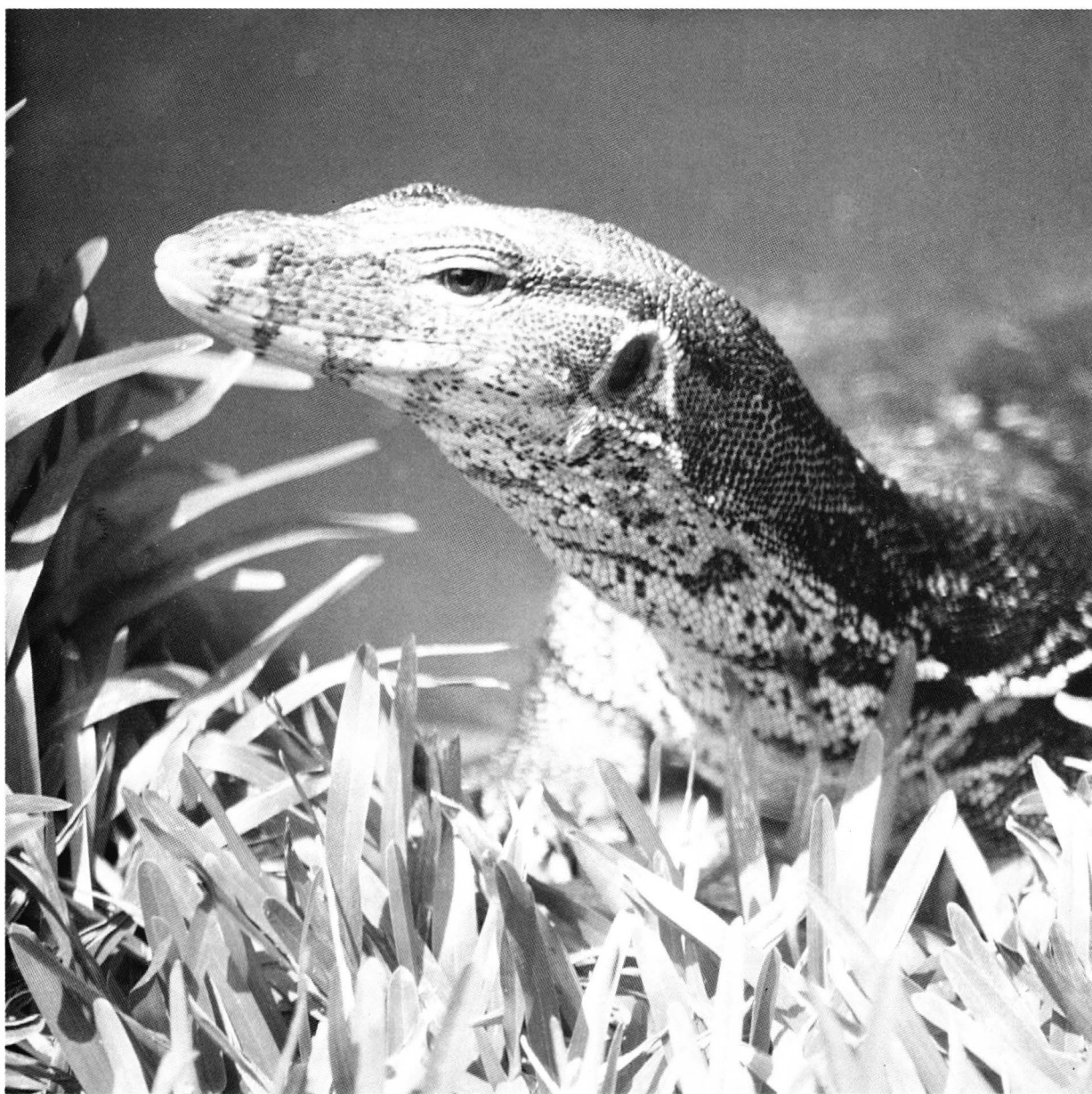


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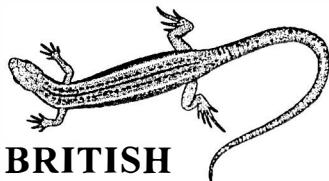
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FRONT COVER: *Varanus salvator* (J. Foster).

ESTABLISHMENT OF POPULATIONS OF THE COMMON FROG, *RANA TEMPORARIA*, AND COMMON TOAD, *BUFO BUFO*, IN A NEWLY CREATED RESERVE FOLLOWING TRANSLOCATION

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The establishment of large populations of common frogs *Rana temporaria* and common toads *Bufo bufo* was monitored for six years in a newly-created reserve, following stocking with spawn of both species and with toads rescued from a site to be destroyed. Frog spawn output reached a peak three years after the initial introduction. There was high mortality and/or emigration (64% loss) during the first year following translocation of over 5,000 adult male toads. Thereafter male mortality decreased and/or site fidelity increased: 39% loss year 2 to 3, 42% loss year 3 to 4. Comparable data were not available for the 795 females translocated, but there is no reason to believe their mortality was lower. Transfer of spawn is probably more effective as a means of establishing a new population of toads than transfer of adults. Counts of male toads peaked after three years, but delayed sexual maturity of females meant that counts of pairs and estimates of spawn output continued to increase for about six years. Age determination in a sample of 43 male toads showed that length was significantly related to age, but there were some notably disparate rates of growth. A sample of 16 females showed no correlation between age and length. The greatest recorded losses of naturally-laid spawn of both species (up to 16% in one year for the frog and 39% for the toad) were due to desiccation, presumed collection by people and fungal infestation.

INTRODUCTION

Amphibian translocations (*sensu* Griffith, Scott, Carpenter & Reed, 1989) are usually performed in response to the need to evacuate a threatened population. The familiar dilemma is to choose a suitable recipient site. If the target site does not contain a population already, the habitat may be unsuitable. On the other hand if a population already exists, introduction is likely to cause it to exceed the carrying capacity of the habitat; the introduction simply leads to increased mortality of either the introduced or the native population, or of both. A more promising situation exists if a new target site is created with "built in" maturity, or a degenerate site is enhanced. In our case the situation was propitious; the creation of an amphibian reserve in Peterborough, at a site previously unoccupied by amphibians, pre-dated by two years, the destruction of a large toad *Bufo bufo* breeding site 50 miles away in Leicestershire. Frogs *Rana temporaria* and smooth newts *Triturus vulgaris* were available for introduction from local threatened sites and from "surplus" spawn. There was no attempt to include crested newts *Triturus cristatus* because of the presence of fish in the new reserve. If rescue is the primary objective of translocation there is often no choice of the component of the population that is moved; only one life-history stage may be available.

There was sufficient warning with the toads so that eggs were available in one year and adults the following year. For the frogs only spawn was available and for the newts only adults.

The Boardwalks Reserve was created in 1985 by the former Peterborough Development Corporation. Of its total area of 6 ha, about 3.5 ha was set aside for amphibian conservation. It is believed that this is the first reserve of this size in Britain to be specifically established for amphibians. Its creation was motivated by the fact that, with the exception of the common frog, all the native British amphibian species appear to be declining (Hilton-Brown & Oldham, 1991). Even for the frog, although there was an increase in many parts of lowland England in the 1980s, probably through its success in garden ponds, large populations in semi-natural habitat, readily accessible to the public, remain a rarity in many areas.

A review by Dodd & Seigel (1991) casts doubt on the effectiveness of RRT (relocation, repatriation and translocation) programmes as a conservation strategy; indeed they could find no recorded instances of success for amphibians (although Reinert, 1991, cites three instances). They emphasize the importance of defining criteria for successful RRT, and of long-term monitoring to determine success, and suggest that success should only be claimed if there is evidence of establishment of "a self-sustaining population" which is "at

least stable". In Britain the crested newt has been the subject of nearly 100 translocation attempts in the late 1980's (Oldham, Musson & Humphries, 1991), but with inconclusive results owing to inadequate attention to monitoring. Dodd & Seigel (1991) recommend that introduced toad populations should be studied for 10 to 15 years. However, as pointed out by Burke (1991), stability is dependent upon timescale and no population is indefinitely and invariably stable. Our intention was to establish self-sustaining and relatively stable populations of significant size for two of the introduced species; frogs and toads. For the relocations to be judged successful, the frog population would need to number in excess of 100 adults and the toad population in excess of 1000 adults (Cooke, 1975). We decided to continue monitoring the site each breeding season until the translocations failed or until the populations stabilised. At the end of each breeding season we assessed whether monitoring would continue. This phase of monitoring is now complete and the results are presented in this paper.

In summary, our aims were: (1) to introduce a frog population using spawn, and to monitor its success at the new reserve; and (2) to introduce a toad population, monitor its success and, if possible, compare the relative merits of introducing spawn and adults.

MATERIALS AND METHODS

STUDY SITE

The Boardwalks Reserve is 6 ha site in size and occupies a low-lying marshy area on the north bank of the River Nene near the western edge of the city of Peterborough. A south-facing embankment runs along the entire northern boundary of the site; beyond that is a playing field. The western part of the reserve was designed as a scrape for wading birds, having a single large pool with an irregular edge and four small islands. The remainder of the site, about 3.5 ha, was created for amphibians in 1985 by excavating 13-16 pools (the number depends on the water level). The largest pool measures about 125 x 15 m with the smallest about 2 m across. The river frontage to the amphibian area is roughly 450 m and its width ranges from 70 to 100 m. In several winters the river has inundated the reserve and presumably as a direct consequence, fish have been recorded in most of the ponds. The marsh vegetation is dominated by common reed *Phragmites communis*, reed sweet-grass *Glyceria maxima* and reed canary-grass *Phalaris arundinacea*. Existing willows *Salix* sp. were retained and much tree planting and seeding of the ponds and their edges were undertaken. The vegetation is now managed by the Peterborough Wildlife Group.

TRANSLOCATION

In the spring of 1986 about 200 clumps of frog spawn were introduced, from garden ponds in the Peterborough area, with a further 150 clumps in 1987

TABLE 1. Introductions of frog spawn, toad spawn and toads to Boardwalks Reserve.

| Year | Frog spawn clumps | Toad spawn (approx. egg no.) | Toad adults |
|------|-------------------|------------------------------|-------------|
| 1986 | 200 | 500 000 | 0 |
| 1987 | 150 | 0 | 5911 |

(Table 1). In 1986 about half a million toad eggs were transferred from a site due to be opencast-mined in Leicestershire. In 1987, 5911 toads were rescued early in the breeding season from the same site and transferred to the Boardwalks reserve; 5116 were males and 795 females. The distal phalanx of one particular toe was removed from 76% of the toads. The remaining 24% were variously tagged as a result of natural injury or toe-clipping at the donor site in the previous year. Apart from relatively small numbers of smooth newts *Triturus vulgaris* released by the first author and small amounts of frog spawn deposited at the site by the public (eight clumps in 1990, four in 1991 and 14 in 1993), no other translocations were recorded. Such deposited spawn can be readily distinguished from spawn naturally laid (Cooke, 1985).

MONITORING

Between 1986 and 1993 the reserve was visited from one to three times per week, from prior to the first spawn being laid until after the spawn had hatched. Monitoring input at other times of year was variable. Routine monitoring visits were always during daylight. In the early years the entire edge of every pool in the amphibian area could be checked easily. All of the edges to all of the ponds were shallow. It was also possible to see into the centre of each pond, water clarity always being good. As freshwater and terrestrial vegetation developed, it became more difficult to check the entire edge of each pond. Any floodwater was thoroughly checked for spawn or adults by wading.

Monitoring of frog reproduction was based on counting spawn clumps. For toads, insufficient time was available to permit mark-recapture estimates of population size during each breeding season. Instead, adults were counted and peak counts for all adults and for pairs were taken as measures of breeding activity that year. An attempt was made to undertake at least one count during peak season for toads during calm, mild and sunny conditions. The duration of the toad breeding season was recorded each year in an effort to assess whether the peak counts were comparable as indicators of the breeding population size. The season was deemed to have started when at least 10 toads were seen in the ponds on a single occasion and to have fin-

ished on the last day that new spawn was observed. As an additional measure of population size, particularly of the female component, an index of abundance of toad spawn was devised. The only reference found in the literature to counting strings of toad spawn was that of van Gelder (1973) and this gave no details about the method used. The technique developed at the Boardwalks reserve involved using a cane to probe through ponds to find and estimate spawn strings by gently lifting them to the surface. The estimation was based on being familiar with what appeared to be a single string and then using this knowledge to estimate by eye the content of masses. During the course of the study guidelines were developed. Thus a mass concentrated more or less in 0.2 m² was taken to be five strings, whereas a larger mass in 1 m² was counted as 20 to 30 depending upon the density of the strings. The total, a spawn count index, was expressed as a range. The technique was developed to make comparisons and was not intended as an absolute measure. One additional comparative use to which it was put was to permit determination of the percentage of spawn lost each year to human collection and other factors. It was of interest to calculate this for both species in view of the huge losses suffered by frogs during the 1970s at a similarly accessible site in the area (Cooke, 1985). The monitoring programme finished in 1993. During that year it was not possible to visit the reserve precisely at peak breeding time for toads, but spawn for both species was still recorded.

From 1988 to 1990 samples of between 100 and 200 toads were caught at the site at night. These were measured (snout to distal tip of the urostyle) and examined for earlier toeclips. Toads already marked were remarked using a "Panjet" and any new toads were marked using a year-specific toeclip. The toe tips removed in 1990 were frozen and a subsample subsequently examined using the technique of skeletochronology described by Hemelaar & van Gelder (1980).

Monitoring also provided a means to enable remedial action to be identified and then taken when necessary during the establishment phase. Examples of this included moving spawn to prevent desiccation, and provision of information on the behaviour of the populations that could be taken into account when planning management of the site.

MONITORING RESULTS

ESTABLISHMENT OF POPULATIONS

No adult frogs or naturally-laid spawn were recorded on the site in 1986 or 1987 (Table 2), but frogs of sub-adult size were seen in 1987. Emergence from the translocated spawn was judged to be good in 1986, with froglets being abundant in mid-summer all over the eastern half of the site. However, in 1987 emergence was evidently much poorer with froglets being hard to find. The population which became established

TABLE 2. Counts during the breeding season (N/A = not available).

| Year | Frog spawn clumps | Peak total toad count | Peak count of pairs of toads | Spawn count index |
|------|-------------------|-----------------------|------------------------------|-------------------|
| 1986 | 0 | 0 | 0 | 0 |
| 1987 | 0 | N/A | N/A | 30-50 |
| 1988 | 92 | 127 | 6 | 22-27 |
| 1989 | 162 | 311 | 7 | 29-34 |
| 1990 | 121 | 181 | 10 | 58-63 |
| 1991 | 147 | 328 | 34 | 100-105 |
| 1992 | 117 | 306 | 54 | 105-110 |
| 1993 | 112 | N/A | N/A | 107-114 |

was therefore assumed to have resulted from the translocated spawn, especially that introduced in 1986. In 1988 92 clumps were laid naturally (Table 2), indicating that many frogs matured in two years. A peak number of 162 clumps was reached in 1989, since when numbers have ranged 112-147.

In 1986 no adult toads were seen at the site, and no naturally laid toad spawn was noticed (Table 2). The first toad spawn recorded at the site was in 1987, presumably laid at least in the main by the introduced adults; no spawn was recorded that spring until after the first adults had been released. This spawn, as well as that introduced in 1986, produced good numbers of toadlets. Their numbers were not estimated, but in late May 1987 there was a visual assessment of tens of thousands of shoaling tadpoles in one pond and thousands in two others.

In 1988, 64% of a sample of male toads, and 89% of a sample of females, were found to be marked, indicating that the majority of the breeding population was originally from Leicestershire. The unmarked toads were either animals which had grown from the toad spawn introduced in 1986 or were "natives", immigrants from surrounding populations. A histogram of length measurements of these toads (Fig.1) suggests that both explanations might apply, with the smaller unmarked toads up to about 57 mm originating from the 1986 spawn and the few above 58 mm being local immigrants. The recaptured males from the original group, introduced in 1987, were clearly larger animals with mean length 59.4 mm (cf. 55.2 mm for all new males). Only adults were translocated from Leicestershire, so if the minimum adult age is assumed to be two

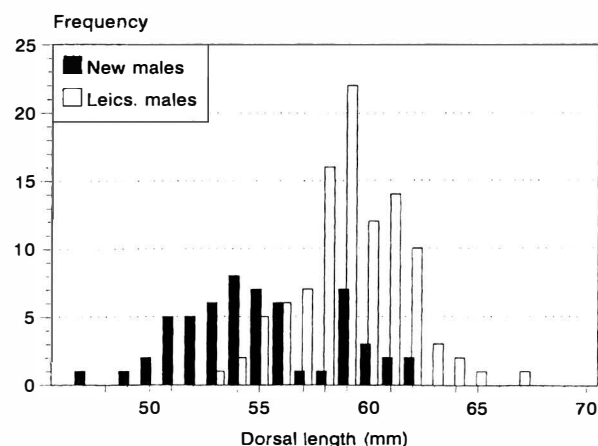


FIG. 1. Length frequency distribution of male toads caught in 1988.

years (Gittins *et al.*, 1985; Reading, 1991), the recaptured males were at least three years old in 1988. Considerably less spawn was apparent in 1988 than in 1987 (Table 2), probably reflecting a reduction in the female population, not yet augmented by new females developed from the 1986 or 1987 spawn.

The first 'peak count' of toads was derived in 1988 (127 total count including six pairs, Table 2). The use of peak counts as indicators of population sizes in successive years depends upon a comparable profile of breeding numbers during each season; a protracted season might result in lower counts than an "explosive" season. We accepted the peak count as a meaningful indicator of population size because the duration of the season each year was relatively constant, with a range from eight to 14 days (standard deviation of 2.5 days). There was no evidence of an inverse relationship between season length and peak count ($r=0.01$).

