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STUDIES ON THE BREEDING MIGRATION AND INTRAMIGRATORY MOVEMENTS OF THE COMMON TOAD (*BUFO BUFO*) USING PANJET DYE-MARKING TECHNIQUES

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INTRODUCTION

The study of the migratory movements of the common toad (*Bufo bufo* L.) has long been hampered by the lack of a satisfactory technique for marking individuals. Some workers (Boulenger, 1912; Moore, 1954; Frazer, 1966; Collier, 1970) have used toe-clipping, but, as Collier (1970) mentions, this can result in inflammation of the digits and in large populations gives a very limited number of feasible permutations. Savage (1934) attached small waterproof labels by string around the waists of frogs and found this method of tagging to be quite successful, if somewhat slow. Moore (1954) attempted to affix what he described as numbered "running shorts" but this proved inoperable, especially at night in heavy rain. Frazer (1966) used permutations of coloured glass beads sewn onto the toad with braided nylon or cotton thread. However, such tags were easily lost and subsequent returns poor. Smith (1969) mentions three other tagging methods, *viz.* attaching a metal clip to the lower jaw, tattooing the web of the foot and tying metal clips around the waist, but gives no indication of their performance.

Fishery biologists have utilized dye-marking techniques alongside more conventional tagging methods. Kelly (1967) described a method of intracutaneous injection of dyes by means of a high pressure jet technique and Hart and Pitcher (1969) discussed the application of the "Panjet" inoculator in field trials, using the dye Alcian-Blue 8GX. Although these techniques are usually applied to large, adult fish similar methods can also be used on small or immature specimens (Riley, 1966; Hart & Pitcher, 1969; Smith, 1970; McIlwain & Christmas, 1975). It was, therefore, thought that the "Panjet" might have potential as a device for marking toads.

Direct colour-marking methods have not been generally employed in the study of amphibian migration, although Moore (1954) states that he marked toads with dabs of blue oil paint. Gittins, Parker & Slater (1980), working during the 1978 breeding season on the toad population at a lake in Llandrindod Wells, Mid-Wales, used "Panjet" marking (with Alcian-Blue dye) in conjunction with toe-clipping, the former providing a date-of-capture mark, the latter, a year-mark.

During the 1979 breeding season, a larger sample of toads from the same population were marked using a slightly modified technique and an estimate of length of stay at the lake attempted.

MATERIALS AND METHODS

The "Panjet"

The "Panjet" inoculator used in this study was obtained from F. H. Wright, Dental Manufacturing Co., Kingsway West, Dundee, Scotland. The device measures 18.5 cm in length and 1.5 cm in width and since it weighs only 270 g it is easy to use in the field. The replaceable glass reservoir holds 3.5 ml of dye solution and this is propelled from the inoculator by means of a mechanical plunger. The dye used was Alcian-Blue (obtainable from Gurrs).

Pitcher & Kennedy (1977) found that roach marked with such equipment retained their marks for as long as 3.5 years.

General Methods

Except when toad activity was curtailed by cold weather, three circuits of the lake (each lasting 20 mins) were made each evening, from the end of February onwards. Toads were located on the perimeter road and path of the lake using powerful torches, collected, brought to a central point for processing and released at the lake margin at the end of the evening's work. Each toad was given a year-mark by removing the outside toe of the right hind foot and was examined for the 1978 year-mark (outside toe of the left hind foot removed). Date-marking, using the "Panjet", commenced on the first night of major movement of the toads to the lake. The eight dye-marking locations on the limbs, shown in Fig. 1 were used either singly or in combination. The "Panjet" was operated at a range of 5 mm or less from the toad's under-limb at an angle of about 45 degrees. Since female toads have thicker, more granular skin, it was often necessary to place the "Panjet" actually against the skin in order to obtain a satisfactory mark. Subsequent recapture of date-marked specimens gave some indication of how long those individuals had been in the vicinity of the lake.

In 1978, Gittins *et al.* applied "Panjet" marks to six locations on the ventral body surface (axilla, centre flank and inner thigh on each side) but this was abandoned in 1979 because the locations indicated in

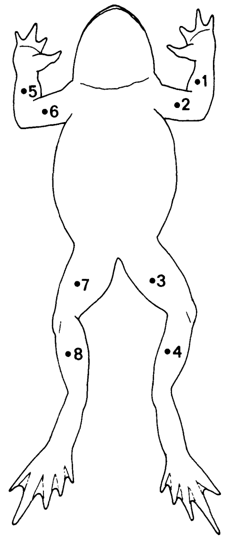

FIG. 1. 1979 marking positions on the underside of a toad.

Fig. 1 allowed for more numerical combinations and reduced to nil the slight risk of rupturing the body-wall.

The data presented in this work represents a synthesis of the total information collected from entire circuits of the lake and for the whole time period. In addition to these data some further information was obtained by erecting a barrier, 44 m in length, along one side of the lake.

This consisted of a double sheet of clear polythene, approximately 20 cm in height, held upright by metal supports at 1.5 m intervals, the bottom edge being held down by bricks. By noting the number of toads on either side of the barrier during each circuit, it was possible to attribute some directionality to the migration. Thus, when spawning had finished and toads were leaving the lake, more toads were found on the lake side of the barrier. This information could not be quantified because the barrier was not extensive enough to preclude movement of individuals around the ends but it served as a useful additional measure of the progress of the migration.

RESULTS

LENGTH OF STAY AT THE LAKE

In 1979, toads were first observed moving to the lake on 24 March, but it was not until 9 April that the first major movement was recorded. On that evening 517 toads were captured and given both year- and date-marks. On 15 April, the first spent females were captured and on 16 April, counts at the barrier revealed that 40.5% of toads were leaving and 59.5% were entering the lake. By 17 April 58.3% were leaving the lake. This was the last day on which male and spent female toads were date-marked. The last day on which gravid females were date-marked was 21 April and the last date on which large numbers of toads were recorded (296) was 22 April. Gravid females were marked for a longer period of time to ensure adequate returns, since female toads formed a much smaller proportion of the migrating population. Very few toads were captured after 22 April and collection ceased on 25 April, although one circuit per night was carried out for the next fortnight to ensure that no major, late migration was missed.

During the migration period 4823 male toads and 1086 females were captured. Of these 3074 males and 826 females, a total of 3900 toads, received a date-mark. Assuming that each individual was recaptured once only, a total of 913 individuals (23% of the total marked in 1979) were recaptured, comprising 782 males (25% of the males marked in 1979) and 131 females (16% of the females marked in 1979).

The results are summarised in Fig. 2. For male toads, recapture peaks occurred at 1 and 4 days after initial capture with smaller peaks at 8 and 12 days. No males were recaptured 15 or more days after initial capture. The recapture peak at 1 day after initial capture may be accounted for by the male toad's habit of returning to the road to await the arrival of females. For female toads, such clear peaks did not exist but the highest recapture rate occurred at 6 days after initial capture, with a smaller peak at 3 days. All female toads recaptured 8 days or more after marking were spent and no females were recaptured 13 or more days after initial capture.

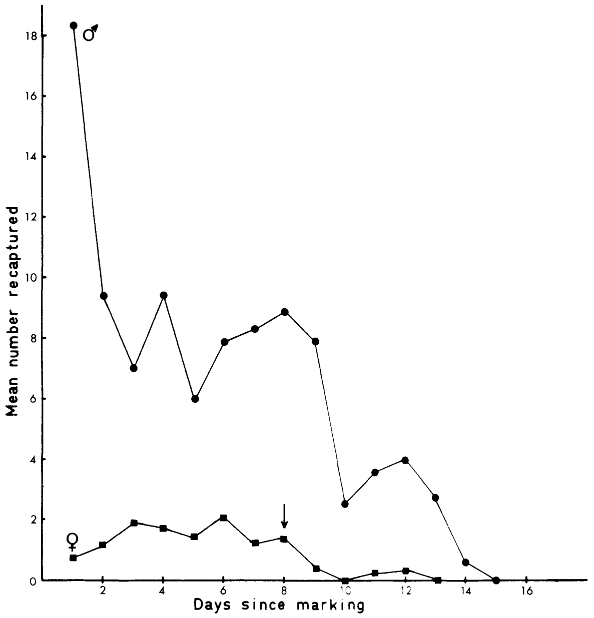

FIG. 2. Time between captures. Mean number of toads recaptured plotted against the number of days since initial capture. All female toads caught on or after the day marked by the arrow were spent. (♂ = male. ♀ = female).

Figure 3 indicates that toads of both sexes marked late in the migration tended to be recaptured after a shorter period of time than those marked at the beginning of the migration. Data for recaptures of male toads occurring on the first day after marking have been omitted since, as Fig. 2 shows, this day had a particularly high recapture rate and these data probably did not represent males actually leaving the lake.

From a plot of the mean number of marked toads as a percentage of each night's catch against date of recapture (Fig. 4), the discrepancy between recapture peaks for males and females can again be seen. Most males were recaptured between 10 and 13 April, as they returned to the road to await the arrival of

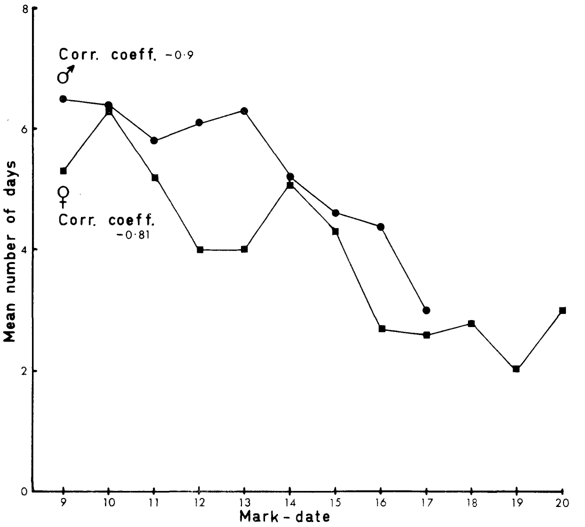

FIG. 3. Length of stay of individual date-batches. Mean number of days until recapture plotted against date of initial marking. Correlation coefficients are given.

females. Despite the fact that 185 females had been marked, only 5 were recaptured during this period, indicating that females were moving directly to the lake. The low number of female recaptures continued until 15 April. From 13–16 April male toad recaptures declined and it is assumed that they had entered the lake to pair since the date on which spawning was recorded (15 April) fell in the middle of this period. From the evening of 15 April female recaptures increased but male recaptures did not show any increase until 16 April. High recapture rates for males were recorded from 16–19 April and this coincided with a decline in female recaptures. During this period it is probable that most females were moving away from the lake. Some males were probably also leaving the lake, while others had returned to the road to await late females. A slump in the number of male and female recaptures on 20 and 21 April may be indicative of a final spawning period, followed by an exodus on 22 April, marked by a sharp increase in the number of recaptures of both sexes.

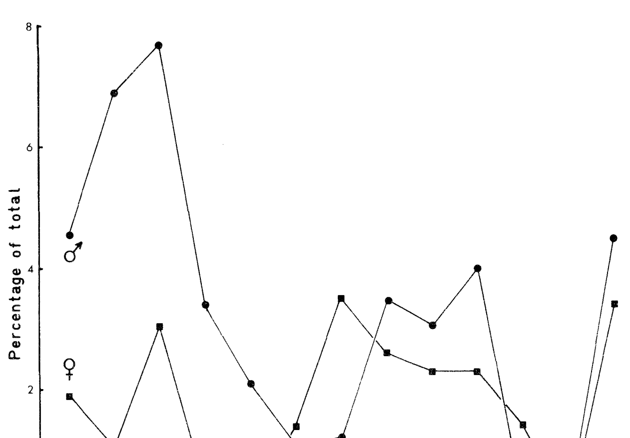

FIG. 4. Fluctuations in the number of recaptures. Mean number of marked toads expressed as a percentage of each evening's catch plotted against the date of recapture in April.

ANNUAL RETURN OF TOADS

Of the 3786 male toads handled once, 1013 had a 1978 year-mark. Similarly, of the 925 female toads handled once, 147 had 1978 year-marks. Some of these toads (between 30 and 70) were still carrying "Panjet" date-marks from the 1978 season.

DISCUSSION

In 1979, eight locations on the underside of the limbs of toads were marked with the "Panjet" and resulted in very few injuries. On two occasions (0.05%) the force of the jet tore a small hole in the skin allowing air and water to enter and to inflate the leg. This proved far more satisfactory than the 1978 technique described earlier.

Returns of 1979 dye-marked toads were good and toads bearing 1978 date-marks were also collected, indicating that this method might be considered for long-term studies. Three disadvantages should, however, be noted:

1. The marks are small and can usually be detected efficiently only by the operators who initially marked the toads.
2. Where combinations of marks are used, failure of one such mark may produce spurious results.
3. Toads proved difficult to hold when marking the forelimbs, especially in the axillary region; this reduced marking efficiency.

The results show that in 1979 the main breeding season lasted for 13–15 days which roughly corresponds to the number of nights of toad activity noted in previous seasons (Gittins *et al.*, 1980). The highest recapture rate for males occurred on the day after initial capture. This may be explained in behavioural terms as several workers (Savage, 1934; Frazer, 1966; Smith, 1969; Gittins *et al.*, 1980) have remarked upon the tendency of males to wait at the margins of the breeding ponds, presumably for the females to arrive. It may be assumed, therefore, that a large proportion of males moved away from the lake and back to the road after being marked, remaining there for at least another night.

Two further peaks occurred, one at 4 days after marking and a smaller one at 8 days. The latter peak occurred 2 days later than the peak for females. Heusser (1968) stated that females left the breeding pond the night following spawning, while the males remained to fertilize further females. It is also likely that some males, having not fertilized any females, remain longer in the lake to mate with late-comers. Similarly, these peaks may indicate that all the females in the lake had paired and spare males returned to the road to await more females. This behavioural difference may also explain some of the disparity between the proportion of each sex recaptured since the longer males remain in the vicinity of the lake, the greater their chance of recapture.

The recapture peaks of 1, 4, 8 and 12 days after initial capture for males and 3 and 6 days for females are probably unique to the 1979 season. Cold spells undoubtedly prolong the breeding season (Fraser, 1966; Smith, 1969). No cold spell interrupted migration or spawning in 1979. Gittins *et al.* (1980), in 1978, recaptured still gravid females 8 days after marking and spent females 9 days after marking, data comparable to those collected in 1979. But male toads were recaptured up to 47 days after marking; this may be explained by the occurrence of several cold spells during the migration period and the much earlier initial start to the migration.

Underlying the afore-mentioned trends are others more closely related to the date of initial capture. By plotting the number of days until recapture for each date-batch it can be seen that toads marked later in the migration stay for shorter periods (Fig. 3). This suggests that the migration is physiologically synchronized towards meeting a certain dead-line, presumably spawning. In 1979 spawning was first recorded, in the Llandrindod Wells area, on 15 April, while in 1978 some spawning had occurred by 12 April (Gittins, *pers comm*). It would appear from examination of data for the start and end of the migration (Gittins *et al.*, 1980) that spawning usually occurs around these dates. The fact, noted earlier, that males tend to frequent the lake longer than the females is also illustrated clearly in Fig. 3.

Many workers (Moore, 1954; Reed, 1963; Frazer, 1966; Collier, 1970; Gittins *et al.*, 1980) have drawn attention to the imbalance in the sex ratio at breeding ponds. Gittins *et al.* (1980) stated that this might result if the females did not breed every year. Frazer (1966) found that only 11% of the males returned to breed the following year and that some females re-appeared at the breeding pond for two successive seasons. The results of the present study seem to suggest that a large proportion of both sexes returned to the lake at Llandrindod Wells in 1979, after being marked in 1978, since 27% of the males captured bore a 1978 year mark as did 16% of the females. The lower percentage returns for female toads may indicate that some females do not breed every year or may simply be indicative of a disparity in "catchability" for each sex, reflecting behavioural differences. It should, however, be noted that these figures are undoubtedly underestimates of the percentage returning to the lake and it is hoped that data collected in the 1980 season may allow a correction factor to be calculated.

