded for the lightest frog caught in 1980. The weight loss during breeding was considerable, being an average of 28% for the eight frogs captured in both February and May 1980 (Table II).

Heusser (1970), working on an established frog population in a Swiss garden, marked 165 froglets in 1963; seven marked males returned to breed for the first time in 1966. Their range of length was about 50–70 mm with a mean length between 60 and 65 mm (lengths taken from a graph in Heusser's paper). So in size, these three year olds tended to be intermediate

Table I. Weights and lengths of male frogs assumed to be hatched from spawn in 1978

		Weight (g)		Length (mm)	
Date of capture	No. in sample	Mean ± SE	Range	Mean ± SE	Range
February 1980	12	29.8 ± 1.7	18–38	58.8 ± 1.0	52–64
May 1980	8	20.3 ± 1.1	14–24	58.4 ± 1.2	51–62
March 1981	8	40.3 ± 2.1	31–52	66.5 ± 1.0	62–70

Table II. Percentage changes in weights and lengths of individual male frogs

		Weight		Length	
Time period	No. of frogs	Mean	Range	Mean	Range
February 1980 to May 1980	8	–28%	–24% to –38%	–1%	–3% to +3%
May 1980 to March 1981	5	+88%	+73% to +111%	+12%	+8% to +15%
February 1980 to March 1981	7	+38%	+26% to +72%	+12%	+7% to +18%

between the Ramsey cohort at age two years and three years.

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PHYSICAL ABNORMALITIES AND ACCESSORY LIMB GROWTH IN THE SMOOTH NEWT, *TRITURUS VULGARIS*

Urodele amphibians are well-known for their capacity of regenerating normal limbs following amputation or injury. (See Scadding, 1981, for a recent survey). A considerable amount of work has been conducted in the laboratory studying the effects of various chemical and physical agents on the normal pattern of regeneration. There are very few reports, however, of the incidence of physical abnormalities in natural populations of amphibians.

A total of 268 (124 male, 144 female) adult smooth newts, *Triturus vulgaris* from a series of small ponds in the grounds of a London college, have been examined for abnormalities in external morphology. 4.1% displayed supernumerary or bifurcated digits (3.7% in male newts; 0.4% in females) whilst 3.7% (1.1% male; 2.6% female) showed evidence of atrophy or loss of digits. Smith (1951) states that the capacity to regenerate is greater towards the posterior part of the body—in the present survey 1.1% of newts bore supernumerary or bifurcated digits on the fore limbs compared to 3% on the hind. The incidence of digital atrophy/loss was 0.7% of fore limbs and 3% hind. Two male newts were found which possessed truncated tails. This resulted in reduced swimming efficiency in both animals by causing excessive lateral movement.

In March, 1981, a female newt was collected that displayed an incompletely developed accessory limb (Fig. 1). The extra structure bore three small digits plus a fourth digit bud and was attached distally to the femoral region of the left hind limb which otherwise appeared normal. In May a second female newt was found (under a large stone on land) which possessed a similar abnormality of the right fore limb *i.e.* an additional growth attached to the elbow bearing three partly-developed digits (Fig. 2). In neither newt did the additional structure appear to impair locomotion.

