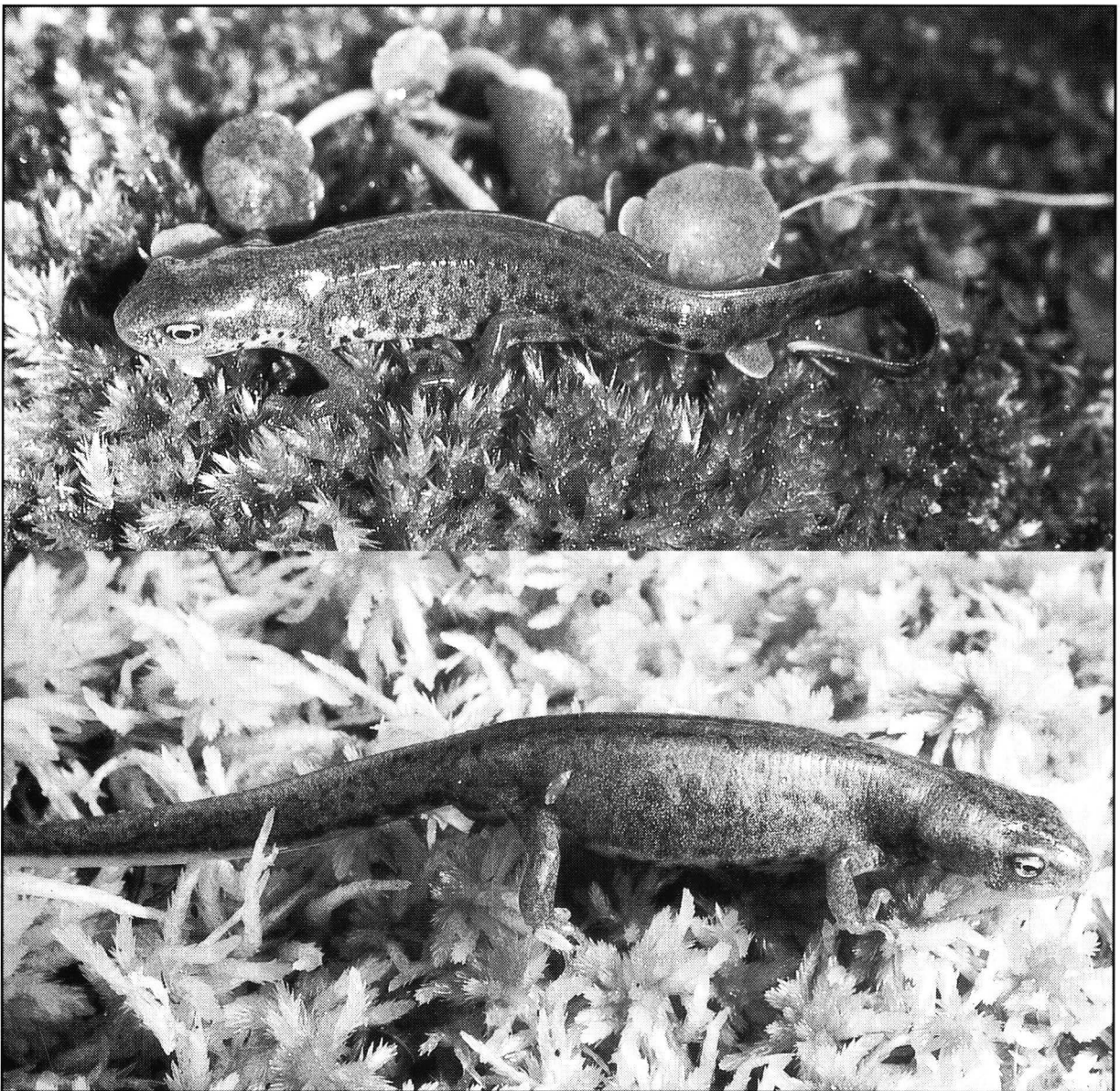


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ABUNDANCE AND SURVIVAL RATES OF GREAT CRESTED NEWTS (*TRITURUS CRISTATUS*) AT A POND IN CENTRAL ENGLAND: MONITORING INDIVIDUALS

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A population of great crested newts (*Triturus cristatus*) in central England was monitored from 1988-1995. Recognition of individuals was used to quantify population dynamics. Adult annual survival varied from 31-100%. Long-term members of the breeding population had a significantly higher rate of annual survival (65%) than individuals breeding for the first time (57%). The population showed variable patterns of recruitment. A period of six years with little recruitment was followed by a rapid increase in population size, more than three-fold, over two years. The change in the population characteristics coincided with a crash in the population of predatory three-spined sticklebacks (*Gasterosteus aculeatus*), raising the possibility that newt recruitment was held in check by predation. Juveniles were rarely captured, but their recapture rate between years (49%) indicated that the rate of annual survival for juveniles in this population could be relatively high (estimated as 59%). Most juveniles matured at two years of age. The study population thus consisted of long-lived adults, showing variable survival, and erratic recruitment. The longevity of adults enabled the population to persist under adverse conditions until beneficial circumstances could be exploited by rapidly increasing the population size. These demographic traits may be common in *T. cristatus* populations.

Key words: *Triturus cristatus*, population dynamics, mark-recapture

INTRODUCTION

Concern over the issue of declining populations of amphibians (e.g. Blaustein & Wake, 1995) has focused attention on the need for greater understanding of amphibian population dynamics. In this respect the population dynamics of *Triturus cristatus* are of particular conservation interest. Although it is widespread throughout its British range, the species has been in decline since before the 1960s and it is the most rapidly declining amphibian in Britain (Beebee, 1975; Cooke & Scorgie, 1983; Hilton-Brown & Oldham, 1991; Beebee, 1994).

Long-term studies (twelve and nine years) have demonstrated that amphibian populations may naturally show large fluctuations (Pechmann *et al.*, 1991; Woolbright, 1996), apparently driven by stochastic, climatic events, such as variable patterns of rainfall (Pechmann *et al.*, 1991; Banks, Beebee & Denton, 1993; Woolbright, 1996) or extreme weather conditions (Woolbright, 1996). However, not all amphibian populations are unstable. Amphibians may have high survival rates and be long-lived (e.g. *Ambystoma talpoideum* [Raymond & Hardy, 1990], *Triturus alpestris* [Schabetsberger & Goldschmid, 1994], *Bombina variegata* [Plytycz & Bigaj, 1993]).

Great crested newts (*Triturus cristatus*) have a wide distribution over northern Europe (Griffiths, 1996) and population data from a number of sites have been summarized by Arntzen & Teunis (1993). The data suggest that population processes vary between sites. Adult *T. cristatus* can be long-lived. Skeletochronological estimates indicate that individuals can live for as long as 14

to 17 years (Hagström, 1977; Dolmen, 1983a; Francillon-Vieillot, Arntzen & Géraudie, 1990; Miaud, Joly & Castanet, 1993). Although adult annual survival varies between sites, it is fairly stable within sites (49% to 78%) (Arntzen & Teunis, 1993). This longevity and constant rate of adult survival create the potential for population stability, which has been recorded for some populations. For example, Glandt (1982) estimated that the size of a breeding population in Germany stayed between 89 and 108 individuals over a four-year period. Hedlund (1990), found that a population on the island of Öland in the Baltic, was relatively stable, staying between 150 and 223, over a five-year period.

However, population fluctuations do occur in this species. Hagström (1979) recorded a halving of population size (500 to 230 adults) between two consecutive breeding seasons, at a site in south-west Sweden, while Miaud *et al.* (1993) noted a doubling of population size (209 to 434) over an equivalent interval at a site in eastern France. Two long-term studies have also detected population fluctuations in this species. Arntzen & Teunis (1993), studying a population in north-west France, estimated that although adult survival was fairly constant (33-57%) over a six-year period, population size ranged from 16 to 346 individuals. Similarly, in England, Cooke (1995) recorded annual mean counts of 3 to 183 for a population over an 11-year period. Although Cooke did not directly measure population size, he concluded that fluctuations in visual counts mirrored changes in population size.

This paper reports the results of a long-term study of a population of great crested newts, *Triturus cristatus*, to provide information on the dynamics of a population, using recognition of individuals to quantify population demography.

MATERIALS AND METHODS

STUDY SITE

The Walton Hall Pond is on the campus of the Open University (52°1'N, 00°42'W, Ordnance Survey grid reference SP 886369), Buckinghamshire, England. It measures 400 m² and is up to 2.5 m deep. It is heavily vegetated and can be regarded as a permanent pond, although it dried out in a drought year, 1976 (Bielinski, 1986). Map records show that the pond has been in existence since at least 1925 (Bielinski, 1986). A steep bank around the pond supports relatively unmanaged vegetation. Beyond this the pond is bordered on three sides by lawns and beyond these, office buildings. There is a road and car park on the fourth side. The pond is the breeding site of the four amphibians indigenous to the area; *Rana temporaria*, *Bufo bufo*, *T. cristatus* and *T. vulgaris*. A population of three-spined sticklebacks (*Gasterosteus aculeatus*) was present in the pond from at least 1980 (Bielinski, 1986) until 1990, spanning the first three years of this study.

The study population was considered to be isolated, with little or no newt movement between this and other ponds. The nearest neighbouring breeding site is 500 m away. Although this falls within the dispersal range of this species (Oldham, 1994) it is separated from the study pond by a main road, and drift fencing erected in 1989 did not detect any newt migration from this direction in 1989.

CAPTURE AND IDENTIFICATION OF NEWTS

The objective of this study was to capture and identify as many individual newts as possible each year. Procedures for capturing and identifying newts were modified over the course of the study, as the most efficient sampling techniques for this particular population became evident (drift fence/pitfall trapping was eventually abandoned in favour of the use of funnel traps). In 1988 newts were captured in funnel traps placed in the pond, during a pilot study of the monitoring program. From 1989 to 1991 newts were captured by the use of both a drift fence/pitfall trap system and by the use of funnel traps. In 1992 only 16 newts were captured at the drift fence, so it was assumed that the population had diminished and that aquatic trapping was not merited. From 1993 to 1995 newts were captured solely by the use of funnel traps in the pond.

The drift fence/pitfall trap system was put in place to coincide with the newts' spring migration to the breeding pond, but was dismantled before emigration, to avoid the disruption of dispersal into the terrestrial habitat. The formally-managed grounds beyond the immediate pond border appear to provide little "newt-friendly" terrestrial habitat, as described by Oldham (1994). Emigrants were not captured to avoid the possibility that trapping and release might have disorientated or detrimentally delayed newts navigating a seemingly harsh terrain. Hence, the drift fence was completed by the end of January, and dismantled as the arrival of im-

migrants ceased (2 March to 5 May). The fence was constructed of 3 mm plastic mesh, stapled to wooden stakes. Since the pond is located in a public area, the fence was designed to be inconspicuous. The fence was 15 cm high, with another 10 cm below ground. The top of the fence was folded at an angle of 90° to the vertical, to provide an 8 cm lip, facing outwards. Pitfall traps were emptied daily.

The population was also sampled later in the season, by trapping aquatic individuals in funnel traps. These were box-like traps (50 x 25 x 25 cm), made from perforated aluminium, with a funnel entrance at one end. The large size of these traps and their placement in shallow water allowed newts to rise to the surface to breathe within the trap. Additionally, each trap had a "chimney" to allow newts access to the water surface should the traps be placed in deeper water. These funnel traps were chosen in preference to the more widely used plastic drinks bottles (Griffiths, 1985) to avoid the possibility of drowning newts, a risk that would be significant over the course of a long-term sampling study such as this. Two to four funnel traps were set at the western end of the pond, the only edge easily accessible due to emergent vegetation (*Carex riparia* and *Sparganium erectum*) surrounding 80% of the pond perimeter. Funnel traps were set during the period lasting from the last week of March to the first week in June and were inspected for newts twice a day.

To provide a means of recognition of individuals, the pattern of black spots on the ventral surface of each newt was photocopied, modifying Hagström's (1973) technique of photographing newts. Newts were anaesthetized by immersion in a 0.1% solution of MS-222 (Sandoz) to facilitate the copying process. This allowed a reference series of uncontorted belly patterns to be created, which allowed easier recognition of recaptured animals than has been reported by Oldham & Nicholson (1986), who photocopied unanaesthetized animals. To minimize any possible detrimental effects of anaesthesia, efforts were made to anaesthetize newts only once during a breeding season. Prior to anaesthesia, newly-captured newts were compared with copies of belly patterns of all newts previously captured that year. However, newts recaptured in successive years were anaesthetized annually to allow changes in body measurements to be recorded (unpublished data).