ACKNOWLEDGEMENTS

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 75–77

REPTILIAN FAT BODIES: A SHORT REVIEW

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Whoever dissects a reptile, particularly a lizard or a snake, must be impressed by the size of the large, pale yellow, lobulated deposits of fat which, starting at the cloaca, may reach or even extend beyond the lower border of the liver. These fat deposits obscure and envelop the intestines to such a degree that some authors (Oldham, Smith & Miller, 1970) have found it necessary to warn their readers not to confuse them with the ovaries. Large fat deposits are found in many vertebrates, but not in all, and in general we are inclined to regard them as a kind of insurance against bad times. If, however, we examine specimens which have definitely died of starvation or at the end of a long and debilitating illness (Fig. 1) we may still find fat bodies in their usual sites and not visibly reduced in size. Therefore, the presumed "larder" is never completely emptied, even though nutrients are urgently required to keep the animal alive. Authors have paid only passing attention to this apparent contradiction. Perhaps even the total depletion of all fat reserves would not keep the reptile alive and the exhaustion of protein or glucose, for example, decides the issue. Nevertheless, it seems worthwhile to consider the opinions which have been expressed on the structure, function and control of the fat bodies. Only those references which are of direct relevance are quoted; many more exist on the seasonal changes in size of the fat body.

One of the earliest major texts on vertebrate comparative anatomy which mentions the fat bodies is that of Waldeyer (1907). He listed the fat bodies with the lymphatic system and described them as consisting of adenoid (*i.e.* lymphatic) tissue, fat and leucocytes. He tentatively proposed a connexion between these bodies and the gonads but without giving any details in favour of this view. His suggestion that the fat bodies should be regarded as modified lymphoid organs was taken up by Butler (1889) but no final agreement on this question has been reached. Gadow (1923) described the fat bodies as "mysterious organs, largest in Spring, extending along the ventral side and largest at the time of reproduction".

At first sight the fat bodies seem to take up all the available space in the pleuro-peritoneal cavity. However, Butler (1889, 1892) demonstrated that they in fact lie outside the pleuro-peritoneal cavity in a lymphatic space of their own which, in the embryo,

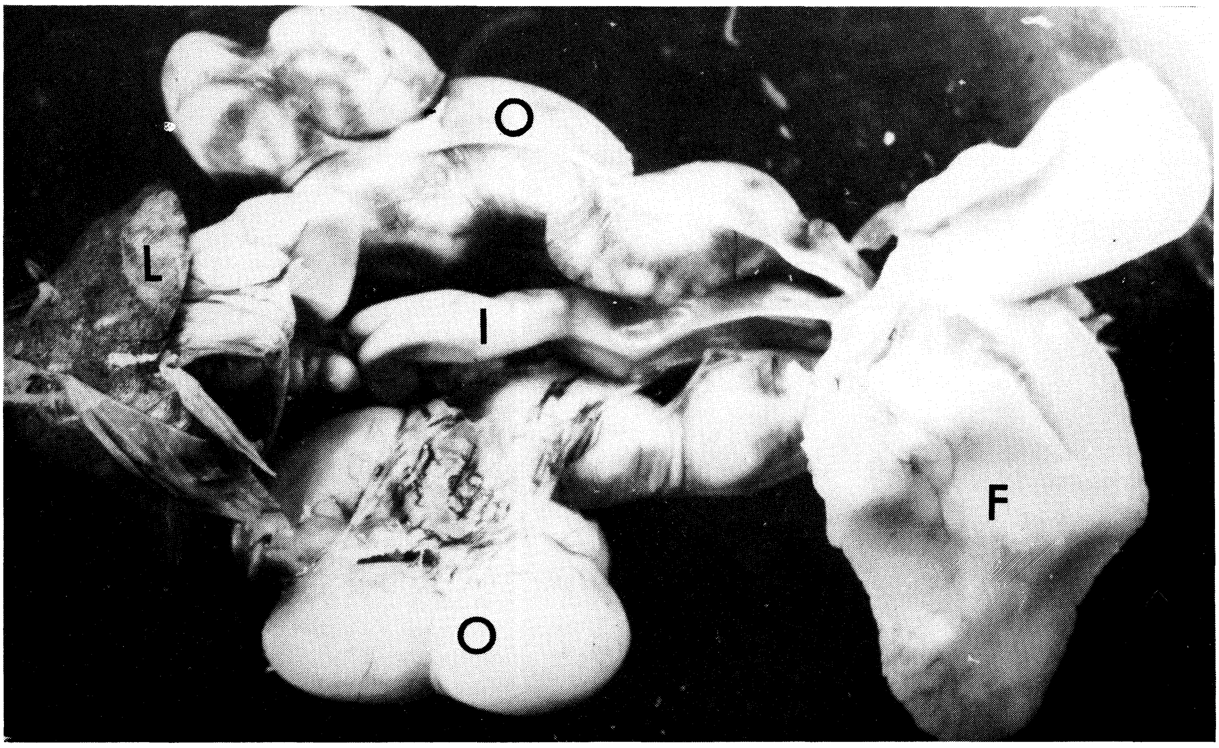

FIG. 1. Part of the viscera of a specimen of the lizard *Physignathus lesueri*. This specimen died from pneumonia in a zoo. F, fat body; O, ovaries; I, intestine; L, liver.

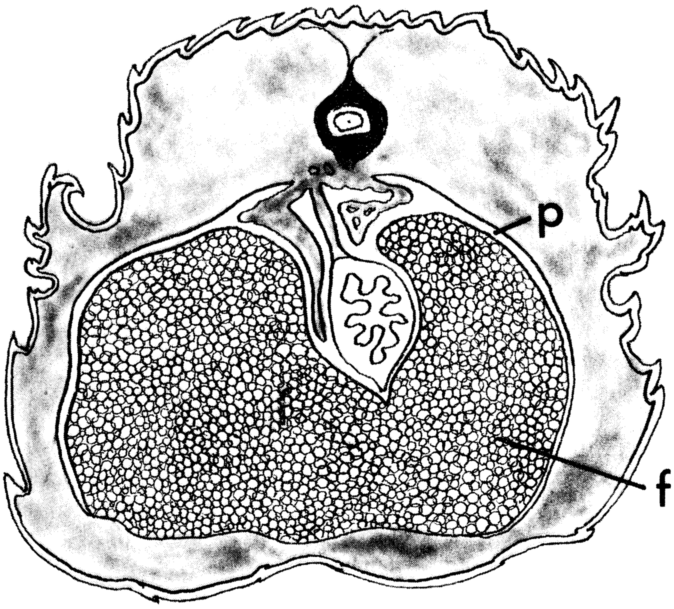

FIG. 2. Diagram of a transverse section through the anterior abdomen of the lizard Lacerta viridis, showing the compression of the pleuroperitoneal cavity (p) by the large fat body (f). Redrawn after Butler (1889).

develops independently from the coelom. Figures 2 and 3 demonstrate the size of these fat bodies in the lizard, *Lacerta viridis*, where the peritoneal cavity is reduced to a potential rather than a real space.

The fact that in the Amphibia, particularly in anurans, the fat bodies are closely adjacent to the gonads, has suggested to many that there might also be a physiological connexion between these organs. This view was strongly supported by Hahn & Tinkle (1956) who investigated the reproductive cycle of the lizard *Uta stansburiana*. They showed that the females do indeed use some of the stored fat for vitellogenesis of their first clutch of eggs in Spring when little or no food is available. These observations agree with those of Bellairs (1969), Chapman & Chapman (1964), Darevski (1957), Hoddenbach (1966) and Rollinat (1934). However, quite different results were obtained by Marshall & Hook (1960), and weight fluctuations unrelated to the reproductive cycle were also reported by Barwick & Bryant (1966). Therefore, since these large deposits are not used up by starvation, hibernation, illness or reproduction (Volsøe, 1944) at least part of their function would seem to lie elsewhere.

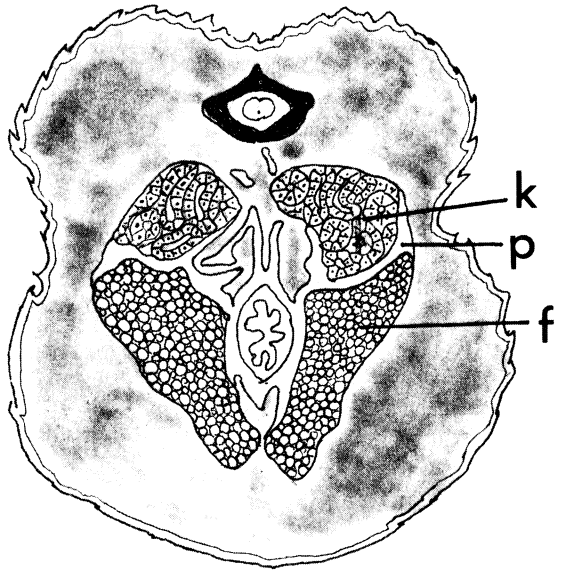

FIG. 3. Same specimen as in Fig. 2; section through the abdomen in the renal region. f, fat bodies; k, kidneys; p, pleuroperitoneal cavity. Redrawn after Butler (1889).

It has been pointed out by Fox (1977) and others that fat bodies are far more prevalent in reptiles from temperate climates than in those living in the tropics. In hot countries, where food is plentiful and hibernation is not required and where young may be produced in any season, fat bodies may be of little use. The one requirement, far more stringent in tropical than in temperate climates, is protection against excessive heat and dehydration. It may not always be possible to agree with Tinkle (1961) that in such circumstances "the fat reserves are not being used for metabolic needs", because the degradation of fat produces not only energy but also a greater amount of water than that of any other foodstuff. In addition, there could be a physical insulating effect of these pads of fat serving to protect the viscera from the hot substratum. Therefore, the value of large fat bodies need not be limited to reptiles in cool climates.

In an attempt to resolve such contradictions authors have divided the fat deposits into two parts—the *élément variable* and the *élément constant* (Rollinat, 1934), the former serving metabolic needs, the latter constituting a purely structural element, cushioning the intestines against heat and injury, and ensuring the proper action of the ventral shields during locomotion (Volšøe, 1944); this structural *élément constant* remains unavailable for metabolic needs. According to this hypothesis it is this part of the fat bodies that we find in animals which have died from starvation.

However, as far as is known, adipose tissue is homogeneous and chemical differences between supposed constant and variable elements have not been observed. Clearly, the mechanism by which the utilisation of stored fat is controlled and arrested in reptiles requires biochemical and endocrinological studies.

The importance of the fat bodies is well illustrated by the fact that they are already well developed in snake embryos (Butler, 1889). The accepted practice of authors of textbooks to mention the fat bodies solely in connexion with the gonads and reproduction is not justified if other potential functions are considered. However, details of their function and control are still almost as great a mystery as they were in Gadow's time.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 79–81

SEASONAL ACTIVITY OF ADULT AND JUVENILE *SALAMANDRA SALAMANDRA* AT THE SOUTHERN LIMIT OF THEIR DISTRIBUTION

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SUMMARY

The activity of adult and juvenile *Salamandra salamandra infraimmaculata* in Israel was studied both by way of observations in the field and in semi-natural conditions in enclosures. The number of adult salamanders met while active was higher than that of juveniles, which made up 10–25% of the total of all salamanders seen in all the localities and throughout the six years of study. Moreover, the activity of juveniles took place only at low temperatures and high relative humidity.

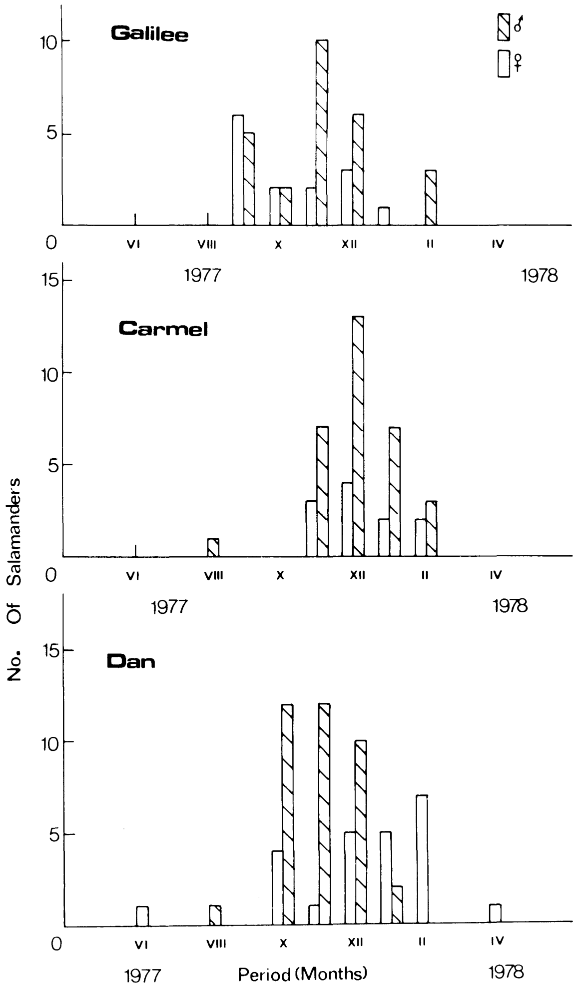

FIG. 1. Distribution of salamanders (male and female) collected from 1977 to 1978, showing month and locality collected.

INTRODUCTION

Salamandra salamandra is found in central and southern Europe, reaching south to Northern Africa and Israel (Eiselt, 1958; Gasser, 1975; Degani, 1979). Salamanders in Israel are considerably larger than specimens in Europe (Eiselt, 1958; Gasser, 1975; Degani, 1979; Degani & Warburg, 1978) and belong to the subspecies *S. s. infraimmaculata.* The population structure and seasonal activity of European *S. salamandra* have been studied by Gasche (1939) and Joly (1959, 1968) and in Israel adult salamanders were studied by Degani & Warburg (1978).

Joly (1968) found that in France only 7.2–11.6% of the salamanders were metamorphosed juveniles.

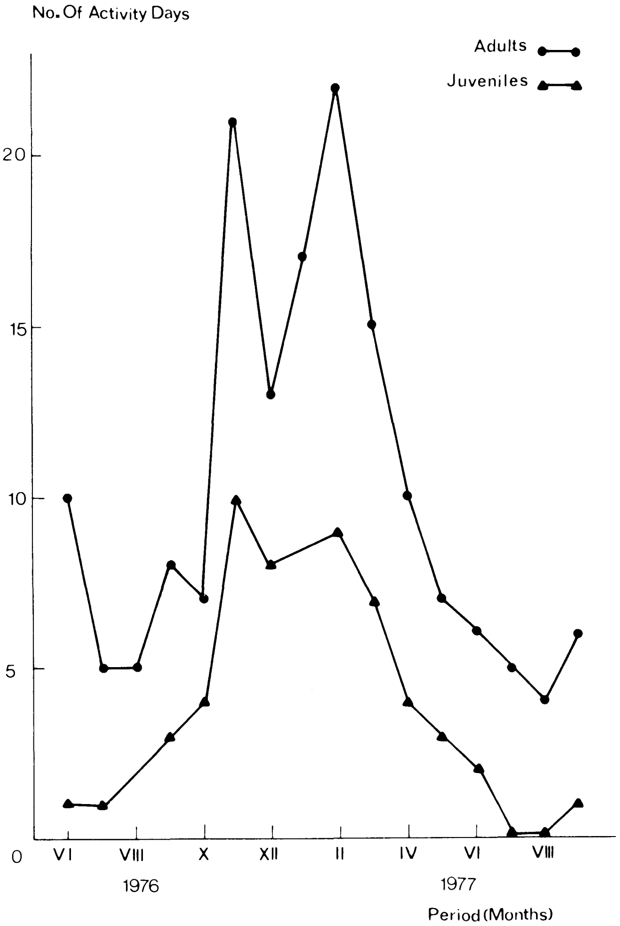

FIG. 2. Comparison of activity of 6 adult and 6 juvenile salamanders in the various seasons.