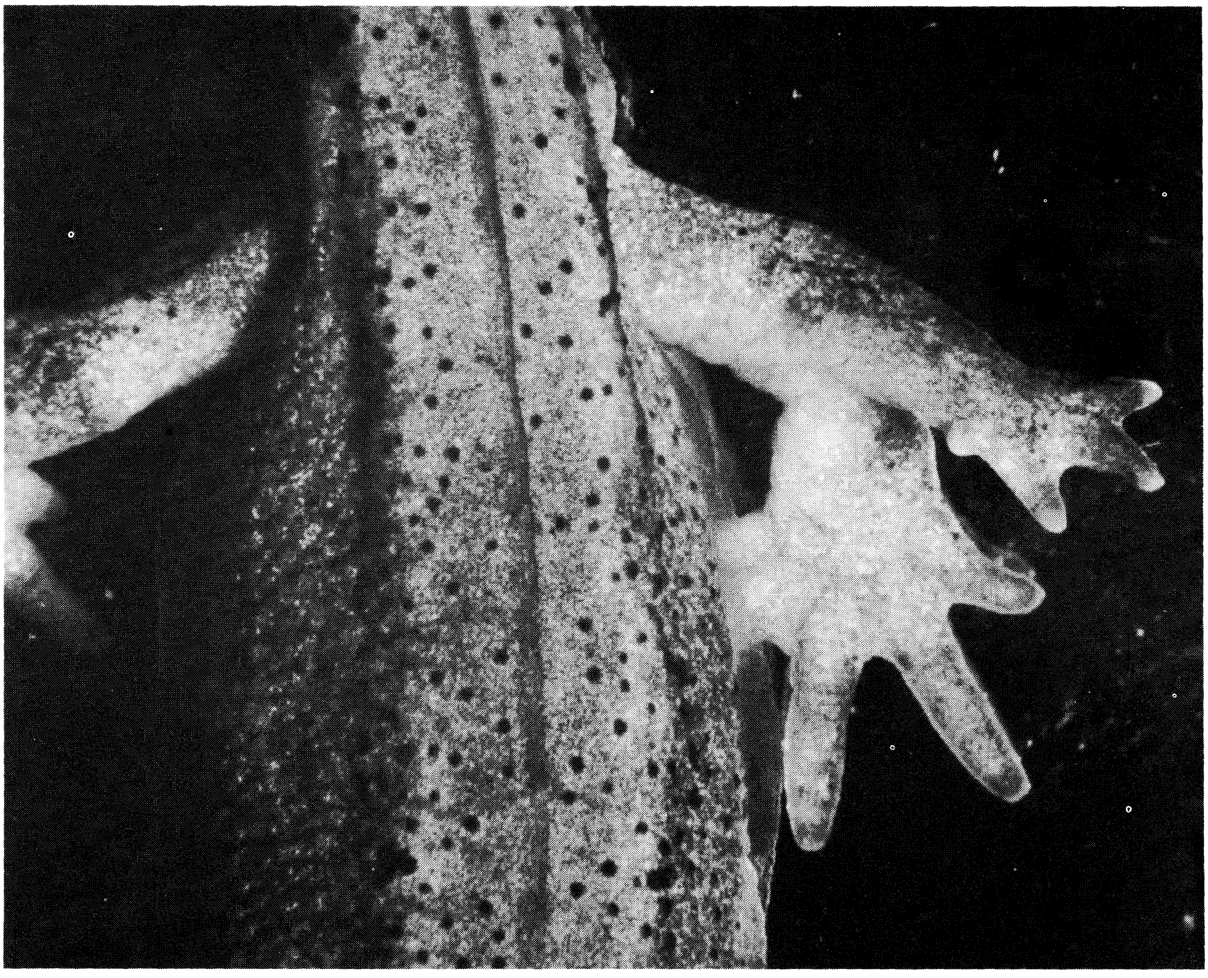

Fig. 1. Accessory limb development on left hind leg of female smooth newt.