POPULATION SIZE ESTIMATES

The Petersen method described in Donnelly & Guyer (1994) was used to calculate adult population size each year. In the years when newts were captured both by drift fence/pitfall trap and by funnel trap, the drift fence/pitfall captures were used as the first sample and captures made in the pond, by use of funnel traps, as the second sample. Newts that were captured in the pond and identified by belly patterns as having also been captured during the first sample, at the drift fence, were regarded as 'marked' animals in the estimation of population size. In 1989 and 1990, some newts were

TABLE 1. Dates of trapping periods (day-month), numbers of adults captured (caps) and efficiency of capture (%), expressed as a percentage of the estimated adult population size, are given for two different sampling techniques (drift fence and funnel traps). The efficiency of both techniques combined is also presented.

	Drift fence				Funnel traps				Fence and funnel traps
	From	To	caps	%	From	To	caps	%	%
1988	-	-	-	-	12-4	28-5	37	35	35
1989	4-2	5-5	47	53	1-4	14-5	57	65	86
1990	30-1	22-4	56	64	12-4	26-4	42	48	79
1991	21-2	21-3	50	65	26-3	10-5	59	77	90
1992	15-2	2-3	16	22	-	-	-	-	-
1993	-	-	-	-	3-4	21-4	66	99	99
1994	-	-	-	-	29-3	3-5	95	78	78
1995	-	-	-	-	4-4	7-6	191	79	79

captured at the drift fence after the initiation of pond trapping. These captures were omitted from the estimation of population size. Funnel trapping was not attempted in 1992, so population size was not estimated.

From 1993 to 1995 the first and second sampling periods were designated by taking the date of the median capture each season as a watershed. Captures up to and including this point constituted the first sampling session, captures after this date were considered the second sampling session.

The use of different capture techniques between the first and second capture sessions within a year and different capture and sampling techniques between years may potentially bias the population estimates. Ideally, similar sampling techniques would be used each year. The present estimates rest on the assumption that any newt captured at the drift fence is no more or less likely to be captured in a funnel trap than newts that were not captured at the drift fence.

ESTIMATION OF SURVIVAL

Survival was estimated as a function of recapture rate between years and sampling efficiency, as follows. A "recapture" between any two years was considered as the capture and identification of the same individual. Recapture rate represents the proportion of individuals recaptured between years. However, not all newts were captured in any year. A measure of sampling efficiency was calculated as the number of newts captured in any one year as a fraction of the estimated population size. When sampling efficiency is less than 100%, recapture rate between years will underestimate survival (some individuals surviving from one year to the next will not be recaptured). To correct for this, an estimate of annual survival was obtained by multiplying the number of recaptures by the reciprocal of sampling efficiency in any particular year.

During the last two years of the study, 1994-95, sufficient adult recruitment had occurred to allow a comparison of the survival of newly breeding adults

with that of long-term members of the breeding population. All new captures in 1994 were regarded as breeding for the first time, since sampling efficiency in 1993 was almost 100%. The annual survival of these first-time breeders was compared with that of the other adults, all of which represented recaptures from previous years.

Recaptures of individuals originally captured as juveniles were used to estimate juvenile survival. Although the belly pattern changes as juveniles grow (Oldham & Nicholson, 1986; Arntzen & Teunis, 1993), the basic pattern is present at transformation. Immobilization of newts prior to photocopying facilitated the recognition of juveniles on recapture in succeeding years.

RESULTS

The numbers of adult newts captured by the drift fence/pitfall system and the funnel traps are given in Table 1. It is estimated that 35-99% of the breeding population was captured and identified each year. Over the course of eight years estimated population size ranged from 67 to 242 adults (Fig. 1). Between 27% and 88% of the newts captured in any one year were recaptured the following year. The recapture interval tended to be one year (83% of male recaptures and 77% of female recaptures). In the cases when individuals were only recaptured at two-year intervals (16% of male recaptures and 22% of female recaptures), 70% of these occurred between 1991 and 1993, spanning the year when funnel trapping was not carried out. One male (1% of male recaptures) was recaptured four years after initial capture and one female (1% of female recaptures) was recaptured three years after initial capture.

The failure to capture all of the breeding population each year made precise assessment of recruitment impossible. Newts being recorded for the first time may have been new recruits to the breeding population, or longer-term members of the population that had evaded previous capture. In the latter case these "new cap-

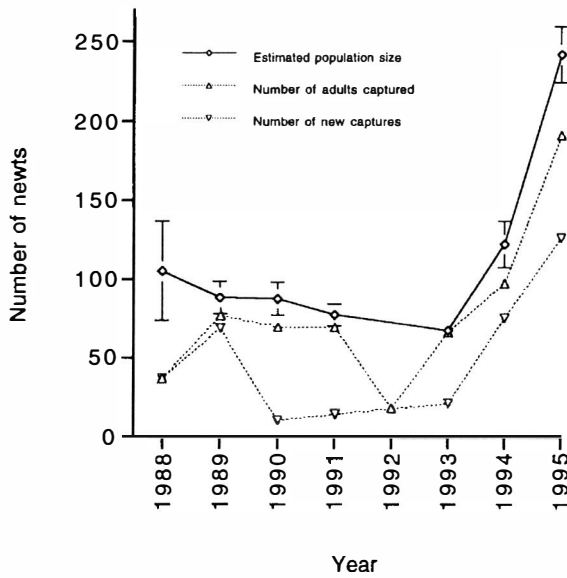


FIG. 1. Estimated population size (± 1 SE) and numbers of adult *T. cristatus* captured at the Walton Hall Pond from 1988 to 1995. "New captures" refers to the number of newts captured in any year that were not identifiable from previous years' records.

tures" will give an overestimate of recruitment. The number of these new captures (10-126 per year, or 14-89% of all newts captured) is shown in Fig. 1.

ADULT SURVIVAL

Estimated adult survival varied between 31% and 100% (Table 2). There was little evidence of a consistent sex difference. Male survival was greater from 1992 to 1994, while females had higher estimated survival rates in the periods 1988 to 1991 and 1994 to 1995. Be-

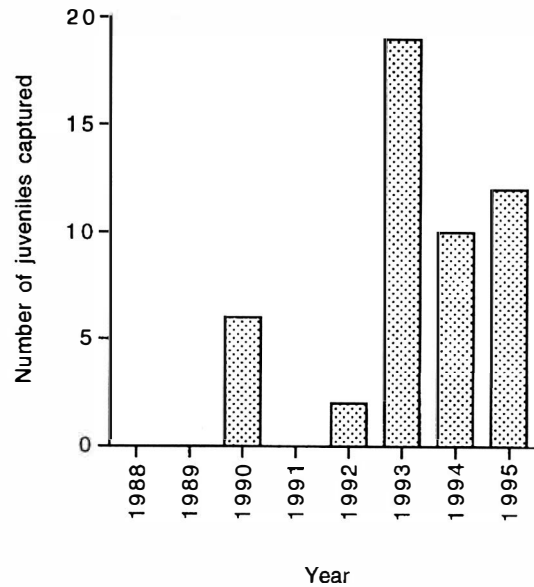


FIG. 2. Numbers of juvenile *T. cristatus* captured from 1988 to 1995.

tween 1994 and 1995, adults breeding for the first time were significantly less likely to be recaptured the following year than long-term members of the breeding population (recorded in the breeding population from two to eight years) $\chi^2 = 6.141$, $P < 0.025$ (Table 2).

The stickleback population was not systematically monitored, but its presence and disappearance was evident since the funnel traps were very effective in trapping these fish. Up to 50 sticklebacks could be captured in a single funnel trap, and from 1988 to 1990

TABLE 2. Annual recapture rates and estimated survival rates of adult *T. cristatus*. Recapture rates represent the number of recaptures as a fraction of the number of individuals captured in the previous year. Figures in brackets are percentages.

(1) Recapture Rates						
Year	1988-89	1989-90	1990-91	1991-93	1993-94	1994-95
Male	5/23(22)	31/36(86)	22/33(67)	24/33(73)	10/32(31)	35/59(59)
Female	5/14(36)	38/42(90)	22/36(61)	22/36(61)	9/34(26)	27/36(75)
Established breeders	-	-	-	-	-	17/19(89)
First time breeders	-	-	-	-	-	45/76(59)
All	10/37(27)	69/78(88)	44/69(64)	46/69(67)	19/66(29)	62/95 (65)

(2) Estimated annual survival(%)							
Year	1988-89	1989-90	1990-91	1991-92	1992-93	1993-94	1994-95
Male	25	100	74	85	85	40	75
Female	42	100	68	78	78	33	95
All	31	100	71	82	82	37	82

sticklebacks were the most abundant animals found in the traps. After 1990 no sticklebacks were trapped or otherwise observed during searches.

JUVENILE SURVIVAL AND AGE AT MATURITY

During the eight-year study period 49 juveniles were captured and recorded (Fig. 2). Eighteen of the juveniles were recaptured over successive years. Since 12 of these juveniles were captured in 1995, juvenile recapture rate was determined to be equivalent to 18/37, or 49%. Juvenile survival, correcting recapture rate for capture efficiency as described for adults, produces an estimated survival rate of 22/37, or 59%.

In assigning an age to juveniles and in determining age at maturity, it was assumed that juveniles captured were one-year-olds. All captures were made during the spring breeding period, so any juveniles present must have originated from eggs oviposited during previous years. The possibility that these juveniles were any older than one year but still at a small body size due to slow growth was excluded because the recapture of juveniles the following year revealed that juveniles grew rapidly. Juveniles captured over two successive years grew by 19 mm SVL (49.5 to 68.5, $n = 16$).

All of the juveniles recaptured, except for one, had reached sexual maturity by the following year, at a presumed age of two years. Even the smallest juvenile captured (SVL = 37 mm) grew to maturity by the succeeding year (SVL = 71.5 mm). A single male and single female were detected as adults two years after capture as juveniles. It is not possible to determine whether these individuals matured at three or at two years of age, but were not captured in their first year of sexual maturity. It can be assumed that the single newt that was captured as a juvenile in two successive years (SVL of 51 and 57.5) certainly did not mature until older than two years.

DISCUSSION

The monitoring methods used during the course of this study demonstrated that funnel trapping was the most effective means of trapping a large proportion of the estimated population. The drift fence used from 1989 to 1991 was only effective in trapping 53–65% of the breeding population, which agrees closely with the 45–61% trap rates of *T. cristatus* achieved by Arntzen, Oldham & Latham (1995). The inability of the drift fence to trap all migrating amphibians is, in part, most likely due to the ability of amphibians to circumvent the fence (Dodd, 1991). There are additional factors which may contribute to the low capture rates of *T. cristatus* at drift fences. *T. cristatus* has a flexible life history. Individuals, particularly newly mature adults, may migrate to ponds in the autumn prior to breeding (Verrell & Halliday, 1985), and some juveniles and adults may remain aquatic all year (Smith, 1964; pers. obs.), thus avoiding drift fences set to capture the spring migration. Also, individuals may spend the terrestrial phase sufficiently close to a pond that they need not cross a

drift fence in order to reach a breeding site. Vegetation prevented the construction of a drift fence immediately along the edge of the Walton Hall Pond, so that a band of 2–4 m of grass and scrub was left between the fence and the pond.

By comparison, funnel traps placed in the pond, even though they spanned only approximately 20% of the pond perimeter, were able to capture as much as 77–99% of the estimated population. Lower capture rates from 1988 to 1990 reflect time constraints on the investigator rather than limitations of the trapping technique itself.

Over the eight years of the study, the population dynamics changed from a stable but unproductive situation to one of rapid population increase (Fig 1). For the first six years the population showed a slow decline from 105 to 67 animals, with recruitment lower than 14–32% of the adult population (as indicated by newly captured newts between 1989 and 1993). However, over the next two years the population showed a dramatic increase in numbers, increasing more than threefold from 67 to 242. These changes in population size are smaller than the three orders of magnitude recorded for four temperate pond-breeders (Pechmann *et al.*, 1991), and the sixty-fold fluctuations in visual counts recorded in *T. cristatus* at a different site in England (Cooke, 1995).

The present data also reiterate the need for studies that are long-term in nature, when examining amphibian population dynamics (Pechmann *et al.*, 1991; Grossenbacher, 1995). For *T. cristatus* this may be of importance in assessing the success of translocation programmes (e.g. Gent & Bray, 1994) or other management practices (e.g. Cooke, 1997). The present population was able to persist for several years with little apparent recruitment. Hence, the presence of adults at a site for several years does not indicate successful breeding or the long-term survival of the population. Conversely, populations that appear to be non-productive over a short time-scale may not be so in the long-term. Breeding failures in *T. cristatus* populations, for up to three years, have been reported elsewhere (Verrell & Halliday, 1983; Oldham & Nicholson, 1986; Griffiths, 1996) and may be a common occurrence for this species.