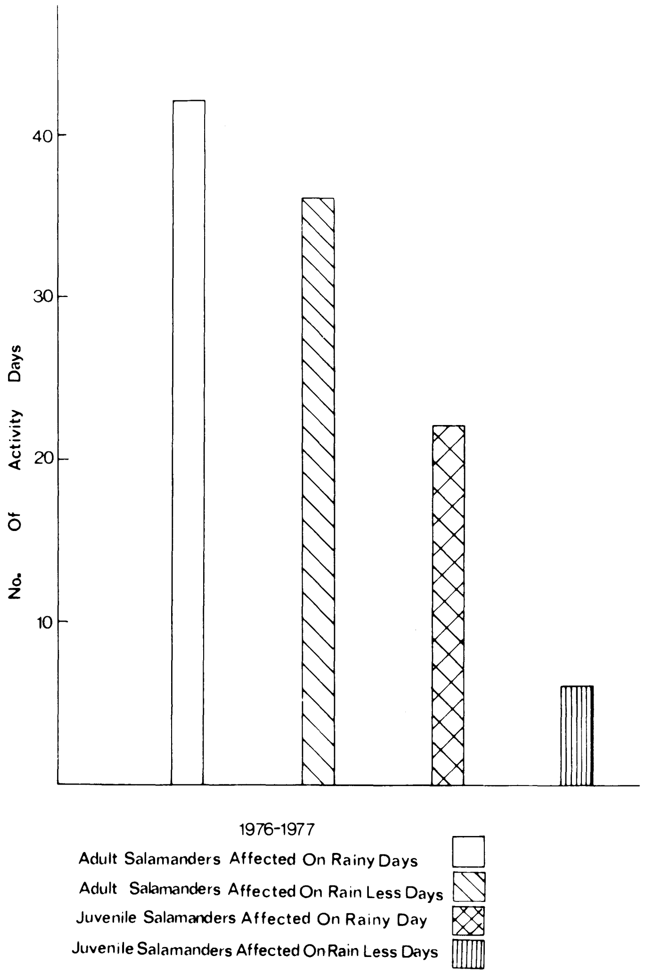

FIG. 3. Correlation between incidence of rain and activity of 6 adult and 6 juvenile salamanders in Galilee.

Degani & Warburg (1978) found that in the Mt Meron area in Galilee the number of tadpoles was much greater than the number of adults. Moreover, water loss through evaporation was greater in post-metamorphosed juveniles than in adult *S. salamandra* (Warburg & Degani, 1979).

In Israel, where *S. salamandra* is found in different habitats, such as Upper Galilee and Mt Carmel, which are both semi-arid, and in a moist habitat (Tel Dan), the activity of juveniles has not been described.

MATERIALS AND METHODS

Field studies were carried out during 6 years in four localities: (i) Kibbutz Sasa, (ii) Hammama spring, (on Mt Meron), (iii) Mt Carmel, (iv) Tel Dan. (see description in Degani & Warburg, 1978; Degani & Mendelssohn, 1979).

The adults and juveniles (post-metamorphosis specimens, 1 and 2 years old, with total lengths of 7–13 cm) were collected at night and released at the place of capture, as previously described by Degani & Warburg (1978). The activity pattern of adult and juvenile salamanders was also studied in two outdoor enclosures, measuring 10 m^2 and 4 m^2 respectively.

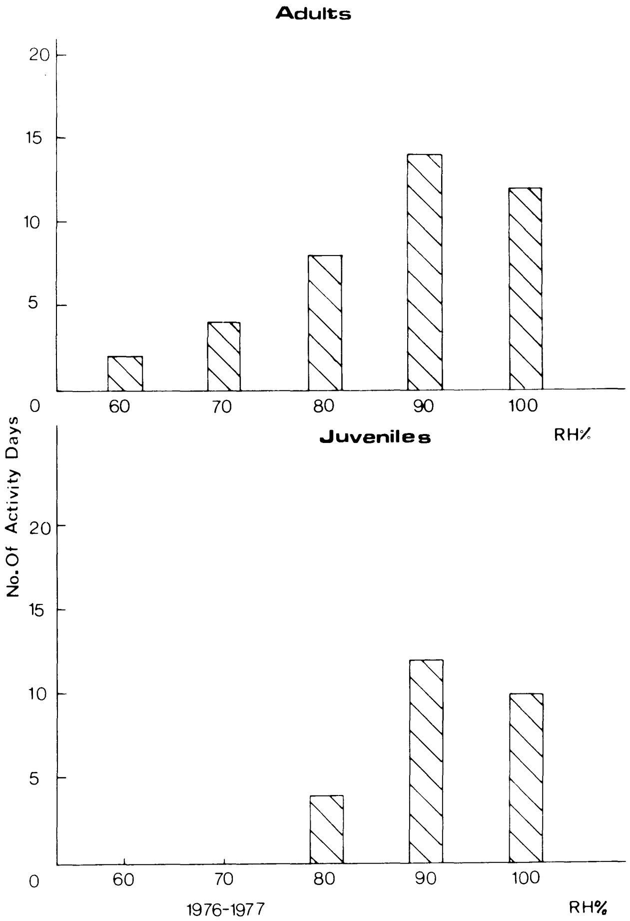

FIG. 4. Comparison of activity of 6 adult and 6 juvenile salamanders as a function of relative humidity.*
* RH% = relative humidity %.

RESULTS

The activity of adult and juvenile salamanders was studied by observation under natural conditions in Galilee (Hammama, Sasa), Mt Carmel and Tel Dan (Fig. 1). Most of the activity took place in winter in all four localities. However, only 10–25% of all the salamanders found throughout the 6 years were juveniles (Table I). Moreover, the relationship between the activity of adults and juveniles observed in semi-natural conditions, in the enclosures, has shown that adults are more active than juveniles (Fig. 2). The activity of juveniles took place mostly during rain (Fig. 3), at high humidity (Fig. 4) and low temperatures (Fig. 5). The activity of adult salamanders was, compared with that of juveniles, less restricted by climatic conditions.

TABLE I. Comparison of the percentage of adults and juveniles in the various populations during 6 years

Locality	No. of salamanders	% Adults	% Juveniles
Galilee	187	86.10	13.90
Carmel	79	81.01	18.99
Tel Dan	160	90.00	10.00
Hammama	84	75.00	25.00
Sasa	58	74.14	25.86

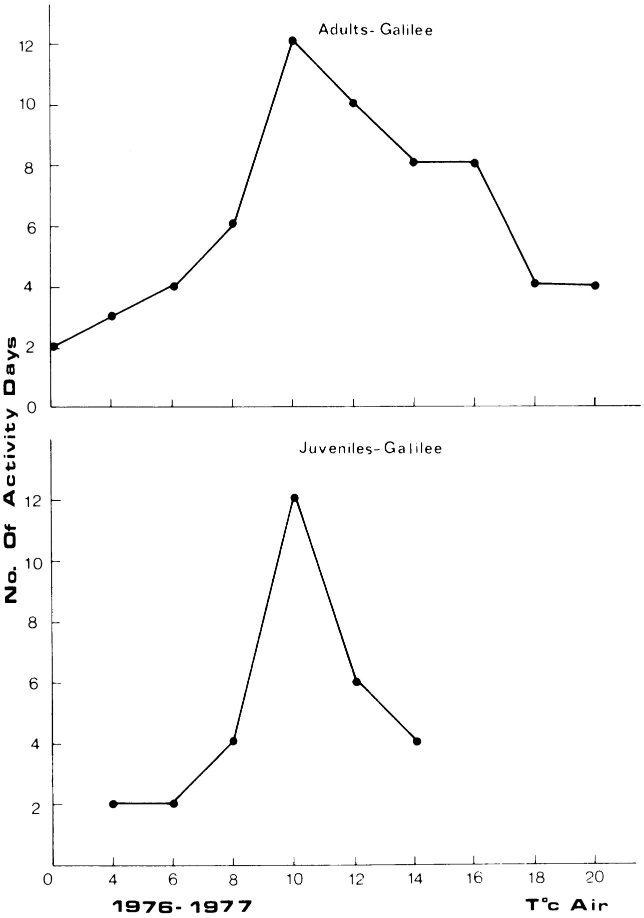

FIG. 5. Comparison of activity of 6 adult and 6 juvenile salamanders as a function of temperature.

DISCUSSION

The activity of adult *S. salamandra* in Europe has been studied by Joly (1968) and in Israel by Degani & Warburg (1978). However, no explanation has been found for the low percentage of juveniles in France (7.2–11.6%, Joly, 1968). Moreover, the populations of tadpoles of the Sasa and Hammama salamander populations seem to be greater than the adult populations and most of the tadpoles from Sasa complete metamorphosis (Warburg, Degani & Warburg, 1979).

According to this study it seems that the explanation of the low percentage of juveniles observed is due to the fact that juveniles are less active than adults (Fig. 2, Table I). Warburg & Degani (1979) found that the rate of water loss in juvenile *S. salamandra* is higher than that of adults.

In this study it was found that juvenile salamanders were mostly active during rain, high humidity (80–100% RH) and low temperature (4–14°C), compared with adults (60–100% RH, 0–20°C) (Figs. 4, 5). From these observations, therefore, it seems that the difference between the activity of juveniles and adults is because of the juveniles' greater sensitivity to water loss. In Israel, in a semi-arid environment, avoiding water loss is extremely important for survival.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 83–85

ANNUAL AND DAILY LOCOMOTOR ACTIVITY OF THE FROGS *RANA ARVALIS* AND *R. TEMPORARIA*

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SUMMARY

The locomotor activity of moorfrogs and common frogs was studied by means of pitfall trapping and with laboratory tests in an actograph. Juveniles of both species were active in day-time, whereas older ones were active at night-time. Older frogs had two activity peaks, one before and one after midnight. During those parts of nights when rain fell, activity increased. Also juveniles were active on these occasions. Common frogs were more active than moorfrogs during late autumn and winter.

INTRODUCTION

This paper reports on field and laboratory studies of the locomotor activity of the moorfrog *Rana arvalis* and the common frog *R. temporaria*. Both species live very similar lives; studies that could reveal any resource partitioning should be of interest as they might suggest resources that are in short supply and thus limit them. The locomotor activity is probably related to weather conditions, activity of prey species, or activity of predators or, more probably, a combination of them. A study of only locomotor activity must thus be extended with further aspects. The present study is intended as a base for future investigations.

STUDY AREA AND METHODS

The study was conducted at the Stensoffa Field Station of the University of Lund in South Sweden (55°40′N, 13°30′E). To study the activity in the field, pitfalls were dug in the ground. They measured 25 × 60 cm with a depth of 45 cm. To prevent the frogs from climbing out, the upper 10 cm of the walls were covered with plastic. The pitfalls were dug at 10 m distance. Two grids with 12 pitfalls in each were situated in a moist meadow and a moist birch forest, respectively. They were operated continuously from September 1972 to August 1974. The pit-falls were checked about twice a week in summer and at least once every two weeks in winter. During a total of nine 24-hour periods in June through September 1972, the pitfalls were checked every second hour.

To test whether adult frogs are repelled by pitfalls, the following experiment was performed. Two pitfalls, 0.25 × 3.0 meters and 45 cm deep, were dug on the opposing sides of a hexagon in a lawn. Frogs were released in the centre and had thus a 33% chance of being caught. The experiment was performed at night and in the day.

The activity during the daily cycle was also studied in a laboratory test. Frogs were put in plastic boxes (30 × 20 × 15 cm high) that were suspended and connected to a pen which registered all movements on a time-chart. A description and figure of the apparatus has been published (Loman, 1974). For the evaluation, every hour was given a score of zero to four, depending on the number of 15-min periods during which the frog exhibited any movement. Sixteen common frogs and 17 moorfrogs were used in these experiments, each for 24 hours.

Juveniles refers to frogs aged no more than one year after metamorphosis.

RESULTS

Daily activity

The experiments on day-time and night-time trapability did not suggest that the frogs were easier to trap during the day than during the night. Eight of 29 frogs were captured during the day (expected number 9.7) but only eight of 48 during the night (expected number 16). This could suggest that the frogs were more difficult to trap during the night, but this seems very implausible. I suggest that this is a random deviation. Any preference for night-time activity found with pit-fall trapping is certainly real.

Juvenile frogs were more active during the day than during the night. This was specially pronounced just after metamorphosis, in June and July. (Table I). Older frogs were more active during night than during day (Table I). A comparison of the species showed that adult common frogs were relatively more night-active than adult moorfrogs ($\chi^2 = 12.7$, $P < 0.001$). Moorfrogs had more tendency for most activity in the hours around dawn and dusk (Table II).

In the laboratory experiments that only included adult frogs, almost all activity took place during the night (Fig. 1). There was a tendency that more activity took place between 2000 h and 2200 h and between 0200 h and 0400 h than between 2200 h and 0200 h. This was significant for moorfrogs ($\chi^2 = 3.84$, $P < 0.05$) (as in the field tests), but not for common frogs ($\chi^2 = 3.47, 0.10 > 0.05$).

TABLE I. Number of frogs trapped in pitfalls during the hours of light and darkness. Frogs were captured during nine 24-h periods, four in June and July (16 L:8 D) and five in late August and September (12 L:12 D). Juvenile frogs were not separated on the two species in June and July. Those two-hour periods during which rain fell are omitted from the computations. Figures given are number of frogs trapped, and in parentheses, the total number of capture hours. The probability values (computed with χ^2-tests) refer to the probability that locomotor activity was the same during light and dark capture hours

	Light hours	Dark hours	χ^2	P
Juveniles				
Rana sp (June, July)	41 (78)	3 (40)	14.4	<0.001
Rana arvalis (Aug., Sep.)	31 (48)	10 (38)	6.49	<0.05
Rana temporaria (Aug., Sep.)	41 (48)	10 (38)	12.4	<0.001
Older				
Rana arvalis (June, Sep.)	11 (126)	16 (78)	4.20	<0.05
Rana temporaria (June, Sep.)	9 (126)	27 (78)	20.5	<0.001

TABLE II. Activity during midnight hours (2200 h–0200 h in June and July, 2000 h–0400 h in August and September) compared with activity during the two preceding dusk hours and two following dawn hours. Two-hour periods when rain fell are omitted. Trappings considered comprised 44 midnight hours and 34 dawn and dusk hours. Figures given are number of frogs trapped. Juvenile frogs are not considered

	Midnight	Dawn and dusk	χ^2	P
Rana arvalis	8	16	5.12	<0.05
Rana temporaria	15	12	0.075	>0.10

The influence of rain

Rain fell on six 2-h periods during the periods when the traps were emptied every second hour. As five of them were at night-time in August and September, only this period is considered in the test of the influence of rain. Both juveniles and older individuals of both species were significantly more active during those periods when rain fell than at other times (Table III).

Yearly activity cycle

The main activity period for both species fell in the period of July to October (Table IV). Among adults, moorfrogs were significantly more active than common frogs in May and September, whereas the opposite applied from October through December. It should be noted that some activity persisted throughout the winter. As the size of the juvenile population changed much during the first year, and distances to breeding places of the two species might influence the result, a species comparison for juveniles cannot be made with much confidence. It seems clear that during winter juvenile common frogs were much more active than were juvenile moorfrogs (Table IV). The high activity for older frogs in March and April coincides with, and is probably due to, the breeding migrations. No information is available about the duration of the breeding migrations, but if the frogs return to their summer home-ranges immediately after breeding, all should be present in the trapping area by May.

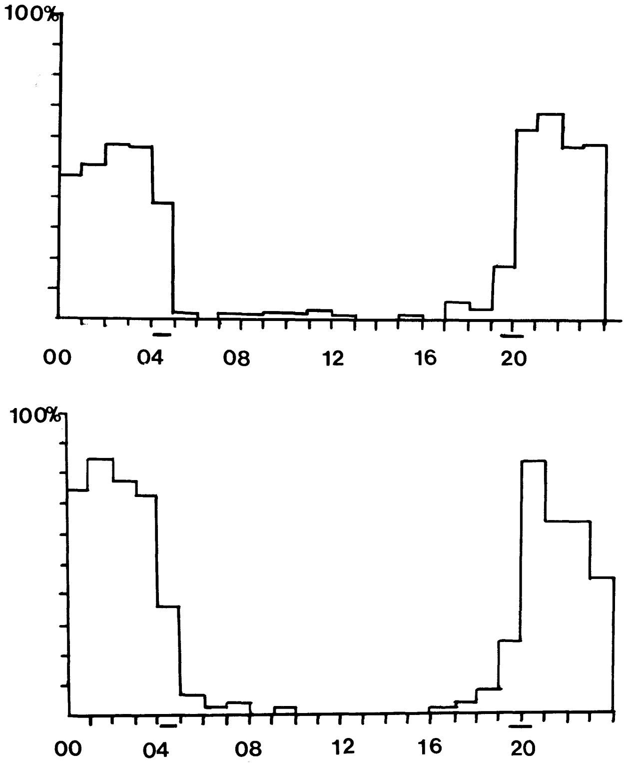

FIG. 1. Relative activity of *R. temporaria* (above) and *R. arvalis* (below) according to the laboratory tests. For each hour, the activity score in relation to the total score possible is given. The score is given according to the number of 15-m periods during which any activity was exhibited. The tests were run under a natural light and temperature cycle during the period 28 July to 15 August 1974. Time of sunset and sunrise is indicated below the time-axis.