By 1989 only 21% of a sample of males caught comprised marked animals from the original Leicestershire group. Their mean length (Fig. 2) was 61.5 mm (cf. 59.4 mm in 1988). The mean length of new males, including those few (2%) marked for the first time in 1988, was 56.8 mm (cf. 55.2 mm in 1988). The range of lengths of the new males had also increased, by 6 mm (48 to 69 mm, cf. 47 to 62 mm in 1988) and there was a complete overlap with the old Leicestershire males at the upper end of the scale. Either there was a disparate rate of growth within the population or there had been an influx of new large males. The wide frequency distribution of the Leicestershire males (Fig. 2) adds weight to the former possibility. The smallest members of this founding population were still only 53 mm, yet they were at least four years old. In 1989, although there was little change in the number of pairs counted or the spawn count index, the maximum count of adults (mainly of unpaired males) more than doubled (Table 2). Most of the newcomers may have been males from the 1986 spawn returning to breed as three

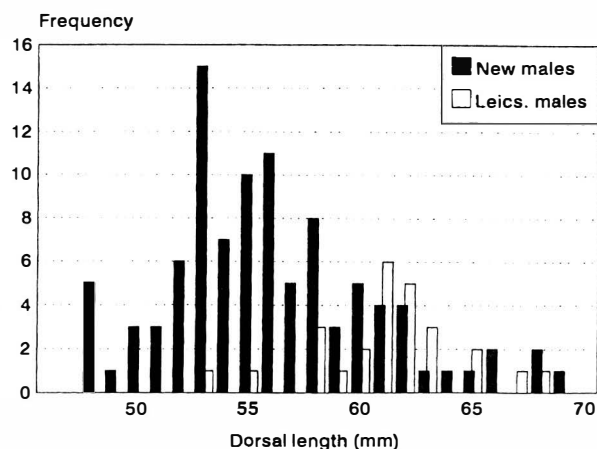


FIG. 2. Length frequency distribution of male toads caught in 1989.

year olds, perhaps with some two-year-olds from the 1987 spawning.

By 1990 the proportion of recaptures from the Leicestershire group had fallen to 15% of the catch. The new males, including the small proportion (4%) first marked in 1988 or 1989, had an average length of 59.0 mm (Fig. 3), the Leicestershire males 61.4 mm, the length range of the former completely enveloping that of the latter.

Toe samples from 43 males and 16 females of the 1990 captures enabled ages to be estimated. 'New' males ranging between 53 and 62 mm in length had ages estimated between two and five years (Fig. 3) whilst eight of the founding population, between 56 and 64 mm, had ages between five and seven years. No allowance was made in the age estimation technique for the possibility of bone resorption (Hemelaar & van Gelder, 1980; Gibbons & McCarthy, 1983), so some of the ages may have been underestimated. Overall, for the males, although there was a significant correlation between estimated age and length ($P<0.001$), only 31% of the variation in length could be ascribed to age. There were several deviations from a straight line relationship (Fig. 3); two individuals had apparently achieved 57 mm in just two years, whilst at the other extreme a six year old was only 56 mm. All of the new males, except two, could have originated from Boardwalks spawn: the four-year-old animals from the spawn introduced from Leicestershire in 1986; the three- and two-year-olds from spawn laid in 1987 and 1988, respectively. Only the two five year old animals (56 & 61 mm, Fig. 3) would seem to have originated from a local site prior to the creation of the reserve. Ages of 16 unmarked females caught in 1990 were determined as three years (nine animals), four years (6) and five years (1). For the females there was no significant correlation between length and age. The smallest and largest females (67 and 85 mm, respectively) were each estimated to be four years old. The five-year-old animal was 77 mm long.

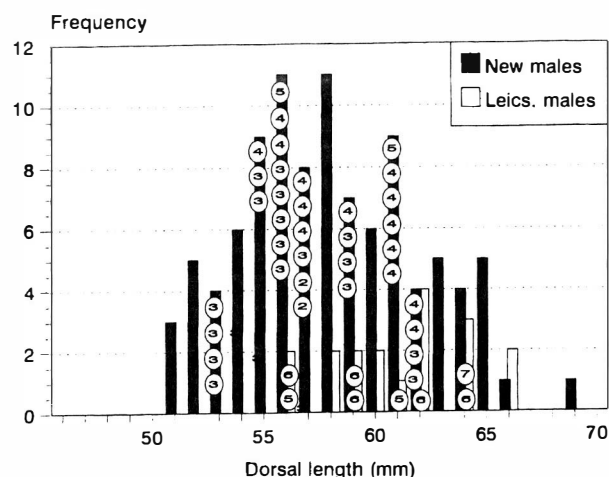


FIG. 3. Length frequency distribution of male toads caught in 1990. Ages of 43 males, estimated using skeletochronology, shown against the appropriate length.

The spawn count index in 1990 showed a considerable increase on 1989 (Table 2), probably a reflection of recruitment of females developed from the 1986 and 1987 spawn.

After 1990 no further captures were made to check for marked toads. There was a major increase in the spawn count index in 1991, coupled with an increase in the peak counts of adults and of pairs (Table 2). Although there was a comparable increase in the peak count of pairs from 1991 to 1992, increases in the spawn count were negligible in 1992 and 1993 (Table 2). It is possible that the population size had more-or-less stabilised by 1993.

Application of Jolly's mark, release and recapture method of population size determination (Blower *et al.*, 1981) to the male segment of the population between 1987 and 1989, if it is assumed that there were no native animals at the site in 1987, suggests the population and survival values shown in Table 3.

There are large standard errors, especially for the 1989 estimate, a reflection of the relatively small samples taken (116 to 159) compared to the number originally marked. Tentative ranges of estimates for 1990 to 1992 are obtained by back calculation from the peak count records of males. We felt justified in this extrapolation since the ratios of peak count to population estimate for 1988 and 1989 (1:19 and 1:24, respectively) are reasonably consistent.

Table 3 also includes estimates of the founding population for males in the first three years following introduction. These are obtained from the ratio of marked to unmarked animals caught in the samples in these years. The proportion of recaptures declined each year, partly because of dilution by new recruits and partly because of mortality or emigration. The results indicate high mortality or emigration in the first year when there were losses of 64%, but reduced mortality or increased site fidelity thereafter; during the second year there was only a 39% loss and even in the third year the loss, estimated at 42%, was still not as high as in the first year, despite the fact that by this time the toads were at least five years old.

TOAD SPAWN ESTIMATION TECHNIQUE

For the period 1988-1992 mean spawn count index was significantly related to the peak count of pairs ($P < 0.01$): \log_{10} mean spawn index = $0.98 + 0.64 \log_{10}$ peak count of pairs. The ability to find spawn was tested in 1989 and 1992 by netting and searching ponds for toad tadpoles in mid-May. During the springs of 1989 and 1992 there was a combined total of 27 separate water bodies. The ten in which spawn had been recorded earlier contained tadpoles in May. Six ponds in which unpaired toads had been recorded and nine others with no records of toads did not appear to contain tadpoles. However, the remaining two ponds (in which adults had been recorded, but no spawn) did

TABLE 3. Annual male toad population estimates. a, known no. introduced; b, Jolly's method; c, from peak count; d, from ratio in sample.

| Year | Est. population size | Survival | Peak count | Founding pop. size | Founding pop. survival | New adults in population |
|------|------------------------|------------------|------------|-------------------------|------------------------|--------------------------|
| 1987 | 5116 ^a | | | 5116 ^a | | |
| 1988 | 2890±1420 ^b | 36% ^b | 121 | 1840 ^{b&d} | 36% ^b | 36% ^d |
| 1989 | 5620±4140 ^b | 66% ^b | 304 | 1120 ^d | 61% ^d | 79% ^d |
| 1990 | 3180-4100 ^c | | 172 | 650 ^d | 58% ^d | 85% ^d |
| 1991 | 5430-7010 ^c | | 294 | | | |
| 1992 | 4660-6010 ^c | | 252 | | | |

contain tadpoles in May. Thus 25 (93%) of the 27 ponds gave the expected qualitative result. Some toad tadpoles were also found in the wader scrape in 1992; although adults were recorded there in the breeding season, no spawn was ever found. Occasionally adult toads were noted in the river, but no spawn or tadpoles were recorded.

The data in Table 2 and the equation above indicate that the ratio, *spawn count index: maximum pairs*, decreases as the pair count increases. For example, from the equation: when the pair count = 5, then spawn index = 27 and ratio = 5.4 and when the pair count = 50, then spawn index = 117 and ratio = 2.3. If the counts are a genuine reflection of numbers present, this relationship suggests that the spawn count technique is less satisfactory as the density of spawn increases; or alternatively pairs may be easier to observe at higher population density. A similar relationship existed on an individual pond basis for water bodies in which both pairs and spawn were recorded between 1990 and 1992 ($n = 15$, $P < 0.01$): \log_{10} mean spawn index = $0.71 + 0.63 \log_{10}$ peak count of pairs.

FATE OF SPAWN

Collection and desiccation proved the most serious forms of loss for frog spawn (Table 4). The only instances of a different type of loss was minor hatching failure in 1992 and 1993. Floodwater was available outside the confines of the ponds in 1988 and 1990, and in those two years frogs laid 88 and 12% of their spawn respectively in the floodwater. In 1988 the first author moved this spawn to deeper water; the floodwater dried out during the tadpole phase. The desiccation losses of spawn in 1990 were almost entirely due to floodwater disappearing during the spawn phase. In

1991 the spawn season coincided with a deliberate lowering of the water level in the River Nene by about 2 m in order to remove rubbish. The ponds are all within 100 m of the river bank. The local water table was evidently affected severely, with the levels in the ponds falling by 0.3-1.0 m depending on their location. As the levels receded, spawn became stranded. Without intervention, 74% of the spawn would have been lost; however, pushing spawn into deeper water restricted losses to 13-16%. Losses, assumed to be due to collection, occurred each year and ranged from 3% to 12%, with an overall loss of 8%.

Unlike frog spawn which suffered some losses every year, toad spawn had no recorded losses in three years out of seven (Table 4). Overall percentage loss of toad spawn did not, however, differ greatly from that of frog spawn. In 1990 up to 12% was lost through being deposited in the shallow edges of ponds in which the water level went down. Partial desiccation resulted in a further unquantified amount of spawn suffering fungal attack. Up to 13% was taken or broken up by people or other animals in the same year. In 1991 desiccation losses of about 31 to 39% occurred following the sudden lowering of the water level in the river (see above). Without intervention these losses may have reached 78%. Actual losses to desiccation in 1991 were thus at least twice as high as losses of frog spawn; the fine strings of toad spawn with a higher ratio of surface area: volume appeared less robust to desiccation stress. In 1993, 31 to 42% of the toad spawn suffered a low hatch rate following fungal infection.

CONCLUSIONS

Many frogs evidently matured in two years as there was substantial spawning in 1988 following the initial

TABLE 4. Percentage of spawn lost through various causes. (* = some loss due to fungal attack, not quantified).

| Year | FROG SPAWN | | | | TOAD SPAWN | | | |
|------|------------------|----------------|-------------------|-------|------------------|----------------|-------------------|--------|
| | Desiccation loss | Loss to humans | Fungus, low hatch | Total | Desiccation loss | Loss to humans | Fungus, low hatch | Total |
| 1987 | - | - | - | - | 0 | 0 | 0 | 0 |
| 1988 | 0 | 8 | 0 | 8 | 0 | 7-9 | 0 | 7-9 |
| 1989 | 0 | 6 | 0 | 6 | 0 | 0 | 0 | 0 |
| 1990 | 12 | 10 | 0 | 22 | 11-12 | 12-13 | * | 23-25+ |
| 1991 | 13-16 | 12 | 0 | 25-28 | 31-39 | 0 | 2 | 33-41 |
| 1992 | 0 | 3 | 1 | 4 | 0 | 0 | 0 | 0 |
| 1993 | 1 | 0 | 2 | 3 | 0 | 0 | 31-42 | 31-42 |

introduction of spawn in 1986. This seems to be typical for introductions to good areas in lowland Britain (Beebee, 1980, 1986; Cooke, 1981). Beebee (1986) describes an introduction to a garden which took five years to attain peak numbers. This contrasts with the Boardwalks, where peak numbers were reached three years after the first introduction of spawn. Spawn introductions at the Boardwalks may have been sufficient for the carrying capacity of the environment to have been quickly attained, especially in view of the good metamorphosis in 1986. Amounts of spawn introduced in 1986 and 1987 were roughly comparable to amounts laid at the site later.

Assuming that all of the frog spawn was found, that an adult female frog lays one clump of spawn per annum and that there is a sex ratio of unity (see Savage, 1961; Blackith & Speight, 1974; but contrast Oldham, 1963; Heusser, 1970), the adult frog population numbers 200-300. Thus we achieved our aim of establishing a frog population with >100 adults. Based solely on the core area of the amphibian reserve, this represents a density during the breeding season of 60-90 adults/ha, but presumably they forage at other times of year into the waderscape area and more widely too. The nearest spawn to the Boardwalks was found 400-500 m away.

The data on toad sizes (Figs. 1-3) and age distribution (Fig. 3) suggest that most of the population characteristics at the site were the result of introduced toads or of introduced spawn, with little contribution from toads native to the vicinity of the Boardwalks Reserve. The population fluctuations indicated by the data in Tables 2 and 3 can, to an extent, be explained on the basis of the difference between cohort success in successive years. The 1987 adult introductions (made up of a series of cohorts beginning life before 1986) provided large numbers of animals, but their success was limited partly because of the high male:female ratio (6.5:1) and partly because of high attrition, whether through mortality or emigration. On the other hand the cohorts starting in 1986 and 1987, when there were good numbers of eggs and evidence of high metamorph production were apparently very successful. The 1988 adult population was a small one because the introduced adults had substantially dispersed and there was still low recruitment from the 1986 cohort. Numbers of breeding females were particularly low in 1988. By 1989 the effect of recruitment from the two successful years (1986 and 1987) was probably having an impact, but mainly on the males. In Britain the age at which male toads attain sexual maturity is given as 2-3 years (Gittins, Kennedy & Williams, 1985), 3-6 years (Reading, 1988) and 2-6 years (Reading, 1991). For female toads, data are 3-6 years (Gittins *et al.*, 1985) and 4-6 years (Reading, 1991). The increases in females after 1989 (Table 2) is consistent with them taking longer to reach maturity. By 1990 female numbers were increasing but the males were being affected by the poor 1988

cohort. In 1991 and 1992 both sexes were on the increase, but not dramatically so, either because of the continuing dampening effect of the 1988 cohort or alternatively because the population was close to the habitat's carrying capacity.

A total of 6000 male toads exceeded our establishment criterion of 1000 adults and represents approaching 2000 per hectare in the core area during the breeding season. But the toads clearly forage further afield after breeding; in the current study dead ones were found up to 400 m from the breeding ponds.

There was some loss of frog spawn to collection each year, the overall loss being 8%. This is similar to 7% collected at St Neots Common 1981-3, but is much less than the 24% recorded as collected at St Neots 1973-80 (Cooke, 1985). During the 1970s, St Neots Common was the best known site for frogs in the old county of Huntingdonshire, and was frequently raided by people requiring spawn for garden ponds. During the 1970s and 1980s, the establishment of frog populations in garden ponds probably resulted in general increases in frog numbers in suburban areas throughout lowland England (Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991). Consequently the collection pressure has probably eased on large populations to which the public has access. Indeed, in 1987 and 1988 it proved relatively easy to find 350 clumps that were regarded as surplus in gardens in the Peterborough area for the initial stocking operation at the Boardwalks. During the period 1988-93, 26 clumps were deposited at the site by the public.

This is the first time that spawn losses for toads have been quantified. No loss was observed in three of the seven years but overall loss of toad spawn was similar to that of frog spawn. Desiccation, collection or destruction by humans and hatching failure were the factors recorded as responsible for greatest loss of toad spawn, but the deliberate lowering of the level of the River Nene represented an unusual local factor. Those responsible were notified of the implications of the lowering of the river and this operation was done about one month later in 1992 with no detrimental consequences being observed.

In 1993 there was significant hatching failure of toad spawn associated with fungal attack. Blaustein, Hokit, O'Hara & Holt (1994) documented even greater egg losses to the fungus *Saprolegnia ferax* in a population of the western toad *Bufo boreas* in Oregon. They speculated that such pathogens may be important in amphibian population declines worldwide. At the Boardwalks, however, major fungal infection has happened only sporadically.

For toads two methods of introduction were used; a large input of spawn in 1986 and a massive input of adults in 1987. It is difficult to unravel the relative contributions of each of these to the eventual success of the Boardwalks population. However, the evidence suggests that the adult introductions were relatively

unsuccessful, with 64% loss of males in the first year. The eventual establishment of the population probably depended upon recruitment from the two sets of spawn in 1986 and 1987. It was not until the females from these cohorts became mature that the population began to stabilise. On the basis of the current study, we suggest the introduction of spawn on three successive years, given suitable habitat, as a means of establishing a viable toad population.

In conclusion, these introductions have succeeded in their primary aim of establishing frog and toad populations of reasonable size where they can be readily seen and enjoyed, especially when breeding, in attractive semi-natural surroundings. They contribute two instances of monitored translocation success, to add to the few available in the literature. The Boardwalks Reserve was declared a Local Nature Reserve in 1991.