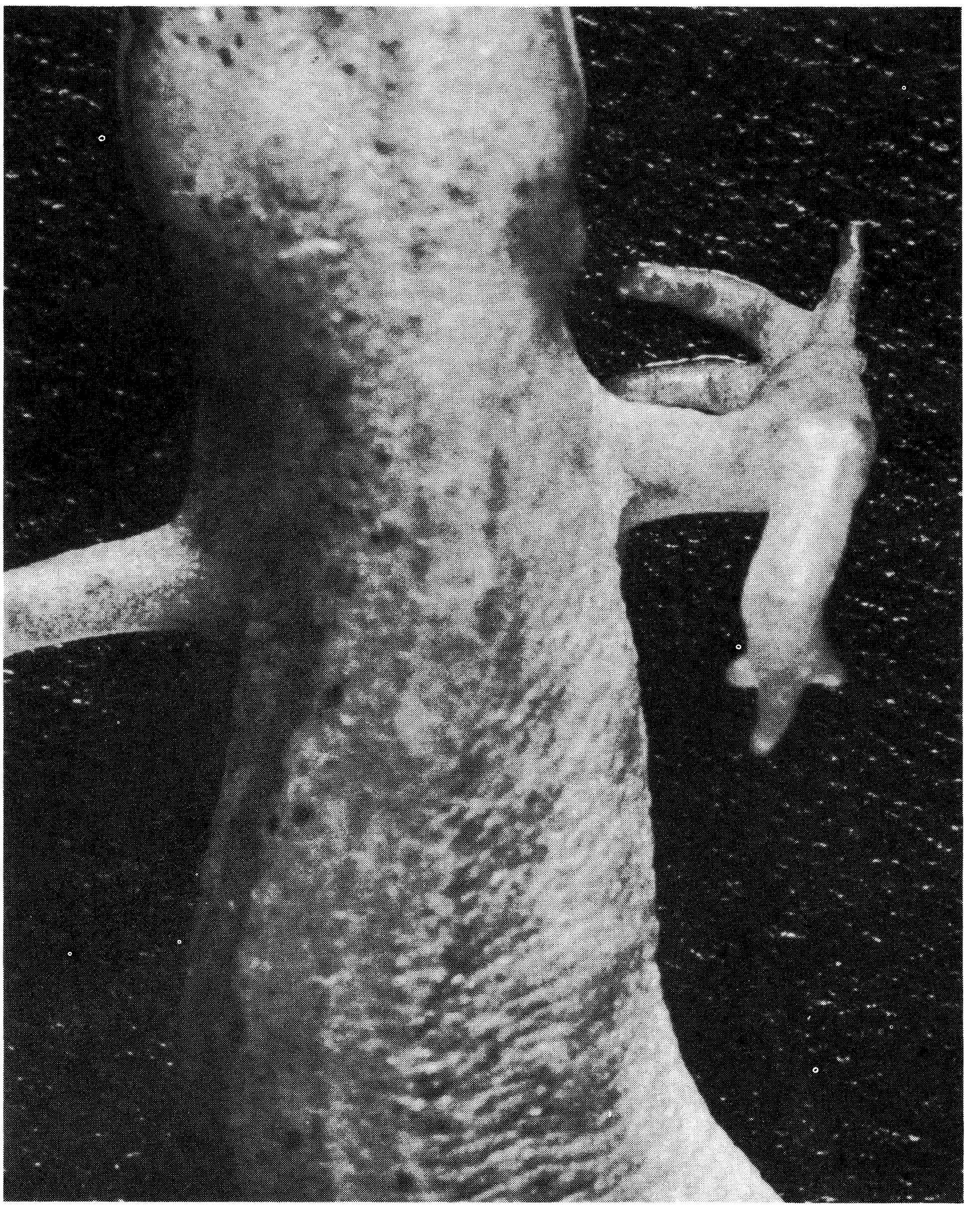

FIG. 2. Accessory limb development on right fore leg of female smooth newt (Photographs: R. Packer).

The most likely cause of such growths would be abnormal regeneration following injury or amputation of the limb. Breedis (1952) who succeeded in inducing accessory limb growth in *Notophthalmus viridescens* by injecting various carcinogenic substances into the forelimb, reported an incidence of limb duplication in only 2 out of 1500 non-experimental animals. Nerves are known to play an important part in the regeneration of a limb. Displacement of a nerve from its normal path such that it emerges at the skin surface may cause an accessory limb to grow from that point (revs. by Rose, 1964; Thornton, 1968). Clean-cut amputations produced in the laboratory then, will usually result in a normal regenerate. Injuries incurred by newts due to natural predation, however, (*e.g.* the bill of a bird) often involve some maceration and shredding of the tissue (personal observation) and would seem more likely to cause deviation of a nerve and hence secondary limb development than an amputation produced cleanly with a scalpel blade.

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SITE TENURE IN *HEMIDACTYLUS BROOKII*

Very little is known of the ecology and spacing patterns of nocturnal geckos other than *Gehyra* spp. (Stamps, 1977), so the observations described below may be worth recording. Ten years ago, in Khartoum, I made a study of site tenure and selection in *Tarentola annularis* and concluded that, although not exactly territorial, these geckos manifest site tenure and disperse very slowly in nature (Cloudsley-Thompson, 1972). This agrees with Stamps' (1977) Type 3 spacing pattern, in which "only one adult of either sex is found per site, which may be shared with juveniles. Implied: adults exclude other adults irrespective of sex".

Throughout January and early February, 1981, whilst visiting the University of Nigeria, Nsukka, I took the opportunity of noting each evening, the position of geckos, *Hemidactylus brookii*, outside the entrance to the Continuing Education Centre (C.E.C.) where my wife and I were living. The entrance was arbitrarily subdivided into five regions, each of about 20 m^2, and the number of geckos in each was counted. The two sides of the cement canopy leading to the door were designated B and C, the recesses on the wall of the main building each side of the door and reaching as far as the drainpipes were designated A and D, while E and F were strips of wall of equal area each side of this. Regions A, B, C and D were well illuminated by electric lights; E and F were in semi-darkness. Nevertheless, although my stay coincided with the dry season, when insect food was scarce, geckos appeared regularly at dusk (about 18.45 hr) and had usually disappeared again by 23.00 hr.

My observations can be summarized as follows: A. Half-grown gecko recorded on 22 out of 35 evenings, plus a different juvenile on two separate occasions; B. An adult recorded twice, and a half-grown specimen with most of its tail missing, on three occasions; C. An adult recorded on one evening—possibly the same as the one noted on other evenings on B; D. Two adults recorded behind drain pipes twice, a single adult behind the pipes on 16 occasions; the half-grown specimen with the broken tail, twice; E. A half-grown individual recorded twice, a juvenile on five occasions. The half-grown specimen was definitely not the same individual as that observed on A; F. No geckos recorded. These sight records clearly indicate the tendency of individual geckos to emerge nightly in the same territory, and suggest that *H. brookii* exhibits Stamps' (1977) Type 3 spacing pattern.