DISCUSSION

Day-time activity for juvenile frogs and night-time for adults has been reported for several other species, including *Rana clamitans* (Martof, 1953), *Bufo viridis*, *B. calamita* (Hemmer & Kadel, 1971), and *B. boreas* (Mullaly, 1968). One possible explanation is that adult frogs are predators on juveniles (Loman in press). The

TABLE III. Activity during periods with and those without rain. Periods with rain are those two-hour periods when at least $\frac{1}{2}$ mm of rain fell. Only activity during night hours in August and September is included. There were altogether 10 hours with rain and 38 without. The figures refer to number of frogs trapped

	Rain hours	Non-rain hours	P (binomial test)
Juveniles			
Rana arvalis	10	10	<0.01
Rana temporaria	19	7	<0.01
Older			
Rana arvalis	6	2	<0.01
Rana temporaria	5	3	<0.05

TABLE IV. Total number of frogs trapped during different months. The χ^2-tests refer to the samples of older frogs and give the probability of a species difference

	Juveniles		Older			
	R. arvalis	*R. temporaria*	*R. arvalis*	*R. temporaria*	χ^2	*P*
September	148	105	30	8	11.4	<0.001
October	102	282	16	35	4.69	<0.05
Nov.–Dec.	27	180	5	26	10.9	<0.001
Jan.–Feb.	1	50	3	6		
Mar.–Apr.	24	26	30	21	1.47	n.s.
May	22	6	17	4	7.05	<0.01
June	30	34	10	7	0.33	n.s.
July	19	186	47	65	1.28	n.s.
August	70	102	20	10	2.92	n.s.
	443	971	178	182		

increased activity of adult frogs, at least moorfrogs, during early and late night compared to the hours around midnight (Table II, Fig. 1), also reported by Inozemtsev (1969), might be related to decreased visibility of prey animals when it is very dark. I do not know, however, whether frogs really have difficulties in seeing their prey. This is also related to the question of whether locomotor activity is related to feeding activity. Dole (1965) reports that leopard frogs *Rana pipiens* adopt a sit-and-wait strategy for the capture of prey, which suggests that there is not necessarily a correlation. However, stomach analyses of newly captured and killed frogs did not show a particularly high proportion of frogs with newly captured prey at any time of the 24-hour cycle for adult frogs and only a tendency that most prey were captured during the day for juveniles (Loman in press). These frogs were captured by hand when flushed, *i.e.* they moved in response to my approach. If they were more easily flushed when active, a correlation that is by no means certain, this suggests that active frogs are feeding frogs. Another explanation of adult frogs being found feeding during the day and also during the night is that they really feed equally during night and day, adopting a sit-and-wait strategy, but that spontaneous movements, *e.g.*, from one feeding site to another, are restricted to night. This could be in order to reduce the risk of predation. Important predators on frogs in the study area are badgers (*Meles meles*) and tawny owls (*Strix aluco*) (night-active), pole cat (*Putorius putorius*) (probably mainly night-active), crow (*Corvus cornix*) and heron (*Ardea cinerea*) (mainly day-active). The risk of predation is thus severe also during night. One important predator, the grass snake (*N. natrix*), is also day-active. It is not found in the study area but could, among others, be responsible for the evolution of night-time activity in these frogs.

It is clear that the tendency to night-time activity was more pronounced in the laboratory test than in the field. I do not think this was because, although it is possible, the traps were less efficient by night than by day, rather it might be because in the laboratory tests, which lasted 24 h for each individual, no prey animals were supplied and the frogs were not disturbed by predators. This is also a warning against drawing too far-reaching conclusions from laboratory tests.

The most striking pattern found in the analysis of yearly activity is that common frogs have a larger part of their activity during the winter months than do moorfrogs. This is probably related to common frogs being more extensively distributed in northern Scandinavia than are moorfrogs.

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, p. 87

LONG DISTANCE MOVEMENT BY A SALTWATER CROCODILE (*CROCODYLUS POROSUS*)

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The saltwater crocodile has the most extensive range of any of the living crocodilians. Until recent massive depletion occurred, following large-scale commercial hunting, its distributional range extended from Cochin in South-west India, East to extreme South China and South through Indonesia, the Philippines, Papua New Guinea and the Solomons to Northern Australia. Within this extensive geographical range, the saltwater crocodile occurs on many small island groups often isolated from adjacent mainland areas by considerable distance of open sea. Clearly, sea-going behaviour, or the ability to survive long distance at sea has been important in achieving the present distributional range of the species.

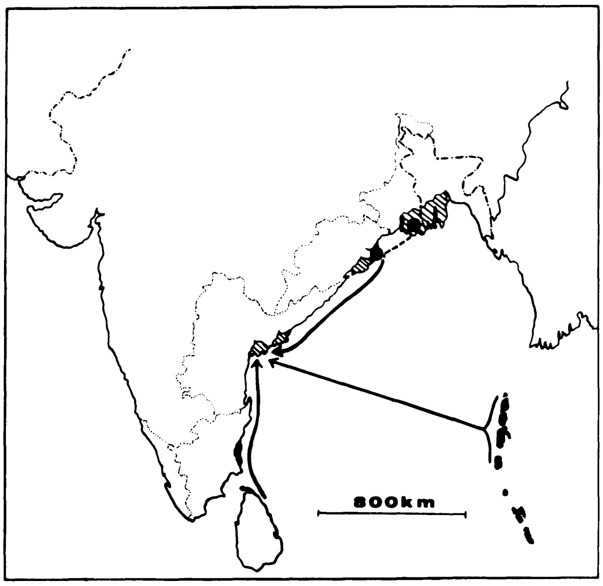

FIG. 1. Possible movement routes taken by the saltwater crocodile to the Krishna estuary. The cross-hatched areas indicate mainland and mangrove forests. The solid circles mainland areas still holding *C. porosus* in Orissa and West Bengal (to the North) respectively. The saltwater crocodile still occurs in the Andaman and Nicobar Islands (solid black) which also still provide extensive mangrove cover.

Recorded long distance movements of *Crocodylus porosus* are given in Table I.

The saltwater crocodile is extinct in South India. The last recorded individual was shot by Biddulph (1936) in Tanjore District of Tamilnadu.

On 11 January 1979 a saltwater crocodile was caught in the Krishna Estuary of Andhra Pradesh by villagers of Pedapatnam. This individual, seen by both of us, measures 3.3 m.

Geographical considerations suggest that the crocodile most likely came from the Andaman Islands, a distance of approximately 1100 km through open sea. This movement, together with other possible movements, is shown in Fig. 1. The shortest of these distances is 800 km.

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TABLE I. Long distance movement records for *C. porosus*

	Recorded at	Nearest breeding population	Minimum distance covered (km)	Reference
1.	Fiji Islands	Solomon Islands	1100	Malcolm Smith (1931)
2.	Palaus	Philippines or West Irian	800 900	Neill (1971)
3.	New Hebrides	Solomons	800	
4.	Cocos–Keeling Islands	Solomons	960	
5.	Ponape Island (Eastern Carolines)	Solomons or Bismark Archipelago	1280	Powell (1976)

BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 89–91

OBSERVATIONS AND COMMENTS ON THE POST-PARTURIENT BEHAVIOUR OF SOME TROPICAL BOAS OF THE GENUS *EPICRATES*

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INTRODUCTION

Although the reproduction of many squamate reptiles has been documented (see Fitch, 1970), very little appears to have been published on their behaviour during and after parturition. Some oviparous lizards and snakes are known to brood their eggs, which provides the eggs with some protection during their incubation period. Only one species, *Eumeces obsoleta*, is known to exhibit any care or interest in the young after they hatch (Evans, 1959). Of the viviparous species, *Xantusia vigilis* and *Mabuya trivitta* have been observed to assist their young in extricating themselves from their foetal membranes (Cowles, 1944; Rose, 1950); however, neither of these species appears to show any interest in its young after the birth process. The young of some viviparous squamates are known to remain close to their parent for short periods (Klauber, 1956; Bellairs, 1969), but no known advantages have been demonstrated for the young or the adults from these associations. Reported here are observations on the post-parturient behaviour of snakes of the genus *Epicrates* that suggest some protective advantages to the adults and their young after parturition.

OBSERVATIONS

During the early morning of 24 October 1978, an adult female Brazilian rainbow boa (*Epicrates c. cenchria*) gave birth to 28 young. These young were still in their foetal membranes at 0800 hours, when they were first observed. At this time, the female was coiled near her young with her head and anterior one-third of her body raised off the floor of the enclosure in a defensive attitude.

When attempts were made to check the condition of the young the female tightened her coils and directed her head toward the intruder's hand. Although no direct aggressive behaviour (striking or biting) was observed, the female vibrated her tail against the floor and walls of the enclosure and closely followed the hand of the intruder during the initial examination of the foetal membranes containing the young. At this time 27 of the young showed signs of life; the remaining juvenile was obviously dead and appeared to be smaller and not completely developed.

Shortly after my examination of the young, the female was observed to touch each of the foetal membranes with her snout and gently push them. The living young usually responded to this nudge by moving in their membranes, some even attempting to break free of them. After the female pushed at the membrane containing the dead juvenile with her snout, she grasped the membrane in her mouth and ingested the dead snake and its foetal membrane. At no time during the examinations of the foetal membranes was the female observed to use her tongue, which indicated that no olfactory cues were apparently utilized in her examination.

All of the live young were allowed to emerge from their foetal membranes on their own, which required as long as 36 hours for some specimens. During the first nine hours that the young were observed, the female repeated her investigations of each membrane several times. No other young died or were eaten during this period. At the end of the day the female was removed from her brood because some of the young had emerged from their membranes and the enclosure was somewhat crowded because of their activity.

DISCUSSION

Neill & Allen (1962) observed a captive female anaconda, *Eunectes gigas* (= *E. murinus gigas*) that produced four live young and 19 large abortive eggs (= undeveloped ova). Most of the undeveloped ova were eaten by this female, but no apparent interest was shown to the live young. Hanlon (1964) reported a captive *Epicrates striatus* that produced 51 young, three of which were found crushed when first observed in the enclosure. As he was removing these young he observed the female eat two of the remaining young. It was not stated, however, if the young that were ingested were alive or dead, but apparently at least one of the ingested young was alive since two of the three dead young were later available for measurements. Boos (1976) observed a female *Epicrates cenchria maurus* eating an undeveloped ova after giving birth to six young. This female later ingested three additional undeveloped ova after her young were removed.

Duval (in litt. to Hans Boos) reported two separate female *Epicrates striatus strigilatus* that ingested some of the birth debris and were also observed to have living young in their mouths. These young were later released unharmed after they began to move. One of these females was also observed to eat one of several dead young that were produced in her brood. Huff (1978) reported a captive female *E. s. strigilatus* that ingested four dead young that were produced in her brood and then was observed eating one of the live young from the same brood. This female also ingested other birth material before eating the live young. He also observed (per. comm.) a female *E. s. striatus* that was eating freshly passed undeveloped ova. He did not know if this female had also produced any young and ingested them before he made his observations, but he suspected that she had since blood and mucus, that is normally associated with the birth of young, were present in the enclosure. Tryon (in litt. to Hans Boos) observed an *E. s. striatus* and an *E. s. strigilatus* eating the undeveloped ova in their broods and the former specimen also consumed her live young. He also observed an *E. fordi* that was suspected of eating some of her live young since only a few juveniles were found in the enclosure after parturition. This same female was observed to eat her live young the next year after five or six had been born. In neither of the instances involving *E. fordi* were undeveloped ova present, but it was stated that these might have been eaten before discovery.

It is interesting to note that the boas that are known to exhibit this unusual post-parturient behaviour are mainly terrestrial species. *Epicrates cenchria* has been found in both terrestrial and arboreal habitats (Beebe, 1946; Duellman, 1978), but it is considered to be primarily a terrestrial snake. It, therefore, would seem that this species has its young on the forest floor. The time that it takes the young to emerge from their fetal membranes (at least several hours) would also indicate that they are born on the ground. Arboreal species such as *Corallus canina* produce their young in the trees and their young leave their foetal membranes as they are expelled from the female (personal observation in captivity). *Epicrates striatus* and *E. fordi* are also found on the ground and in arboreal situations (Sheplan & Schwartz, 1974) and observations on captives indicate that they deliver their young on the ground. *Eunectes murinus* is aquatic, but may also have its young in terrestrial environments; however, both terrestrial (Neill & Allen, 1962) and aquatic births (Deschanel, 1978) have been reported for captive specimens.

The reasons that these snakes ingest their birth debris and dead young cannot be completely explained yet, particularly since on several occasions some of the live young were also consumed. This latter behaviour might be influenced by captivity or possibly the living young that were ingested were poorly developed and/or in a weakened condition and would not have survived. However, because this behaviour has only been reported in species that produce their young in terrestrial and aquatic situations where the chances of predation are high, it might be related to the protection of the adults and young from potential predators. Neill & Allen (1962) suggested that female snakes might obtain some physiologically and metabolically useful substances by eating their own birth debris. This certainly would be an advantage to snakes that produce their young alive, particularly since much energy is expended during parturition and any substances that would help replace some of this lost energy would be beneficial to the adult. They also state that a more obvious survival value can be obtained by eliminating the strong and characteristic odours that are produced by the birth debris. These odours might attract carnivores or other predators to the birth site, and by removing this material the adult might reduce the possibilities of predation to herself and her young. The fact that it requires several hours for the young to free themselves from their foetal membrane supports this conclusion, because the young would be more vulnerable to predation while enclosed in their membranes.

It may also be significant that the adult *Epicrates cenchria* reported here appeared to stimulate her young to leave their membranes by pushing at them. This behaviour might help reduce the time that these young remain in their membranes and thereby reduce the possibilities of predation to them. Another indirect advantage that the live young might obtain from the removal of the dead young and other birth debris is that they would have less exposure to bacterial infections that could contribute to the mortality of the litter. This latter suggestion is based on the fact that 10 of the 27 live *E. cenchria* reported herein developed a bacterial infection of the umbilicus, possibly as a result of prolonged contact with the degenerating foetal membrane.

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HABITAT SELECTION BY AMPHIBIANS DURING THEIR TERRESTRIAL PHASE

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SUMMARY

The summer quarters of 9 amphibian species were studied in an area of inland dunes, mostly covered with woods and the remainder with heath, fens, cultivated land and some patches of drift sand. They were *Bufo bufo*, *B. calamita*, *Pelobates fuscus*, *Rana arvalis*, *R. esculenta*, *R. temporaria*, *Triturus alpestris*, *T. cristatus* and *T. vulgaris*. Data were obtained through direct observations during nightly searches and by means of a trapping programme. These two methods proved to complement each other. *Bufo bufo* appeared in nearly all habitats; *B. calamita* selected drift sand habitats; *Rana arvalis* and *R. temporaria* chose humid grassy habitats with *R. temporaria* avoiding acid environments. *Rana esculenta* appeared to remain in the close vicinity of water though it might be found everywhere during rainy nights. *Pelobates fuscus* and the *Triturus* species offered very few data.

INTRODUCTION

In the years 1971–1973 a study was made in the reserve *Overasseltse en Hatertse Vennen* near Nijmegen in the Netherlands concerning the summer quarters of the amphibian species occurring there. There is a fair amount of literature on habitat selection of amphibians, but nearly always only the habitat preferences during the aquatic phase are reported (see Cooke, 1975; Strijbosch, 1979). In some papers (*e.g.* Beebee, 1977) there is information on the habitats of the terrestrial environment but then the places of reproduction are clearly accented. In this study we restricted ourselves to the habitat preferences during the purely terrestrial phase of the amphibians. In our area there are 9 different amphibian species, namely, *Bufo bufo* (L.), *B. calamita* Laur., *Pelobates fuscus* (Laur.), *Rana arvalis* Nilsson, *R. esculenta* L., *R. temporaria* L., *Triturus alpestris* (Laur.), *T. cristatus* (Laur.) and *T. vulgaris* (L.). The systematic position of *Rana esculenta* has been amply discussed of late (see *e.g.* Berger, 1973): within the *Rana esculenta* complex one can distinguish the forms *"esculenta"*, *"ridibunda"* and *"lessonae"*. According to more recent studies (Wijnands & van Gelder, 1976) the form *Rasa lessonae* chiefly occurs on the present site with, to a lesser extent, *R. esculenta*. This distinction could not be made during this study and the old name *Rana esculenta* has been used. The investigation was almost completely restricted to the months July and August presuming that the amphibians were certainly present in their summer quarters by then. Juveniles which might possibly show dispersal during that period have been excluded from this study. The data have been collected by means of direct observations during the night and by means of a trapping programme. All habitats present in this area were included, except the open water.