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HABITAT SELECTION AND THERMAL ECOLOGY OF THE SYMPATRIC LIZARDS *PODARCIS MURALIS* AND *PODARCIS HISPANICA* IN A MOUNTAIN REGION OF CENTRAL SPAIN

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We studied habitat selection, field body temperatures (TB) and activity cycles in sympatric populations of the lacertid lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain area in Central Spain. Different patterns of habitat selection for the two species were found: *P. muralis* occupies N and NW facing talus sites, while *P. hispanica* shows a less habitat-specific distribution at the study site. Inter- and intraspecific differences in TBs were found, while thermoregulatory precision analyses showed differences between adult male and female *P. muralis*. Hypotheses based on activity cycles, habitat selection and basking behaviour are discussed to explain such results in two closely related species.

INTRODUCTION

Thermoregulatory behaviour and habitat selection are intimately related and strongly influence life history traits and fitness of lizards (Ouboter, 1981; Huey, 1982; van Berkum, Huey & Adams, 1986; Adolph, 1990). Many authors have approached the study of interactions between the conditions of the habitat occupied by a given species and its thermal behaviour (Hillman, 1969; Moermond, 1979; Roughgarden, Porter & Heckel, 1981; Hertz & Huey, 1981; Tracy & Christian, 1986; van Damme, Bauwens, Castilla & Verheyen, 1989; Marquet, Ortíz, Bozinovic & Jaksic, 1989), as well as focusing on the connection between thermoregulation and activity time (Porter & Tracy, 1983; Grant & Dunham, 1988).

We here report a study of body temperatures, activity cycles and features of habitat selection in the lizards *Podarcis muralis* and *Podarcis hispanica*, that are sympatric in some areas of the Iberian Peninsula, including the Sierra de Guadarrama (Central System, Spain), where this study was undertaken. The analysis of thermoregulatory precision, activity cycles and basking behaviour have been developed through field observations, and the conclusions extracted are therefore mainly directed towards suggesting working hypotheses for future studies.

Our main objectives were to: (1) quantify habitat occupation by the two species in the area, and identify any intra- and interspecific differences between them; (2) determine some aspects of their thermal ecology, and relate these to the habitat selection features; and

(3) inspect whether differences in thermal ecology could be found between the two species.

MATERIAL AND METHODS

ANIMALS

Lizards of the lacertid genus *Podarcis* from the Iberian Peninsula seem to be very similar in basic ecological characteristics such as diet composition, foraging behaviour, activity cycles and thermoregulatory behaviour (Arnold & Burton, 1978; Pérez-Mellado, 1983a,b; Arnold, 1987; Gosá, 1987). These similarities are especially strong between *P. muralis* and *P. hispanica*, two species so closely related that there are some problems for their systematic distinction over a wide part of their distribution range (e.g. Martínez-Rica & Laplaza, 1989). These two small lizards are similar in size (adult snout-vent length 49.7-67.6 mm and 46.7-66.8 mm respectively, personal data), morphology (Pérez-Mellado & Galindo, 1986) and habitat requirements (Arnold, 1987). *Podarcis muralis* occupies a wide range of latitudes in Europe -the southwestern extreme of which is the Sierra de Guadarrama-, while *P. hispanica* is limited to the Iberian Peninsula, southern France and northern Africa.

STUDY AREA

The study area is located in the westernmost part of the Sierra de Guadarrama, Spain, a mountain range reaching a maximum altitude of 1902 m. The altitudinal range surveyed extended from 1450 to 1902

m. The dominant vegetation consists of *Pinus sylvestris* forest, widely spread throughout the whole mountain range. In the high mountain areas, the forest was gradually replaced by small shrubs, with *Juniperus communis* subsp. *nana* being the dominant species. Below 1550 m, the forest becomes very open, and *Quercus ilex* subsp. *ballota* is the predominant tree species. Important habitat differences occurred resulting from the topography: the southern slopes of the mountains present a greater number of open habitats with Mediterranean shrubs such as *Cistus laurifolius*, *Halymium viscosum*, *Erica arborea* and *Thymus bracteatus*. The northern slopes exhibit closed *Pinus* forests with a few accompanying scrubs (mainly *Arctostaphylos uva-ursi*) and have much higher humidity.

METHODS

Observations were made at monthly intervals from May 1988 to September 1989. We captured lizards by hand or noose, and recorded the following data upon each capture: species, date, time, age, sex, reproductive condition of females, behaviour (basking or active), orientation of slope (N, NW, W, SW, S, SE, E, NE), altitude, body temperature (cloacal = TB), air temperature (shaded bulb, 10 cm above substrate = TA), and substrate temperature (shaded bulb = TS). Temperatures were measured with a Schultheis thermometer to the nearest 0.1°C.

Three age classes were considered: juveniles, the individuals born in the year of capture; subadults, one-year-old individuals, which have not yet reached sexual maturity; and adults, sexually mature individuals.

Activity rhythms were determined from the frequencies of lizard observations made in the different months and time intervals (data from 1988 and 1989 were pooled since no differences were detected). Correction indices (Tellería, 1986) were used to avoid possible biases caused by an irregular survey intensity.

The microhabitat selection field study was developed between April and August 1989, at monthly intervals. A 5 x 5 m square was used as the survey unit, the centre of which was a lizard previously observed (these observations were made randomly, using two hour intervals and considering the first lizard seen after each of these periods of time). Within each square we estimated 28 variables: (1-5) percentage cover at ground level of gravel, grass, fallen leaves, rock and soil; (6-10) percentage cover of vegetation layers with heights <25 cm, 25-50 cm, 50-100 cm, 1-2 m, >2 m; (11-15) percentage cover of walls, and rocks with heights <25 cm, 25-50 cm, 50-100 cm, >100 cm; (16) percentage cover of talus structures; (17-18) percentage cover of dead tree trunks and branches; (19-20) percentage cover of 0-20° and 20-40° slopes; (21-28) SW, S, SE, E, NE, N, NW or W dominant orientations. Percentages were calculated as means of estimates made by eye by two independent observers. Similarly

we estimated the availability of microhabitats in the environment by measuring the same variables in squares for which the centres were the points occupied by us after stopping every two minutes during random directed walks.

STATISTICAL ANALYSIS

We used one-way analysis of variance (ANOVA) and Bonferroni's multiple comparison test (see Keppel, 1991) on arcsin x^{-1} transformed data to examine differences between samples (*P. muralis*, *P. hispanica* and availability) for each microhabitat variable. When variances were heterogeneous across samples (Bartlett's test) we used the non-parametric Kruskal-Wallis test, followed by Dunn's multiple comparison test (Dunn, 1964; see Hollander & Wolfe, 1973).

Thermoregulatory precision was estimated by the slope of the least square regressions of TB on TA or TS. Differences between lizard species and age/sex groups were assessed by analyses of covariance (ANCOVA). As another indicator of thermoregulatory precision we employed the interquartile range. To analyse differences between two means we used the two-tailed Student *t*-test, with the Welch approximation (t_w) in case of heterogeneity of variances, or a Z-test for $n > 50$. Frequency distributions of distinct behavioural categories were compared with χ^2 tests. The significance level used was $\alpha = 0.05$.

RESULTS

HABITAT SELECTION

Podarcis muralis occupied a narrower altitudinal range in the study area (1490-1725 m; Fig. 1), while *P. hispanica* was present along the whole surveyed range (1450-1900 m).

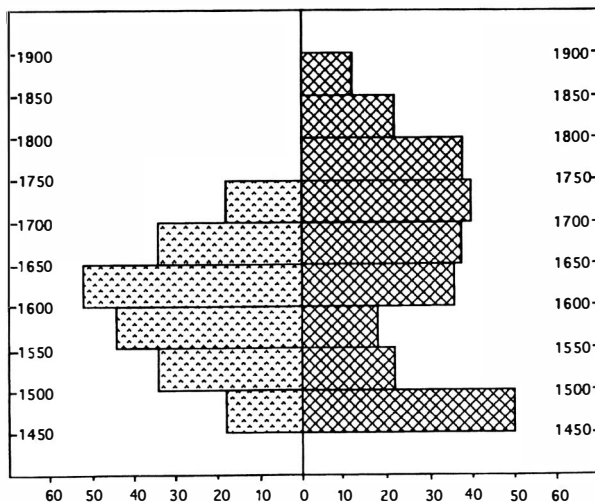


FIG. 1. Absolute frequencies (on horizontal axis) of *Podarcis muralis* (left hand) and *Podarcis hispanica* (right hand) lizards seen at the different altitude intervals (on vertical axis).

TABLE 1. Average percentages and standard deviations for the three groups considered: Availability, *P. muralis* and *P. hispanica*.

| | Availability (n=45) | | <i>P. hispanica</i> (n=24) | | <i>P. muralis</i> (n=22) | |
|--------------------|------------------------|------|-------------------------------|------|-----------------------------|------|
| | mean | SD | mean | SD | mean | SD |
| Gravel | 2.2 | 14.7 | 16.7 | 37.3 | 15.5 | 34.6 |
| Grass | 72.6 | 41.4 | 41.7 | 49.3 | 13.2 | 30.3 |
| Withered leaves | 8.8 | 28.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| Slab | 4.1 | 16.8 | 9.4 | 18.1 | 3.4 | 11.4 |
| Soil | 12.2 | 30.3 | 24.0 | 38.1 | 67.9 | 43.2 |
| Trees: | | | | | | |
| >2m | 20.0 | 27.1 | 3.1 | 13.5 | 6.2 | 18.4 |
| <2m | 1.2 | 5.3 | 6.7 | 10.1 | 8.6 | 13.9 |
| Shrubs: | | | | | | |
| <25cm | 8.0 | 15.2 | 2.5 | 5.9 | 2.8 | 9.8 |
| 25-50cm | 15.3 | 20.6 | 6.8 | 9.1 | 9.7 | 12.9 |
| >50cm | 3.8 | 10.3 | 4.0 | 8.3 | 2.5 | 10.9 |
| Wall | 0.0 | 0.0 | 2.3 | 5.2 | 0.0 | 0.0 |
| Rocks: | | | | | | |
| <25cm | 9.1 | 10.3 | 17.3 | 12.6 | 19.2 | 12.3 |
| 25-50cm | 2.6 | 4.9 | 15.0 | 14.6 | 2.7 | 5.0 |
| 50-100cm | 2.2 | 11.2 | 2.4 | 5.7 | 0.5 | 1.7 |
| >100cm | 0.7 | 3.3 | 2.7 | 7.2 | 0.0 | 0.0 |
| Talus | 0.0 | 0.0 | 7.8 | 21.1 | 34.8 | 30.2 |
| Slope: | | | | | | |
| 0-20° | 80.0 | 40.0 | 77.2 | 37.2 | 46.5 | 31.3 |
| >20° | 20.0 | 41.5 | 22.8 | 37.2 | 53.4 | 31.3 |

In the analyses of variance and Bonferroni tests, made with the percentages obtained in the microhabitat selection study (Table 1), *P. muralis* exhibited significantly higher percentages for the variables soil, talus and 20-40° slope, and lower ones for grass and the 0-20° slope. Both *P. muralis* and *P. hispanica* showed significantly higher percentages than available for rocks under 25 cm (Table 2).

In the group of variables analysed through non-parametric tests, significant results were found for the following variables: trees (>2 m high vegetation cover) and <25 cm scrubs were more available than utilized. Regarding interspecific comparisons, *P. hispanica* selected rocks of heights between 25 and 50 cm.

BODY TEMPERATURES AND THERMOREGULATORY PRECISION

Body temperatures for all age/sex classes are shown in Table 3. TBs are significantly higher in *P. muralis* than in *P. hispanica*, regarding the whole species ($Z=4.07$, $P<0.001$), and for adult males ($t=2.54$, $df=79$, $P<0.05$) and subadults ($t_w=5.05$, $df=47$, $P<0.001$).

TABLE 2. Results obtained in the habitat selection study. (* $P<0.05$; ** $P<0.01$. The last three variables were analysed using non-parametric tests).

| Variables | Availability/ <i>P. hispanica</i> | Availability/ <i>P. muralis</i> | <i>P. muralis</i> / <i>P. hispanica</i> |
|---------------|--------------------------------------|------------------------------------|--|
| Grass | - | * | * |
| Soil | - | * | * |
| Rocks < 25cm | * | * | - |
| Talus | - | * | * |
| Slope 0-20° | - | * | * |
| Slope >20° | - | * | * |
| Trees >2m | * | * | - |
| Shrubs < 25cm | * | * | - |
| Rocks 25-50cm | * | - | * |

Both in *P. muralis* and in *P. hispanica*, the juveniles exhibited lower mean TBs than the other age groups, which did not differ significantly (ANOVA, $F=5.64$, $df=2-81$, and 3.24 , $df=2-116$ respectively, $P<0.05$; Bonferroni test, $P<0.05$).

The interquartile range of TB was lower in males of *P. muralis*, followed by the adult females of both species. Regression slopes of TB on TA and TS (Fig. 2) are similar for adults of the two species; but considering the two sexes separately, we notice that in adult male *P. muralis*, the slopes are not statistically different from 0 ($b=0.22$ and 0.08 ; $t=1.62$; $df=25$ and 1.45 ; $df=22$ for TA and TS respectively), whereas adult females have high slope values ($b=0.60$ and 0.50). *P. hispanica* shows, instead, more similar values for males and females ($b=0.47$ and 0.41 respectively for TA; $b=0.38$ and 0.50 for TS). The results of the analyses of covariance show no differences between *P. hispanica* males and females, while differences were detected in the slopes of males and females in *P. muralis* ($F=6.31$, $df=1-54$ $P<0.05$ for TA; $F=9.05$, $df=1-47$ $P<0.01$ for TS).

The regression slopes of gravid and non-gravid females were analysed, and differences have not been detected between the two groups for either of the two species.

ACTIVITY CYCLES AND BASKING BEHAVIOUR

Annual and daily activity periods of adult males and females, and subadults, of both species are shown in Fig. 3. Activity cycles differed between sex/age groups considered.

Frequencies of basking individuals for adults of both species show low differences among groups, as follows: *P. muralis* males, 57.1% and females, 60.7%; *P. hispanica* males, 64.7% and females, 66.7%. There are no intraspecific differences in the proportions of

TABLE 3. Statistics (mean ± SE, range in parentheses, interquartile range, and sample size) of body (TB), air (TA), and substrate (TS) temperatures for *P. muralis* and *P. hispanica*.

| <i>P. muralis</i> | | | | <i>P. hispanica</i> | | | |
|-------------------|--|--|---|---------------------|---|--|--|
| sex/age group: | TB | TA | TS | sex/age group: | TB | TA | TS |
| adult males | 32.60 ± 0.69 (24.0 - 38.0) 3.2 28 | 19.22 ± 0.96 (12.5 - 31.1) 6.0 27 | 26.37 ± 1.45 (13.6 - 39.0) 11.4 24 | adult males | 30.16 ± 0.59 (21.4 - 36.0) 5.7 53 | 16.97 ± 0.69 (9.6 - 26.0) 8.7 48 | 25.13 ± 0.78 (14.0 - 34.0) 6.0 41 |
| adult females | 31.08 ± 0.72 (23.3 - 36.8) 5.3 30 | 18.80 ± 0.98 (8.8 - 31.1) 8.4 30 | 25.78 ± 1.24 (13.6 - 37.0) 11.7 26 | adult females | 30.20 ± 0.55 (21.4 - 36.6) 4.5 45 | 19.07 ± 0.82 (10.9 - 28.5) 8.8 40 | 26.03 ± 0.77 (15.6 - 34.0) 6.7 34 |
| subadults | 34.10 ± 0.44 (30.3 - 37.8) 1.9 17 | 22.58 ± 0.85 (17.8 - 28.1) 6.1 17 | 28.75 ± 1.24 (17.0 - 27.0) 10.0 15 | subadults | 29.99 ± 0.68 (22.0 - 36.0) 5.9 31 | 19.10 ± 0.90 (11.0 - 26.9) 5.6 24 | 25.49 ± 1.39 (14.0 - 40.0) 9.6 21 |
| juveniles | 29.02 ± 0.94 (26.2 - 32.6) 2.8 6 | 17.50 ± 0.78 (15.6 - 20.0) 4.0 6 | 20.0 ± 1.58 (17.0 - 27.0) 4.8 6 | juveniles | 26.07 ± 1.89 (22.0 - 34.5) 9.0 7 | 14.04 ± 2.01 (9.6 - 23.0) 9.9 7 | 18.77 ± 2.72 (14.2 - 29.0) 11.2 6 |
| total | 31.99 ± 0.40 (23.3 - 38.0) 4.2 81 | 19.32 ± 0.51 (8.8 - 31.1) 7.0 80 | 25.12 ± 0.70 (13.6 - 39.0) 12.0 71 | total | 29.79 ± 0.36 (21.4 - 36.6) 6.5 136 | 17.42 ± 0.44 (9.6 - 28.5) 8.6 119 | 23.67 ± 0.54 (14.0 - 40.0) 9 102 |

basking or active individuals in either of the two species ($\chi^2=0.07$, $df=1$ for *P. muralis*; $\chi^2=0.042$, $df=1$ for *P. hispanica*). After pooling the data, we found no interspecific differences ($\chi^2=0.69$, $df=1$).