Fish predation may have had some role in the regulation of the population of great crested newts in the Walton Hall Pond. While sticklebacks were present in the Walton Hall Pond there was very little recruitment to the adult population, but after the disappearance of the fish the newt population grew rapidly. Predatory fish can affect amphibian distribution (Bradford, 1989; Brönmark & Edenhamn, 1994; Fisher & Shaffer, 1996) and reduce the species richness of amphibian communities (Hecnar & M'Closkey, 1997). Great crested newts seem particularly sensitive to fish predation (Smith, 1964; Beebee, 1985; Oldham & Nicholson, 1986; Arntzen & Teunis, 1993; Swan & Oldham, 1993), probably due to the nektonic behaviour of the

larvae (Dolmen, 1983b). In spite of a prolonged period of low reproductive success in the Walton Hall Pond, the adult newts continued to return to the pond to breed. The apparent failure of adult *T. cristatus* to detect and respond to the presence of predatory sticklebacks by altering breeding site selection, may be due to the inability of the newts to respond to a small, gape-limited predator which preys on newt larvae rather than on adult newts. Alternatively, the lack of other breeding sites nearby may have prevented movement away from Walton Hall Pond.

One curious aspect of the recovery of the study population from the surmised predatory effects of sticklebacks is a delay in the newt population size increase. No sticklebacks were found in the pond in 1991 or later years. Since it takes two years to attain maturity, the newt population might be expected to have increased in 1993. However, the population did not show signs of growth until 1994 (Fig. 1). The reason for this one-year delay in population size increase is not known. It is possible that the stickleback decline occurred in 1991, so that some fish survived long enough to prey on newt eggs and larvae. Alternatively, factors other than fish predation may have been involved.

Estimated adult survival ranged from 31%–100% per year. Between most years adult survival appears to have been very high, ranging from 76%–100%. However, in the periods 1988–89 and 1993–94, it was markedly lower, at 31% and 37%. The low adult survival between 1988 and 1989 may be attributable to some aspect of the handling and registration procedure. This conclusion is reached since the change in estimated population size, a drop of 17 from 105 to 88, is more than accounted for by the disappearance of those individuals that were captured, anaesthetized and photocopied in 1988 (only 10/37 individuals from 1988 were recaptured in 1989). Handling procedures were similar in 1988 and succeeding years, hence the detrimental aspect of the procedure has not been identified. The cause of low survival between 1993 and 1994 is also not known. However, the monitoring of individuals reveals that, during this period, an increase in population size occurred even though this was a period of relatively high adult mortality. The remaining years showed survival rates (76–100%) comparable to, or higher than, the upper ranges previously recorded for *T. cristatus* (70–80% [Hagström, 1979] and approximately 65% [Hedlund, 1990]).

The lower recapture rate of new recruits, compared to older individuals suggests that first-time breeders experienced lower survival (59%) than older newts (89%). This difference in survival between first-time breeders and older adults was also found by Hedlund (1990).

Juvenile productivity was not measured in the Walton Hall population. Moreover, the pitfall trapping and funnel trapping methods used to sample the adult population revealed very few juvenile captures, only 49 over the course of the study. The use of the aquatic en-

vironment by juvenile *T. cristatus* varies between populations (Bell, 1979), so the low capture rate of juveniles during the present study is not atypical. More striking was the complete failure to detect newt larvae over seven years of funnel trapping. It is possible that the design of funnel traps used in the present study is less effective in catching larvae than are the bottle traps (Griffiths, 1985) used in other studies (e.g. Cooke, 1995). Alternatively, the low capture rate of juveniles, and the lack of evidence of larvae may reflect the low productivity of this population. The low rate of recruitment to the breeding population from 1989 to 1993 indicates that this population underwent at least a five-year period with very low productivity of juveniles.

The annual recapture rate of juveniles (49%) and the estimated annual survival rates of juveniles at this site (59%) are relatively high compared to other temperate pond-breeding amphibians. This may be typical of newts in the genus *Triturus*, since *T. cristatus* and *T. vulgaris* have the highest juvenile survival rates of temperate pond-breeders reviewed by Beebee (1996). This high rate of juvenile survival in *T. cristatus* may compensate for periods of low productivity and the relatively low fecundity of this species. Fifty per cent of all eggs die at the tail bud developmental stage (Horner & MacGregor, 1985) leaving mean clutch sizes of approximately 100 viable eggs (Hedlund, 1990; Griffiths, 1996).

For those few newts that were identified as newly metamorphosed juveniles, and later as sexually mature adults, it appears that most individuals achieved sexual maturity at two years. This agrees with Beebee's (1980) observations made at a site in southern England, and also with the skeletochronological work on French populations (Francillon-Vieillot *et al.*, 1990; Arntzen & Teunis, 1993) which suggests the attainment of sexual maturity at two to three years.

The current data also demonstrate the unreliability of counts as measures of population size. For example, in 1992 very few newts were captured at the drift fence. If drift fence captures had been used as a count to indicate population size then the population would have appeared to have crashed that year. However, monitoring the following year revealed that 68% of the newts captured in 1993 were recaptures from 1991, indicating that many of the individuals that evaded detection at the drift fence in 1992 were nevertheless still alive. A possible explanation for the lack of newts captured at the drift fence may be yearly variation in weather patterns, although the mechanism of the impact on the newts is not known (other local migrations were observed to occur as expected; pers. obs.). However, it is interesting to note that 1992 also resulted in Cooke's (1995) lowest mean count. In this latter study, as well, the increase in the numbers of newts counted in the following year seems unlikely to be due entirely to new recruits to the breeding population. Cooke's larval catches were minimal for the years 1990 to 1992, making it unlikely that the adults observed in 1993 were the resultant, newly

breeding animals. These findings support the notion that newt counts do not necessarily reflect population size (Griffiths & Raper, 1994).

Monitoring individuals in the present study reveals information about population fluctuations. It demonstrates that a single population of *T. cristatus* can rapidly change in its demographic nature. Over the course of this study the population switched from a stable population, with low recruitment, to a rapidly increasing population. Rapid changes in *T. cristatus* population size have been noted elsewhere (Arntzen & Teunis, 1993; Cooke, 1995); however, the current data provide information on the population processes occurring during these fluctuations.

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BREEDING SITE FIDELITY IN THE JAPANESE TOAD, *BUFO JAPONICUS FORMOSUS*

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A breeding population of Japanese toads, *Bufo japonicus formosus* was studied at two ponds in Yamakita-machi, Kanagawa Prefecture, Japan, during the three breeding seasons of 1992-1994. The movement of toads between the ponds was monitored by mark-recapture studies. Although the two ponds were only 30 m apart, most toads did not switch ponds within or between years. A binomial test and bootstrap simulation rejected the null hypothesis that individual toads selected their breeding ponds randomly from year to year. Mating success and other ecological and behavioural characteristics were compared between male toads that exhibited site fidelity and those that switched ponds during the study period, but we could not detect any significant differences between them. This study demonstrated strong site fidelity in *B. j. formosus*, but failed to show quantitative advantages or disadvantages of returning annually to the same pond.

Key words: *Bufo japonicus formosus*, site fidelity, movement between ponds, mating success

INTRODUCTION

Many species of anurans spend their non-breeding season in terrestrial home ranges although they breed in wetlands such as ponds. Therefore, they must undertake seasonal migrations to and from the ponds. In some species, breeding adults move annually to the same sites instead of randomly searching for new ones. Such strong fidelity to a particular breeding site within a single season or between years has frequently been reported in anuran species (e.g. Berven & Grudzien, 1990; Reading, Loman & Madsen, 1991; Ritke, Babb & Ritke, 1991; Sinsch, 1991; Lüddecke, 1996).

The Japanese common toad (*Bufo japonicus formosus*) is a large and robust species reaching sizes in excess of 100 mm snout-vent length (SVL). It is very common in eastern Japan from southern Hokkaido to the Kinki and San'in districts of Honshu. It lives in a variety of habitats from sea level to high mountains, and breeds explosively in early spring in still waters such as small ponds (Maeda & Matsui, 1989). Adult *B. japonicus* have been shown to be relatively sedentary during summer months and to return annually to the same pond for reproduction (Okuno, 1984, 1985; Hisai, Chiba, Yano & Sugawara, 1987). Most studies of breeding site fidelity in anurans were conducted at ponds that were relatively distant (≥ 100 m) from each other (Okuno, 1984, 1985; Hisai *et al.*, 1987; Berven & Grudzien, 1990; Ritke *et al.*, 1991; Lüddecke, 1996). The fact that movement between such ponds is rare

does not necessarily indicate that toads actively select particular ponds. In fact, Reading *et al.* (1991) showed that in *B. bufo* the degree of relocation between ponds is correlated negatively with the distance between ponds. If the degree of relocation is low between ponds that are sufficiently close to each other, this would strongly suggest that toads prefer particular ponds.

Here, we report on within- and between-year breeding site fidelity in *B. j. formosus*, assessed by monitoring the breeding activity in three consecutive years at two ponds that are only 30 m apart.

MATERIALS AND METHODS

STUDY SITE

The breeding population of *B. j. formosus* was studied at Hanna-in temple (35°21'N, 139°06'E) in Yamakita-machi, Kanagawa Prefecture, between early and late March in 1992-1994. The temple is located at the foot of a hilly region at an altitude of 100 m. A brief description of the areas surrounding the study site was given in our previous report (Kusano, Maruyama & Kaneko, 1995). Two small ponds in the temple garden are used by *B. j. formosus* for breeding, and there are no other breeding ponds near the temple, at least within a radius of a few hundred metres.

Pond A is natural, and since it is located at the foot of a small hill ridge on the western edge of the garden, it gets little sunshine. A small spring supplies the pond with water, but the water supply has recently become very poor, and therefore prolonged drought sometimes causes the pond to dry up. Three species of frogs, *Rana ornativentris*, *R. rugosa* and *Rhacophorus schlegelii*, also breed in this pond. Pond B is artificial and located

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in a sunny area on the southern side of the garden. Water temperature is therefore always a few degrees higher in pond B during the breeding season than in pond A. Since pond B is artificially supplied with water, the pond has never dried up. Apart from *B. j. formosus*, only *R. ornativentris* breeds in pond B but carp are also raised. Both ponds are 7-8 m long and 2-3 m wide; the water is 0.2-0.4 m deep. The linear distance between the two ponds is 30 m. There are no obstacles between the ponds, and we could easily hear the toads calling from one pond while positioned at the other.

CENSUS OF BREEDING ACTIVITY

In March of 1992-1994, daily visits were made to the study site to survey the breeding population. Censuses were made by two or three researchers in the temple garden, especially at the two breeding ponds. Since the preliminary survey showed that in the population studied, breeding toads appeared and called in the ponds throughout the day, except for the early morning, we censused the breeding population at least four times a day; at 1400 hr, 1600 hr, 1900 hr, and 2100 hr. Toads were captured by hand or a dip net, measured for SVL to the nearest 0.5 mm, and weighed to the nearest 2 g. In 1992, toads were individually marked by toe-clipping, while the toads that were first captured in 1993-1994 were marked to denote the year of first capture by clipping a portion of the hind leg webs. A numbered rubber tag (15 mm x 15 mm) was glued with a small amount of adhesive to the head to allow individual recognition without capture. Breeding behaviour of these marked toads was observed using binoculars to determine which pond each toad used for breeding. This was done to quantify the within- and between-year movements of breeding toads between the ponds. Mating success of each male toad was also determined by counting the number of females with which he paired in the season.

AGE DETERMINATION

Toes clipped for individual identification in 1992 were stored in 10% buffered formalin. Age was determined by counting year rings in the haematoxylin-stained cross-sections of these phalanges (Hemelaar & van Gelder, 1980; Kusano *et al.*, 1995).

STATISTICAL ANALYSIS

Statistical analyses were mainly performed with the Statistical Analyses Software version 6.03 (SAS Institute Inc., 1988). We analysed the data on ecological and behavioural characteristics of male toads using ANOVA. Age was compared between toads that exhibited site fidelity and those that switched ponds using one-way ANOVA. Other characteristics were analysed by repeated measures ANOVA. The number of matings and duration of residence were analysed after they were $\log(x+1)$ -transformed to homogenize variances. The significance level used in all tests was $P=0.05$. Accept-

ance levels for simultaneous statistical tests were adjusted by the sequential Bonferroni procedure (Rice, 1989).