STUDY AREA

This study was made in the reserve *Overasseltse en Hatertse Vennen* at 5°48′E Long., 51°48′N Lat. in the Netherlands. This is an area with inland dunes of about 300 hectares along the north-eastern Maas border near Nijmegen. The amphibians occurring there breed in a great number of fens covering about 30 hectares. The greater part of this reserve, about 165 hectares, is woodland. The original forest type was oak-birch wood, but at present this type only occurs as coppice on about 15 hectares. The remainder, about 150 hectares, is coniferous plantation especially *Pinus sylvestris* (but also other *Pinus* species), *Larix leptolepis* and *Pseudotsuga menziesii.* These plantations were started in 1912. About 45 hectares of the reserve consist of heath and some patches of open drift sand. The remainder of the area, about 60 hectares, is cultivated farmland comprising pastures, meadows and fields. This farmland has an occasional strip of coppice between the various plots.

METHODS

Sampling methods

The data of the occurrence of the various amphibian species were exclusively collected from late June till the beginning of September, *i.e.* the period in which the amphibians of this area (with the exclusion of *Rana esculenta* and partly *Triturus cristatus*) lead a purely terrestric life. Direct observations were used in 1971, and traps in 1972 and 1973.

The direct observation method worked as follows: at night a car with dimmed headlights was driven through every road, lane and path of the area at a speed of 5–10 km/h, carefully scanning the ground when doing so (cf. Heusser, 1968). These searches were spread in time and space so that all places had an almost equal frequency of visitation. Every time an amphibian was seen its species and size were established. Also the traffic casualties were included. We assumed that every amphibian seen came from the habitat next to the road or path. This habitat was then assigned one point. If the road or path formed the borderline between two different habitats (*e.g.* woodland/pasture or coppice/cropfield) these two habitats were each scored 0.5. Thus, if amphibians showed a preference for transitions in their habitat this possibility has been neglected.

In spring 1972 a vegetation map (scale 1:5000) was drawn and 104 pitfall traps were placed in the various vegetation types, 43 of which in the various types of woodland, 18 in the heathland, 23 in the moist surroundings of the fens and 20 in the cultivated farmlands. These pitfalls consisted of plastic buckets with a diameter of 37 cm and a height of 40 cm, which were dug into the ground. They were emptied twice a week during the experimental period of 1972 and 1973; they were closed during the remaining time of these years. We restricted ourselves to these periods because certain amphibian species show migration from the spawning sites to their summer quarters as late as June, and in September the migration to hibernation sites might already have started. Juveniles were excluded from this study because in their dispersal they might cross habitats not suitable as summer quarters for them.

Vegetational data

In order to establish the precise nature of the plant communities around the pitfalls phytosociological relevés were made in 1973 using the method of the Zurich-Montpellier School (Braun–Blanquet, 1964; Westhoff & van der Maarel, 1973; cf. also Shimwell, 1971). To indicate the nature of the plant communities we took as a basis the level of alliances as they are described for the Netherlands by Westhoff & den Held (1969). The alliances found are given in Table I. They can be characterised as follows: all woodlands originally belonged to the Quercion robori-petraeae, acidophilous oak woodlands. For these deciduous woods we made a distinction between woods growing on a dry substratum (the main grass-species in the herblayer being *Deschampsia flexuosa*) and those growing on a humid substratum (the main grass-species in the herblayer being *Molinia coerulea*). All coniferous plantations can be considered as substitution communities for the Quercion robori-petraeae. This study distinguishes between plantations of pines, larches and douglas firs and within the pinewoods covering by far the largest surface, between those growing on dry places and those growing on humid places. The larch and douglas fir plantations are all respectively nearly all planted on humid soils. The Thero-Airion is here represented by the communities Agrostietum tenuis and Festuco-Thymetum serpylli, both ± closed herbaceous vegetations of sand dunes and other acidic sandy soils, often on deserted fields *etc.* The Polygono-Chenopodion comprises the weed communities of rootcrop fields. The Aphanion comprises the weed communities of grain fields. The farmyards mainly had the community Lolio-Plantaginetum (alliance Lolio-Plantaginion). This is a vegetation of small plants with a rather open structure occurring on frequently trodden places. The Agropyro-Rumicion crispi comprises the moderately humid permanent pastures, strongly fertilised and intensively grazed on. The Arrhenatherion elatioris comprises the moist hay meadows. These meadows are here often used as grazing pastures for a short time during summer. In this area the most frequent plant community within this alliance is therefore the Lolio-Cynosuretum. Ditches are often present in these meadows. The Salicion cinereae comprises the *Myrica* and *Salix* scrubs along the fen borders. Within this alliance this area has the Myricetum gale, the Frangulo-Salicetum auritae and the Alno-Salicetum cinereae. They are nearly always rather narrow belts around the eutrophicated fens. The Caricion curto-nigrae comprises the rather low, mainly grassy communities occurring along the borders of the eutrophicated fens to a certain distance into the water. The Erico-Sphagnion comprises the vegetations of ombrogeneous peats. These peats were developed in many fens and they emerge above the water surface. They are also frequently seen in the eutrophicated fens. The vegetations in and around the still oligotrophic fens nearly all belong to the alliance Rhynchosporion albae. As a result of periodic inundations wide zones of *Molinia coerulea*-dominated communities often occur on the borders of the fens and these zones were sampled during this study. Within the Ericion tetralicis of this area the Ericetum tetralicis is mostly found. This community occurs only around the rather undisturbed, acid fens, on moist places. And finally the Calluno-Genistion comprises the species-poor acidophilous grass-heaths of this area. The more humid places often have *Molinia coerulea* by the side of *Calluna vulgaris*, on the drier places it is combined with *Deschampsia flexuosa*. On spots where the top-layers of soil have been disturbed this latter species often dominates.

TABLE I. Code and name of the plant communities

Code:	Name:
Qrpd	Quercion robori-petraeae (dry)
Qrpm	Quercion robori-petraeae (humid)
Pid	plantations: dry pine wood
Pim	humid pine wood
Lam	humid larch wood
Psm	humid Douglas fir wood
Th-A	Thero/Airion
P-Ch	Polygono-Chenopodion
Aph	Aphanion
L-P	Lolio-Plantaginion
A-Rc	Agropyro-Rumicion crispi
A.e.	Arrhenatherion elatioris
Sal.c.	Salicion cinereae
C.c.n.	Caricion curto-nigrae
E-S	Erico-Sphagnion
Rh.a.	Rhynchosporion albae
Er.t.	Ericion tetralicis
C-G	Calluno-Genistion

RESULTS

The results of the direct observation method are given in Table II. The clearly distinguishable habitats are mentioned with the percentage of how much of the study area they cover given in the first column. It is clear that the newts were not captured with this method. All 325 captures were anurans, *Bufo bufo* clearly being the most frequently captured species, *Pelobates fuscus* the least. The following things can be said about the occurrence of the different species: *Rana arvalis* seems to occur relatively often near the coppice strips; *R. temporaria* was seen relatively often in the grasslands and the coppice strips between them (this species was found only in these two habitats and in the woodlands); *R. esculenta* was also relatively often observed in grasslands and coppice strips and furthermore quite often in the neighbourhood of the fens (heathland and fields are seemingly not visited); *Bufo bufo* shows a relative preference for the cultivated lands (pastures and arable fields and the coppice strips between them) and it proves to dislike heathland; *B. calamita* is the only species occurring frequently in the patches of open drift sand and besides that also in heathland—relatively few of them were found in the woods and within the sphere of cultivated lands the arable fields are preferred to pastures. It is a pity that only 10 *Pelobates fuscus* were captured; the discussion about its habitat selection remains very speculative. With necessary reservation it might be said that this species does not avoid the woodlands and cultivated soils though it might avoid heath.

To make the distributions found suitable for statistical analysis Table III gives the occurrence in three major habitats. Now the border zone habitat is left out because this type cannot be alloted to one of the three major habitats. Still the values for *Rana arvalis* and *Pelobates fuscus* are too low to make a meaningful statistical analysis (cf. Siegel, 1956), but now the habitat selection of the remaining *Rana* species and the *Bufo* species can be analysed. *Rana temporaria* significantly avoids the combined habitat heath and drift sand and prefers the combined habitat pastures, fields and farmyards ($\chi^2 = 8.50$, $P < 0.02$). According to Table II this latter preference must concern the grasslands. *R. esculenta* significantly avoids the combined habitat heath and drift sand ($\chi^2 = 7.09$, $P < 0.05$). *Bufo bufo* also avoids significantly the heath-drift sand habitat and shows a clear preference for the open habitats strongly influenced by man ($\chi^2 = 27.09$, $P < 0.001$). *B. calamita* very significantly prefers the heath-drift sand habitat and avoids the forest habitats ($\chi^2 = 49.31$, $P < 0.001$). According to Table II this latter preference likely must concern the open drift sand habitat.

Figure 1 shows the results of the trapping programme. The abscissa of all histograms is indicated by the schematic diagram with 18 different habitats. An indication of what plant communities are present is given per habitat. The relative sizes of the various habitats in the diagram bear no quantitative relation to reality. The woodlands, especially the pine and larch woods cover a far greater part of the area than is suggested by the diagram, whereas the willow scrubs, the communities within the Caricion curto-nigrae and the Ericion tetralicis are rather narrow zones around the fens. Also the order of habitats can locally vary from the order in the diagram. Figure 1 also shows the number of traps used per habitat and the total number of weeks of their operational use (= trapweeks). As not all habitats have been sampled equally intensively and as it happened a few times that the traps were found and consequently emptied by unqualified persons a relative standard was used when drawing up the

TABLE II. Surface share of the habitats and the occurrence of anurans in them given in percentages of the total capture (= n) per species

Habitats	Percentage of the total area*	*Rana arv.* n = 25	*Rana temp.* n = 27	*Rana esc.* n = 33	*Bufo bufo* n = 181	*Bufo cal.* n = 49	*Pel. fusc.* n = 10
Forest†	54.0	56	52	52	53	29	70
Coppice strips	3.9	16	15	18	14	—	—
Pastures and meadows	10.2	12	33	24	17	6	10
Agrarian fields	5.3	4	—	—	9	10	10
Farmyards	0.4	—	—	—	1	—	—
Border zone vegetations	3.5	4	—	6	2	—	10
Heath	12.6	8	—	—	2	22	—
Open drift sand	3.2	—	—	—	2	33	—

* The remaining 7% consist of open water which has not been sampled.
† Mainly Pine plantations.

TABLE III. The occurrence of anurans in some major habitats (*i.e.* combinations of the habitats given in Table II)

Major habitats	Percentage of the sampled area	*Rana arv.* n = 24	*Rana temp.* n = 27	*Rana esc.* n = 31	*Bufo bufo* n = 178	*Bufo cal.* n = 49	*Pel. fusc.* n = 9
Closed (forest + coppice)	64.6	18	18	23	121	14	7
Open and strongly influenced by man (pastures + fields + farmyards)	17.8	4	9	8	49	8	2
Open and less influenced by man (heath + drift sand)	17.6	2	—	—	8	27	—

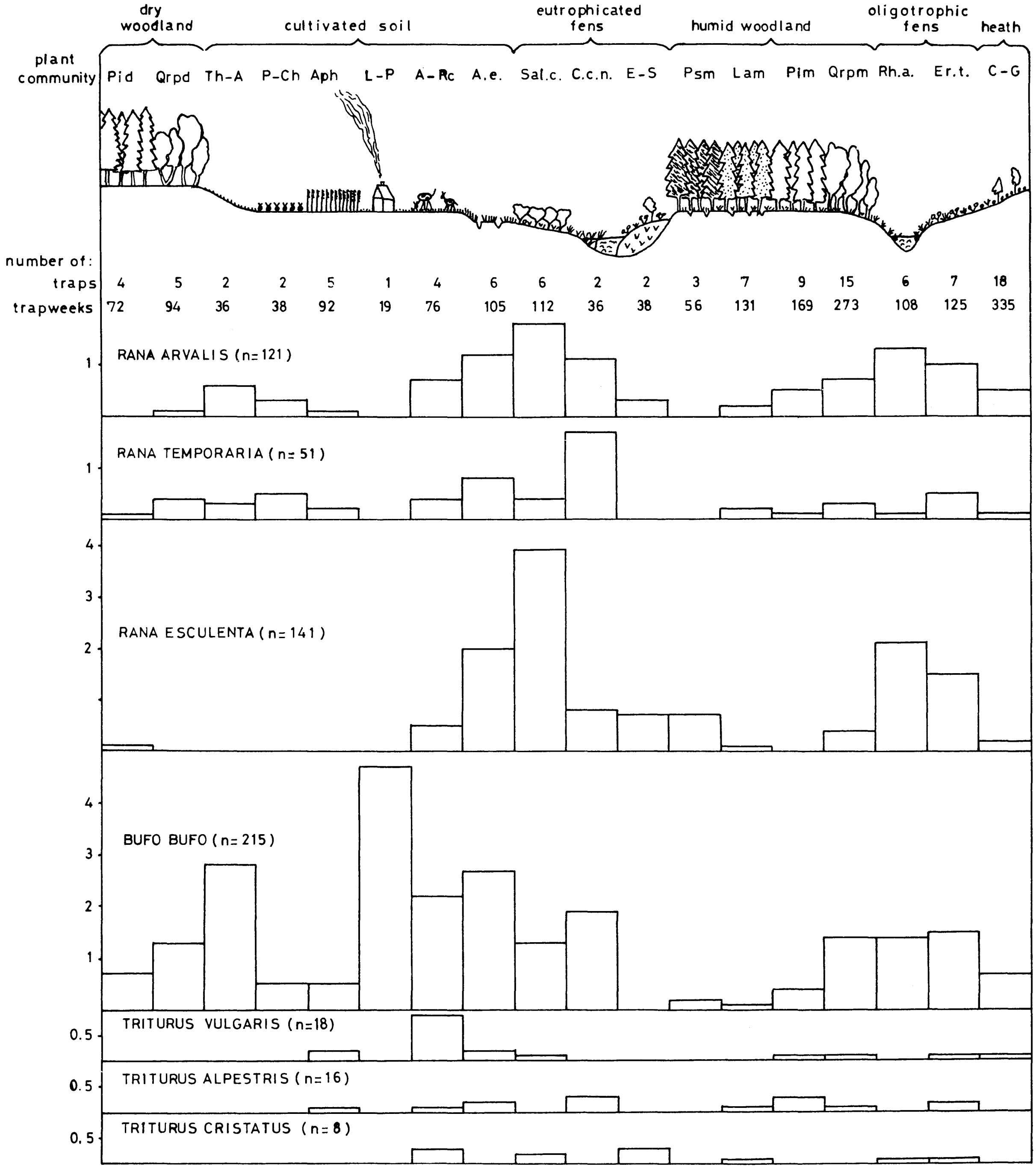

FIG. 1. Capture per period of 10 weeks in the traps in the months July and August 1972 and 1973 (the code of plant communities is given in Table I).

histograms, *viz.* the capture per operational period of 10 weeks.

The total capture of this study was 572. *Rana arvalis* turns out to occur especially in the moist habitats around the fens. This species is found less frequently in the woodlands and the dark douglas fir woods are probably completely avoided. On the cultivated lands it prefers the grassy lands to the arable fields and within the grassy lands it seems to like those of the more humid places better. *Rana temporaria* shows a preference for the moist, grassy surroundings of the eutrophicated fens and for the hay-meadows. This species was captured less frequently around the oligotrophic fens and it was not captured at all in the Erico-Sphagnion, indicative of an acid environment. The difference in occurrence on grasslands and fields is less marked than for *Rana arvalis. Rana esculenta* clearly occurs in and around the vicinity of the fens. Most captures were made in the narrow willow scrubs around the eutrophicated fens but this species also occurs frequently in the borderzones of the oligotrophic fens. Furthermore many of them were caught in the hay-meadows where there are many ditches. Probably it avoids arable fields. *Bufo bufo* is the sole species abundant in the close vicinity of farmsteads. It appears from this study that this species occurs more frequently on open land than in woods. The grasslands are well-beloved summer quarters for this species, they also enjoy a marked preference to fields. In the grassy deserted fields they do occur again rather abundantly. As far as they occur in the woodlands they show a marked preference for the deciduous woods, whether in dry or humid environments; the coniferous plantations are more or less avoided, especially those in humid environments. The more acid surroundings of oligotrophic fens and the heath are not avoided; whereas the Erico-Sphagnion, indicative of a very acid and moist environment, is the only habitat of this area where these toads were never found. The remaining anurans were caught only once during this study, *Bufo calamita* in a pine wood near drift sand, *Pelobates fuscus* in a permanent pasture near a farmstead. These captures have not been worked into Fig. 1. The total capture of newts is also only very low, probably too low to make well-founded statements. In general the three species were found somewhat more frequently on the cultivated lands and less frequently in the woods and the more acid surroundings of the oligotrophic fens. In all probability these species do not migrate very far from the water and for breeding they are dependent on the eutrophicated water of the fens in the cultivated land. *Triturus cristatus* was even exclusively caught in traps very close to open water. This species, as opposed to the two other newts, often remains aquatic till August (van de Bund, 1964; Smith, 1969).