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COMMON TOAD MIGRATION–A POSTSCRIPT

In December 1980 I described the migration of female common toads to a series of dry concrete basins in Sussex; these basins, artificial pools maintained by the local authority, normally hold water and had been traditional breeding sites for the toads for many years previous to 1980. In that year they had been drained for repair, with the rather striking consequence that although a large number of female common toads (82) still migrated to them at breeding time, only a few (6) males turned up.

By the spring of 1981 repairs were complete and the ponds refilled; since aquatic vegetation had been given little time to extablish itself, observations were particularly easy to make. To cut a long story short, the colony reverted to a more "normal" sex ratio *i.e.* there were at least as many males as females present. I made several visits throughout the breeding season, and though a detailed mark/recapture study was not attempted it was easy to see 10 or more pairs of toads on any particular visit (cf. the total of 6 males in 1980) and unpaired females were never seen.

So whatever kept the males away in 1980 was a temporary, readily-reversible phenomenon. The colony now appears quite healthy again, and despite the ravages of local children thousands of tadpoles and good numbers of toadlets were produced.

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ANNOUNCEMENTS

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following Opinions have been published recently:

No. 1176 *Echis colorata* [sic] Guenther, 1878 (Reptilia, Serpentes) given nomenclatural precedence over *Echis froenata* [sic] Duméril, Bibron & Duméril, 1854.

No. 1186 *Tanystropheus* H. von Meyer, [1852] (Reptilia) conserved.

The Commission gives notice of possible use of its plenary powers as follows:

Case no. 1920 TEIIDAE Gray, 1827 (Reptilia, Sauria): proposed conservation. Correspondence should be addressed to The Secretary, c/o British Museum (Natural History), London SW7 5BD, as soon as possible.

OBITUARY: DONALD STREET

It is with considerable sadness and shock that we must announce the untimely death of Donald Street, on November 5th, after a sudden and unheralded illness.

Although only 40 years old, Don was already the most travelled and experienced field-worker on European reptiles in our Society. Indeed, it now appears that only Finland and Turkey had escaped his discerning attention! For those of us who worked with him it was soon evident that he used careful observation and recording from these trips to document not just which species were present, but in which habitats and why, and how safe was their future. If one aspect of his work deserves special note it would be the way in which it was achieved. As devotees of our chosen pursuit most of us might hope to try and combine some field observations with our holidays abroad, but Don's travels were usually planned with herpetology as the main object. Not only that, but his inability to travel by car meant that those many remote hillsides and meadows, especially in eastern Europe, had all to be reached by trains and foot-slogging. Surely a lesson in endeavour to us all.

These journeys never diminished his concern for conservation at home, for born and raised in Christchurch, his love of our lowland heaths and their rare reptiles ensured his active contribution to the work of our Conservation Committee. Two weeks before he died he had submitted a masterly report to the public enquiry on the future of Sopley Common, an important reptile site in his beloved Avon Valley. It is sad, but so typical of him, to report that even as he lay ill he had requested that his parents bring a local paper so that he might appraise the progress of that enquiry.

At a forthcoming Council of Europe environmental meeting Don was to have given the invaluable depth of his experience from his particular field interest in the ecology and conservation of the endangered *Vipera ursinii rakosiensis*, a species whose habitat he had travelled many times to Hungary to study and explore. Those members who were lucky enough to hear his illustrated talk on the reptiles of Hungary this year will be in no doubt as to the depth of his knowledge on this his favourite region. It now remains for us to see that his findings are applied toward conservation of this species within the Council for Europe area, the present subject of their 'Critical Habitat' deliberations.

With his achievements in herpetology, it comes as rather a surprise to realise that Don was known more widely as an accomplished musician, having studied orchestral composition at Berlin! If there was one fault, it was surely modesty, and so to those of our far-flung membership who did not know Don personally we ask that you read again his inspiring book 'Reptiles of North and Central Europe' and reflect on the loss to BHS.

A paper is soon to be published in our Journal on his work to determine the differences he found between the eastern and western forms of *Coronella austriaca*; an apt last work perhaps because this was the species he most admired from his schooldays spent on his ever favourite site of St. Catherines Hill. Apt too therefore that we were able to join his friends and relations in contributing, in his name, to the current Dorset Trust appeal for funds to acquire this site as a nature reserve.

None the less, we believe that our most fitting tribute is to ensure that his pioneering field-work continues as he had intended. The BHS will therefore initiate from 1982 onwards the Donald Street Fellowship which will each year contribute toward the travel costs of reptile field projects in Europe with an applied conservation value for relevent species and their habitats, and we would seek to give preference to participation by our younger members.