RESULTS

WITHIN-YEAR SITE FIDELITY

Breeding activity occurred continuously for 6-17 days: on 12-17 March in 1992, 18-29 March in 1993 and 13-29 March in 1994. We captured 95 male and 31 female toads in 1992; 77 and 36 in 1993; and 113 and 37 in 1994. Their SVLs ranged 94-168 mm for males and 105-155 mm for females, and age was estimated at 1-8 and 2-7, respectively.

Since some toads were captured in the temple garden but not observed at either pond, we were able to determine the breeding ponds for 94 males and 28 females in 1992, 68 and 33 in 1993, and 97 and 26 in 1994, respectively (Fig. 1). Most toads (>96%) did not switch ponds during a breeding season, irrespective of their sex.

Since the proportion of toads that used pond A, pond B or both ponds did not vary significantly from year to year (males: $\chi^2=7.293$, $df=4$, $P=0.121$; females: $\chi^2=4.480$, $df=2$, $P=0.107$), the probability of appearing in either or both ponds was estimated from the pooled data. Of 259 males and 87 females examined in total for all three seasons, 76 (29.3%) and 34 (39.1%) used only pond A, and 175 (67.6%) and 54 (62.1%) used only pond B within a season. Toads that switched ponds within a season accounted for only 8(3.1%) males and 2(2.3%) females.

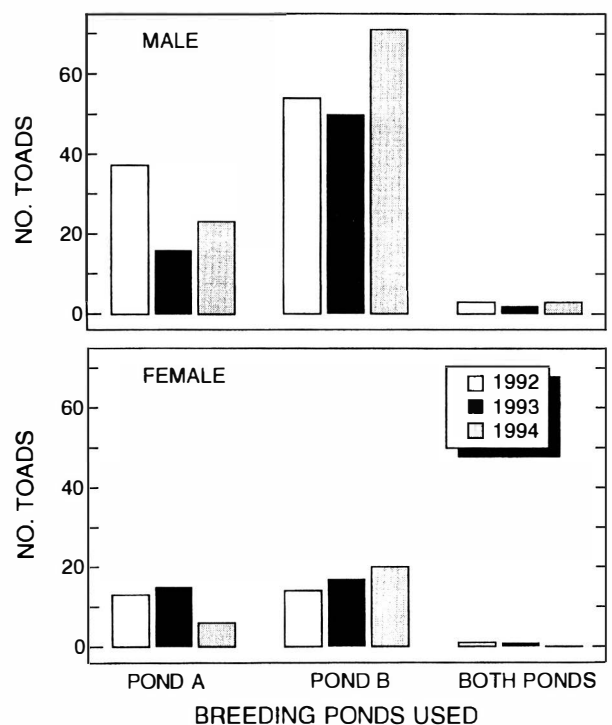


FIG. 1. Frequency distribution of the number of toads that appeared at ponds A and B for breeding in consecutive seasons, 1992-1994.

TABLE 1. Yearly change in breeding ponds used by individual toads during 1992-1994. ? indicates that the toad was captured in the temple garden during the season, but we could not determine its breeding pond.

Pattern of breeding			No. toads	
1992	1993	1994	male	female
A	A	A	5	0
A	A		3	4
A	?	A	1	0
A		A	2	0
?	A	A	0	1
B	B	B	12	2
B	B		6	0
B	?	B	1	1
B		B	2	3
A	A	B	1	0
A	B	A	1	0
A	B	AB	1	0
A		B	1	0
AB	A	B	1	0
AB	A		0	1
AB	B	B	1	0
AB	AB	A	1	0
Total			39	12

BETWEEN-YEAR SITE FIDELITY

To evaluate the between-year movement of breeding toads between ponds, we analysed recapture data for toads that were marked in the 1992 breeding season and thereafter recaptured in at least one other season (Table 1). Most individuals did not shift their breeding ponds from year to year, irrespective of their sex (Table 1). Thirty-two of 39 males (82.1%) and 11 of 12 females

(91.7%) were observed exclusively at one pond for two or three seasons, while only seven males and one female were observed to have changed their breeding ponds (Table 2).

To test whether individual toads selected breeding ponds randomly from year to year, a binomial test was conducted: the probabilities of using pond A, pond B or both ponds within a single season were obtained from the data in Fig. 1, as mentioned above. Table 2 shows that individual toads were unlikely to select ponds randomly, but preferred specific ponds for breeding from year to year, although the sample size was too small to draw definite conclusions in the case of females.

We also tested the null hypothesis mentioned above, using a bootstrap method (see Efron & Tibshirani, 1991). The bootstrap sample was generated from the original data set in Table 1, and the toads that did not switch ponds for the study period were counted. The bootstrap sampling was repeated 100,000 times, and we calculated the probability (P) that the number of toads that did not switch ponds is equal to or larger than the observed number (32 for males and 11 for females; Table 2). The results are similar to those obtained with a binomial test: $P < 0.00001$ for males, $P = 0.0121$ for females. Both statistical tests supported rejection of the null hypothesis that toads select their breeding ponds randomly. The breeding toads exhibited strong site fidelity to a particular pond, at least for two or three seasons.

SITE FIDELITY AND MATING SUCCESS

We compared some ecological and behavioural characteristics such as age, body size, and mating success between male toads that exhibited strong site fidelity and those that changed breeding ponds. We observed breeding behaviours of marked toads during the study period, and counted the number of matings for each toad. Of 95 males that were individually marked in

TABLE 2. Yearly change in the breeding ponds which individual toads used in consecutive seasons. This table is based on data for the toads that were marked in the 1992 breeding season and thereafter recaptured in at least one other season, either 1993, 1994, or both. Acceptance levels were adjusted by the sequential Bonferroni procedure. * significant at a table-wide $\alpha = 0.05$

		No. toads using same or different pond			
	No. seasons examined	No change N_{nc}	Change N_c	Rate $N_{nc}/(N_{nc} + N_c)$	Binomial-test P
<hr/>					
Males					
	2	15	1	0.94	0.0008*
	3	17	6	0.74	0.0001*
Total		32	7	0.82	
<hr/>					
Females					
	2	9	1	0.90	0.0102*
	3	2	0	1.00	0.0729
Total		11	1	0.92	

TABLE 3. Comparison of mating success between males that used the same pond and those that changed ponds during the three seasons, 1992-1994. This table is based on the data for 23 males that appeared at one or both ponds in all three breeding seasons. Statistical tests were conducted using repeated measures ANOVA except for age (standard ANOVA). The number of matings and duration of residence were analysed after they were log-transformed, because of heterogeneity of variances. Acceptance levels were adjusted by the sequential Bonferroni procedure.* significant at a table-wide $\alpha=0.05$

Variables	Year	Ponds used				Repeated measures		
		No change		Change		ANOVA		
		Mean \pm SD	<i>n</i>	Mean \pm SD	<i>n</i>	Source:	<i>F</i>	<i>P</i>
Age	1992	4.4 \pm 1.5	16	4.2 \pm 0.8	6	Change	0.18	0.6725
SVL (mm)	1992	130.6 \pm 12.4	17	131.7 \pm 10.9	6	Change	0.35	0.5594
	1993	134.9 \pm 8.8	17	138.8 \pm 8.1	6	Year	13.45	0.0001*
	1994	137.4 \pm 9.5	17	140.2 \pm 5.6	6	Year x Change	0.43	0.6544
Body mass (g)	1992	224.9 \pm 53.7	17	250.0 \pm 61.2	6	Change	1.33	0.2626
	1993	219.7 \pm 43.8	17	253.3 \pm 51.3	6	Year	4.36	0.0191
	1994	248.2 \pm 55.5	17	266.7 \pm 33.1	6	Year x Change	0.45	0.6397
No. matings	1992	0.35 \pm 0.49	17	0.67 \pm 0.82	6	Change	1.22	0.2828
	1993	0.59 \pm 0.87	17	0.33 \pm 0.52	6	Year	0.08	0.9255
	1994	0.18 \pm 0.39	17	0.67 \pm 0.82	6	Year x Change	1.50	0.2339
	Total	1.12 \pm 1.05	17	1.66 \pm 1.03	6			
Duration of residence (days)	1992	1.94 \pm 0.97	17	2.00 \pm 0.89	6	Change	0.34	0.5667
	1993	5.06 \pm 2.38	17	5.33 \pm 3.27	6	Year	21.29	0.0001*
	1994	1.88 \pm 1.17	17	2.50 \pm 1.52	6	Year x Change	0.13	0.8783

1992, we could determine the breeding ponds and seasonal mating success in all three seasons spanning 1992-1994 for 23 males. Of these males, 17 toads returned annually to the same pond for breeding, while only six toads switched ponds during the three consecutive years. We could recognize no significant differences in ecological or behavioural characteristics between these toads (Table 2). In addition to the parameters described in Table 3, we detected no significant difference in any other parameters examined, e.g. date of appearance at the ponds, and annual growth rate.

DISCUSSION

This study demonstrated that breeding adults of *B. j. formosus* exhibited strong fidelity to a particular pond, and their movement between breeding ponds was rare within a season or between seasons, even if these ponds were very close to each other. We considered the reasons for the toads' fidelity to a particular breeding pond. Since adult *B. japonicus* are relatively sedentary during the summer months and return annually to the same pond for reproduction (Okuno, 1984, 1985; Hisai *et al.*, 1987), we first considered that each toad might simply choose the breeding pond nearest its summer home range. Using radio-tagged toads, Kusano *et al.* (1995) showed that the spatial distributions of the summer home ranges were not distinct for toads that bred at either pond. Therefore, breeding toads did not necessarily appear at the ponds nearest their summer home

ranges. This result strongly suggests that toads actively select a specific pond for breeding.

In some anuran species, breeding adults return to their natal pond; e.g. in *Bufo woodhousei* (Breden, 1987), *B. bufo* (Reading *et al.*, 1991), and *Rana sylvatica* (Berven & Grudzien, 1990). Ishii, Kubokawa, Kikuchi & Nishio (1995) demonstrated that *B. japonicus* used an olfactory map for orientation to the breeding pond. They suggested that newly metamorphosed toadlets remember the route of their post-metamorphic dispersal employing this olfactory sense and return to their natal pond after sexual maturity using a memorized olfactory map. At present, however, we do not have reliable data that *B. japonicus* exhibits natal philopatry.

What is the adaptive or evolutionary significance of a toad's preference for a particular breeding pond? To understand the evolutionary significance of breeding site fidelity, we examined the effect of site fidelity on male mating success. The detection of differences in mating success between male toads that exhibited site fidelity and those that switched ponds might provide an insight into the adaptive value of breeding site fidelity of toads. However, we could not detect any significant differences (Table 3).

In general, natural selection may favour homing behaviour to specific ponds under the condition of scarcity of appropriate localities for breeding. Homing is obviously a strategy to minimize time and energetic

expenditure for breeding migration as compared to a random search for new sites (see Sinsch, 1991). This study demonstrated strong site fidelity to a breeding pond in *B. j. formosus*, but failed to show quantitative advantages or disadvantages of returning annually to the same pond. Further studies are needed to clarify the advantages and disadvantages of breeding site fidelity and understand its adaptive and evolutionary significance.

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MEASUREMENT OF TIME BUDGETS FROM CONTINUOUS OBSERVATION OF THREAD-TRAILED TORTOISES (*KINIXYS SPEKII*)

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Five thread-trailed hingeback tortoises (*Kinixys spekii*) were observed continuously for a total of 260 hr on four hot days (at intervals of 1-2 weeks) in the rainy season. Activity occurred in all hours from 06.00-19.00 hr; the population daily activity period was 13 hr. The daily duration of surface activity of individuals was on average 8.2 hr day⁻¹ between first and last daily movement. The daily time budget included 1.95 hr locomotion, 0.86 hr feeding, and 5.2 hr stationary above ground (including long periods in indistinct surface refuges). There were no significant differences in total activity between individual tortoises or study days. Combining the daily activity period of the population and data from single sightings would greatly overestimate the amount of time spent active; observations over complete days are necessary for a true time budget. Increasing the number of days of observation of each individual decreased the variability of the data only slightly.

Key words: *Kinixys*, tortoise, time budget, activity pattern

INTRODUCTION

Breder (1927) devised the technique of thread-trailing to obtain more data on the behaviour of terrestrial chelonians than available from chance sightings or the infrequent recapture of marked individuals. She listed several aspects which could be investigated by this method: movements, home range, homing; searching for nesting sites, water, sun and shade; correlations with sex, season, and weather. Thread-trailing has subsequently been used to describe the home range and homing ability (Stickel, 1950; Chelazzi & Francisci, 1979); seasonal and sexual variation of movements (Hailey, 1989; Diaz-Paniagua, Keller & Andreu, 1995); the intensity of use of the home range (Hailey & Coulson, 1996a), the relation between activity and weather (Hailey & Coulson, 1996b), and movements to nesting sites (Hailey & Coulson, 1997) and areas of mineral-rich soil (Marlow & Tollestrup, 1982; Hailey & Coulson, 1996a) in a variety of terrestrial chelonians. Thread-trailing provides more information than radio tracking for many of these questions, as it records the exact path followed by an animal (except in very open habitats).