DISCUSSION

Methods

The two methods of investigation do not always show corresponding results. Thus the direct observation method suggests that nearly all anurans occur at random in the woods (Table II), whereas Fig. 1 clearly shows that the number of captures in the woods is relatively low, especially in the coniferous plantations. A striking difference between the two methods concerns the observations of *Bufo calamita.* This species was, excepting *Bufo bufo*, seen most frequently during the nightly searches but it was not caught in the traps (only one specimen). The direct observation method shows that drift sand enjoys the preference of this species. This habitat is, in our study area, represented by some open patches of drift sand, kept open by day-trippers, and some wide footpaths, also kept open by the strong recreational pressure. We often found *Bufo calamita* to be very active by night on this open sand. This is a habitat, however, which cannot possibly be sampled with traps, the very reason being the high concentration of day-trippers on these places. The occurrence found in the woods and on the heaths (see Table II) can be explained by the fact that these habitats often scored captures because they were situated next to a drift sand habitat. The only specimen of *Bufo calamita* captured in the traps was found in a pine wood near an open patch of drift sand.

The newts also show different results for the two methods. They were never noticed when making direct observations, which is undoubtedly due to their small size. The few captures in the traps might also possibly indicate that they are rather inactive in summertime. Some authors (*e.g.* Heusser, 1961) state that these species rest in summer for considerable periods. The fact that many newts do occur in this area is proved every spring when they populate the eutrophicated fens in large numbers.

The statement made by Heusser (1968) that these two methods of investigation into the summer quarters of amphibians are equally suitable does not apply always and everywhere.

Amphibians

Rana arvalis: The summer quarters of this species are situated in the humid grassy parts of this area, often having an acid substratum. The hay-meadows in the neighbourhood of fens, sometimes with wild willow shoots on the edges or coppice between them, the wide zones with *Molinia coerulea* and the humid grassy heathlands around the oligotrophic fens are likely to be the three most important habitats for this species. These conclusions agree to what is mostly said about it in literature (van de Bund, 1964; Smith, 1969; Fretey, 1975; Trutnau, 1975). A preference for woodlands as mentioned for Poland by Kminiak (1966) and Zimka (1971) was not seen in this area. It is remarkable that this species occurs in the habitats indicated by the Thero-Airion. These are in general rather dry grassy plots of land on which the above vegetation mostly develops on deserted cultivated land. *Rana arvalis* was found less frequently on the fields still in use. This might also indicate a preference for a more or less acid substratum.

Rana temporaria: Heusser (1968) gives for this species the woods as its summer quarters and also the surroundings of humid grasslands. In our study area the cultivated land and the surroundings of the eutrophicated fens in it form the most important summer quarters. Relatively few captures were made in the woods. This species is seen considerably more frequently in the neighbourhood of the eutrophicated fens than in the more acid neighbourhood of the oligotrophic fens. Therefore in this area this species can perhaps be considered as anthropochorous.

Rana esculenta: This species stays in or near the water also in the summer months (van de Bund, 1964; Kminiak, 1966; Smith, 1969). According to Juszczyk (1951) and van Gelder & Hoedemaekers (1971), however, specimens of this species show migrations outside its spawning period (in this area this is May–June). During this study a number of trap captures have indeed been made on places, rather far from open water and even some of them on very dry spots (heathland and dry pine wood). Also during the nightly searches this species was sometimes seen in places far from water. Migrating *Rana esculenta* were nearly always observed during nights when it was raining. By far the largest number of captures, however, was made in the close vicinity of the fens. The number of captures of this species in acid environments is not distinctly higher or lower than in less acid environments. A marked optimum in the captures lies in the narrow willow scrubs around the fens. Also the hay-meadows with ditches appear to function as summer quarters. *Rana esculenta* was never found to breed in these ditches.

Bufo bufo: This species behaves in this area as an anthropochorous animal. In the habitat most strongly influenced by man, the farmyard, it is the sole species found (and in large numbers at that!), while the habitat least influenced, the ombrogeneous peat, is the only habitat in which it was never found. The phenomenon that this species occurs more on open land than in woods is in flat contradiction to Heusser's conclusions (Heusser, 1968). In his experimental area (near Zurich in Switzerland) the toads resorted to the woods and avoided the grasslands between them.

Bufo calamita: The marked preference of this species for a sandy environment (van de Bund, 1964; Tinbergen, 1971; Presst, Cooke & Corbett, 1974) was confirmed during this study. In this area the patches of drift sand present here and there can be considered its preferred summer habitat (see discussion on methods).

Pelobates fuscus: In the Netherlands this species shows a distinct preference for the ridges of drift sands along the river borders in the east of the country (Pelt & van Bree, 1965; Oomen, 1966, Oomen & van Gelder, 1967). The summer captures mentioned by them were nearly all made on sandy fields, only very few in woods on a sandy substratum. During this study this species was caught only 11 times. All these captures were made in the south-eastern part of the study area, where there is also a concentration of fens eutrophicated by agrarian activity (spawning sites!). Probably this area houses only a small population which does not go very far away from the fens during summer.

Triturus sp.: Both methods of investigation appear less suitable for the newts. Finding the summer quarters of these species seems to require a more intensive procedure, especially because of possible periods of rest in summer, *i.e.* periods with very little activity.

In general we can say that nearly all species prefer deciduous woods to coniferous woods and also that the presence of coppice strips or the remainders of woods in cultivated land is likely to promote the occurrence of amphibians on it.

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OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOUR OF THE EASTERN INDIGO SNAKE, *DRYMARCHON CORAIS COUPERI*, IN CAPTIVITY

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SUMMARY

Four complete courtship episodes between a mature pair of eastern indigo snakes, *Drymarchon corais couperi*, in captivity, revealed three new male motor patterns. The behavioural sequence followed the triphasic colubrid pattern but with a longer Phase III duration and a lack of courtship/copulatory biting.

A pair of mature (SVL 1533 mm ♂ and 1479 mm ♀; both 9+ years of age) eastern indigo snakes (*Drymarchon corais couperi*) were observed in four courtship sequences, three of which concluded in mating. Complete behavioural sequences were documented on Super-8 movie film and analysed frame by frame.

The courtship motor patterns observed followed the basic triphasic colubrid pattern including touch-mount, dorsal advance movement, chase-chase-mount, writhe-bump, tail-search copulatory attempt (TSCA) and caudocephalic waves (Table I) and are described elsewhere (Gillingham, 1979). However, the following three new and mutually exclusive male courtship events were observed in the tactile-chase phase (Gillingham, Carpenter, Brecke & Murphy, 1977) of the courtship sequence.

Nudge. The mounted male made contact with the female's body with his snout and forcibly pushed at the point of contact. Often the body of the female moved several cm across the substrate as a result of this nudge. This motor pattern differs from the touch-mount in its increased intensity and in that it is exhibited from the mounted position (Fig. 1a).

Neck-curl. The mounted male slid his head and neck under the female's neck, passed to the opposite side of

TABLE I. Courtship motor patterns and observed frequency for *Drymarchon corais couperi*

Motor Pattern	Frequency (%)
Touch-Mount	9.9
Dorsal Advance Movement	18.3
Chase-Chase Mount	5.6
Writhe-Bump	4.2
Nudge	28.2
Dorsal-Pin	25.4
Neck-Curl	1.4
Tail-Search Copulatory Attempt	4.2
Caudocephalic Waves	2.8

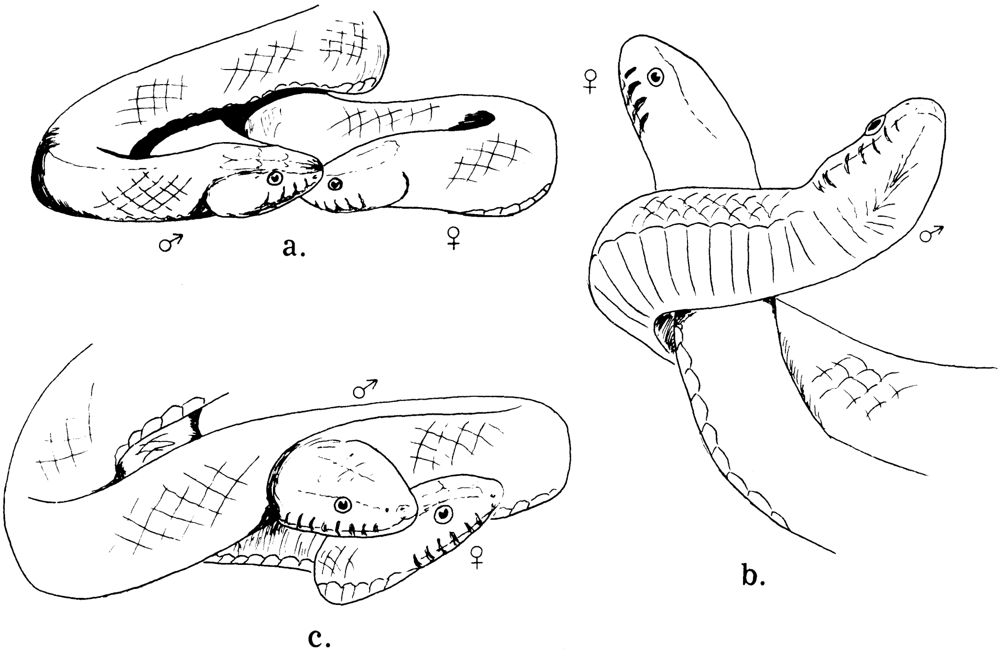

FIG. 1. Sketches from the cinematographic record of courtship postures in *Drymarchon corais couperi*. a. Nudge, b. Neck-Curl and c. Dorsal-Pin.

TABLE II. Comparisons of time durations for three phases of courtship behavior and Tail-Search Copulatory Attempt (TSCA) frequencies for various colubrid species

Species	Phase I	Phase II	Phase III	TSCA	Source
Drymarchon corais	12.0 min	8.5 min	193.0 min	3.5	This study
Elaphe v. vulpina	12.5 min	9.9 min	20.3 min	6.2	Gillingham, 1977
Elaphe o. bairdi	45.0 min	—	40.0 min	—	Brecke *et al.*, 1976
Elaphe o. obsoleta	10.3 min	18.3 min	20.7 min	7.9	Gillingham, 1979
Elaphe g. guttata	5.0 min	4.5 min	25.3 min	2.8	Gillingham, 1979
Lampropeltis mexicana	7 sec–50 min	2 sec–3 min	4–15 min	—	Murphy *et al.*, 1978
Lampropeltis t. sinaloae	5.5 min	33.0 min	20.6 min	10	Gillingham *et al.*, 1976

her body and lifted her upwards. He then curled his neck posteriorly cradling the female's anterior body on his dorsum. In many cases the female responded by forming a corresponding neck-curl and moved her head in the opposite direction thus effecting an overall "lyre-shaped" configuration (Fig. 1b).

Dorsal-pin. The mounted male made a U-shaped curve with his neck and used it to force the female's anterior trunk down to the substrate. It was usually exhibited when the female began to glide forward as a result of the male's dorsal advance movements. This action has been observed in the combat context for *Elaphe o. obsoleta* (Gillingham, 1980) (Fig. 1c).

All motor patterns observed, from initial male contact of the female until either intromission or disinterest, were tallied sequentially and a frequency distribution of observed motor patterns was created (Table I). The new motor patterns described above have not been observed in either *Elaphe* or *Lampropeltis* but are apparently important in the overall courtship sequence since they represent a cumulative contribution of 55% to motor patterns exhibited (Table I). Phases I, II and III (Gillingham, 1979) lasted 12.0, 8.5 and 193.0 min, respectively. The phase I and II values do not differ appreciably from those recorded for *Elaphe* (Brecke, Murphy & Siefert, 1976; Gillingham, 1979) or *Lampropeltis* (Gillingham *et al.*, 1977; Murphy, Tryon & Brecke, 1978). However, Phase III shows a marked departure from *Elaphe* and *Lampropeltis* with an intromission and coitus length averaging 193.0 min (Table II). This phase was also characterised by a considerable amount of movement on the part of both snakes. Although the small sample prohibits any statistical validity, inspection alone results in the conclusion that there is a significant temporal extension of coital duration. The adaptive significance of this difference remains to be determined.

Overall the courtship and mating behaviour fits the colubrid pattern, but it is interesting to note that no biting (by either sex) was observed in any of the interactions. Tinkle (1951) described a similar sexual encounter as being quite violent, with much biting occurring. Coital biting (male grasping the female during all or part of coitus) is known to occur in *Elaphe v. vulpina* (Gillingham, 1977) and appears to be fairly nonviolent with a stimulus and/or anchorment function. Male *Elaphe obsoleta spp.*, however, resort to courtship biting in cases where the female is not immediately receptive to his advances. In these instances the biting is prefaced by a significantly large number of TSCA's. In one episode in the present study the male indigo snake exhibited 46 successive TSCA's without intromission and, interestingly, without a single biting incident.

In summary, the eastern indigo snakes observed here exhibited a courtship pattern similar to other colubrids but with the addition of three different motor patterns. The coital duration was longer than that recorded for *Elaphe* and *Lampropeltis*, and was not characterised by the biting often exhibited by the former.

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WEST INDIAN IGUANAS OF THE GENUS *CYCLURA*: THE THREAT OF HABITAT DESTRUCTION IN THE CAYMAN ISLANDS

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SUMMARY

During the end of January and beginning of February 1979 the islands of Grand Cayman, Cayman Brac, and Little Cayman were visited and a search made for their rare endemic iguanas. A population of *Cyclura nubila caymanensis* was found on Little Cayman about two miles east of West End Point and about half a mile inland from the South Coast. These iguanas are threatened by the intention of the Cayman Government to allow a large crude oil transhipment terminal to be built on this area. The probable effects of this construction and increased human population are discussed, and recommendations made for the conservation of surviving iguanas.

INTRODUCTION

Large ground iguanas of the genus *Cyclura* are found on numerous islands and cays in the Caribbean, including the Bahamas, Cayman Islands, Virgin Islands, and the Greater Antilles. These inoffensive lizards, some species exceeding four feet in length, are primarily herbivorous and are found typically in xeric limestone and sandy habitats remote from man's activities. For centuries they have been hunted for food by natives and sailors, and in more recent times they have been shot for sport.

Populations of *Cyclura* still thrive on many islands which remain so far unspoilt by man; for example *Cyclura cychlura figginsi* of the Exumas (Carey, 1976), and I personally have seen healthy colonies of *Cyclura cornuta cornuta* on Haiti, and *Cyclura c. cychlura* on several cays in the Bahamas. However, it is considered that 75% of extant species are in a depleted state, and in all cases of population depletion indirect human intervention is the primary cause. Increasing pressure on the habitats of these lizards for commercial building, tourism, and from domesticated animals such as dogs, cats and grazing stock, are causes for serious concern. Carey (1976) has reported that on Anegada *Cyclura pinguis* faces possible extinction via the ravages of introduced goats and cattle which run feral and compete with the iguanas for the vegetation part of their diet. The Jamaican Iguana (*Cyclura collei*) had been considered extinct since the 1940s, mainly due to the introduction of the mongoose which preyed upon the young lizards and eggs (Lewis, 1944), but a recent report suggests that there may still be a few individuals living in the Hellshire Hills of Southeastern Jamaica (Woodley, 1971). In 1941 remnant colonies of *Cyclura collei* still survived on the Goat Islands where the mongoose had been introduced at a later date than on the main island, but the growing ichneuman population virtually wiped them out. The few remaining specimens were caught and kept in a pen at the Institute of Jamaica, where they were eventually killed by dogs. Now the existence of the Cayman Island Iguana (*Cyclura nubila caymanensis*) is threatened by the intention of the Cayman Government to allow a large crude oil transfer terminal to be built on Little Cayman, an island which has kept its natural fauna because it has only a small human population.