DISCUSSION

HABITAT SELECTION

Probably, the genus *Podarcis* was present in the Iberian Peninsula from the Upper Miocene (Vives-Balmaña, 1982, 1984). There is no agreement about the ancestral species inhabiting this area (Busack, 1977; Blasco, 1980; Vives-Balmaña, 1980). In any case, the available data indicate an almost general distribution of *P. hispanica* throughout the area, occupying several Mediterranean habitats (Salvador, 1985; Barbadillo, 1987), while *P. muralis* is restricted to mountain areas of the northern half of the Iberian Peninsula. Usually, the species show there a parapatric microdistribution, lacking altitudinal overlap in their ranges; for instance, in the Pyrenees mountains, *P. hispanica* reaches a maximum altitude of 1600 m, co-

inciding with the lowest of *P. muralis* (Vives-Balmaña, 1982; Martínez-Rica & Laplaza, 1989). For this reason, the situation in the Sierra del Guadarrama seems to be especially suitable to investigate factors segregating both species.

Our results show that *P. hispanica* has a less microhabitat-specific distribution at the study site, although it is partially dependent on rocky habitats. *Podarcis muralis* exhibits a greater habitat-specificity, occupying ground talus in humid slants. This picture is the inverse of the situation in other northern populations of the Iberian Peninsula, where *P. muralis* occupies a greater number of habitats and *P. hispanica* is limited to a narrow spatial distribution (Braña, 1984; Gosá, 1987).

FACTORS INFLUENCING THE LOCALIZED DISTRIBUTION OF *P. MURALIS*

We could argue that microhabitat differences between these species are due to their different physiological and historical constraints, i.e., a greater adaptation of *P. muralis* to its originally more mesic

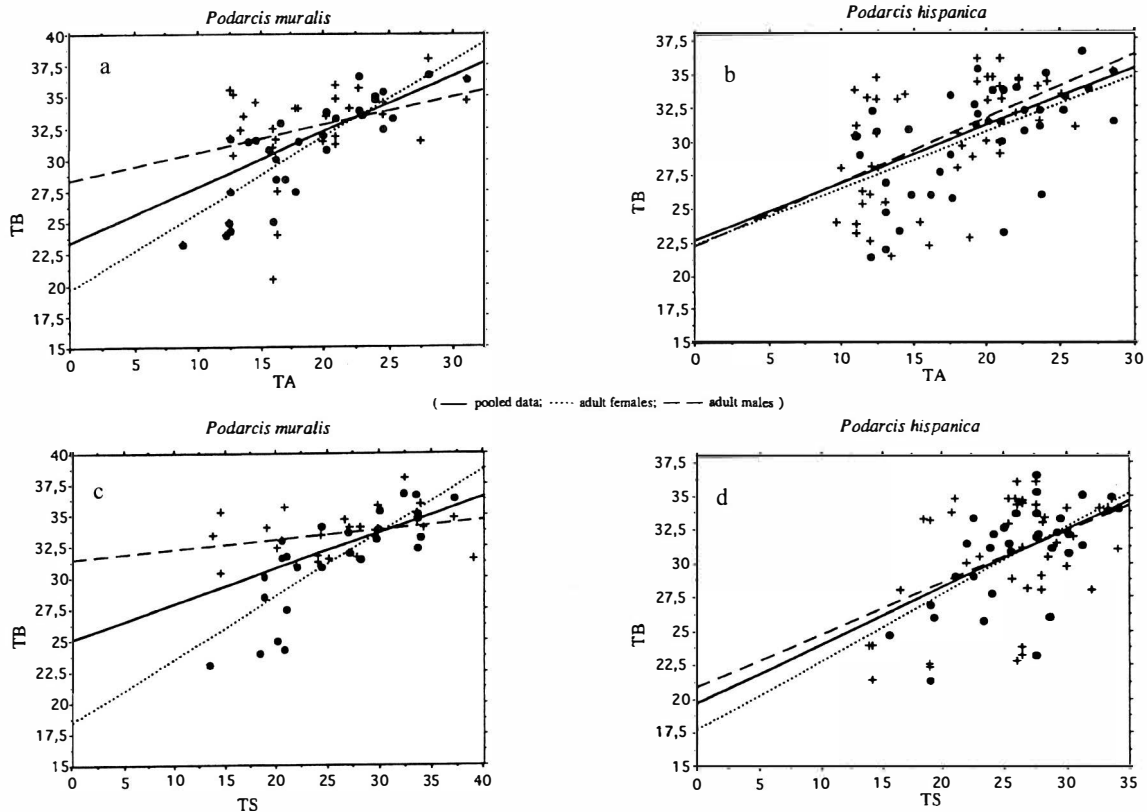


FIG. 2. Regression scatterplots of body temperatures (TB) on air (TA) and substrate (TS) temperatures. Dashes and crosses represent adult males, points and solid circles represent females, while solid lines show regressions after pooling the data of both sexes. Correlation coefficients and equations of regression lines are:

- (a) TB/TA *P. muralis*: Males ($r=0.30$, $TB=28.30 + 0.22 TA$); females ($r=0.83$, $TB=19.73 + 0.60 TA$); pooled data ($r=0.59$, $TB=23.47 + 0.44 TA$).
 (b) TB/TA *P. hispanica*: Males ($r=0.52$, $TB=22.24 + 0.47 TA$); females ($r=0.55$, $TB=22.35 + 0.41 TA$); pooled data ($r=0.52$, $TB=22.65 + 0.42 TA$).
 (c) TB/TS *P. muralis*: Males ($r=0.30$, $TB=31.55 + 0.08 TS$); females ($r=0.82$, $TB=18.50 + 0.50 TS$); pooled data ($r=0.58$, $TB=25.18 + 0.28 TS$).
 (d) TB/TS *P. hispanica*: Males ($r=0.43$, $TB=20.92 + 0.38 TS$); females ($r=0.62$, $TB=17.79 + 0.50 TS$); pooled data ($r=0.50$, $TB=19.72 + 0.43 TS$).

microhabitats of Central Europe and the xeric adaptation of *P. hispanica* in Mediterranean habitats (Arnold, 1987). Roughgarden, Porter & Heckel (1981) mention the importance of humidity as a variable favouring the thermoregulatory processes in some species. The presence of more mesophytic plant species in the talus indicates greater soil moisture, probably favouring *P. muralis*.

An alternative hypothesis could be that competition with *P. hispanica* is the primary determinant of the distribution of *P. muralis*, since the former species should exploit the rocky microhabitats, showing several ecomorphological traits specially adapted to crevice occupation (Arnold, 1987), i.e., a flattened head morphology (Pérez-Mellado & Galindo, 1986; García-Fernández, Martín-Vallejo & Pérez-Mellado, in prep.), which is thought to favour access to narrow shelters and crevices, as well as greater climbing abilities (Arnold & Burton, 1978; Arnold, 1987). A similar situation has been recorded in other areas of southern

Europe, where *P. muralis* occurs sympatrically with other lacertid species, e.g., in Greece, with *Podarcis erhardii* (Strijbosch, Helmer & Scohlte, 1989; and pers. obs.), and in the Balkans area with *Lacerta horvathi* (Arnold, 1987). In both cases, *P. muralis* restricts its microhabitat to soil dwellings in shaded zones, while the other species occupies sunny and rocky microhabitats.

Hence, our results would support the two hypotheses mentioned above, the second of which needs to be verified with an experimental design consisting of displacements of one species from the area (see, for instance, Nevo, Gorman, Soule, Yung Yang, Clover & Jovanovic, 1972). However, the restricted mountainous distribution of *P. muralis* in the Iberian Peninsula mentioned above could favour the acceptance of the first hypothesis of physiological constraints, indicating a residual situation of this rock lizard population at the very edge of the species' geographical range (Pérez-Mellado & Galindo, 1986).

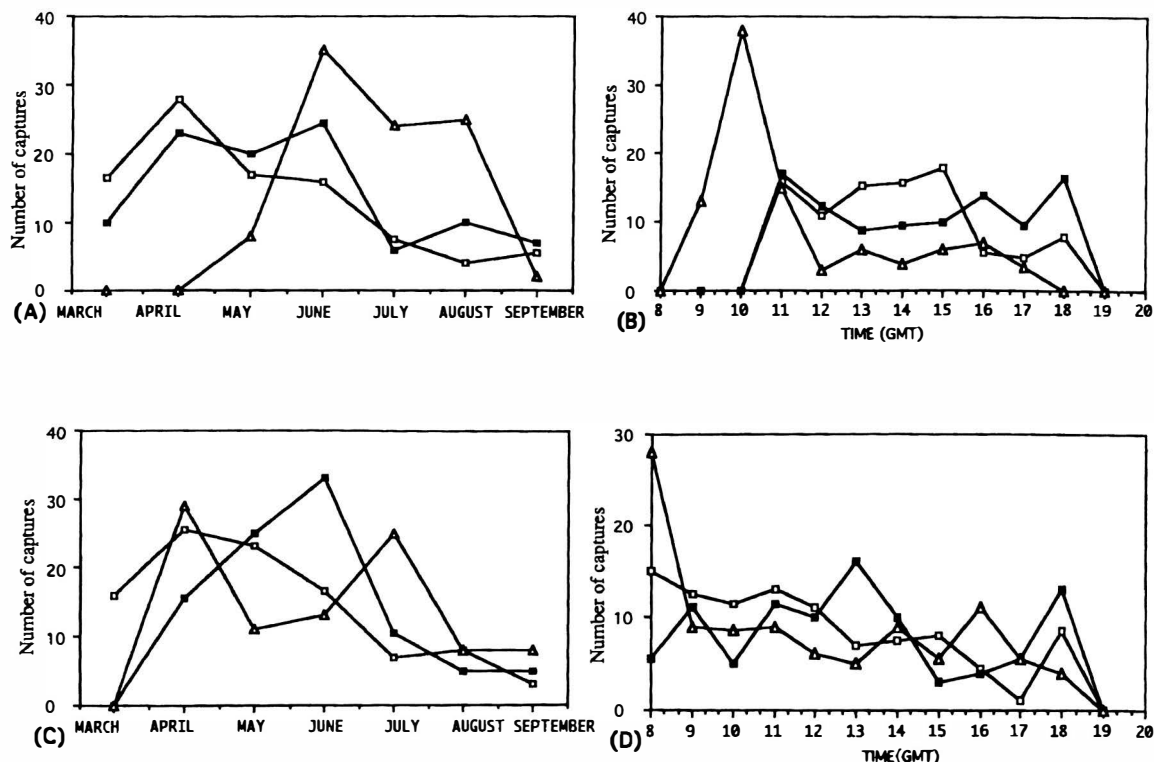


FIG. 3. Annual and daily activity rhythms of *P. muralis* (A and B) and *P. hispanica* (C and D). White squares represent adult males and black squares adult females, triangles stand for subadults.

THERMAL ECOLOGY AND ACTIVITY

The average TBs reported here for *P. hispanica* are somewhat lower than those recorded at lower altitudes (Pérez-Mellado, 1983b). These differences are not likely to be due to physiological changes, but rather to a slightly less effective thermoregulation; or to physical limitations derived from the higher altitudes, that would not let them achieve the TBs they exhibit at lower sites (van Damme, Bauwens & Verheyen, 1990).

FACTORS INFLUENCING THERMOREGULATORY PRECISION IN MALE *PODARCIS MURALIS*

Differences in TBs between two species could be due to differences in their thermal preferences or thermal physiology. In this particular situation, intraspecific differences in selected body or optimal temperatures have not been detected (Bauwens, pers. com.). Therefore, differences in TBs should not be due to physiological differences. Hertz & Huey (1981), van Damme *et al.* (1989, 1990) point out three possible behavioural causes to explain a greater independence from the environmental conditions in some reptiles: habitat shifts; increases in basking intensity; and changes in activity times.

However, the hypotheses concerning habitat shifts would be valid only for *Podarcis muralis* adult males, since females achieve a thermoregulation pattern similar to *Podarcis hispanica*, i.e., greater dependence on

environmental temperatures. If we still would consider a differential microhabitat use as a hypothesis to explain the interspecific variations we ought to verify whether males and females use space differently. We have not detected intraspecific differences in microhabitat selection in either of the two species (see results).

The second of the possible factors mentioned by van Damme *et al.* (1990) is an increase in basking intensity. Significant intra- or interspecific significant differences in the frequencies of various types of behaviour have not been detected, therefore this hypothesis would not be valid either to explain the thermoregulatory differences.

The third hypothesis explains the differences with changes in activity periods. *P. muralis* exhibits shorter activity periods than *P. hispanica*, which appears to be because the talus is less exposed to the sun (most talus areas are in shade during the first morning hours, from 8-11 hr). This could also explain the thermoregulatory imprecision of *P. hispanica*, i.e., it may sacrifice a higher thermal control for longer activity times (Bowker, 1986).

Another hypothesis is linked to food availability. Huey & Slatkin (1976) predict that increased habitat productivity should cause increased thermoregulatory benefits; in this sense, Lee (1980) affirms that in an environment with abundant trophic resources, lizards are expected to thermoregulate more precisely, since

the time inversion in feeding behaviours decreases. The mean number of available prey items per day (García-Fernández, Martín-Vallejo & Pérez-Mellado, in prep.), an estimate of the relative abundance of prey in the environment, is lowest in habitats occupied by *P. muralis*, which contradicts this hypothesis.

Finally, intraspecific differences in TBs found in *Podarcis muralis* could be due to differences in reproductive condition. More cryptic behaviour in females, related to the survivorship of themselves and their offspring could explain these differences, since they would invest less time in thermoregulation. The high reproductive effort made by females of this species, with very high clutch sizes (mode=8; unpub. data) could support this hypothesis. However, we found no differences in TB-TA regression slopes between gravid and non-gravid females of *P. muralis*. We therefore conclude that sexual differences in thermoregulatory precision in *P. muralis* are unlikely to be the result of possible behavioural modifications induced by the females reproductive condition.

The third hypothesis mentioned above (changes in activity periods) could likewise explain intraspecific differences in *Podarcis muralis*: adult males have greater frequencies of activity at midday (Fig. 3), while females exhibit more bimodalism with a greater presence at less thermally favourable hours. However, if we inspect the regression scatterplots, we notice that the points concerning these particular hours (with lower TA and TS), show higher TBs again in males. This, together with some occasional observations in the field, suggested a new hypothesis: adult males *Podarcis muralis*, because of their more aggressive and territorial behaviour (Boag, 1973; Mou, 1987; Edsman, 1990), would exploit small sunny patches at early times, when the talus is almost completely in shade, so that in the moment of capture, they could have already achieved high TBs. Magnuson, Crower & Medvick (1979) and Edsman (1990) report the influence of territoriality on the thermal ecology of lizard species, in the sense that dominant animals occupy the best basking sites to achieve high temperatures as soon as possible. In our study area, subadults begin their annual cycle in May, with the highest frequency occurring in June, possibly to avoid interactions with adult males that would exhibit intense territorial behaviour in the months dedicated to reproductive behaviour.

In summary, both species showed at the study site a similar thermal biology with only apparently slight interspecific differences linked to their different microhabitat selection and changes in activity periods. Microhabitat selection arises as a major factor in species segregation, but the observed pattern could be explained by several alternative hypotheses only testable within an experimental framework.

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SEXUAL MATURATION IN *VARANUS SALVATOR* (LAURENTI, 1768), WITH NOTES ON GROWTH AND REPRODUCTIVE EFFORT

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In captivity, *Varanus salvator* attains sexual maturity when they are just over one metre in total length and 50 cm snout-vent length. Maturity can be attained at the end of two years. Males and females tend to grow throughout the breeding season. Egg-laying seasons are closely synchronized with those in the wild. No significant difference was noticed in clutch and egg sizes of younger females when compared to those of older and larger females.

INTRODUCTION

Little is known about the age at which the water monitor lizard (*Varanus salvator*) attains sexual maturity. Determining the age of wild-caught animals is difficult. Most captive specimens are wild-caught and lack sufficient life history data. Vogel (1979) estimated the age at maturity to be three to four years in the case of females and four to five years in the case of males. Authors have assumed age at maturity to be three years (Andrews & Gaulke, 1990; Daltry, 1991). Some smaller species like *V. bengalensis* mature at the end of the second year or beginning of the third year (Auffenberg, 1983, 1988).

For *V. salvator*, size at maturity has been noted previously. Vogel (1979) reported 1.4 m total length for females, 1.7 m for males in the wild and 1.2 m as the minimum size of a female breeding at the Zurich Zoo (Honegger, in Vogel, 1979). A wild-caught pair consisting of a 1.4 m female and a 1.5 m male, both of unknown age, bred in captivity at the Ahmedabad Zoo (David, 1970). Jasmi *et al.* (1986) designated wild-caught animals over 1.6 m in total length as adults, and a smaller size class of 1.3-1.6 m as sub-adults. Luxmoore & Groombridge (1990) report that size at maturity may vary between populations and could be dependent on the maximum adult size attained. Hairston & Burchfield (1992) reported two females of unknown age and total length 1.5 m and 1.6 m that bred at the Gladys Porter Zoo, and 1.6 m and 1.8 m total length for breeding males. However, it is not mentioned if these females had previously nested. In *V. olivaceus*, males and females appear to mature when just over a metre in size (Auffenberg, 1988). Of the 37 wild-caught males sampled by him, sperm was detected in the seminiferous tubules of animals with total length of 1.2 m and snout-vent length over 0.45 m.

The results of a captive breeding programme at the Madras Crocodile Bank indicate that *V. salvator* in captivity reach sexual maturity when males and females are just over a metre in total length, and 50 cm snout-vent length at the end of the second year. In this paper, I present observations and measurement data of two groups of captives that have been monitored from the time of hatching. In the discussion, I relate these findings to conservation and management programmes based on captive populations of *V. salvator*.