An additional use of thread-trailing would be to track individuals during continuous observation, to give information on activity and time budgets. Studies of tortoise activity face the problem that individuals may be inactive and difficult to locate for much of the time. For example, the use of standard transect sampling techniques (which correct for the difficulty of

observing animals further away) in areas of known population density showed that only 10-25% of individual *Testudo hermanni* were active even during peak activity periods (Hailey, 1988). Inactive tortoises are very difficult to locate by undirected searching (rather than any form of tracking), so that a time budget based on single sightings would overestimate the level of activity of individuals. In this study, thread-trailed hingeback tortoises were observed continuously during the complete daily activity period to produce a time budget for one set of weather conditions. The bias likely to result from the use of single sighting data was then assessed.

METHODS

Tortoises were studied in the Sengwa Wildlife Research Area, Gokwe District, Zimbabwe, in open miombo woodland and bushed grassland (the habitat is described in more detail by Hailey & Coulson, 1995). Five adult *Kinixys spekii* (two females and three males) were each followed by thread-trailing from 5 January to 14 February 1993 (Hailey & Coulson, 1996b), and were observed continuously on four days at intervals of 1-2 weeks; 12 and 23 January and 6 and 12 February. The tortoises had thus been trailed for at least one week before the first day of intensive observations. The four days were all within the rainy season, and had similar, partly cloudy weather; the mean percentage of cloud cover was 48%, 50%, 55%, and 32%, respectively, and there was some cloud cover at most times on each day. Nevertheless, the days were all hot, with maximum shade air temperatures of 31° and 32°C (A study of the thermoregulation of *Kinixys spekii* defined hot days as those with maximum shade air temperature above

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29°C, when activity is bimodal; Hailey & Coulson, 1996c).

Activity was recorded at 5 min intervals from 06.00 hr (shortly after dawn) to 19.00 hr (dusk), after the tortoises had been followed to a refuge the previous evening. A total of 12 observers, mostly game scouts who were skilled trackers (Cumming, 1975), were used in shifts up to 5 hr long. Tortoises were observed with binoculars from 10-20 m, the distance depending on the level of cover available to the observer. The trailed tortoises appeared to be unaware of the presence of the observers; they showed visible reactions to other causes of disturbance.

Studies of reptiles have used a wide range of meanings for activity, ranging from walking only, through inclusion of other types of behaviour (such as feeding), to all time when the animal is away from its overnight refuge. The need for precise definitions is particularly important in *Kinixys spekii* as animals were often stationary on the surface for long periods during the day, but not in distinct refuges; tortoises simply stopped in a patch of scrub or long grass, and remained alert for long periods, changing position if the sun moved on to them. Behaviour was recorded as one of the following: *Locomotion* - walking, without other behaviour; *Feeding* - ingesting food or pausing between bites at a single food item (a tortoise which paused during a period of foraging, in which it moved between different food items, was classed as stationary above ground); *Courtship* - any interaction between a male and a female; *Nesting* - digging a nest; *Stationary above ground* - not moving or engaged in any other behaviour, and not in a burrow. Basking was not seen in *Kinixys spekii* at Sengwa (Hailey & Coulson, 1996c). The term 'specialized activities' is used to indicate animals which were undoubtedly active, and includes locomotion, feeding, courtship and nesting. The daily activity period was used as a population measure - the times of day (or period of time) when specialized activities occurred in the population. A different term was used for measurements on individuals; the duration of daily activity was the period between the first and last specialized activity on one day, including time 'stationary above ground' but excluding time in a burrow. Statistical significance was accepted at $P < 0.05$.

RESULTS

ACTIVITY

Specialized activities were observed in *Kinixys spekii* all hours from 06.00 hr to 19.00 hr. Tortoises were already active when located at 06.00 hr on only two occasions, and these animals had apparently only recently become active: one had moved 1 m from its hole, the other had moved 5 m from the cover where it was left the evening before. Only one tortoise was active after 19.00 hr: a female which was still digging a nest as darkness fell at 19.10 hr (Hailey & Coulson, 1997). Activity outside the period 06.00-19.00 hr was thus infrequent, and probably restricted to just before or after this time, so that the daily activity period of the population was 13 hr. The behaviour of the five individuals was assumed to be representative of that of the population as a whole on hot days. There were no significant differences in the number of observations of different types of activity among individuals or days (Table 1), so that the data were not biased by inclusion of outliers. The non-parametric Kruskal-Wallis test gave similar P values to the analysis of variance shown in Table 1.

All five individuals used burrows during the continuous observations, but only 15 of the overnight refuges were burrows, the other 24 being in surface cover (the nesting female was not followed to an overnight refuge). The proportion of refuges which were burrows (38%) was significantly lower than the 66% found by Hailey & Coulson (1995) ($\chi^2 = 6.69$, $df = 1$, $P < 0.01$). That study did not follow animals until they became inactive, and could only identify obvious refuges from the trailed threads. The difference between the two studies is thus probably due to the indistinct nature of most surface refuges. Burrows were also only rarely used as temporary refuges during the day. Entry into a burrow and re-emergence on the same day was only observed four times (in three individuals), for durations of 5, 15, 20, and 70 min respectively.

TIME BUDGETS

A total of 3117 observations was recorded at 5 min intervals. Time budgets based on these observations are shown in Table 2; the small percentage of time

TABLE 1. Test of differences in activity among individuals and days. The mean number (\pm SD) of observations of each type of activity is shown for individuals, averaged across days. Values of F and P for ANOVAs are for individuals (averaged across days) and days (averaged across individuals), respectively.

	Individuals			Days	
	Number	$F_{4,15}$	P	$F_{3,16}$	P
Locomotion	25.7 \pm 9.0	1.3	0.31	0.7	0.55
Feeding	8.6 \pm 3.9	2.0	0.14	0.7	0.55
Reproduction	1.8 \pm 1.9	0.6	0.66	1.0	0.41
All specialized activities	36.0 \pm 12.7	1.6	0.23	1.0	0.41

TABLE 2. Time budgets for *Kinixys spekii*, based on: (1) the population daily activity period; (2) the duration of daily activity of individuals; (3) simulation of undirected searching. The upper section shows the mean time represented by the total number of observations, and that spent in different types of behaviour, each day. The lower section shows the percentage of the total time made up by each behaviour; values of hr d⁻¹ in the lower section of budget 3 are based on the population daily activity period of 13 hr.

Time budget	(1)	(2)	(3)
Total no. of 5 min observations	3117	1963	894
Mean total time (hr d ⁻¹)	13.0	8.2	3.7
Specialized activity (hr d ⁻¹)	3.0	3.0	3.0
Stationary above ground (hr d ⁻¹)	7.8	5.2	0.7
In burrow (hr d ⁻¹)	2.2	-	-
Locomotion (% , hr d ⁻¹)	15.0, 1.95	23.8, 1.95	52.2, 6.79
Feeding (% , hr d ⁻¹)	6.6, 0.86	10.4, 0.86	22.9, 2.98
Courtship (% , hr d ⁻¹)	1.0, 0.13	1.6, 0.13	3.6, 0.47
Stationary above ground (% , hr d ⁻¹)	60.1, 7.81	63.3, 5.18	19.5, 2.53
In burrow (% , hr d ⁻¹)	16.8, 2.18	-	-

unaccounted for in the table was due to nesting by one female (Hailey & Coulson, 1997). The first time budget is based on all observations made during the daily activity period of 13 hr, including time in burrows and before the start and after the end of individual tortoises' activity each day. This time budget shows a low proportion of the day spent active – for example, 15% locomotion and 6.6% feeding. Note that these are proportions of the potential activity time of the tortoises, when they could have been active – as some members of the population were at any given time within the daily activity period.

The second time budget is based on the daily duration of activity of individuals, between the first and last observation of specialized activity each day, excluding only time in burrows. The mean duration of daily activity was 8.2 hr. This time budget includes a greater

percentage of specialized activities, for example 23.8% locomotion. Nevertheless, although the percentage of specialised activities increased, this was out of a shorter total time; the actual duration of these activities was of course unchanged. There were 3.0 hr of specialised activity per day, of which 2.1 hr was spent in movement (locomotion and courtship) and 2.8 hr was potentially foraging (locomotion and feeding).

Tortoises remained stationary above ground for periods ranging up to several hours (Fig. 1). There was an inflection in the frequency distribution, which was used to separate short pauses during activity (1 or 2 consecutive observations) from inactivity in surface refuges (three or more consecutive observations). The third time budget (Table 2) simulates the results of undirected searching, by including the specialized activities and short pauses, but excluding inactivity in surface refuges. This budget shows a much greater percentage of specialized activities, but of a much shorter total time. A calculation based on the behaviour of tortoises found by undirected searching and the population daily activity period would grossly overestimate daily activity – for example, 6.79 hr of locomotion compared to the true 1.95 hr (Table 2). A time budget based on short periods of observation of focal individuals (for example, for 30 min; Ruby *et al.*, 1994) would also be biased if the animals were active when first located (not shown).

DISCUSSION

ADVANTAGES OF CONTINUOUS OBSERVATION

Undirected searching and focal studies clearly overestimate the level of activity of tortoises, as suggested by Moskovits & Kiester (1987), and give no information on the daily duration of activity of individuals. Combining data from undirected searching with the population daily activity period is particularly misleading, giving for example a three-fold overestimate of locomotion in *Kinixys spekii*. Undirected searching or

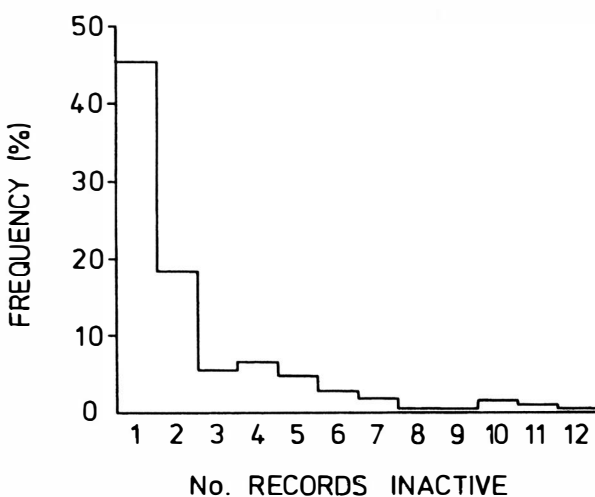


FIG. 1. The frequency distribution of the length of periods stationary above ground, shown as the number of consecutive observations at 5 min intervals, excluding time before the first and after the last specialized activity each day. In addition to those shown, 10.8% of periods stationary above ground were longer than 60 min, with a mean of 193 min.

focal observations may be used to compare the proportions of different types of behaviour – for example, between seasons (Meek, 1988). Comparisons of the level of activity or true time budgets require information on individuals observed through the complete daily activity period.

There were no significant differences between individuals or days, so that the data were not distorted by outliers and can be considered representative of the activity of the population in general during this type of weather. *Kinixys spekii* has a short annual activity period at Sengwa, limited to 4–5 months in the rainy season (Hailey & Coulson, 1996b), and pronounced seasonal variation within this period is therefore unlikely. There is, however, likely to be a strong effect of weather. The daily movement distance of *Kinixys spekii* increases on cool days (Hailey & Coulson, 1996b), so that an increase in locomotion, and possibly other types of behaviour, would be expected in cool weather. This hypothesis, and others such as differences between sexes or species, should be tested using individual tortoises as the basis of analysis (for example, the data in Table 1), rather than pooled time budgets. Repeated observations are useful in increasing the reliability of data for each individual, but do not increase the sample size as such.

The collection of behavioural data is time consuming, and the question is: are repeated observations worth the extra effort? As an example, the mean number of observations of specialized activities was 36 ± 17 on the first day of observation (\pm SD among individuals). The number was 32 ± 17 on days 1 and 2, 38 ± 11 on days 1–3, and 36 ± 13 on days 1–4 (Table 1). Repeated observations therefore had little effect in reducing the inter-individual variability of these data, and thus the confidence interval and usefulness for testing hypotheses. The best allocation of resources would therefore be to observe as many individuals as possible, each for one day in each situation of interest (type of weather, season).