The Cayman Island Iguana (*Cyclura nubila caymanensis*)

Introduction. The three Cayman Islands are situated some 180 miles west-north west of Jamaica (Fig. 1). The largest, Grand Cayman, in the Western Caribbean, lies 80 miles to the west of Cayman Brac and Little Cayman, which are separated by a five mile wide channel. Grand Cayman is approximately 76 square miles in area; Cayman Brac 14 square miles, and Little Cayman only 10 square miles. Grand Cayman and Little Cayman are made up of low lying limestone, but Cayman Brac is distinguished by a limestone bluff rising to 140 feet.

Distribution. Cyclura nubila caymanensis is endemic only to Little Cayman and Cayman Brac, although Carey (1975) has reported that a pair had been released on Grand Cayman and had subsequently reproduced. This is unlikely to be a good thing since they may threaten, through competition or intergradation, the rare endemic iguana *Cyclura nubila lewisi*, about which very little is known.

OBSERVATIONS

During my brief visit to the Caymans in January/February 1979 all three islands were visited and a search made for iguanas; unfortunately time was short and the search far from thorough. About four days were spent investigating wild areas on the eastern end of Grand Cayman and a couple of days on the north-western coast of Cayman Brac, and no iguanas were seen. Carey (1966) reported finding an isolated colony on the south side of Cayman Brac from a point

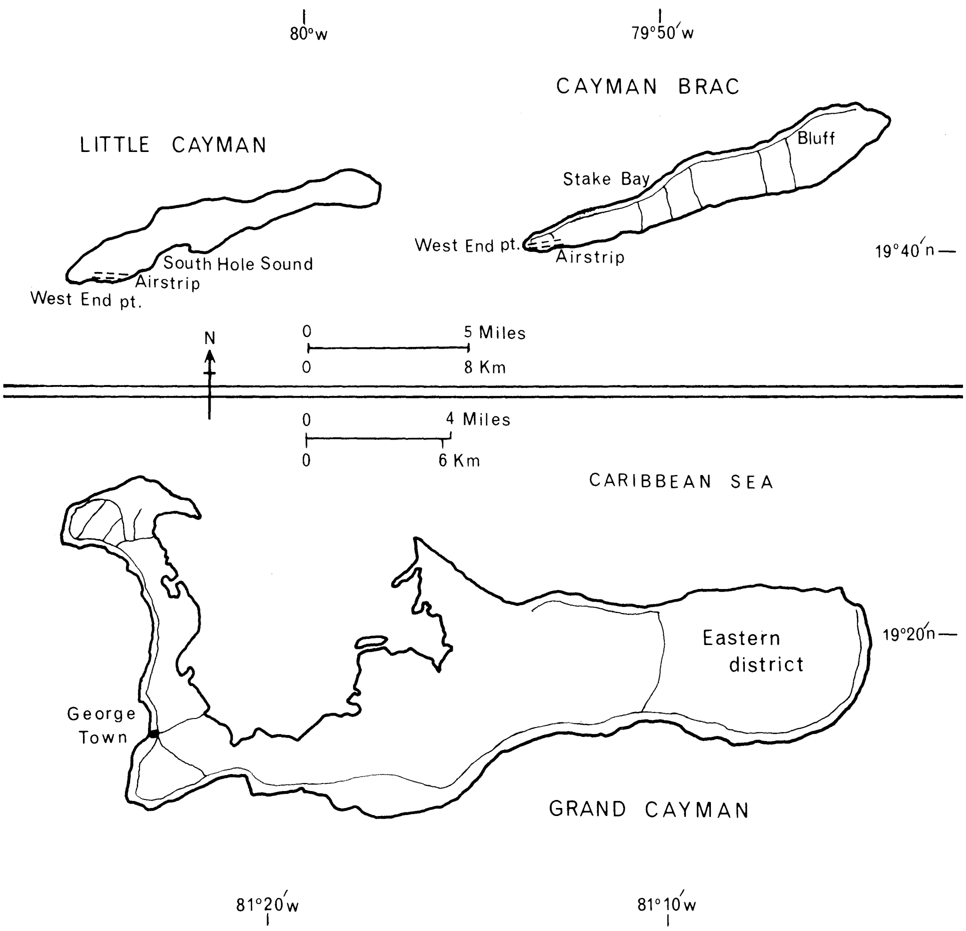

FIG. 1. Map of the Cayman Islands. The roads are indicated by thin lines.

PLATE 1. Xeric limestone habitat of the Cayman Iguana.

two miles east of the Settlement of West End, where the Bluff begins to rise, to the area about one mile south of Stake Bay. In the time available I was not able to search this area.

Little Cayman is the least populated of these islands, with only about twenty people living mostly along the coast between the grass airstrip and South Hole Sound. Virtually the whole island is still in its natural state, with no paved roads, shops, or public amenities. Much of the island is covered with dense stunted trees; these areas are unsuitable for iguanas, which prefer more open habitats (Plate 1) where the limestone is partly covered with plants such as *Cordia caymanensis*, *Sauriana maritinia*, *Erodea littoralis*, *Tournefortia graphalodes* (Grant, 1940), and *Hippomane mancinella* (Carey, 1966).

On the first day of searching I was lucky enough to come across a small colony of iguanas about two miles east of West End Point and about half a mile inland from the South Coast. This group consisted of a large adult male (Plate 2) and female, two smaller females, (probably subadult), and several babies, all of which seemed to range over an area of between three to five acres. The male was characterised by its stocky build, enlarged dorsal crest and dewlap, and sagging jowl masculature. When approached it began head-nodding and broadside challenge displays, puffing itself up to appear larger. The iguanas were not usually seen before about 10.00 a.m. when they began to emerge from the holes and water-eroded passages in the limestone. They were most active during the hottest part of the day when there was frequent interaction between the four larger lizards, with the male usually chasing the larger female, and this female sometimes chasing off the smaller females. A total of nine baby iguanas (hatched 1978) were seen throughout the same area, each of which was solitary and well spaced from the next. After several days of observation the larger iguanas and most of the babies could be individually identified at a glance, and I am confident that this was probably the extent of this population.

The North and South Coasts at the western end of the island and the area between them was searched over a period of seven days, and no other iguanas were seen. Grant (1940) reported that iguanas were found all over Little Cayman, but that the populations were being rapidly reduced by dogs; he also reported a large colony on the south shore of Little Cayman at mid-island which was sufficiently isolated to escape persecution; unfortunately I did not have enough time to investigate this area or the eastern part of the island.

DISCUSSION

In January 1979 the surveying work for the planned crude oil transfer terminal had been completed and building was due to start in February; the most recent information I have is that building still had not started by January 1980 because of commercial problems, but that construction would start as soon as possible. Drawings of the proposed project show a large area at the western end of the island, stretching east to the beginning of South Hole Sound, covered with oil storage tanks and other buildings which were presum-

PLATE 2. Large male *Cyclura nubila caymanensis* on Little Cayman.

ably offices and accommodation for the crews. This would completely destroy the area inhabited by the colony of iguanas described previously.

Although I think it likely that other populations of iguanas exist on Little Cayman, it is clear that however dense they may be, the total population is bound to be precariously small simply because of the small size of the island. Even if we assume that groups of iguanas exist which are not in the immediate vicinity of the oil terminal, then their existence is bound to be threatened by the arrival of large numbers of people to build and operate the plant, and from man's pet and domestic animals. It has been clearly established that dogs will attack and kill iguanas of all sizes, and that rats and cats will prey on juveniles and eggs (Carey, 1975). Grazing animals such as goats have been responsible for the decimation of other ground iguana populations, such as those of the genus *Conolophus* on the Galapagos Islands (Hillaby, 1964), where the goats compete with the lizards for food. It is also likely that if the vegetation were to become well grazed, the juvenile iguanas would become much more susceptible to predation by birds (Dowling, 1964).

It is my opinion that the prospects for this lizard are poor indeed, since man leaves no room for animals which require specialised or restricted habitats such as these. Since 1940 when Grant described *Cyclura n. caymanensis* as common on Cayman Brac, the population there has been reduced to a single isolated colony (Carey, 1966)—this being solely due to the presence of man and the changing land use. The oil transhipment terminal proposed for Little Cayman is of such magnitude (in fact, the largest in the world) that the existence of surviving iguana populations will be threatened both from direct habitat destruction and from the greatly enlarged human population. However, steps must be taken as far as possible to ensure that this species does not follow the same fate as the Jamaican Iguana.

RECOMMENDATIONS

(I) A comprehensive survey should be carried out on all three Cayman Islands to determine the status and distribution of both *Cyclura n. caymanensis*, and *Cyclura n. lewisi.*

(II) Iguanas in the immediate vicinity of the project should be captured and removed to a safe place.

(III) A suitable area of the island should be left wild and designated as a nature reserve. However, this seems to be an extremely unlikely possibility, since the island is so small the presence of a large number of people is bound to affect surviving iguanas, and there will be increasing pressure to develop the tourist industry.

(IV) Although not a problem at present, domestic livestock should be kept within certain boundaries and feral cats and dogs destroyed. Local people and visitors should be made aware of the situation.

(V) Young iguanas should be removed, particularly from the area to be built on, for captive breeding projects, so that there will be a "reserve" of this species in captivity should anything happen to the rather small wild population. Grant (1940) reported that this species does well in captivity, and this has certainly been my impression of the six juveniles I captured and took to England. Although so far as I know *Cyclura n. caymanensis* has not been bred before in captivity (in fact I know of no zoos or other institutions keeping them), other species of *Cyclura* have been bred successfully (Haast, 1969; Roman, 1979; Shaw, 1954, 1969; Burchfield, 1973).

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BRITISH JOURNAL OF HERPETOLOGY, Vol. 6, pp. 105–108

LETTERS TO THE EDITOR

HISTORICAL ASPECTS OF BRITISH HERPETOFAUNA DISTRIBUTION

Yalden's recent article (*British Journal of Herpetology* **6,** 37 (1980)) following my own on this subject (*British Journal of Herpetology* **5,** 763 (1978)) may have caused some confusion because of implied differences of opinion which I suspect do not really exist, at least not to the extent suggested by Yalden. I would like to state straight away my view that the Yalden scenario for the events of 10,600 to 5000 years BP is a highly plausible one and it seems quite possible that the original invasion of Britain by *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* happened much as he suggests. This, however, was not the point of my own article.

The essence of my argument is that, irrespective of how the species originally became established, the creation of heathlands (including perhaps the Midland corridor) may have increased the mobility of populations in relatively recent times, *i.e.* over much of the last 1000 years, relative to that in very recent times, *i.e.* the last 100 years or so. I was careful to emphasise that the heathlands were probably never contiguous through the midlands, but it is important to bear in mind firstly that farmland has only recently become as neatly organised as it now is and that in the past quite large amounts of rough country may have connected the true heaths; and secondly that there have been mini-optima of temperatures which might have made such habitats acceptable to the rare herpetofauna. I believe that such a picture has merit in explaining the perpetuation of recent distribution patterns; for example, Yalden's attempt to explain the absence of the three species from most Welsh and south-west English dunes seems a strange cause of special pleading for chance effects to be geographically linked.

It will probably never be possible to prove or disprove much of this, but I would suggest the following overall scheme(s):

1. Invasion by the three species (among others), 10,000–9000 years BP 2. Restriction due to forest growth, 9500–500 years BP followed by expansion around developing heathlands etc.	All as per Yalden

OR

1. Invasion over period >7000–5000 BP, restricted to few suitable areas by prevalence of forest. 2. Expansion around coasts or with heaths, or both, after 5000 BP	As per Spellerberg/ Beebee

More evidence, *e.g.* from fossils, will be needed to clarify these events.

THEN

3. Population fluidity maintained along suitable corridors, varying substantially within historical times (e.g. inversely with Royal Forest protection), perhaps between >1000 to 100 years BP. 4. Increasing isolation of colonies as heathlands designed, 100 years BP to present.	As per Beebee

It was only to parts 3 and 4 that my 1978 article was addressed, and it was not proposed that the midland corridor represented the *original* route of colonisation nor that this took place within historic times (*i.e.* the last 1–2000 years). Neither of these would seem at all likely, though it is only fair to add that there is as yet no direct evidence precluding them.

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A REPLY

If my general thesis (Yalden, 1980) is acceptable to Beebee, it seems that our disagreement is largely concerned with the hypothetical corridors, through the West Midlands to north-west England, and through Essex to East Anglia, along which "population fluidity" was supposedly maintained during the last 1000 years. What evidence have we that these corridors existed? What evidence have we that they were relevant to herptile species?

The existence of the corridors is hypothesised solely from the "heath" place names. This is not persuasive evidence; "heath" is an Anglo-Saxon name, and from Beebee's map (Beebee, 1978, Fig. 1) seems to have been very widely used throughout the region formerly settled by the Anglo Saxons. One could not expect "heath" place names in Celtic, Gaelic, or Norse areas. Beebee (1978) asserts, "it is intrinsically unlikely that so complete an occupation of the north-west dune systems would have been maintained in isolation for thousands of years without some random loss of species. The most likely explanation of this must surely involve periods of greater population mobility". It is not at all clear to me why the north-west duneland populations of *Lacerta agilis* and *Bufo calamita* should not have been isolated for several thousand years; their populations were, until recently, estimated in thousands. There is other evidence that the north-western dunes have been biologically isolated for a long time. Thus there is a subspecies of Larger Wintergreen, *Pyrola rotundifolia maritima* which, in Britain, is only found there; the Tiger Beetle *Cicindella hybrida* also seems to be confined (in Britain) to those dunes, other species of *Cicendella* occurring in its place on the southern heaths and dunes. The orchid *Epipactis dunensis* is known from only eleven sites, mostly on the Lancashire dunes, but also from Anglesey and Northumberland, while the grass *Cornephorus canescens* is known from the north-west dunes and East Anglia (Perring & Farrell, 1977; Perring & Walters, 1962). The occurrence of these "dune specialists" in the north-west, despite their absence in southern England, argues for a long perpetuation of dune habitat, or something similar, in north-west England. There is no need to postulate a corridor through the English Midlands.

Is there, though, any real evidence that such a corridor existed? Beebee seems to have no clear idea of when he would expect such a corridor to be in existence, which makes it difficult to compile evidence either for or against it. If it is generally agreed (as the "ley" place names suggest—"ley" being a pasture cleared out of a wood) that the clay valleys were largely woodland until the Anglo-Saxon farmers colonised them, then the corridor would have to post-date that time. Darby (1977), evaluating the Domesday geography of 1086 AD, suggests a strongly wooded belt of country through the west Midlands from Gloucestershire to Cheshire and Derbyshire, with farmland further east. This more easterly farmland belt became the mediaeval "open field" area, now the "planned countryside" of Rackham (1976, p. 17); Beebee's assertion that "farmland has only recently became as neatly organised as it is now" is quite unjustified. Neither of these belts of country, at any time since the Norman conquest, seems especially suitable to allow or encourage the passage of *Lacerta agilis* or *Bufo viridis* to or from the north-west. And while it is true that the climate was somewhat warmer from 1000–1300 AD (Lamb, 1965) than now, the improvement was modest; it allowed some vineyards to be established in southern England, as far north as the Fenlands and south Herefordshire. Evidently viticulture was, even then, a fairly chancy business. The "mini-optimum" seems to have involved summer temperatures of a fairly modest 1.5°C warmer than now. Given our more oceanic climate, this change hardly seems great enough to allow the passage of the rarer herptiles to the north-west. If we had evidence of mediaeval vineyards in Cheshire and south Lancashire, the argument would be more convincing, but we do not.

Finally, I am accused of special pleading for chance effects to be geographically linked. Why is that special? The ice cap covered Scotland and northern England, but not the south; Scotland was depressed by the weight of the ice, below even the reduced sea level, whereas southern England was about 60 m above sea level; since the ice melted, Scotland has been rising by 3 mm/year, whereas southern England has sunk by 2 mm/year (West, 1968, p. 139). This last, in particular, will have tended to flood early-forming dune systems in south-west Britain. Interestingly, north-west England seems to be on about the axis of this tilting, this implies that the land has remained fairly level relative to the sea, and could go some way towards explaining the regular inundations which Tooley (1978) proposes for the north-west coast. Certainly, in any case, chance effects *will* have been geographically linked.

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FIRST CAPTIVE BREEDING OF THE GHARIAL (*GAVIALIS GANGETICUS*)

The gharial has bred for the first time in captivity in Nandankanan Biological Park, Orissa (Eastern India) in a pool specially designed by the senior author in 1974 and constructed by the Government of India the following year. The female, reared in captivity from a juvenile caught in Mahanadi river, Orissa, mated with a male of unknown origin obtained on a breeding loan from Frankfurt Zoological Society. Courtship and copulation in February 1980 were followed by egg-laying on 10 March. Twenty-five eggs were laid and twenty-four young hatched on 7 May 1980. The young are doing well. Full details of the design of the breeding enclosure, the technique used, and the breeding event will be published later.