MATERIAL AND METHODS

The study animals consisted of captive-bred *V. salvator* maintained at the Madras Crocodile Bank (see Andrews & Gaulke, 1990; Daltry, 1991). All animals were individually marked by tail-notching and housed in a small enclosure. Initially, as hatchlings, the animals were measured (total body length, TBL; snout to vent length, SVL) and weighed every month for the first year, and subsequently at intervals of two or three months. The first group (Group 1) comprising four males and 11 females, were all captive-bred at the Madras Crocodile Bank in 1988 and 1989. Incubation and growth records of this group in the first year have been reported by Andrews & Gaulke (1990). On April 14, 1990 animals of this group were measured, weighed and moved to a large breeding enclosure (Enclosure 1), which housed a large-size wild-caught male from the initial breeding group. These animals were measured and weighed again on July 6, 1990 (Daltry, 1991). Several females from this group laid eggs in 1990. In October 1990, the large wild-caught male was transferred to a separate enclosure. The second group (Group 2), offspring of animals belonging to Group 1, comprising six males and two females, were hatched in captivity in 1991. This second group of animals were

maintained in a separate enclosure. One of these females nested in this enclosure in 1993.

RESULTS

1990 NESTING - 1991 HATCHING

Egg incubation extends for seven to nine months in this species; an increase in incubation temperature reduces the incubation period (Andrews & Gaulke, 1990). Two clutches laid by two females of Group 1 in 1990 went undetected until the following year. On March 31, 1991, three hatchlings were noticed in the enclosure, and on April 16 eight more hatchlings were observed emerging from a burrow. All 11 hatchlings were transferred to a hatchling pen. Excavation of the burrow revealed 11 hatched egg shells with longitudinal cracks all around and an opening at one end.

The second clutch hatched on April 22, 1991. Eight hatchlings were observed emerging from a burrow at 0730 hrs and were immediately removed. On closer examination, the hatchlings revealed the presence of an egg tooth, fresh umbilical scars and a few of them had extended umbilical cords. On excavating the burrow, eight freshly hatched egg shells and one whole egg was found which had completely dried out. Considering the extended incubation period, these two clutches were probably laid in July or August 1990.

1991 NESTING - 1992 HATCHING

During the 1991 breeding season, mating among the two- and three-year olds was noticed in April and May. Between May 31 and July 15, four females were observed nesting. Eggs were removed, measured, weighed and candled to determine fertility rate, and fertile eggs were incubated. Each female was measured and weighed immediately after she had nested. On July 15, 1991, all the animals of Group 1 were measured, weighed and transferred to a new, larger breeding enclosure (Enclosure 2).

On March 4, 1992, 25 hatchlings were recovered from Enclosure 1 and seven hatchlings were recovered from Enclosure 2. The recovery of these 32 hatchlings indicate that two females had nested in Enclosure 1 before being transferred to Enclosure 2 and another female of the same group (Group 1) had nested in Enclosure 2 immediately after the transfer.

SEXUAL MATURITY IN FEMALES

In 1990, the exact sizes of the two-year old females that nested could not be determined, because the animals could not be identified. However, measurements and weights of all the animals taken at the onset of the breeding season (April, 1990), and during the egg-laying season (July, 1990), show that sizes of the two year old females during the egg-laying season ($n = 6$) ranged from 108 cm to 125 cm (mean 113.8 cm) TBL; 45 to 49 (mean 46.5 cm) SVL and 1.3 to 2.5 kg (mean 1.87 kg) weight. The two-year old females that nested for the first time in 1991 and 1993 were 114.5 cm TL and 47 cm SVL, and 123.5 cm TL and 48 cm SVL (Table 1). Egg-laying by the two females in 1990 and the results of 1991 and 1993 breeding season show that female *V. salvator* reach sexual maturity at the end of two years.

Continual growth monitoring helped ascertain age and size at maturity. Measurements taken in April and July 1990 (a 76 day interval) show that females continue to grow even during the breeding season (Table 2).

SEXUAL MATURITY IN MALES

Although mating activity was observed among members of Group 1, it was not possible to determine whether the two-year old males fertilised the females of this group in 1990, due to the presence of the old, wild-caught male from the initial breeding stock. This was later determined when one of the females of Group 2

TABLE 1. Reproductive effort and size of two and three year old *Varanus salvator* females taken immediately after nesting. (TBL = total body length; SVL = snout-vent length).

| Female code | Year hatched | TBL (cm) | SVL (cm) | Wt. (g) after laying | Date laid | Clutch size | Egg wt. (g) range | Clutch wt. (g) | Clutch wt. % body wt. |
|-------------|--------------|----------|----------|----------------------|-----------|-------------|-------------------|----------------|-----------------------|
| 10 | 1989 | 114.5 | 47.0 | 1700 | 31.5.91 | 11 | 64.15-58.4 | 678.4 | 39.90 |
| 07 | 1988 | 124.0 | 50.5 | 2325 | 9.6.91 | 12 | 64.7-52.9 | 689.5 | 29.65 |
| 04 | 1988 | 132.5 | 54.5 | 2320 | 10.6.91 | 14 | 62.65-47.10 | 768.6 | 33.12 |
| 02 | 1988 | 133.0 | 53.3 | 2520 | 15.7.91 | 9 | 65.9-59.9 | 563.2 | 22.34 |
| 11 | 1991 | 123.5 | 48.0 | 2350 | 21.6.93 | 8 | 78.8-60.8 | 520.3 | 22.14 |

TABLE 2. Growth and size of female *Varanus salvator* recorded in April and July 1990 in the second year, and July 1991 in the third year.

| Female code | Year hatched | TBL (cm) | | | SVL (cm) | | | Weight (kg) | | |
|-------------|--------------|----------|-------|--------|----------|------|--------|-------------|------|--------|
| | | (1990) | | (1991) | (1990) | | (1991) | (1990) | | (1991) |
| | | 14/4 | 6/7 | 15/7 | 14/4 | 6/7 | 15/7 | 14/4 | 6/7 | 15/7 |
| 01 | 1989 | 84.0 | 95.5 | 116.0 | 33.3 | 38.4 | 47.5 | 0.76 | 1.18 | 2.10 |
| 02 | 1988 | 111.0 | 125.0 | 133.0 | 45.0 | 48.0 | 55.3 | 1.32 | 1.80 | 2.52 |
| 03 | 1988 | 75.7 | 94.0 | 124.0 | 30.5 | 37.0 | 50.0 | 0.57 | 1.98 | 2.52 |
| 04 | 1988 | 109.0 | 120.0 | 133.0 | 45.0 | 45.0 | 54.0 | 1.42 | 2.32 | 2.30 |
| 05 | 1989 | 85.3 | 99.0 | 120.0 | 32.8 | 39.0 | 49.0 | 0.71 | 1.00 | 2.72 |
| 07 | 1988 | 104.7 | 108.0 | 124.0 | 43.7 | 45.0 | 50.5 | 1.42 | 1.30 | 2.52 |
| 08 | 1988 | 106.5 | 112.0 | 130.0 | 41.5 | 45.0 | 53.0 | 1.37 | 1.70 | 3.12 |
| 09 | 1988 | 102.0 | 112.0 | 131.0 | 40.0 | 47.0 | 53.0 | 1.20 | 1.62 | 2.33 |
| 10 | 1989 | 106.5 | 116.0 | 123.0 | 42.8 | 49.0 | 50.0 | 1.77 | 2.50 | 3.72 |
| 12 | 1989 | 97.9 | 104.0 | 126.0 | 40.2 | 42.0 | 52.0 | 1.00 | 1.30 | 2.62 |
| 17 | 1989 | 69.2 | 80.4 | 94.2 | 27.4 | 31.0 | 40.0 | 0.41 | 0.60 | 1.52 |

TABLE 3. Growth and size of male *Varanus salvator* recorded in April and July 1990 in the second year, and July 1991 in the third year.

| Male code | Year hatched | TBL (cm) | | | SVL (cm) | | | Weight (kg) | | |
|-----------|--------------|----------|-------|--------|----------|------|--------|-------------|------|--------|
| | | (1990) | | (1991) | (1990) | | (1991) | (1990) | | (1991) |
| | | 14/4 | 6/7 | 15/7 | 14/4 | 6/7 | 15/7 | 14/4 | 6/7 | 15/7 |
| 06 | 1988 | 115.0 | 135.0 | 149 | 46.4 | 53.5 | 63.0 | 2.12 | 3.22 | 5.17 |
| 07 | 1988 | 104.0 | 115.0 | 130 | 42.7 | 48.0 | 56.0 | 1.77 | 2.25 | 3.67 |
| 11 | 1989 | 84.0 | 95.5 | 119 | 33.3 | 38.4 | 47.5 | 0.76 | 1.18 | 2.62 |
| 13 | 1989 | 77.6 | 92.2 | 116 | 31.0 | 36.0 | 45.0 | 0.56 | 0.9 | 2.26 |

(hatched in 1991) nested in June 1993 in a different enclosure, which housed both males and females of the same age group. The sizes of the males from this group ($n = 6$) were TBL = 111 to 133.6 cm, SVL = 46 to 55.5 cm, weight = 1.5 to 3.35 kg. Table 3 shows size and growth at one, two and three years of age. Thus the results of the 1993 breeding season demonstrate that both males and females can attain sexual maturity at two years of age.

REPRODUCTIVE EFFORT

Clutch weight ($n = 5$) ranged from 520.3 to 768.6 g, comprising 22.3 to 39.9% of the body weight of the females after nesting (Table 1). Clutch sizes of the smaller two year old females ($n = 5$) ranged from eight to 14 when compared to older and larger females of the initial breeding stock ($n = 6$), which ranged from seven to 17 (Andrews & Gaulke, 1990). Egg sizes ($n = 54$) of the two year old females from five clutches ranged from 67.8 to 89.1 mm in length (average 79.4 cm) and weight ranged from 52.9 to 78.8 g (average 59.6 g).

Egg sizes from the older and larger wild-caught females of the initial breeding stock; ($n = 76$) from six clutches ranged from 67.2 to 82.6 mm and averaged 73.11 mm; egg weights ranged from 33 to 82 gm, average 63 gm. There was no significant difference in egg size and weight of young females nesting for the first time when compared to that of older and larger females.

Since 1987, the timing of the egg-laying season at the Madras Crocodile Bank has varied. The initial breeding stock that was acquired from north-east India laid eggs in May and again during August of 1987. In their second year of breeding here, in 1988, eggs were laid in September and October, respectively.

Offspring from the initial breeding group laid at the end of May and the other females laid in June and July. In 1992 females laid in July, and in 1993 two females nested in June.

DISCUSSION

The above observations and results clearly demonstrate that male and female *V. salvator* are sexually mature when they are just over a metre in total length and 50 cm in snout-vent length, at the end of their second year.

In the first three years of growth there was no marked difference in size between females, and males ($n = 4$) grew 5.0 - 7.1 cm (mean $5.63 \pm \text{SE } 0.50$) in 76 days, while females ($n = 10$) grew 1.3-7.0 cm (mean $4.42 \pm \text{SE } 0.65$), in the same period. Within the year (358 days), the same males ($n = 4$) grew 8.0 - 9.5 cm (mean $8.90 \pm \text{SE } 0.32$), while the same females ($n = 10$) grew 1.0-13.0 cm (mean $7.99 \pm \text{SE } 0.93$). Comparisons of growth rates between the sexes show no significant differences (Mann-Whitney *U*-test; $U = 3$, $P > 0.05$, in both cases).

Enhanced feeding regimes under captive conditions may result in early sexual maturity, in which case sexual maturity will be dependent on growth, rather than age. This feature has been demonstrated for various species of crocodilians (Andrews, *unpubl. obs.*). Bustard & Singh (1981) reported that captive *Crocodylus palustris* under optimum husbandry conditions exhibit rapid growth, thereby leading to early onset of sexual maturity. They also demonstrate that breeding can be hastened and sexual maturity is dependent on growth, rather than age. Nichols & Chabbeck (1980) reported that enhanced feeding leads to faster growth rates, resulting in early breeding in alligators. Joanen & McNease (1975) have also reported that sexual maturity is dependent on size rather than age for alligators. However, this aspect is still to be tested in *V. salvator* when comparative information from the wild becomes available.

The oviposition cycle in *V. salvator* has been discussed by several authors. At the Nandankanan Biological Park, Orissa, eastern India, eggs were laid in July for two years in captivity by a female (Biswas & Acharjyo, 1977) and by another in June in the same Park (Acharjyo & Mohapatra, 1980). Khan (1969) reported that different wild individuals in the Malay peninsula are reproductively active throughout the year, with a peak from September to October. Erdelen (1991) thought that it is likely that *V. salvator* in south Sumatra reproduce continuously throughout the year, with egg-laying peaking at the same time as in the Malay peninsula, as reported by Khan (1969). Gaulke (1992) found considerable variation in the breeding season between wild populations found in the various islands of the Philippine archipelago. For example, nesting in May was observed in one island and in November in another. Hairston & Burchfield (1992) reported marked oviposition cycle differences in two breeding females in captivity. These females laid eggs in December, April, July, August and September. Authors have also reported multiple clutches by the females in a single year, a phenomenon reported by Andrews & Gaulke (1990).

At the Madras Crocodile Bank, where the rainy season starts in June, the 1991, 1992 and 1993 egg-laying seasons closely synchronize with that reported by Smith (1935), namely, eggs being laid in June at the onset of the rainy season in Thailand. A female in captivity was also reported to have laid 14 eggs in June (Whitaker, 1978). June has also been reported as the egg-laying season coinciding with the south-west monsoon season in north-east India, Bangladesh and Andaman and Nicobar Islands (Whitaker & Khan, 1982). Biswas & Kar (1981) also reported that in north-east India, egg-laying in the wild occurred in June. Keatzer (1973) also reported egg-laying in July. Similar findings of eggs being laid from May through July in the north-eastern India population (R. Ghosh, *pers. comm.*) are known.

V. salvator has the largest distributional range of all the varanids (Gaulke, 1991). It is also the most exploited species for skin and meat throughout its range. (Das, 1989; Luxmoore & Groombridge, 1990). Habitat destruction also poses a major threat for the species' survival (Andrews & Gaulke, 1990; Erdelen, 1991).

Previous observations in captivity have demonstrated that the species can be bred in captivity with a high degree of success (Andrews & Gaulke, 1990). Considering the growth rate of the species, hatchling survival rate and their ability to breed in two years under captive conditions, the species can easily be made a resource for skin and meat. In countries of tropical Asia, captive-breeding for farming can be taken up under eco-development programmes for the benefit of local people, thereby reducing the pressure on wild populations.

Captive-breeding can also serve as a conservation tool, and for maintaining gene pools. Besides farming, offspring raised to the appropriate size can be restocked in habitats where populations have been decimated. Thus, besides facilitating a better understanding of the biology of *V. salvator*, captive breeding can greatly aid in the management and conservation of the species.

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SHORT NOTES

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PREVALENCE OF ENDOPARASITES
IN ROUND ISLAND REPTILES

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Round Island is a half-eroded volcanic cone rising out of the 50 m deep coastal shelf 21 km NNE of Mauritius in the Indian Ocean. This 151 hectare outcrop of tuff holds a reptile population consisting of three species of gekkonid lizards, three species of skink and two species of bolyeriid snakes (Vinson & Vinson, 1969; Bullock, 1986). Of these eight species, four, the gecko *Phelsuma guentheri*; the skink *Leiopisma telfairii* and the bolyeriid snakes *Casarea dussumieri* and *Bolyeria multocarinata*, are found solely on Round Island, whilst two others (the gecko *Nactus serpensinsula* and the skink *Scelotes bojerii*) also occur on smaller nearby islets, with *S. bojerii* having a further small relict population on mainland Mauritius. Fossil evidence shows that most of these reptiles previously occurred on mainland Mauritius (Arnold, 1980); therefore, Round Island represents a last refuge for an important relict herpetofauna.

It is thought that this unique fauna has only survived due to the lack of carnivorous mammals; however, the introduction of rabbits (*Oryctolagus cuniculus*) and goats (*Capra hircus*) sometime between the early 1600's and 1840's has led to decimation of the native vegetation and severe loss of soil cover (North & Bullock, 1986; Bullock, 1986). Rabbits and goats have now been eradicated (Merton, 1988) but despite the subsequent increase in soil cover, one of the endemic snakes (*Bolyeria multocarinata*) has not been seen since 1975 and is now almost certainly extinct (Bullock, 1986). The reptile fauna remains extremely endangered and at risk from ecological disturbances such as introduction of rats and mice, introduction of non-indigenous weed species, and cyclone damage.

Parasitic infections of reptiles have been studied by numerous authors, and their pathological implications are fairly well known (see Cooper & Jackson, 1981). It has recently been shown that parasitic infection may cause a major loss of reproductive capacity in wild reptiles (Schall & Dearing, 1987; Pence & Selcer, 1988). Papers have been published concerning parasite prevalence in reptiles (see Telford, 1970) and descriptions of new species often contain prevalence data. There appears to be no information pertaining to the parasites of Round Island species in the refereed literature. Goldberg & Bursey (1990) undertook a study of en-

doparasite prevalence in the endangered island night lizard (*Xantusia riversiana*) and found that prevalence of the gall bladder protozoon *Eimeria noctisauris* was higher than that of similar parasites in similar mainland reptiles. These results suggest that parasitic infection is naturally elevated in island populations, and therefore represents another ecological pressure on these species.

The present study was undertaken as part of a Raleigh International expedition to Round Island (Daszak, 1994). The aims were to ascertain as far as possible the prevalence and identity of the endoparasites infecting the populations of Round Island reptiles and to deduce the possible impact of parasitism on this fragile fauna. In the present paper, information on prevalence of coccidial infection in wild reptiles is collated from 150 sets of data in 44 papers published between 1923 - 1994 describing new species of coccidia. These data are used to investigate the influence of insularity and other factors on coccidial infections of reptiles.