The number of individuals observed in any set of conditions depends on the reliability required for the time budget. Using the example of the number of observations of specialized activities, the SE was 21% of the mean with five individuals each studied for one day. A sample size of $n=22$ would be needed to give a SE of 10% of the mean, and $n=89$ to give a SE of 5% of the mean. A very large number of individuals would thus only increase the reliability of the estimate by a moderate degree. The sample size needed also depends on the variability of behaviour between days. For example, activity of *Testudo hermanni* varied greatly in summer, with about 50% of individuals being completely inactive on any given day (Hailey, 1989). Study of time budgets by continuous observations would be impractical in these circumstances, as a very large sample size would be needed and much of the time would be wasted on inactive animals.

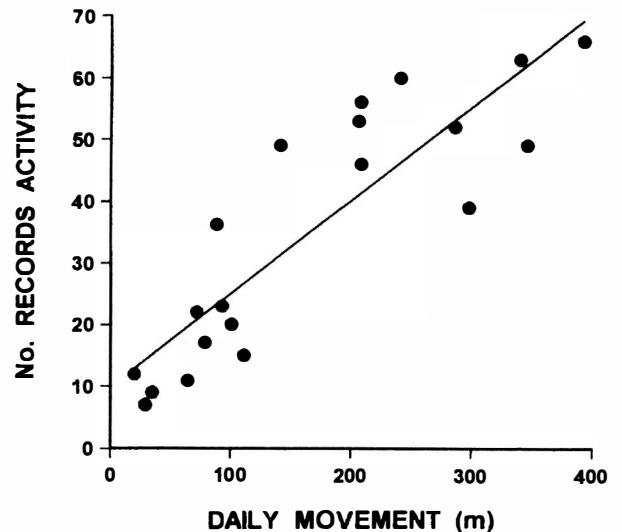


FIG. 2. Relationship between behavioural activity (the number of records of locomotion, feeding and courtship in one day) and the daily movement distance. Regression equation: $y = 10.0 + 0.15x$ ($r^2 = 76.3\%$).

Time budgets in seasons of low or variable activity are best estimated by calibrating data from single sightings or focal individuals. It would be necessary to collect such data in seasons of both low and high activity, together with a detailed time budget in the season of high activity and a measure of total activity (such as the daily movement distance of thread-trailed animals) in both seasons. This method depends on a strong relationship between behavioural activity and daily movement distance (Fig. 2). Rarely observed types of behaviour present a similar problem, as their occurrence is likely to vary widely between individuals and days. For example, the SE of the number of observations of reproduction was nearly 50% of the mean, even after averaging across four days of observation (Table 1). The level of such rare types of behaviour is also best estimated from short-term observations, calibrated using the total level of activity from continuous observations.

Continuous observation would also be useful when assessing thermoregulation by animals in novel circumstances, for example to show the effects of climate (Hailey & Loveridge, 1998) or familiarity with the home range (Chelazzi & Calzolari, 1986). It is necessary to show that any differences in body temperature are responses to the thermal environment, rather than to disturbance. For example, Chelazzi & Calzolari (1986) found that translocated *Testudo hermanni* had daily mean body temperatures different to those of resident animals, but these were measured automatically by radiotelemetry throughout the daily activity period without reference to activity of individuals. Chelazzi & Francisci (1980) noted altered behaviour of translocated tortoises, including both an initial period of inactivity lasting up to 4 days, followed by hyperactivity with unusually linear movements. Both of these

types of behaviour suggest that thermoregulation was partially abandoned (within the constraint of avoiding critically high body temperatures) rather than made more difficult. Detailed behavioural observations of translocated and resident animals would resolve this question.

ACTIVITY AND TIME BUDGETS

Activity of *Kinixys spekii* on hot days can be compared to the scanty data for other species of tortoise, from long-term observations, thread-trailing, and radiotelemetry. The duration of daily activity of 8.2 hr was rather longer than the 3 hr reported for *Gopherus agassizii* (Nagy & Medica, 1986), the only other tortoise for which this has been measured. This difference is probably due to the severe thermal constraints on activity of the desert tortoise (Zimmerman *et al.*, 1994), which is supported by the difference in daily movement distance between these species. *Kinixys spekii* moved on average 172 m on hot days (Hailey & Coulson, 1996a), compared to about 35 m in *Gopherus agassizii* (Ruby *et al.*, 1994).

Kinixys spekii was moving for 2.1 hr out of the 8.2 hr duration of daily activity, thus spending 26% of time moving. This value is exactly the same as that found in *T. graeca* observed for long periods (Meek & Jayes, 1982). The population daily activity period (13 hr) is similar to the 12.5 hr reported for two other tropical tortoises, *Geochelone carbonaria* and *G. denticulata* (Moskovits & Kiester, 1987). It is possible to calculate that the latter two species spent about 1.7 hr moving each day, similar to the 2.1 hr in *Kinixys spekii*. Huot-Daubremont, Grenot & Bradshaw (1996) studied activity of *T. hermanni* in a large outdoor enclosure. Feeding made up about 4% of the daily activity period of 11 hr (periods 2 and 3 in that paper) during July and August, similar to the value of 6.6% for *Kinixys spekii*.

Results for activity of *Kinixys spekii* are thus generally similar to the little data available for other tortoises. More data are available for lizards: values for the time spent moving each day are of particular interest, in relation to the exercise physiology of lizards and tortoises. Reported values are: 0.4 hr in *Egernia cunninghami* (Wilson & Lee, 1974); 0.8 hr in *Varanus rosenbergi* (Christian & Weavers, 1994); 1.5 hr in *Cyclura nubila* (Christian *et al.*, 1986); 1.6 hr in *V. gouldi* (Christian *et al.*, 1995); 1.7 hr in *Conolophus pallidus* (Christian & Tracy, 1985). *Kinixys spekii* (and *Geochelone* spp.) thus spent more time moving than most lizards, even the particularly active Varanidae. The only exception was *V. panoptes* which moved for 3.5 hr day⁻¹ in the dry season, when making daily journeys to forage around water courses (Christian *et al.*, 1995). The comparison of lizards and tortoises therefore supports the conclusion that exercise physiology is related to the intensity of activity, not to the time spent moving each day (Christian & Conley, 1994).

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APPENDIX

Nesting by one of the trailed tortoises was described by Hailey & Coulson (1997). That note was not seen in proof and contains some errors. Page 13, last line should read: 17.16 hr digging under *Mundulea sericea* tree (nest 3); 18.32 hr digging under *Pseudolachnostylis maprouneifolia* tree (nest 4). Page 16, line 6: 100 mAs should read 10 mAs. Page 17, line 15: 80°S should read 8°S.

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GEOGRAPHIC VARIATION IN BODY SIZE AND LIFE-HISTORY TRAITS IN BOSCA'S NEWT (*TRITURUS BOSCAI*)

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Body size of newts from five populations of *Triturus boscai* was measured and the age of the newts was estimated using skeletochronology. Variation in adult body size was observed throughout the range of the species, with largest individuals of the southernmost populations being smaller than the smallest adults of the northern localities. Sexual dimorphism in body size was detected in all populations studied. A tendency towards older mean ages was also observed from southern to northern populations. The age of youngest breeders, modal age at which growth slows, and mode of the age structure showed geographic variation, with the greatest differences in life-history traits being between northernmost and southernmost populations, survival being optimized in the north by delaying either the age of maximum reproductive output or sexual maturity. The variation observed may have been due to evolutionary changes, though more extensive information on genetic and morphological interpopulational differences is needed to support a taxonomic differentiation.

Key words: geographical variation, newt, life history, *Triturus boscai*

INTRODUCTION

Geographic variation in body size is frequently associated with differences in several life-history traits throughout the range of a species, such as fecundity, age at maturity and longevity. These, in turn, may be associated with variation in morphological characteristics, such as body size and growth rate (Roff, 1992; Charlesworth, 1994).

Plasticity in phenotypic and life-history traits is not unusual in amphibians, and has been frequently reported to occur in urodeles (e.g. Hanken & Wake, 1993 and references therein; Tilley & Bernardo, 1993 and references therein; Kalezić, Cvetkovic, Djorovic & Dzukic, 1994). In some cases the variation is supported by genetic differentiation resulting from adaptive plasticity through evolutionary processes, while in other cases non-adaptive plasticity is observed, and the variation may be regarded as a response to local environmental characteristics (Bernardo, 1994).

In urodeles, and in particular in the genus *Triturus*, a decrease in body size has been observed for certain species throughout their range, occurring mainly under extreme environmental conditions (Beebee, 1983; Dolmen, 1983; Díaz-Paniagua, Mateo & Andreu, 1996). The small body size in some *Triturus* populations has led to the description of different taxonomic groups (Wolterstorff, 1905; Raxworthy, 1988; García-Paris, Herrero, Martín, Dorda, Esteban & Arano, 1993). A small body size confers some advantages to individuals, as it reduces nutritional requirements (Clarke, 1996) and their maintenance costs (Bernardo, 1994). Size reduction is normally associated with variation in life history traits such as

fecundity, age at maturity, longevity and reproductive life span (e.g. Roff, 1992).

Triturus boscai is an endemic species from the western half of the Iberian Peninsula, and is considered to be closely related to other small-bodied *Triturus* species (e.g. Macgregor, Sessions & Arntzen, 1990; Halliday & Arano, 1991). No subspecies have been described for *T. boscai*. However, variability in colouration (Malkmus, 1980-81) and genetic patterns (Herrero, 1991; Arano, Herrero, García-Paris, Mateo & Sanchíz, 1997) have been reported throughout the species range, and substantial differences in adult body size among populations are evident from studies from different localities (Malkmus, 1980-81; Caetano, 1982). The aim of this paper is to describe the variability in adult body size and some life history traits in *T. boscai* along a north-south gradient across its geographic range. The observed variation constitutes an interesting basis for *a posteriori* analyses of taxonomic differentiation including a more extensive study on morphological and genetic differentiation among populations.

METHODS

We analyzed the characteristics of newts from five populations located along a latitudinal gradient across the range of the species, which can be classified as: northern populations: Pontevedra-Bueu (P), Lugo-Ancares (L); central population: Salamanca-Candelario (S); and southern populations: Huelva-Aroche (H), Huelva-Doñana (D) (Fig. 1). A description of the main characteristics of each locality is given in Table 1.

Individuals from all localities, except D, came from the scientific collection of the Estación Biológica de Doñana (CSIC), and all were mature newts collected during the aquatic phase within one breeding season in each locality. Newts from D were live individuals, captured during the breeding season of 1994 and 1995, which were released in the field after being measured

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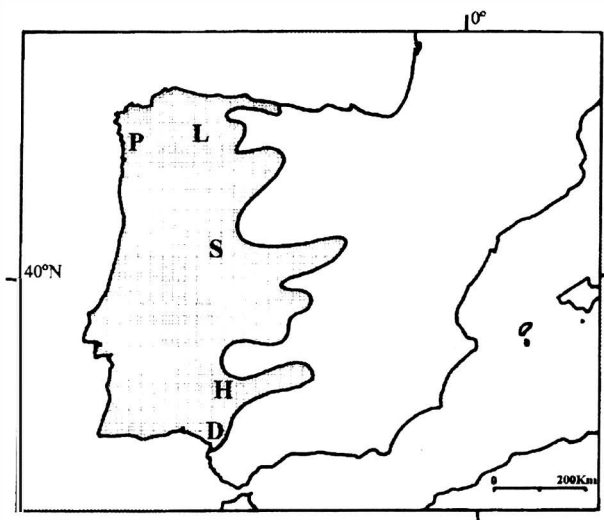


FIG. 1. Locations of sampling sites within the range (shaded area) of *Triturus boscai*.

and weighed. We clipped and preserved one toe for age determination from each of 60 individuals. The absence of preserved newts from D forced us to compare their measures with those from preserved individuals, which may have contributed towards an increase in the observed differences, mainly because of a wider variation in the measures recorded for D newts. We assumed, nevertheless, that the data satisfactorily reflect the range of body length within each population, although some distortion may be expected in preserved specimens (Verrell, 1985).