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AMPHIBIAN GROWTH RATES

There seems to be considerable disagreement in the literature over the times taken by various species of European amphibians to reach sexual maturity in the wild. This was brought back to my attention by the brief comments of Cooke *et al.* (*British Journal of Herpetology* **6**, 45 (1980)) concerning newts. There have been widespread suggestions that three years or more are generally required by most species, and though no doubt there are real differences across Europe I would like to recount a few observations which stem from essentially wild populations using garden ponds as breeding sites.

1. Introductions of common frog *Rana temporaria* spawn, on four separate occasions to newly-made ponds in four different places has invariably resulted in large numbers of adults returning to spawn twenty-four months later (and every year subsequently). None appeared after twelve months, suggesting that the ponds were not simply being utilised by animals that happened to be present in the districts.
2. Parallel observations have been made on two occasions with *Triturus vulgaris* and *T. helveticus* and once with *T. cristatus*; in these instances very small numbers of adults introduced one year were followed by similar or smaller numbers returning twelve months later, and then huge increases twenty-four months after the original introduction. One particular juvenile *T. cristatus*, recognisable by belly pattern, had a habit of returning regularly to a small pool in the garden during its second year of life and the astonishingly high growth rate could be "seen" from month to month.
3. A similar experiment with *Triturus alpestris* gave different results; the large increase in adult numbers occurred after thirty-six months.
4. Observations on the growth of young *Rana esculenta* in garden ponds confirm firstly that some individuals can attain maturity after twenty-four months in Britain, but also the enormous variation between individuals. In one pool at the time of writing there are animals of *c.* 25 mm and *c.* 65 mm length from the same batch of tadpoles (only one batch has been put in) and all are only one year old.

Unfortunately I have no comparable information on bufonids, but it is certain that at least in southern England a high proportion of individuals of many species of amphibians attain maturity in two years. Also, there is no evidence of sexual disparity in this regard.

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GROWTH IN THE GHARIAL

Growth in crocodilians has been a confusing and little-known topic; most "growth" data resulting from one or a few individuals kept far from their natural habitat, often under totally unsuitable husbandry conditions. We here present the first published growth data on the Gharial (*Gavialis gangeticus*) during the first four and a half years of life.

	Mean ± S.D. (range)		
	Length (cm)	Weight (kg)	Number of Individuals
At hatching	36.1 ± 1.1 (34–38)	0.095 ± 0.006 (0.088–0.101)	39
1 year	90 ± 9.5 (71–108)	1.298 ± 0.470 (0.552–2.225)	37
2 year	142 ± 16.4 (120–159)	6.85 ± 2.58 (3.070–9.515)	10
3 year	210 ± 9.7 (193–222)	23.9 ± 2.58 (19.8–27.1)	6
4 year	248 ± 5.9 (238–353)	48.9 ± 3.25 (44.7–53.4)	5
4.5 year	256 ± 4.4 (251–263)	59.2 ± 4.05 (55.1–64.5)	5

These data are based on results of Indian Gharial grown under simulated natural conditions within the range of the species 100 m from the bank of the river Mahanadi at Satkoshia Gorge, Orissa.

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A SEX-SPECIFIC MIGRATION OF COMMON TOADS

Events at a breeding site of common toads *Bufo bufo* in the Brighton area during the spring of 1980 seemed sufficiently unusual as to warrant comment. I have inspected the breeding ponds, which are two artificial and interconnected concrete pools each some 5 m in diameter, quite regularly over the last three years and previous to 1980 the toad colony appeared normal in every way. The ponds were quite heavily vegetated and contained a few fish, and in 1978 and 1979 the toads arrived sometime during March, spawned over a period of a week or so and then dispersed in the usual manner. Very few other amphibians use these pools.

In March 1980 however the concrete basins were dry due to preparations for repair work on a leak. Nevertheless, very suddenly (over the night of 27–28 March) sixty-three adult toads appeared on the dry pond floors. These were followed the next night by twelve more animals, and finally on the night of 29–30 March by a further thirteen; eighty-eight in all. However, the most dramatic observation was that eighty-two of these toads were females. Only six males ever turned up at the site, which had been watched closely for over a month before these events and also was observed for two weeks afterwards.

All of this necessitated a rescue operation because the site is readily accessible to, and much frequented by children who carry toads away in dozens given the chance. To cut a long story short, males were obtained from two other local toad colonies operating normally (*i.e.* with excess males) and most of the females paired and spawned in captivity; these were later released in the vicinity of their dry "home" ponds since these should be available again in 1981. The spawn was allowed to develop in my own garden ponds with the hope of initiating a new colony. Because eighty-two females were too many to deal with in one garden, some were released at other local toad sites but more than fifty were ultimately returned to their area of origin.

The interesting question is, of course, why such a dramatic imbalance in the sex ratio occurred under these unusual conditions. Population studies of *Bufo bufo* at several other disparate sites by a number of workers have yielded male: female ratios in the region of 4–6:1, whereas here the ratio in 1980 was about 0.073:1. In 1978 and 1979 the usual type of male excess was observed at the site, though no counts were done, and the phenomenon seems to have been a result of the state of the ponds in 1980.

Do male and female common toads respond to different cues at breeding time? Most of the females were large and presumably quite old animals. It seems to me that they must have found their way to the ponds by memory alone, with no olfactory or other senses being involved. I do not know whether younger females strayed away or whether there has been little recent recruitment (child predation of spawn is very heavy) so that young females are rare. Male toads, on the other hand, usually arrive first and may respond to the "smell" of the water as frogs do. I cannot however think of any convincing reason by natural selection should have favoured the emergence of such sex differences and perhaps one should not read too much into one year's observations of a single colony. It will certainly be interesting to see what happens in 1981.

One other pertinent fact is that the females all arrived over the same period that other toad colonies were starting to breed in Brighton, so their timing was unaffected by the lack of water in the ponds.

I would be most interested to hear of any comparable observations or any possible explanations.

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BOOK REVIEWS

WILDLIFE INTRODUCTIONS TO GREAT BRITAIN. Report by the Working Group on Introductions of the U.K. Committee for International Nature Conservation. Published by the Nature Conservancy Council, 1979. 32 pp, £1.20p.

This document represents a major attempt by the Nature Conservancy Council to come to grips with an increasingly important issue in wildlife conservation and management. Both the extent to which alien species have invaded the U.K. (with more than a little help from *Homo sapiens*) within historical times and the problems of understanding and controlling the effects of such species are discussed. The terms of reference of the working group are clearly spelt out, and it is made plain from the start that the publication does not (yet at least) mirror government policy nor are the recommendations specifically supported by law. Advice was sought from some fifty individuals and organisations including the British Herpetological Society.

After an initial discourse on definitions and a summary of relevant topics such as convergent evolution, island biogeography and the poverty of the U.K. flora and fauna the real substance of the discussion is dealt with under "benefits", "problems" and "actual impact" of introductions, reintroductions etc. Much of this has little relevance to herpetology, since (for example) the economic consequences of introductions feature strongly in general discussion but scarcely apply to reptiles and amphibians unless perhaps we start eating frogs' legs. However, some points are worthy of note. The use of introductions and reintroductions as positive conservation tools received qualified support; on the other hand, problems which could apply to herpetofauna translocations include predation of or competition with native species, depletion of the source material from its original habitat and genetic mixing. The latter is dealt with rather vaguely in the report, and is a bogey which the conservation committee has had the most trouble with in debate. Poorly thought-out genetic arguments can be unnecessarily restrictive in the field of conservation, and it will surely prove impossible to make general rules on this point without much more debate. The working group also concedes that only a very small proportion of introduced species has become widespread and even fewer have posed problems as a result, putting the issue in some sort of perspective. Nine species of reptiles and amphibians are listed as recent introduction, only one of which (*Rana ridibunda*) is considered to have become quite widespread and none of which could be described as troublesome. Finally, there are the policy guidelines. The use of legislation to restrict imports of exotic species is recommended (some of which already exists) and with regard to introductions either between countries or within a country it is suggested that: these be considered "guilty until proved innocent"; an appropriate "Introductions Authority" be set up to vet and monitor proposals; and that the possibility of a "low risk" category of species (which may well include herpetofauna) be examined. Reintroductions should be subject to similar controls except that the premise against them be "less forceful" (whatever that means), and perhaps without statutory controls when translocations are within the same country though guidelines are still required.

Whether or not such formal machinery is ever set up it is evident that the movements of all animals and plants will be increasingly scrutinised in the future. There are some aspects that could relate to herpetofauna which are not spelt out in this report: I would like to have seen some comment that introductions from distant continents such as North America are more likely to be harmful (in a competitive sense with native species) than those from Europe; and difficulties in defining what is an introduction as opposed to a reintroduction, which within a country often depends upon very inadequate historical recording, are important problems in practise when trying to justify a proposed translocation of animals and likely to become even more crucial if the report's recommended guidelines are formally adopted. Nevertheless, this is an interesting publication well worth reading by anyone involved in this contentious field.

There are three annexes: introduction and reintroduction policies expounded by IUCN, SPNC and WWF; a list of species already introduced into the U.K.; and current legislation (no less than 28 Acts since 1932!) relevant to these issues.

T. J. C. BEEBEE

BIOLOGY OF THE REPTILIA, Volumes 9 and 10. *Neurology*, Edited by R. G. Northcutt and P. Ulinski (1979). 462 pp. London and New York: Academic Press, £30.

The contributors to, and publishers of, these volumes are to be congratulated for the high standards to which they have adhered. There can be no doubt that the books make a major contribution to our knowledge of reptilian nervous systems. All libraries that cater for vertebrate zoologists, comparative physiologists or comparative neurologists will undoubtedly need to acquire them.

Although the actual formulation of the individual contributions inevitably reflects the particular preoccupations of the late 70's they cover most aspects of reptilian neurology. It may just seem that to have one whole article on the parietal-pineal eye complex, and another that covers all aspects of the brainstem, will seem odd when looked at with hindsight in the future. Nevertheless, the reader who wishes to obtain a topical review of, for example, paleoneurological, embryological or forebrain studies will find a wealth of information here. Furthermore, the data are frequently discussed alongside brief reviews of the situations in other taxa, thereby encouraging a commendable panoramic approach.

I personally found the contributions of Donkelaar and Nieuwenhuys, Schwab, Parent and Belekhova dealing with the brainstem, monoaminergic systems and forebrain the most informative. However, it is clear that this just reflects my own idiosyncrasies and I do not hesitate to urge all workers who have an interest in brain studies to peruse these books. They will undoubtedly find something that furthers their education and many will find that most of the articles make a sound addition to their teaching and research.

R. PEARSON

TURTLES: PERSPECTIVES AND RESEARCH. Edited by Marion Holmes and Henry Morlock (1979). 695 pp. New York, Chichester, Brisband and Toronto: John Wiley & Sons, £30.

This is a massive book—695 pages containing 26 chapters. These are divided into sections on: taxonomy, evolution and zoogeography; methods; vital functions; sensory processes; behaviour; population dynamics. From the outset it should be stated that the book is not about turtles, it is about chelonians in general, and that the balance of subjects is rather heavily weighted towards the behavioural sciences. Perhaps neither of these points is surprising since the book is American and the editors are psychologists.

Like most multi-authored books, the quality is highly variable; some articles are excellent, others are mediocre, and some are bad. In testing its value, I applied my usual criterion of looking at subjects I know something about and at some of those I know nothing about. For the former I chose the chapters on laboratory maintenance (Campbell & Busack), anaesthesia and surgery (Maxwell) and feeding, drinking and excretion (Mahmound & Klicka); for the latter, I chose collecting and marking (Plummer), population dynamics of sea turtles (Bustard) and rhythms (Gourley).

The chapter on laboratory maintenance I found useful although there was evidence of lack of understanding of underlying principles. Thus bone phosphates are recommended as a dietary additive to provide extra calcium. What is needed of course is a non-phosphate source of calcium to obtain a correct calcium:phosphorus ratio in the diet. Shell disease rates but one paragraph. The chapter on anaesthesia and surgery I found useful although the description of some procedures was so perfunctory that a simple reference to published work would have been just as useful. The chapter on feeding, drinking and excretion I found poor, particularly the section on excretion; there was no evidence of breadth or depth of knowledge.

Plummer's chapter I found very useful, as I did that of Bustard on turtles because it reveals what little is really known of turtles in the wild. Again Gourley's short chapter points the way for research on biological rhythms in chelonians.

In all I would recommend this book to all engaged in research on chelonians and to those with a scientific interest in these fascinating animals.

M. PEAKER

TORTOISES OF AUSTRALIA. By J. Cann (1978). Melbourne: Angus and Roberton. $A 10.95.

Cann's book is the first published for over ten years devoted to Australian fresh water tortoises (Chelidae). It covers all known species of Australian tortoises, together with concisely arranged details of their distribution, description and habits, including information on food preferences in the wild and in captivity, and the treatment of common diseases in captivity. The text is accompanied by excellent colour photographs, not only of individual specimens, but also the habitats in which they are found. Of particular note is the chapter concerned with collecting tortoises, outlining the methods and equipment associated with diving and fishing for tortoises. Further details of the soft-shelled tortoise *Carettochelys insculpta*, first recorded in Australia in 1969, are given, together with preliminary notes and photographs of eleven so far undesribed specimens, (including the possible re-discovery of *Emydura victoriae* Gray 1842).

Overall the book is well recommended as an up-to-date and authoritative work on an often neglected group of reptiles.

R. N. PADDLE

AMPHIBIANS OF SOUTH AUSTRALIA. By Michael J. Tyler (1978). 84 pp. Adelaide: South Australian Government Printer. $A 2.40.

This is an excellent publication that makes an informative companion to the two other guides covering all of the Australian anuran fauna (Cogger, H. G. 1979. *Reptiles and Amphibians of Australia*; Barker, J. and Grigg, G. 1977. *A field guide to Australian frogs*). It is something more than just a book on South Australian frogs. The author devotes thirty pages to discussions on the biology, systematics and zoogeography of Australian frogs. It is well illustrated with colour and black & white photographs, maps and drawings. The section on South Australian frogs has detailed information on the genera and species. The glossary is useful and the references are a handy introduction to the Australian anuran literature. The frog *Ranidella deserticola* was included although it had not been recorded from South Australia. However, it has been collected recently in that State (Brooks, J. (1980). *Sth. Aust. Nat.* **54,** 55).

The only reservation to consider when buying this book is that South Australia has a depauperate frog fauna (22 species) compared to the rest of Australia excepting Tasmania (160 species).

G. J. INGRAM

ENCYCLOPAEDIA OF TURTLES. By P. C. H. Pritchard (1979). 895 pp. Hong Kong: TFH Publications.

This massive book is an updated version of the author's *Living Turtles of the World* (1967) and is about chelonians, not just (marine) turtles. In many respects it is an old-fashioned natural history à la Gadow, and to review it requires that the book be divided into text, illustrations and production.

Much of the early part of the book is concerned with anatomy and physiology. Here the author falls between two stools—insufficient breadth (there are some glaring omissions in physiology) or depth for the professional, far too much abstruse osteology for the amateur (and many a professional). Nearly all the rest of the book (and the reason why sales will be high) describes the individual extant (and sometimes extinct) species and sub-species, often in great detail. The text is often ponderous and unbalanced in coverage (but the author's enthusiasm does shine through) but it is generally valuable and clearly the author has performed a great service in bringing the information together. The chapters on conservation and exploitation are well worth a read but that on captive care is too short and contains too little modern information.

Some of the colour illustrations are excellent, others have gone awry in terms of colour rendering. Unfortunately, colour plates bear little relation to the text and cross-reference is difficult. It is made even more difficult by plates from the 1967 book being put in completely out of order! The black-and-white illustrations are horrid and are so badly reproduced that many of them are useless. Similarly, some of the unlabelled line diagrams serve no useful purpose.

The quality of production is by no means high. Flaws in the type, badly positioned illustrations and legends all mar the book and there are errors which should have been spotted at the proof stage.

The book as a whole seems to lack the touch that can only be achieved by a good editor and sub-editor, and the whole style seems wrong. Surely, a species-by-species account could by hard editing and good production techniques have been achieved with headed sections and illustrations within the text.

There is no doubt that cheloniophiles will find it very useful even if the information is hard to extract. I would expect sales to be high even if for only it covers all species of the world. Thoughtful presentation, good editing and production could have made this into a classic.

M. PEAKER