Faecal samples were collected between 1 August and 15 September 1993 during a Raleigh International expedition to Mauritius, Round Island and Rodrigues. Due to the rarity of the animals it was considered unethical to kill specimens; therefore, presence of infection was ascertained by examination of faecal samples for parasite eggs. Reptiles were captured by hand and placed in cloth bags for up to two days and subsequently released at the site of capture. Faecal samples were removed from the bags, split into two and portions placed in one of either 5% aqueous formalin (to fix helminth eggs) and 2.5% aqueous potassium dichromate (to allow sporulation of coccidian oöcysts for subsequent identification). Suspensions of faeces were examined in the UK by wet mounts on a Zeiss photomicroscope. Samples which showed no parasite ova were filtered and treated with saturated saline to float off parasite eggs (see Whitlock, 1948). It was decided that counts of parasite eggs or oöcysts present in individual samples or incidence scores would yield no useful information, since counts may vary over the course of a single day or throughout an infection (Levine, 1942; Stanton *et al.*, 1992).

Table 1 shows the results of the faecal survey. In addition to the data in Table 1., dual infections of two species of coccidia were observed in 16.7% (2/12) *P. guentheri*, 33.3% (2/6) *P. ornata* and 31.2% (5/16) *N. serpensinsula*. Dual infections of coccidia and helminths were observed in 11.1% (2/18) *S. bojerii* and 20.0% (2/10) *C. dussumieri*. 40.0% (4/10) specimens of *P. ornata* of mainland Mauritius origin (Flic en Flac, Rivière-noire) contained coccidial oöcysts, with 0.0% (0/10) containing helminth eggs.

Identification of the helminth parasites was hampered since internal examinations were not possible and therefore no adult worms could be retrieved. Identification down to class or genus was possible using egg morphology. In 62.5% (10/16) of the *L. telfairii*

TABLE 1. Prevalence of endoparasite infection in Round Island reptiles.

| Reptile species | % prevalence coccidia | % prevalence helminths | % infected (total) |
|---------------------------------|--|---------------------------|-----------------------|
| Gekkonidae | | | |
| <i>Phelsuma guentheri</i> | 33.3 (4/12) | 0 (0/12) | 33.3 (4/12) |
| <i>Phelsuma ornata</i> | 66.7 (4/6) | 0 (0/6) | 6.6 (4/6) |
| <i>Nactus serpensinsula</i> | 50 (8/16) | 0 (0/16) | 50 (8/16) |
| Scincidae | | | |
| <i>Leiolopisma telfairii</i> | 0 (0/40) | 40 (16/40) | 40 (16/40) |
| <i>Scelotes bojerii</i> | 61.1 (11/18) | 44.4 (8/18) | 66.6 (12/18) |
| <i>Cryptoblepharus boutonii</i> | No specimens collected from this species | | |
| Bolyeriidae | | | |
| <i>Casarea dussumieri</i> | 60 (6/10) | 20 (2/10) | 60 (6/10) |
| <i>Bolyeria multocarinata</i> | No specimens collected from this species | | |

samples positive for helminths, an unidentified species of nematode was found, and in 37.5% (6/16) of the positive samples, one species of the Order Oxyurida. One hundred percent (8/8) of the *S. bojerii* samples positive for helminth ova appeared to represent an unidentified oxyurid species, similar to those from *Leiolopisma telfairii*. Helminth eggs from *C. dussumieri* samples belong to an unidentified species of nematode.

Measurements of the coccidian oöcysts were taken and it appears that the majority of the species found have not previously been described (Daszak & Ball, in prep.). One hundred percent (6/6) of the coccidia-positive *P. guentheri* faeces contained a subspherical *Eimeria* species, and 33.3% (2/6) of the positive samples contained *Isospora* oöcysts mixed with the *Eimeria* sp. All (6/6) of *P. ornata* *Eimeria*-positive samples contained oöcysts which were subspherical and 33.3% (2/6) of the samples contained both the *Eimeria* sp. and a subspherical *Isospora* species. It is interesting to note that 16.7% (2/12) of the mainland Mauritius *P. ornata* samples contained three different groups of oöcysts: a subspherical *Eimeria* sp. similar to those from the Round Island samples, a more ellipsoidal *Eimeria* sp. with larger oöcysts and an *Isospora* species similar to those from the Round Island samples. All (8/8) coccidia-positive *N. serpensinsula* samples contained subspherical *Eimeria* oöcysts, with 62.5% (5/8) of these positive samples showing the presence of a spherical *Isospora* species. All *S. bojerii* oöcysts examined were of a similar morphology (ellipsoidal *Eimeria* sp.) and measurement range. The coccidium found in samples from *C. dussumieri* is a *Caryospora* sp. and has a fairly uniform morphology and size range between samples. *Caryospora* spp. have a life cycle which alternates between asexual division in muscle cysts within a prey host, and the sexual reproduction within the intestine of a predator host

(see Upton, Current & Barnard, 1986). It is probable that the asexual cycle occurs within the skeletal muscle of one of the Round Island lizard species which appear to be the snake's main prey (Bullock, 1986; Jones, 1988; Cundall & Irish, 1989); however, none were examined for cysts.

In addition to the data in Table 1, 2.5% (1/40) *Leiolopisma telfairii* faecal samples contained very low numbers (two observed) of coccidian oöcysts. The oöcysts were measured and appeared conspecific with the *Eimeria* species found in *Scelotes bojerii*. *L. telfairii* was observed to eat *Scelotes bojerii* during the course of this study (Daszak, 1994) and it is probable that the presence of these oöcysts is spurious. Oöcysts of an *Adelina* species were identified in 18.7% (3/16) of *Nactus serpensinsula*. Measurements of these oöcysts fell within the range of an *Adelina* species (Daszak & Ball - in prep.) isolated from Round Island centipedes (*Scolopendra abnormis* sp. nov. - Lewis & Daszak, in prep.), and it is likely that *N. serpensinsula* preys on these.

To make sense of the prevalence data it is important to realise the limitations of faecal egg surveys. Firstly for helminth infections, it may be that not all females present in the host intestine are laying eggs at the time of sample collection. Secondly, for the coccidian infections, it is known that oöcyst counts (and by deduction the number of individuals passing detectable numbers of oöcysts) vary over the duration of an infection and throughout each day (Levine, 1942; Stanton *et al.*, 1992). Therefore, estimates of prevalence will tend to be slightly lower than actual prevalence.

Goldberg & Bursey (1990) showed that prevalence of *Eimeria noctisauris* infection in the island night lizard *Xantusia riversiana* from small islets off California is higher than the prevalence of similar eimeriid parasites from similar mainland lizards (comparison of three sets of island lizard prevalence data with seven

sets of mainland lizard prevalence data). The present study investigates this phenomenon further - by collating the prevalence data of 105 species of coccidia in 2038 individual reptiles ($n = 2205$ due to some individuals harbouring more than one species). The sources of data were 44 papers describing new species of reptile coccidia published between 1923 and 1994 in addition to the data from Round Island reptiles presented in the present paper. The scope was worldwide, with data from reptiles of Africa, North and South America, Europe, Russia, India, the Far East and islands in the Pacific, Indian and Atlantic Oceans. Infection was assessed by microscopic examination of faeces.

Reptiles show a wide range of prevalences with often 50.0 - 100% reported. For *Caryospora* species from snakes the mean prevalence is 58/151 (38.4%). For lizard *Eimeria/Isospora* spp. the mean prevalence from 75 sets of data is 677/2051 (33.0%). Coccidial prevalence in island-dwelling lizard data is higher (43.6%, $n=626$) than mainland species (26.7%, $n=1425$). However, the possibility that host insularity leads to elevated levels of coccidial infection must be questioned, since the mainland data include a high proportion of desert-dwelling lizards (62.9% of the total number of mainland reptiles). It is known that coccidial oöcysts require moisture for survival and that a higher percentage will survive under higher relative humidity (Fayer & Reid, 1982). Furthermore, it has been suggested that prevalence of coccidial infection in desert-dwelling reptiles is limited by the low resistance of oöcysts to desiccation, and therefore low numbers of viable oöcysts present in the environment for infection of new host individuals (Ovezmukhammedov, 1974).

In order to test the influence of insularity and desert habitation on prevalence of infection, the data in the present study have been divided into three groups. The snake data have not been analysed by habitat since there is a paucity of information on *Caryospora* prevalence in desert- and island-dwelling hosts. Island host lizards (defined as having been captured on a landmass with an area of less than 2000 km²) showed a prevalence of 275 infected out of 626 examined (43.9%). Desert mainland hosts were defined as having been captured in a region having an average annual precipitation of less than 250 mm and in a landmass of area greater than 2000 km², and revealed a prevalence of 134 infected out of 896 individuals examined (15.0%). Non-desert mainland hosts (originating from area of land greater than 2000 km² and with more than 250 mm rainfall p.a.) had a prevalence of 243 out of 529 infected (45.9%). All of the islands studied (including those in the California channel studied by Golberg & Bursey, 1990) had rainfall substantially greater than 250mm per annum, and therefore cannot be classified as desert habitat (Moore, 1975). Chi-squared analysis showed that the three sets of data differed highly significantly ($\chi^2=137.4$, $df=2$, $P<0.001$). Testing the

island against the non-desert mainland data showed no significant difference ($\chi^2=0.241$, $df=1$, $P>0.05$). Finally, testing island and non-desert mainland data against desert mainland data revealed a highly significant difference ($\chi^2=137.7$, $df=2$, $P<0.001$).

Thus it appears that insularity is not a significant factor in coccidial prevalence, whereas occurrence in desert hosts is highly significant. The effect of high humidity habitats (e.g. rainforests) on prevalence was not tested. Other factors affecting prevalence are host population density, age structure of the population, altitude, sunlight and most probably behaviour (e.g. territoriality), season (especially with respect to mating), and weather prior to collection of samples (Telford, 1970; Fayer & Reid, 1982; Aquino-Shuster, Duszinski & Snell, 1990).

Publications particularly pertinent to the Round Island data are those by Brygoo (1963), Upton & Barnard (1987), Upton *et al.* (1990) and Daszak & Ball (1990) concerning parasites of reptiles from Madagascar (the nearest landmass to Round Island greater than 2000 km²). Barré (1982) published parasite data from a survey of 23 reptiles collected on the island of Réunion 200 km southwest of Mauritius. Barré (1982) found 20.0 - 66.7% prevalence of various species of nematodes and cestodes in three species of geckoes and one species of iguanid, and 50.0% prevalence of a cestode in one snake species. These results cannot be usefully compared with the Round Island data as they concern only non-native reptiles. The prevalence data from Upton & Barnard (1987) and Daszak & Ball (1990) cannot be used for comparison with the data presented in this paper, since these studies concern imported reptiles, which often show elevated levels of infection (see Telford, 1970). Brygoo (1963) reported coccidial infection in the gall bladders of *Phelsuma lineata* from Madagascar however, no prevalence data was presented. Upton *et al.* (1990) published eight sets of prevalence data for five species of *Caryospora* and listed prevalences of 16.6% up to 100% with a mean of 45.0% ($n=29$). The Round Island boa *Caryospora* data is well within this range although higher than the mean prevalence for all reports analysed (38.4%, $n=151$). The data on helminth prevalence compare well to data on similar helminths from mainland species of reptiles (see McAllister *et al.*, 1991); however, helminth prevalence data were not analysed by habitat.

Therefore it seems that Round Island reptiles support parasitic infections of average prevalence. No unduly large parasite burdens were observed, and no clinical signs of illness (eg. diarrhoea) were seen other than an emaciated juvenile Round Island boa (no parasite ova were detected in the faeces of this animal). The parasites infecting Round Island reptiles belong to groups that are not usually associated with acute disease in reptiles (Cooper & Jackson, 1981). However, it has been demonstrated that intestinal parasitic infec-

tion in reptiles may lead to a lowering of the reproductive output of females (Pence & Selcer, 1988). Furthermore, it is known that the presence of other disease agents in the host, environmental factors such as nutritional status of the host, the close confinement with other infected individuals and stress related to lowering of external temperature may significantly affect the prevalence, incidence and pathogenicity of coccidial infections (Hammond, 1973; Long, 1973; Fernando, 1982). On Round Island, drought or prolonged cyclone conditions may lead to an increase in coccidial prevalence and outbreak of disease - however, no data on this has been collected. Recent increases in the population of the reptiles (Tonge, 1989; North, Bullock & Dulloo, 1994) suggest that the population is healthy despite the prevalences reported in the current paper.

It is known that captive reptiles may continue to pass coccidian oöcysts for several months following confinement, and this is thought to be due to continual reinfection with oöcysts from the substrate (Ball & Daszak, in press). It would be extremely difficult to ensure that captive stock of Round Island reptiles (maintained as part of the captive-breeding programme) are free of coccidia. It would therefore be interesting to compare the prevalence of parasites in the captive colonies of Round Island reptiles with those in the wild populations. Should the captive-bred animals be free of parasites, this could lead to problems if or when they are reintroduced to the wild population (Jacobson, 1993).

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SHORT NOTES

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**MELANISM AND FORAGING
BEHAVIOUR IN AN INTERTIDAL
POPULATION OF THE MADEIRAN
LIZARD *PODARCIS* (= *LACERTA*)
DUGESII (MILNE-EDWARDS, 1829)**

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The Madeiran lizard *Podarcis* (= *Lacerta*) *dugesii* (Milne-Edwards) is a common lacertid 'wall' lizard occurring throughout the Madeiran archipelago, particularly in the orchards and vineyards of the main island where it occurs in large numbers and has been regarded as an agricultural pest for centuries by the Madeirans (Forster, 1777). *P. dugesii* is omnivorous, eating vegetation, fruit and even nectar as well as insects and other terrestrial invertebrates (Elvers, 1977, 1978; Sadek, 1981; Beyhl, 1990).

P. dugesii is a polymorphic, adaptable species that occurs in a variety of morphological types and colours (Cook, 1979; Crisp *et al.*, 1979) and is found at all altitudes in Madeira, from sea level where air temperatures range between about 18°C in winter and 32°C in the summer, to mountainous areas up to 1850 m where summer temperatures may be as low as 20°C and snow falls in the winter.

The investigation reported here was carried out on a melanistic population of *P. dugesii* that was seen to be exploiting the intertidal zone, an unusual ecological niche particularly given the high-energy (i.e. exposed to heavy wave action), stony nature of Madeiran shores.

The study was carried out at a beach at Caniço, Southern Madeira, about 15 km east of Funchal. The whole beach, about 1 km long, consists of small outcrops of dark coloured lava interspersed with long stretches of mixed dark grey boulders, cobbles and pebbles. These latter portions of the beach were regularly resorted by the advancing and receding tides since Madeira features strong breezes and heavy oceanic swells. The jumble of boulders, cobbles and pebbles was generally at least 0.3 m thick and overlaid coarse gravel. Although the uppermost layers of this substratum rapidly dried out on sunny days, the deeper layers were always damp. Most of the dampness was due to seawater, but there were some freshwater inputs to the beach too.

In common with most of such high energy boulder/pebble beaches there was little sign of animal life save for substantial numbers of an isopod, *Ligia italica* Fabricius. *L. italica* is a large (<16 mm body length in females; Vandel, 1960) plant and debris-eating isopod and browses particularly (in daylight hours) upon lichens, microbial films and, on large boulders and fixed rocks, upon green macroalgae (especially *Cladophora* sp.). Lizards that were black dorsally and blue-grey ventrally were seen in the intertidal zone during most daytime visits to the beach at Caniço, though sightings were rare before mid-morning. They occurred from the top of the shore down to about low water neap tide level though they were never seen nearer to the water's edge than about 1-2 m.

Melanism. To determine whether the 'intertidal' population differed in colour and morphology from the 'terrestrial' population, 115 lizards (58 'intertidal'; 57 'terrestrial') were collected (between 15.11.93 and 16.2.94) in fruit-baited bucket traps set in the intertidal zone and nearby terrestrial area (pyroclastic pebbles and earth, with some vegetation). Measurements were made to the nearest mm: snout-vent length (SVL), tail length (TL; only for specimens with undamaged tails.); and to the nearest 0.1 mm: head width (HW), right forearm length (RFAL) and length of 4th digit of right forelimb (FIL; 'finger length'). The colour of lizards was ranked on a scale from 0-5 (5 being completely black, 0 being sand-coloured). This study confirmed that intertidal lizards were almost black (mean score = 4.4, SD = 0.5, $n=58$), while terrestrial lizards were dark brown (mean score = 3.1, SD = 0.6, $n=57$); the difference was statistically highly significant (Mann-Whitney *U*-test: $U = 2293$, $P < 0.001$). Intertidal lizards were also significantly bigger (mean SVL = 58.0 mm SD = 7.0, $n=58$) than terrestrial lizards (mean SVL = 51.8 mm, SD = 9.4, $n=57$; Mann-Whitney *U*-test: $U = 2293$, $P < 0.001$). There was a weak, but significant, influence of body size on colour rank (colour score = $0.05 \text{ SVL} + 1.16$; $r^2 = 0.24$, $P < 0.001$). However, ANCOVA established that, for the same body length, intertidal lizards were always darker than terrestrial animals ($P < 0.001$). To correct for body size, slopes and elevations of the regressions of TL, HW, RFAL and FIL on SVL were compared for both lizard groups. No differences in slopes were detected (ANCOVA, homogeneity of slopes) for any of the measurements. However, for a given SVL, intertidal lizards had longer tails and longer fingers than terrestrial lizards as there were significant differences in elevations for TL (ANCOVA: $F = 11.6$, $n = 105$, $P < 0.001$) and FIL (ANCOVA: $F = 18.9$, $n = 113$, $P < 0.001$). The regression equations are listed in Table 1.