As measures of newt size we recorded: (a) body length (BL) from the snout to the anterior tip of the cloaca; (b) body plus vent length (SVL) from the snout to the posterior tip of the cloaca; and (c) total length (TL) from the snout to the tip of the tail. These were recorded with vernier callipers to the nearest 0.5 mm. SVL and TL are given to enable comparisons with other studies. Because SVL may show wide variations

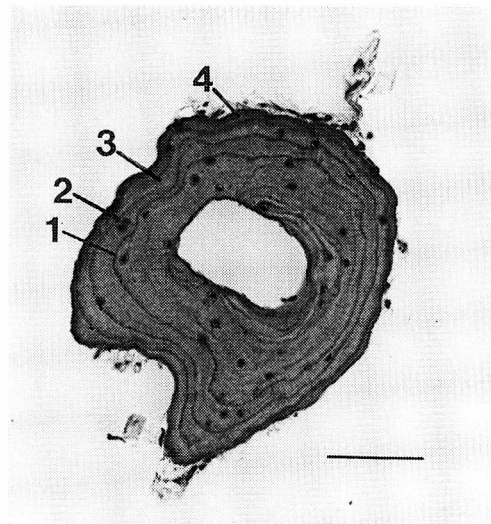


FIG. 2. Stained sections of a humerus of a male *T. boscai* from S, showing 4 LAG (1 wide band + 2 medium bands + 1 narrow band + the last incomplete band) and PAM = 2 yr. Scale bar = 100 μ .

depending on the sex and on the reproductive stage of individuals, and the tail is frequently broken or regenerated, we used only BL in comparisons between populations.

We estimated the age of newts by skeletochronology (see Fig. 2). Sections of decalcified humeri of preserved newts were obtained with a freezing microtome and stained with Ehrlich's hematoxylin (see details of the technique in Castanet, 1982; Leclair & Castanet, 1987; Castanet & Smirina, 1990). Following Caetano, Castanet & Francillon (1985), Francillon-Viellot, Arntzen & Géraudie (1990) and Miaud (1991), we considered the lines of arrested growth (LAG) to correspond to periods of inactivity, while the zones of bone layers between LAG (hereafter referred to as bands) correspond to the periods of activity and growth (Caetano *et al.*, 1985; Verrell & Francillon, 1986; Miaud, 1991; Caetano & Castanet, 1993). Growth bands should therefore form annually, as demonstrated

TABLE 1. Main characteristics of the five localities of newts considered in this study, listed from south to north. Temperature (T^a) data for H, S, L and P come from Montero & Gonzalez (1983). (See Material and methods for complete locality names).

Locality	Altitude	Rainfall	July T^a	Jan T^a	Substrate	Vegetation
D	10-20 m	585 mm	24.5°C	10.6°C	Sandy	Mediterranean shrubland
H	350-500 m	832 mm	25.3°C	7.7°C	Plutonic	<i>Quercus</i> and <i>Eucalyptus</i> woods with Mediterranean shrubland
S	1000-1050 m	1111 mm	22.6°C	5.5°C	Plutonic	<i>Quercus</i> woods with Mediterranean shrubland
P	10-60 m	1727 mm	20.0°C	9.0°C	Plutonic	<i>Eucalyptus</i> spp. forests with Mediterranean shrubland
L	800-1100 m	1901 mm	15.3°C	1.2°C	Siliceous	Clear <i>Quercus</i> and <i>Castanea</i> woods with Mediterranean shrubland

TABLE 2. Mean and standard deviation of snout-vent length, body length, total length, and mass of *T. boscai* from five localities along a latitudinal gradient across its distribution range (body mass of fresh specimens were only available from D and S).

		Body length (mm)			Body+vent length (mm)			Total length (mm)			Body mass (g)		
		Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
D	Male	24.9	2.26	93	25.1	2.24	22	45.2	3.78	38	0.47	0.05	93
	Female	26.0	2.43	61	27.2	4.73	16	55.0	4.53	31	0.58	0.16	61
H	Male	28.2	1.31	40	32.7	1.57	25	66.1	3.12	40	1.14	0.33	40
	Female	34.0	1.59	37	37.2	2.61	37	72.8	3.90	37	1.51	0.42	37
S	Male	28.1	1.67	33	32.1	2.1	33	63.0	3.87	33	-	-	-
	Female	34.1	1.49	37	36.9	1.59	37	72.7	4.31	37	-	-	-
L	Male	30.7	1.33	29	35.1	1.56	29	66.7	3.87	29	-	-	-
	Female	37.0	3.27	33	40.4	2.35	33	79.3	3.99	33	-	-	-
P	Male	32.0	1.40	26	36.3	1.63	26	68.9	3.53	26	-	-	-
	Female	39.0	2.09	37	41.9	1.99	37	81.8	4.06	37	-	-	-

for the sympatric and congeneric species *Triturus marmoratus* by Caetano (1990). In newts from D, the same technique was used in phalanx sections. We confirmed the same number of bands in humeri and phalanges of 14 preserved individuals (6 from D, 6 from S, 2 from L). Caetano (1990) confirmed the same number of LAG in humeri and in phalanges of *Triturus marmoratus*, and Marnell (1997) obtained similar results in a small-sized newt, *Triturus vulgaris*. Double lines were detected in a small percentage of individuals from different localities and they were considered as corresponding to one year with several shorter inactivity periods (e.g. Caetano, 1990).

The relationship with body size was analysed by considering the number of bands rather than LAG, in order to differentiate the newts captured at the beginning of the activity period from those recorded after growing during the activity season. We did not consider 5.2% of 286 individual stained bone sections (2.1% from D, 1% from H, 1.75% from L and 0.35% from S), because LAG were not clearly visible or the zone of endosteal resorption was too large, which could have affected the number of LAG estimated.

The age at maturity is commonly considered to be associated with a decrease in the growth rate and some authors have considered it to correspond with the age when LAG become closer (Leclair & Castanet, 1987; Mateo & Castanet, 1994), although for some newt populations sexual maturity has been demonstrated to occur before the age of growth decrease (Francillon-Viellot *et al.*, 1990). In this study, the irregularity of the bands, especially those of phalanges, prevented precise width measurement. Therefore, we classified bands in three relative width categories (wide, medium and narrow), and considered that the growth rate decreased when narrower bands appeared

after wide or medium ones. The number of wide bands was assumed to correspond with the probable age at maturity (PAM hereafter). PAM was considered only for newts showing a decrease in growth rate. We compared the modes of PAM distribution with the modal and minimum classes of the age distributions for each breeding population.

Differences in body size and age distributions were analysed by means of two way ANOVAs in which the effects of locality and sex were tested. Student-Newman-Keuls *a posteriori* tests were employed with one way ANOVAs.

RESULTS

A significant variation in body size was observed for *T. boscai* throughout its range ($F_{4,272} = 569.5$, $P < 0.001$) (Table 2). The smallest newts were observed in the southernmost populations, from Doñana National Park (D). These averaged 24.9 mm and 26.0 mm in BL (males and females respectively) while the newts from H, about 50 km to the north, were about 4 mm (males) and 8 mm (females) longer on average. In the centre of the range, in S, the newts did not significantly differ in size from H (after Student-Newman-Keuls *a posteriori* test), with an average BL of 28.2 mm and 33.9 mm for males and females, respectively. They also differed from newts from northern populations: in L, males averaged 30.7 mm and females 37.0 mm; and in P, 32.0 mm and 39.0 mm respectively (Table 2).

Sexual dimorphism also contributed to interpopulational differences, as reproductive males were significantly smaller than reproductive females ($F_{1,272} = 320.19$, $P < 0.0001$) in each locality. However, the difference between BL of males and females was much smaller in newts from D than in the other localities (Table 2).

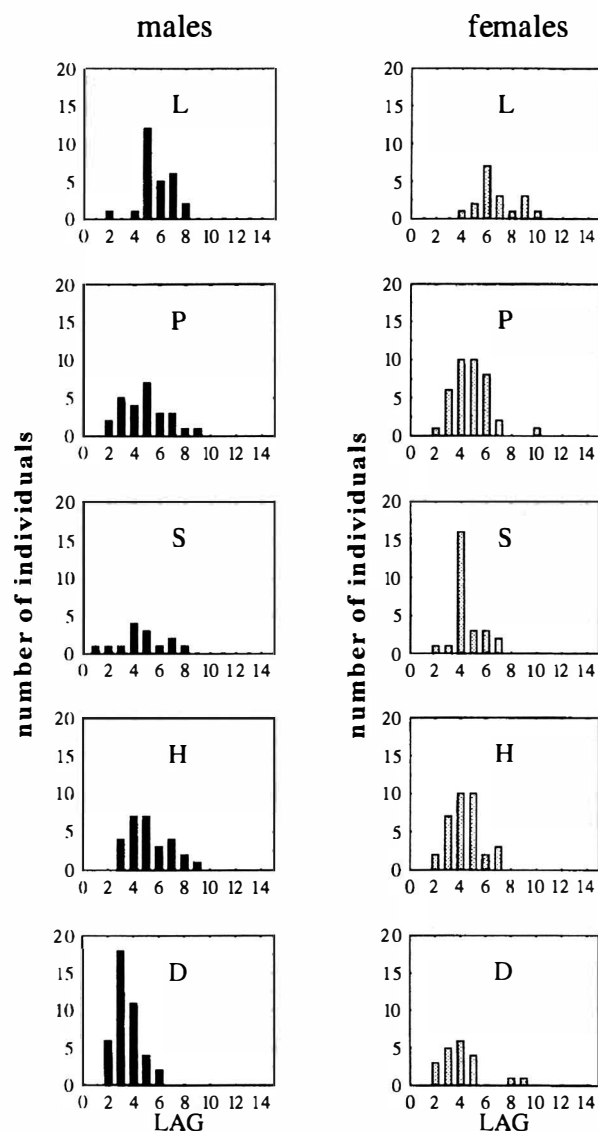


FIG. 3. Age structure of male and female newts in the five populations studied. Age is expressed as the number of lines of arrested growth (LAG) counted in bone sections.

The age structure also varied significantly among populations ($F_{4,260} = 16.99$, $P < 0.0001$), with older mean ages tending to be observed in the northern populations (Fig. 3). Mean age of reproductive newts varied from 3.5 LAG in D to 5.6 in L (males), and from 4.1 LAG in D to 6.8 LAG in L (females). No differences were observed between age distributions of males and females within populations, except in L ($F_{1,45} = 5.84$, $P = 0.0198$).

Maximum longevity was registered for a female from L, with 10 LAG, and a male from P, with 9 LAG. However, there did not appear to be any consistent differences in longevity between the sexes (Fig. 3).

Regarding the youngest breeding individuals, one male from S was aged 1 yr, while all males were over 2 yr in P and D, and over 3 yr in H. It is remarkable that the age distributions did not show decreasing frequencies from lower to higher age classes, but instead displayed two-tailed distributions (Fig. 3). The modal age class varied among populations according to the latitudinal gradient, from 3 yr in males from D, to 6 yr in females from L. In these two populations the modes corresponded with older age classes in females than in males, females also achieving greater longevity. In the remaining populations, males and females had similar modal ages and a higher frequency of males was observed in the older age classes. The difference between the age of the youngest breeding individual and the mode differed among populations from one year in males from D and H to three years in newts from L, P and S (Fig. 3).

Body size was not significantly correlated with age in any population, a wide range of body sizes being observed for most age classes (Fig. 4). The largest males and females from D were both smaller than the smallest individuals of the same sexes at any other locality. Mean body size of 3 yr males from D was about 5 mm smaller than in similar aged males from S and H, and 9 mm smaller than the mean size of P newts. Even larger differences were observed for females: mean body size of all age classes from D was about 7 mm smaller than mean BL in other populations. On average, 4 yr old females from D were 15.4 mm smaller than 2 yr old females from L.

Most bone sections exhibited wide bands corresponding with the earliest ages, followed by medium or narrow bands which were assumed to correspond to post-maturation years with lower annual growth rates. Table 3 shows the number of individuals in each population showing 1, 2, 3 or no bands formed before the decrease in growth rate occurred (through the detection of subsequent narrow bands).

A small percentage of breeding males from D, H, L and P showed no wide bands, probably indicating that they had matured during the first activity period after metamorphosis (PAM = 1). All males (except one from D) also exhibited one to six medium bands, possibly

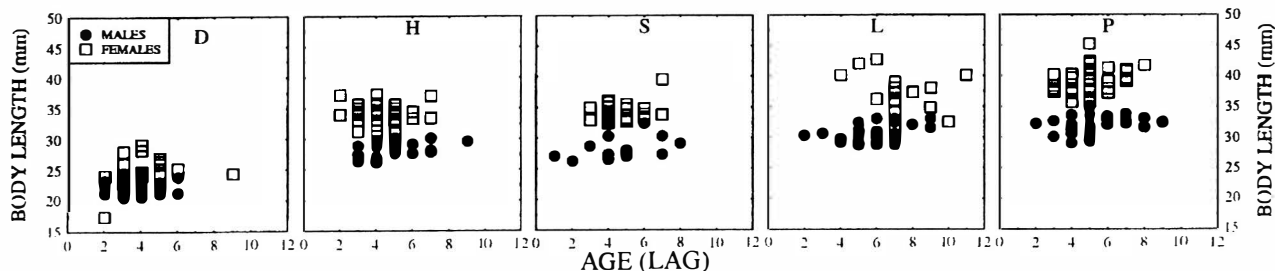


FIG. 4. The relationship between age (number of LAG) and body length (imm) of newts in the five populations studied.