These data show that the intertidal population differs significantly in both colour and morphology from its terrestrial near-neighbours. The differences in morphology might, perhaps, have been explained by a difference in sex ratio, since Sadek (1981) reported

TABLE 1. Regression equations of tail length (TL), head width (HW), right forearm length (RFAL) and finger length (FIL) on snout-vent length (SVL) for intertidal and terrestrial lizards or, if ANCOVA stated no difference between regressions, for pooled data.

| Variable | Slope | Constant | r^2 | P |
|------------------|-------|----------|-------|--------|
| TL(intertidal) | 1.41 | 13.04 | 0.49 | <0.001 |
| TL (terrestrial) | 1.62 | 9.09 | 0.64 | <0.001 |
| HW (pooled) | 0.08 | 0.98 | 0.58 | <0.001 |
| RFAL(pooled) | 0.20 | -0.44 | 0.67 | <0.001 |
| FIL(intertidal) | 0.10 | 0.56 | 0.50 | <0.001 |
| FIL(terrestrial) | 0.10 | 0.21 | 0.83 | <0.001 |

that females have relatively shorter tails and hind legs than males. However, although the lizards of this study were not sexed directly, the head width data were analysed (c.f. Sadek, *op. cit.*) and this analysis showed that there was no significant difference in sex ratio between the populations, reinforcing the hypothesis that the intertidal population of lizards is morphologically distinct.

Foraging behaviour. Specimens of *P. dugesii* were regularly seen along the whole of the beach; direct visual observation of their behaviour was carried out whenever possible over a period of two weeks in the summer of 1993. Four melanistic specimens of *P. dugesii* were trapped in a banana-baited trap at mid-tide level. The banana bait was wrapped in perforated plastic film so that it could be smelt, but not eaten. One of the animals was sacrificed humanely for dissection and analysis of stomach contents; the others were held separately unfed for 24 hr so that their droppings could be collected. These three animals were then offered specimens of *L. italica* and their behaviour was observed.

On several occasions intertidal lizards were seen to eat discarded fruit remnants (particularly banana skins) left behind by tourists. However, they were also seen to exhibit alertness whenever specimens of *Ligia* were visible nearby. Often they were seen to stalk isopods, but usually disappeared from view in the jumble of beach pebbles before food capture was observed. However, on the afternoon of 17.8.93 two black lizards were seen to capture and eat *Ligia*. One caught a single isopod (capture and handling taking 5 s), but the other first chased two large groups ($n > 20$) of isopods without success, ceasing pursuit within 0.2–0.4 m. It then chased, caught and swallowed a large isopod (catching and handling time 10 s), rested for 60 s before jumping in the air to catch a dipteran fly. It ate another *Ligia* before disappearing into the pebble substratum in pursuit of another isopod.

The single animal dissected was a mature male (overall length 134 mm; snout-to-vent length 61 mm). On dissection the stomach contents were found to consist wholly of five large, partly digested *Ligia*. The isopods were in pieces; all of the heads were separate from the bodies. The droppings of the three other captured lizards revealed the following material:

Lizard 1: Parts of the exoskeleton of a large cockroach (attracted into the banana-baited trap?), several parts of *Ligia* exoskeleton, particularly the eyes, plus a small piece of polythene sheet.

Lizard 2: Droppings contained *Ligia* exoskeleton pieces, two dipteran pupal cases, and parts of a large cockroach.

Lizard 3: Beetle elytrae and large numbers of *Ligia* eyes.

The three animals held captive after trapping took specimens of *Ligia* offered to them immediately after collection of droppings (i.e. when they had fasted for 24 hr). They were subsequently held for several months during which they were fed exclusively on a diet of *Ligia* and talitrid amphipods.

In conclusion, the observations recorded in this study indicate that there is a separate population of melanistic *P. dugesii* that forages entirely or predominantly between the tidemarks at Caniço, Madeira, the most important item of diet being the large, amphibious isopod *L. italica*. The population appears to be readily separable from nearby terrestrial populations by virtue of its black coloration, though there are subtle morphological differences too. Although Sadek (1981) included 'beach' populations in his study of the diet of *P. dugesii* on Madeira, he makes no reference to melanistic lizards on the main island of Madeira, and it seems likely that he caught supralittoral/terrestrial predators rather than intertidal foragers, particularly as the diet of his 'beach' specimens was dominated by ants, beetles, flies and amphipods (which may well have been terrestrial talitrids, common on Madeira (Dahl, 1967)). Both Crisp *et al.* (1979) and Bischoff *et al.* (1989) also fail to mention melanistic lizards on the main island of Madeira.

Other carnivorous lizard species are known to forage entirely within the intertidal zones of islands: *Anolis agazzi* and *Diploglossus haycocki* which both eat intertidal crustaceans on the Isla Malpelo, Colombia, and the skink *Cryptoblepharus boutoni* which eats insects, crustaceans and juvenile fish on Madagascar (Fricke, 1970), migrating up and down the shore in similar fashion to *P. dugesii*. Although no other lacertid lizard has been reported to use the intertidal zone in this fashion, such behaviour might be expected from other wall lizards living on islands (e.g. in the eastern Mediterranean) where *L. italica* is to be found.

The following factors may have encouraged the development of intertidal foraging on Madeira. On most Atlantic coastlines the productivity of cobble/pebble beaches is dominated by strandlines at the top of the shore where rotting wrack supports a diverse talitrid

amphipod and insect (dipterans and beetles) fauna. Such strandlines are less important on a volcanic island like Madeira whose seaweed beds are very limited in extent. Instead, the dominant animals are large *L. italica* that feed on green algae on boulders and in pools, but also eat detritus, lichens and microbial films as they move up and down with the tide. On most eastern north Atlantic shores a different member of the genus is found, *Ligia oceanica* L. (see Vandel, 1960 for discussion). However, *L. oceanica* is a nocturnal species (Nicholls, 1931) that hides under stones throughout the day, whereas *L. italica* (at least on Madeira) is a day-active isopod that hides at night when predatory grapsid crabs (mainly *Pachygrapsus maurus*) are numerous and active on the wet rocks. Lizards are diurnal visual foragers, too slow-moving in the cool of the night to catch fast-moving animals, so the daytime coincidence of *P. dugesii* and its isopod prey is important. Additionally, in most coastal intertidal environments there is an alternation of predatory influences with fish and crabs dominating when the tide is in, and sea birds dominating when the tide is out, at least during the day. On Madeira the influence of birds on the intertidal zone is very limited since the number of resident seabirds is low (e.g. Jepson & Zonfrillo 1988), there are no members of the crow family on Madeira (Bannerman & Bannerman, 1965) and even migrant waders are sparse (Zonfrillo, pers. comm.). Both *P. dugesii* and its prey avoid predation at high tide and/or night by moving off the shore or hiding amongst the pebbles of the substratum; they can both exploit the intertidal zone during the day with little or none of the risk that they would face during the day if there were more wading birds, or if corvids were present.

The reliance of a population of *P. dugesii* on a diet of intertidal isopods poses a number of interesting questions regarding salt and water regulation. No data concerning the osmoregulatory capacity of *L. italica* appear to have been published, but the related *L. oceanica*, *L. occidentalis* and *L. pallasii* are all powerful osmoregulators at low salinities and are actually hyperosmotic to full sea water (Parry, 1953; Wilson, 1970). This suggests that the body fluids of the isopods will have osmolarities of at least 1000–1100 m Osmoles kg⁻¹, some 2–3 times the likely plasma osmolarity (probably ca 350–400 m Osmoles kg⁻¹) of the lizards. Although the ready availability of *Ligia* will provide abundant food for intertidal *P. dugesii*, the lizards must incur a considerable salt load when exploiting this resource. Whether the lizards cope with this salt loading behaviourally by seeking out freshwater for drinking, or physiologically by extra-renal salt secretion is as yet unknown.

The melanistic nature of the intertidal *P. dugesii* is undoubtedly cryptic, given the unrelieved black/grey colour of the rocks and stones of the Madeiran intertidal zone. The small body size of the species makes it unlikely that the black colour provides any ther-

moregulatory advantage; Crisp *et al.* (1979) have already provided good experimental evidence dismissing this possibility for the melanistic *P. dugesii* living on the Desertas islands. The differences in size and proportions exhibited by the intertidal population of *P. dugesii* are more difficult to understand, although the Galapagos marine iguana (also melanistic) has similarly well developed toes and claws for maintaining purchase on a slippery substratum (Bell, 1825; Trillmich & Trillmich, 1986).

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FORUM

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TADPOLE GROWTH: IS THERE
AN INTERFERENCE EFFECT
IN NATURE?

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The effects of crowding on growth-suppression in tadpoles have been the subject of laboratory studies for more than thirty years. Ever since the pioneering work of Richards (1962) and others, a unicellular organism has been implicated in an interference-type of competition that seems to operate on tadpoles of many different anuran species. Only recently, however, have intensive efforts been made to try and discover the mechanism of this process and, most importantly, whether it occurs in the field as well as in the laboratory. These new results are, at first sight, somewhat confusing and possibly contradictory.

In two recent papers (Petranka, 1989; Biesterfeldt, Petranka & Sherbondy, 1993), Petranka's group has reported experiments carried out at natural sites used by various anurans but especially the southern leopard frog *Rana utricularia* and the wood frog *R. sylvatica* in the USA, including studies with water taken from these sites and subsequently transferred to the laboratory. Broadly speaking, the experiments indicated, or were interpreted to indicate, that: (1) even in ponds with very high densities of tadpoles, it was rare (<25% of samples) for water from those sites to cause growth inhibition of other (target) tadpoles. This was true whether experiments were carried out *in situ*, or after transfer of water back to the laboratory. And (2), when growth inhibition was observed in field samples, the unicellular organism implicated as the crucial mediator in laboratory trials was probably not responsible.

By contrast, growth inhibition of small *Bufo calamita* tadpoles by large larvae of *Rana temporaria* has been demonstrated in the UK by Griffiths and his colleagues (Griffiths, 1991; Griffiths, Edgar & Wong, 1991; Griffiths, Denton & Wong, 1993) using replicated outdoor ponds which closely mimicked many natural ones used by these species. Although variable in degree, an interference-type mechanism was commonly observed and so was production of substantial numbers of the implicated unicells in the tadpole faeces. Studies by my group (Beebee, 1991; Beebee & Wong, 1992; Wong & Beebee, 1994) have confirmed that the organism involved is an unpigmented alga (genus *Prototheca*), and that purified cells cause growth

inhibition in small tadpoles under laboratory conditions by diverting them away from higher-quality food sources. More recently, we have also found that these cells were produced in large quantities by tadpoles in two natural ponds where densities were high, though the water from these ponds was not tested for growth inhibitory properties (Wong, Beebee & Griffiths, 1994).

Can these disparate results be reconciled? With respect to the significance of interference competition in the field, two aspects may be important: the availability and type of food consumed by tadpoles, and the abundance of *Prototheca* pathogens. Most laboratory experiments, and some of the replicated ponds used by Griffiths' team, received an artificial food (dried vegetable matter in pellet form). Since *Prototheca* seems to act by diverting tadpoles from alternative food sources, its efficiency in causing growth inhibition may be critically related to the type of food it is competing with. Perhaps it is much less successful when pitted against natural periphyton. Furthermore, we have also shown (Wong, Beebee & Griffiths, 1994) that a bacterial pathogen of *Prototheca* is widespread in natural pond silts. This pathogen is able to reduce *Prototheca* numbers drastically within a few days, and when present as an accidental contaminant can have similar effects in laboratory studies.

All of this means I share Petranka's view that interference competition may be less likely in natural than in laboratory situations. However, unlike Petranka I believe that the evidence clearly implicates *Prototheca* as a causative agent when this type of competition does occur, even in the field. Aside from the published evidence on this matter, and our findings of protothecans at high abundance in natural ponds, the data of the most recent paper by Petranka's group (Biesterfeldt *et al.*, 1993) gives some support to this hypothesis. Although the authors interpreted their data to mean that growth inhibition was caused by agents other than *Prototheca*, there is in fact an interesting relationship if the data in their Tables 2 and 3 are analysed. Thus, the numbers of *Prototheca* cells in fresh, wild-caught tadpole guts (Table 2) were negatively correlated with the arcsin-transformed percentages of growth relative to controls that can be calculated for the "target" tadpoles of Table 3. Both sets of data are normally distributed by the Shapiro-Wilk test and $r = -0.770$, $df = 6$, $P < 0.05$. Although there was no relationship between growth inhibition and *Prototheca* numbers in tadpoles kept for three days to condition water, this is not especially surprising. Feeding will have purged them of many cells (passage time, at least in *Rana temporaria* larvae, is >10 hours), and it is these which, in the conditioned water, probably caused the growth inhibition documented in Table 3. It is very likely that *Prototheca* numbers would have risen again in these tadpoles had they been kept longer; single cell-division times for these algae are usually about 24 hr in our ex-

perience, depending upon temperature. There was also almost a significant relationship, in Biesterfeldt *et al.*'s data of Tables 1 and 2, between *Prototheca* numbers in wild-caught tadpoles and tadpole mean local density per square metre of pond (a more meaningful measure than per cubic metre for a sediment organism of this kind); $r = 0.654$, $df = 6$, $P > 0.05$.

It is quite likely, therefore, that at least in site 2 of the Biesterfeldt *et al.* (1993) study *Prototheca* was mediating growth inhibition. This looks much less probable for the other two "inhibitory" sites, 5 and 6. However, the method used (assaying water taken from the sites) does not distinguish between inhibition due to interactions between tadpoles, and inhibition of growth that might be quite unrelated to tadpole products. Water samples from these ponds may have contained thermolabile toxins/inhibitors from other sources, and thus have nothing to do with competition between tadpoles. An interesting control would have been to screen water from a series of randomly-chosen ponds without any tadpoles at all.

Finally, bioassays in the Biesterfeldt *et al.* (1993) study were carried out in the presence of excess food and with only a single (initial) water addition. In our experience these conditions minimise *Prototheca*-mediated interference competition, which is more severe under laboratory conditions when food supply is limiting (Beebee, 1991; Griffiths, Denton & Wong, 1993) and may be weak if *Prototheca* is not continually replenished (as would of course occur in the wild). Growth inhibitors may therefore have been more prevalent than the bioassays revealed. Although *Prototheca* numbers in wild-caught tadpoles were generally much lower than those seen in laboratory stocks, this may not relate in any simple way to an effect on growth inhibition because *Prototheca* acts by resource diversion (and this might happen even at quite low cell numbers in faeces) and not by direct competition for nutrients within the tadpole guts (Beebee & Wong, 1992).

So where do we go from here? In my opinion, there are at least two areas which merit further research. Firstly, we need to identify what it is that makes interference competition happen in the field in those (possibly rare) places where it does occur. Is there something unusual about the natural food supply, or the abundance of *Prototheca* pathogens? Growth rates of *Bufo calamita* larvae in natural ponds are usually limited by food availability (Banks & Beebee, 1988), and this might make them especially susceptible to *Prototheca*-mediated growth inhibition; but in replicated pond trials, interference competition was more marked at high rather than at low food levels (Griffiths, Denton & Wong, 1993). This paradox needs further study. Secondly, the significance of overall competition (i.e. exploitation + interference) needs more attention both in the field and the laboratory. It is, after all, this holistic scenario that tadpoles nor-

mally face and in the case of tadpoles the distinction between the two types of competition is blurred; both are undoubtedly influenced by the quantity and quality of food available.

Despite some apparent discrepancies between recent studies, I am optimistic that within a few years we should have a much better idea about what really goes on in amphibian nurseries.

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INTERFERENCE COMPETITION IN TADPOLES: ARE MULTIPLE AGENTS INVOLVED?

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The inconsistent results of recent research concerning water-borne growth inhibitors in tadpoles is part of a bothersome trend that has occurred over the last thirty years. Several factors have contributed to confusion about the agents involved in growth inhibition, and the role that these agents play in regulating natural populations of tadpoles. First, there has been much disagreement on the exact nature of growth-inhibiting agents found in tadpole guts, with candidates including proteinaceous compounds, fungi, and algae (Beebee, 1991). Second, researchers have not used standardized laboratory procedures. Differences in temperature, tadpole densities, tadpole size distributions, food types, feeding schedules, and methods used to isolate and culture growth-inhibiting agents may in part explain why conflicting results have sometimes emerged over the years. Beebee (1991), for example, found that the degree of growth inhibition in *Prototheca* increased with the number of cells that tadpoles were fed, while West (1960) found the opposite. Although *Prototheca* has been implicated as the primary growth-inhibiting agent in tadpoles, Steinwascher (1978; 1979a,b) found that water-borne agents other than *Prototheca* inhibit tadpole growth in the laboratory. Specifically, he found that tadpole growth is inhibited in a dose-dependent manner when tadpoles are fed different concentrations of yeast (*Candida humicola*) that were isolated from a natural habitat. Finally, all but the most recent studies were conducted under artificial laboratory conditions that may not reflect the biological complexities of natural ponds.

Despite these limitations, there are many points upon which researchers do agree. One is that *Prototheca* can reach very high levels in crowded laboratory animals and can strongly inhibit tadpole growth. A second is that *Prototheca* can inhibit the growth of laboratory animals in a dose-dependent manner that could potentially act as a regulating agent in natural populations. A third is that *Prototheca* occurs in many natural populations. Finally, *Prototheca* infections are not species-specific (Licht, 1967) so that *Prototheca* could potentially be important in mediating competitive interactions in tadpole guilds that occur in breeding ponds.

My research (Petranka, 1989; Biesterfeldt, Petranka, & Sherbondy, 1993) has focused on determining whether water-borne growth inhibitors play a key role in regulating natural anuran populations. We have addressed this primarily by testing water collected from natural breeding ponds for inhibitory qualities, by conducting field experiments that control the degree to which test animals are exposed to tadpole faeces, and by examining the relationship between *Prototheca* densities in wild-caught tadpoles and the extent to which water from natural breeding sites is inhibitory. Surprisingly, we found that in most cases water from ponds containing high densities of tadpoles was not inhibitory. Although *Prototheca* appears to be present in most natural populations of wood frog tadpoles in North Carolina, we find it to be uncommon or rare in faecal samples from individual tadpoles, and have never found it to occur at the high levels that typify laboratory stock. Previous laboratory studies have shown that *Prototheca* will not stunt the growth of laboratory stock when at low densities (Richards, 1962). Consequently, we have questioned whether levels of *Prototheca* infections in wild-caught tadpoles are sufficient to cause growth inhibition.

At wood frog sites where growth inhibitors were detected and *Prototheca* was present, was *Prototheca* acting as a density-dependent regulating agent? Although this question cannot be answered with certainty, we did not find compelling evidence to support this hypothesis. First, *Prototheca* was relatively rare in tadpole guts at all sites. Secondly, tadpoles from sites with inhibitors did not contain more cells on average than those from sites without inhibitors. In fact, we often found contradictory results. Tadpoles from Site 3 of Biesterfeldt *et al.* (1993), for example, had the highest density of *Prototheca* in tadpole guts even though water from this site was not inhibitory. In contrast, water from Site 5 was very inhibitory even though tadpoles had one of the lowest densities of *Prototheca* cells of any population sampled. Overall, the extent to which water from natural sites inhibited the growth of test animals was independent of *Prototheca* density in wild-caught tadpoles, with *Prototheca* density explaining only 2% of the variation in growth rates of test animals relative to controls. When tadpoles from the sites were returned to the laboratory and crowded for 72 hr, virtually all populations produced inhibitors even though levels of *Prototheca* did not increase in tadpole guts. Collectively, these trends led us to suspect that *Prototheca* was not functioning as an effective density-dependent regulating agent in most populations, and that other growth-inhibiting agents may have contributed to the inhibitory qualities of water collected from certain wood frog breeding sites.

Whether growth-inhibiting agents other than *Prototheca* contribute to interference competition in natural tadpole populations is unknown. In a general sense, we know that every vertebrate species has a wide

array of faecal-borne pathogens, parasites, and disease agents that can slow growth or cause weight loss (certainly, the number in well-studied species such as humans must number over a hundred!). Consequently, I strongly suspect that the number of water-borne agents that affect tadpole growth is far greater than the number documented to date. Our studies were not designed to determine the specific agents causing growth inhibition. However, they do provide evidence which suggest that multiple agents may be involved in growth inhibition in natural populations.

Experiments conducted by Griffiths, Edgar & Wong (1991) under semi-natural conditions suggest that agents other than *Prototheca* may be involved in inhibiting growth of tadpoles. In one sample taken during the first week of their experiment, for example, *Prototheca* was not evident in tadpole faecal samples even though tadpoles were stunted. After four weeks, *Prototheca* occurred in low-to-moderate numbers in the faeces of stunted tadpoles. These observations along with data from our own studies suggest to me that faecal-borne agents in addition to *Prototheca* may be involved in growth inhibition under natural or semi-natural conditions. *Candida* is not a likely candidate since there is no evidence that it reaches high densities in tadpole faeces under natural conditions. However, bacterial and viral infections could be important and would be impossible to detect using standard microscopic examination of faeces. Perhaps the tendency of researchers to focus too narrowly on *Prototheca* has led us to ignore other faecal-borne, growth-inhibiting agents. A well-trained microbiologist might surprise us if she or he were to examine the growth inhibiting capabilities of the array of faecal-borne bacteria that inhabit tadpole intestines.

My scepticism should not downplay the important contributions that Beebee, Griffiths, and their colleagues have made in understanding the importance of *Prototheca* in regulating natural populations of tadpoles (see summaries in accompanying articles). Their work has provided much support for the argument that *Prototheca* may be an important density-dependent regulating agent in some (perhaps a small percentage) of amphibian populations. Wong, Beebee & Griffiths' (1994) recent discovery of two natural populations of tadpoles with high densities of *Prototheca* in their guts is significant. If they can further demonstrate that water from these sites is inhibitory, and that *Prototheca* is acting in a density-dependent manner to regulate these populations, they will be the first to demonstrate convincingly the ecological relevance of this phenomenon in nature. Given the experiences that my research group has had, I remain sceptical in pronouncing *Prototheca* the primary agent that is responsible for the growth-inhibiting properties of water that we have collected from anuran breeding sites.

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DETERMINING COMPETITION MECHANISMS IN TADPOLE ASSEMBLAGES

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Amphibians and reptiles have proved to be popular organisms in competition studies, and have played an important role in influencing competition theory. Testing for interspecific competition requires the demonstration of a negative effect of one species on another. This may take the form of a shift in the distribution, or a decline in population size, of the inferior competitor. The practical demonstration of competition may therefore require long-term study. In the short term, though, variables such as growth and survival may provide an adequate reflection of competitive effects. Such variables are readily measured in small, rapidly growing animals such as tadpoles. The vast majority of studies, however, have treated competitive interactions between species as an ecological 'black box'; very few workers have attempted to unravel those mechanisms underlying the observed effects.

Traditionally, competition mechanisms have been divided into those concerned with 'exploitation' and those concerned with 'interference'. Exploitation competition reflects differences between species in their ability to utilize essential resources. One competitor will suffer because it will be deprived of resources, such as food or hiding places, by another superior competitor. The most overt form of interference competition is direct physical interaction between individuals (e.g. aggression), with the outcome of such contests often depending on the relative sizes of the competitors. A more subtle form of interference is the release of molecules or cells which may be toxic to inferior competitors, or may exert a negative effect on growth and survival via some other pathway. Interference mechanisms are unlikely to evolve unless resources are sufficiently scarce, and those based on the release of toxic chemicals or inhibitory cells are rare in nature (Schoener, 1982, 1983). The challenge for herpetologists is to open up the black box and tease apart the role of different mechanisms under field conditions.

Despite the flurry of work on tadpole growth inhibition between the 1950's and 1970's (e.g. Richards 1958, 1962; Rose, 1960; Licht, 1967; Heusser, 1972; Steinwascher, 1979a,b) unequivocal identification of the inhibitor involved has had to await the develop-

ment of the microbiological tools of more recent years. A combination of ultrastructural, cytological, nutrient assimilation and immunological methods has firmly established *Prototheca richardsi* as the mediator of growth inhibition, at least in laboratory cultures of British anurans (Beebee, 1991; Wong & Beebee, 1994). As discussed in the previous essays by Beebee (1995) and Petranka (1995), the next stage is to determine the importance of *Prototheca*, or possibly other interference mechanisms, as mediators of growth inhibition in the field.

The evidence for *Prototheca* as a mediator of competition in natural populations of tadpoles can be summarised as follows:

- (1) In laboratory bioassays, tadpoles treated with >98% pure *Prototheca* isolated from tadpole faeces suffer growth inhibition. Testing of other fractions from tadpole culture water fails to produce the same effect (Beebee, 1991).
- (2) In semi-natural replicated ponds, tadpoles treated with the faeces of superior competitors are inhibited. The faeces of both 'donor' and 'recipient' tadpoles in these experiments contain *Prototheca* (Griffiths, Edgar & Wong, 1991).
- (3) In natural ponds used by anuran populations, *Prototheca* has been detected in tadpole faeces and pond sediments. The density of *Prototheca* in pond sediment shows a seasonal trend related to the presence of tadpoles. In natural ponds not used by anurans no *Prototheca* have been detected at any time of the year (Wong, Beebee & Griffiths, 1994). Petranka (1995) acknowledges that competition in tadpoles can be mediated by a faecal-borne inhibitor under natural conditions, but argues that this mechanism is unimportant in nature and that *Prototheca* is unlikely to be the main organism involved. The evidence that he and his co-workers produce for this is as follows:

- (1) When water taken from natural ponds containing high densities of tadpoles is tested for inhibitory properties, positive results are obtained at only a few sites (Petranka, 1989).
- (2) The numbers of *Prototheca* in the guts of tadpoles taken from natural ponds is not clearly related to the growth inhibition observed (Biesterfeldt, Petranka & Sherbondy, 1993).
- (3) Even in those tadpoles which are inhibited and show relatively high numbers of *Prototheca*, the number of cells observed in the gut is too low to explain the growth inhibition seen (Biesterfeldt *et al.*, 1993).

There is agreement between both schools in that (1) *Prototheca* mediated inhibition may be more prevalent in simplified laboratory systems than in the field, and (2) that the role of *Prototheca* in the field may be subservient to exploitation competition. As Petranka (1995) points out, apparently disparate results may be a reflection of differences in methodology.

So what experiments are necessary to show unequivocally that *Prototheca* is, or is not, an agent within tadpole faeces that causes growth inhibition under natural conditions?

There seem to be two basic approaches to the problem. The first is that already taken by Petranka and his co-workers, where water taken from natural tadpole ponds is tested for inhibitory properties. At those ponds where inhibitors are thought to be present, further fractionation and testing of the water and/or sediment needs to be conducted to isolate the organisms or molecules concerned. Wong *et al.* (1994) have described two natural ponds which had high densities of both tadpoles and *Prototheca*. Petranka (1995) suggests that if water from these sites was shown to be inhibitory then this would be the first convincing case of *Prototheca* acting as the mediator under natural conditions. However, to test the hypothesis that multiple agents are involved the same water would have to be carefully screened and tested for other putative inhibitors.

The second approach would be to dose natural populations of tadpoles with *Prototheca* isolated from the faeces of superior competitors, themselves raised under natural conditions. In our replicated pond experiments we have gone some way towards achieving this by showing that *Bufo calamita* treated with *Prototheca*-laden faeces from *Rana temporaria* were inhibited (Griffiths *et al.*, 1991). Petranka (1995) suggests that some other component of the faeces may have been responsible for the reduced growth. We have not attempted to test tadpoles by dosing with pure *Prototheca* in replicated ponds for purely practical reasons. If a system can be established for isolating *Prototheca* in sufficient numbers from the faeces of tadpoles raised under natural conditions, then it may be possible to attempt such an experiment in the future.

A further problem lies in identifying the importance of growth inhibitors relative to other exploitation and interference competition mechanisms in nature. Certainly, tadpoles are frequently food-limited in natural ponds which suggests that exploitation competition for food may be most important (e.g. Seale, 1980). However, ponds are dynamic environments, and the abundance and quality of the resources they contain may change rapidly over time. Temporary ponds may deteriorate as nutrients are depleted by animal and plant growth, and then exported from the system as tadpole metamorphosis occurs (Wilbur & Alford, 1985; Morin, Lawler & Johnson, 1990). There is also considerable variability between ponds in the microhabitats and food that they support. As Beebee (1995) points out, the effectiveness of *Prototheca* as a growth inhibitor seems to depend on tadpole food supply, and the variability of this resource between ponds could explain why Petranka (1989) found evidence of growth inhibitors in some ponds but not in others. In replicated ponds we have shown that *Bufo calamita* tadpoles which have access to *Rana temporaria* faeces

but are otherwise physically separated from the latter, display a level of inhibition which is intermediate between control (no *R. temporaria*) and fully interacting (*R. temporaria* + *B. calamita*) treatments (Griffiths *et al.*, 1991). This implies that exploitation and/or direct interference competition supplements that mediated by growth inhibitors. This approach could be extended to natural ponds by performing food manipulation experiments using tadpoles raised in enclosures. Treating tadpoles with various combinations of food supplements and growth inhibitors could shed further light on the relative importance of different competition mechanisms. It would be necessary to perform such manipulations on a wide range of ponds (i.e. encompassing both 'resource-poor' and 'resource-rich'), and at the same time collect baseline data on natural food resources contained within the enclosures.

The role of *Prototheca* and/or other agents which mediate competition in tadpole assemblages is unlikely to be resolved overnight. The lack of realism inherent in many rigorous experiments performed in the laboratory will continue to confound extrapolation to the field; the lack of rigour inherent in pond-based experiments will continue to confound the unequivocal identification of inhibitors in natural systems. The essays by Beebee (1995) and Petranka (1995) highlight the value of both approaches in experimental ecology. They also emphasize that some problems cannot be resolved in the short-term by a single, clean-cut experiment. A steady accumulation of evidence, gleaned from both the laboratory and the field, will ultimately lead to a resolution of the problem.

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BOOK REVIEW

Last Chance Lost? Can and should farming save the green turtle? The Story of Mariculture, Ltd.,-Cayman Turtle Farm. Peggy and Sam Fosdick. (1994). 440 pp. Irvin S. Naylor, York, Pennsylvania. \$49.95. (cloth).

Seldom can a book that features recipes for cooking turtle steak have been reviewed in a herpetological journal, but this is a most unusual work dealing with a quite unique subject.

Turtle farming and ranching have long been subjects that have evoked strong opinions, both for and against them. The Cayman Turtle Farm, as a high-profile commercial organization, run in a highly professional manner, has a particularly critical part to play in the debate. If it is to be condemned as having a negative effect on the conservation of the green turtle, then there can be few establishments throughout the world involved in marine turtle culture that might be deemed acceptable. On the other hand, if it is judged to be beneficial to the continuance of the species involved, then it must stand as an example to be followed by others.

The Cayman Turtle Farm has featured in articles and papers in both the British Herpetological Society's *Bulletin* and the *British Journal of Herpetology* (and more recently, *The Herpetological Journal*) for some twenty years, and regular readers will have been able to piece together at least parts of the story for themselves. Now, however, the whole saga is presented in a single volume, together with a wealth of other relevant information - there are no fewer than 14 appendices, running to a total of 82 pages.

Peggy and Sam Fosdick, of New Freedom, Pennsylvania, have backgrounds in journalism, and this is apparent from their writing, but the style is not inappropriate to the telling of such a tale of high adventure, intrigue, and even humour. The driving force behind the project was Irvin Naylor, a director of the farm, and a number of other individuals who might be considered to have vested interests contributed to the effort. In spite of this, the authors seem to have succeeded in providing a solid, dispassionate, account of events, presented with objectivity, clarity, and balance.

The basic structure of the 18 chapters comprises the history of Mariculture, Ltd. since 1968. The biology of *Chelonia mydas*, though, features strongly, reflecting its fundamental role in the development of the company. Larger-than-life characters abound amongst the human participants in the drama, ranging from leading turtle biologists to politicians, industrialists, and even an influential economist admired by Margaret Thatcher, the former British Prime Minister.

Probably the most difficult task that the authors had to carry out, and perhaps the most important, was to reflect the varied (and often changing) opinions of the

parties to the farming/ranching controversy. It is to their credit that they have treated with respect the holders of views that have inevitably on occasions been at odds with their own.

The standard of production of the book is excellent, with high quality materials and the minimum of errors. There are plenty of colour photographs and diagrams, and the extensive appendices include a number of interesting papers, as well as the recipes referred to above.

This, then, is a publication that will be essential reading, not only for many herpetologists, but also for adherents to a number of other disciplines; it would also appeal to those who simply like a good story! Whatever the motivation, after completing this book the reader will certainly be in a good position to give an informed response to the question posed in the title. The debate will no doubt continue.

Leigh Gillett

British Herpetological Society

ANNOUNCEMENTS

The following applications were published on 30 September 1994 in Vol. 51, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

Case 2936:

CAECILIIDAE Rafinesque-Schmaltz, 1814 (Amphibia, Gymnophiona) and CAECILIIDAE Kolbe, 1880 (Insecta, Psocoptera): proposed removal of the homonymy by the revocation of Opinion 1462 and the adoption of the spelling CAECILIUSIDAE for the psocopteran family name

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Abstract. The purpose of this application is the conservation of the very well known family name

CAECILIIDAE Rafinesque-Schmaltz, 1814 for caecilian amphibians. This name is a senior homonym of the insect name CAECILIIDAE Kolbe, 1880. Because it had been suggested that the emendation CAECILIUSIDAE of the latter would be non-euphonious, the amphibian name was emended to CAECILIAIDAE in Opinion 1462 (December 1987). The reversal of this ruling is sought in pursuit of both stable usage and adherence to priority; furthermore CAECILIAIDAE is both non-euphonious and cumbersome.

Case 2362 :

**PHRYNOBATRACHINAE Laurent, 1941
(Amphibia, Anura): proposed conservation**

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Abstract. The purpose of this application is to conserve the name PHRYNOBATRACHINAE Laurent, 1941 for a subfamily of frogs (family RANIDAE) found throughout sub-Saharan Africa. The name is threatened by three earlier potential synonyms, HEMIMANTIDAE Hoffmann, 1878, PETROPEDETINAE Noble, 1931 and CACOSTERNINAE Noble, 1931.

Case 2875:

***Coluber poecilogyrus* Wied-Neuwied, [1824] (currently *Liophis poecilogyrus*) (Reptilia, Serpentes):
proposed conservation of the specific name**

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Abstract. The purpose of this application is the conservation of the widely used specific name of a South American snake, *Liophis poecilogyrus* (Wied-Neuwied, [1824]), by the suppression of the unused senior synonyms *Coluber m-nigrum* Raddi, 1820, *Coluber alternans* Lichtenstein, 1823 and *Natrix forsteri* Wagler in Spix, 1824.

THE HERPETOLOGICAL JOURNAL

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(revised January 1992)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.
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Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

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

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

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

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