TABLE 3. Number and percentage (in parentheses) of individuals with 0, 1, 2 or 3 wide bands formed in bone sections before medium or narrow bands, indicative of the age of growth decrease (only individuals presenting narrower bands after wide bands were considered). The percentage of individuals with double lines (DL) is also shown.

	Males					Females				
	No. wide bands				DL	No. wide bands				DL
	0	1	2	3		0	1	2	3	
D	6 (27.3)	15 (68.2)	1 (4.5)	0	0	1 (6.3)	15 (93.7)	0	0	3.02
H	6 (25)	9 (37.5)	9 (37.5)	0	32.0	3 (9.4)	10 (31.2)	16 (50)	3 (9.4)	5.9
S	0	4 (44)	5 (55)	0	7.1	0	11 (44)	12 (48)	2 (8)	7.4
L	3 (12)	15 (60)	7 (28)	2 (7.4)	38.9	10 (58.8)	6 (35.3)	1 (5.9)	0	25
P	2 (8.7)	12 (52)	9 (39)	0	8.3	3 (9.6)	9 (28.1)	17 (53.1)	3 (9.3)	7.7

corresponding to medium growth before or after maturity. More than 50% of males in D, L and P showed one wide band, probably corresponding to sexual maturity during the second year of life (PAM = 2 yr). In H, a similarly high proportion of one and two wide bands comprised up to 75 % of cases. All individuals from S had one or two wide bands, suggesting that PAM = 2 or 3 yr. In L and P a small percentage of males had three wide bands (PAM = 4 yr). Double lines were observed in all populations except in D (Table 3).

A small proportion of breeding females in D, H and P presented no wide bands, but showed up to three medium bands, indicating a relatively low growth rate during their first years of life. In L, a high proportion of females did not exhibit wide bands, with a maximum of three medium bands. All females from S had more than one wide band (PAM > 1 yr). In D, 93% of females showed only one wide band (PAM = 2 yr), while in S and H, high percentages were similarly distributed between one and two wide bands. A small proportion of females with three wide bands (PAM = 4 yr) were found in H, S and P. Double lines were observed in all populations, most frequently in L and D (Table 3).

DISCUSSION

Triturus boscai shows a latitudinal variation in body size which may have important implications, such as the prevention of interpopulational mating, considering that body size may influence sexual selection (Halliday & Verrell, 1986; Verrell, 1989). The populations from S and H did not differ widely, despite the large distance that separates them. The highest variation was observed in the populations located close to the northern and southern limits of the range of the species. The very small body size of D newts, especially males, indicates that this population is considerably isolated and differentiated from the nearby population at H. D is located at the southern limit of the species range, where the sympatric species *Triturus marmoratus pygmaeus* displays a similar variation in body size (Díaz-Paniagua *et al.*, 1996), suggesting that the characteristics of the biotope favour the attainment of small adult body sizes, as Hanken & Wake (1993) commented for certain environments. Although it is not demonstrated which

environmental characteristics at D favour the diminution of body size, several habitat features, such as low annual rainfall and temporary ponds with a long desiccation period, coincide with those of habitats of other small subspecies of *Triturus* (Raxworthy, 1988).

Sexual dimorphism was also evident in body size, and contributed to an increase in the differences between populations. Geographic variation in sexual size differences has also been reported in other species of *Triturus*, and was explained as a consequence of population specificity in sexual growth rates (Kalezic, Crnobrnja, Djorovic & Dzukic, 1992). The ratio of sexual size dimorphism was smallest for D newts, which may be a further consequence of the particular ecological characteristics of this area.

The latitudinal variation in body size corresponded with the variation in age structure. In a previous study, Caetano (1990) observed that populations of *T. boscai* from southern and northern Portugal, and from low and high altitudes, did not differ in age at maturity, reaching a maximum longevity of 7 to 8 years. In our study we have considered populations of a wider latitudinal range, and, although we agree with Caetano (1990) in general aspects, we have found variation in both parameters, mainly between the most extreme populations, which are out of the range studied by Caetano (1990). Although this author, based on the spatial pattern of LAG, found that newts reached maturity at 3 yr, in our study the minimum age of mature newts was 2 yr in most populations.

It is remarkable that the age structure in all studied populations did not show a decrease from younger to older age classes. In a study on three other *Triturus* species Miaud (1991) described decreasing age structures for females, while male frequencies decreased only from the second age class on. His interpretation was that most individuals matured at the modal age class. In the present study we found that the modal age class of *T. boscai* was from one to three years higher than the minimum age of breeding newts, and did not coincide with the mode of PAM distribution. This difference may be explained by the possibility of lower reproductive frequencies of younger adult newts, which could be associated with the relatively high frequency of indi-

viduals with medium instead of wide initial bands. A lower than annual reproductive frequency in a portion of the population is not uncommon in *Triturus* and has been proposed previously for *T. vulgaris* in an urban population from England (Griffiths, 1984) and for females of *T. marmoratus* from D (Díaz-Paniagua, 1998).

The modal age class seems to be population specific. As occurred with body size, mean age of breeding individuals was higher in northern (L and P) and lower in southern populations (D). This is probably associated with a delay in sexual maturity and/or a decrease in reproductive frequency of younger individuals, which is likely to have important repercussions in life history traits such as fecundity, survival and longevity within each population (e.g. Stearns, 1976; Roff, 1992). The differences observed suggest that at least northernmost and southernmost populations have different life history traits, northern populations optimizing survival of individuals by delaying the age at maturity and/or the seasons of maximum reproductive output, whereas in the central and southern populations a higher reproductive investment occurs in the earlier years, resulting in lower survival probabilities and reduced longevity.

As observed in other urodeles (Halliday & Verrell, 1988), body size of *T. boscai* cannot be considered a reliable predictor of newt age. Age and body size were not correlated in any population, and we even found negative tendencies, with smaller individuals in the older age classes. This may be explained by the drastic decrease of growth rates after sexual maturity is attained, as well as by the different interannual reproductive effort of individuals, resulting in different individual growth trajectories.

The variation in reproductive investment in the early age classes may not be the cause of the differences in body size observed among populations, since all individuals from the southernmost population were smaller than the youngest from the northern populations. Therefore, sexual maturity is reached at different body sizes in populations from different localities, independently of age. Differences in age at maturity and growth rate were detected in two populations of the salamander *Desmognathus ochrophaeus*, where the variation in growth was found to be dependent on environmental factors, while age at maturity was established genetically, suggesting that both parameters may evolve independently (Bernardo, 1994).

In other *Triturus* species variation in body size has been considered to characterize different taxonomic groups within species, as is the case of the dwarf subspecies of smooth newts, *T. vulgaris schmidtlerorum* from Turkey (Raxworthy, 1988), and *T. marmoratus pygmaeus* in the southern half of the Iberian Peninsula (García-Paris *et al.*, 1993). The variation in body size of *T. boscai* has a geographic basis and occurs between distant populations which have evolved different life history traits. However, more information on the genetic and morphological variation among populations is needed to identify taxonomic differentiation.

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SHORT NOTE

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**DIET OF THE MOORISH GECKO
TARENTOLA MAURITANICA IN AN
ARID ZONE OF SOUTH-EASTERN
SPAIN**

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The Moorish gecko, *Tarentola mauritanica*, is a rock-dwelling and broad-fingered gecko distributed throughout the Mediterranean region, from the Iberian Peninsula to Greece in the north, and from Morocco to Libya in the south (Martínez-Rica, 1997). The species can be found in very different natural habitats, from rock cliffs in relatively wet and woody zones, to true deserts. In addition, this reptile shows marked anthropophilous behaviour, and is common in human habitations; in fact, because it thrives in urban (towns) or developed (farms, agricultural landscapes) habitats, most studies carried out on this species focus on these non-natural environments. For instance, the diet and feeding habits of the Moorish gecko have been studied in various zones of its distribution area, but mainly in habitats developed by man (Martínez-Rica, 1974; Seva, 1988; Gil, Pérez-Mellado & Guerrero, 1993; Capula & Luiselli, 1994; Gil, Guerrero & Pérez-Mellado, 1994; Pérez-Mellado, 1994) and rarely in truly natural sites (Mellado, Amores, Parreño & Hiraldo, 1975; Salvador, 1978). The typical behaviour of the Moorish gecko, hunting close to artificial lights, has given this species a widely accepted image as a sit-and-wait predator (Seva, 1988; Gil *et al.*, 1994; Pérez-Mellado, 1994), despite the fact that this is quite different from natural situations. In the present work, we discuss the dietary composition and feeding habits of this gecko in a natural site in south-eastern Spain. Our aim is to determine the extent to which the diet of this animal in a natural landscape compares with previous studies carried out in developed landscapes.

The study area is located in the Guadix-Baza region (SE Spain), a Neogene basin at 700-1100 m asl surrounded by high mountains (1700-3000 m asl). The climate is continental Mediterranean, with warm, dry summers and cold winters (average temperature 25°C in July and 0.5°C in January), and roughly 300 mm average annual rainfall, sparsely distributed between autumn and spring, although the study site, in the lower part of the basin, is drier (Castillo-Requena, 1989).

Field work was carried out in a *rambla* (a seasonal watercourse) named Barranco del Espartal (UTM 30sWG2754, 750 m asl). The sample site is a badlands landscape, with a substrate of silt with gypsum sediments. The vegetation is sparse: 46% bare ground, 21% grassland and 33% shrub cover (see Hódar, Campos & Rosales, 1996, for details), and a mean shrub height of 80.5 cm. The main plant species include *Salsola vermiculata*, *Artemisia herba-alba* and *Gypsophila struthium*, with scattered shrubs of *Retama sphaerocarpa* and *Tamarix gallica*.

Diet analysis was based on faecal samples, collected every two weeks between April and September 1995, a period usually free of nocturnal frost (Castillo-Requena, 1989), which hampers gecko activity. Faecal analysis provides accurate information on diet (Fitch, 1987; Rosenberg & Cooper, 1990; Tucker & Fitzsimmons, 1992), and permits dietary analysis without the killing of animals, and thus is especially useful when working with protected species, as in our case. On the other hand, this type of analysis does not allow identification of the individuals from which samples are taken, thereby preventing the evaluation of direct predator-prey relationships (e.g. size relationships).

Faeces were collected by surveying two marked walls (ca. 110 m² total surface area surveyed) in silt cliffs, the result of water erosion. Geckos take refuge during the day in fissures of these walls (pers. obs.). During each visit, we collected all the faeces found, but only complete faeces were preserved. No other gecko species is present in the zone, and the only other lizard species that inhabit cliffs, *Podarcis hispanica*, is scarce at the sampling site (only three records since 1989, with more than 340 days of field work), and its faeces are clearly different from those of geckos (*Podarcis* faeces are darker in colour, and do not remain attached to the wall). Medium-sized lizards such as *Acanthodactylus erythrurus*, *Psammodromus algirus* and *P. hispanicus* are abundant, but they do not climb on cliffs in the study site. Since sampling was conducted consistently on the same area of the cliffs, and all faeces were collected, we assumed that every gecko living on the cliffs had the same probability of being sampled, thereby eliminating the risk of pseudoreplication.

Faeces were dispersed in water and examined under a 10-40x binocular microscope equipped with a micrometer (0.1 mm precision). Prey remains were identified, sorted and measured. Prey were determined to the lowest taxonomic level possible, and later assigned to OTUs (Operational Taxonomic Units, *sensu* Sneath & Sokal, 1973). Measurements of characteristic body parts provided an estimate of the body size and dry mass of each prey item by means of regression equations previously developed by using arthropods collected in the study area (Hódar, 1997). Statistical analyses of prey size and mass were made only with those prey for which body lengths or dry mass were either measured or estimated. However, for any prey with no estimated biomass, we assigned the average biomass

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TABLE 1. Taxonomic composition and biomass of the diet of *Tarentola mauritanica* in the Barranco del Espartal (SE Spain). %N, percentage of numeric frequency; %B, percentage of biomass; %P, percentage frequency of occurrence of plant remains. Prey length and biomass are expressed as mean+SE. Means followed by different letters (a,b) are significantly different according to Dunn's *a posteriori* comparisons between all pairs of months ($P < 0.01$). * excluding spiders.

Prey	April		May		June		July		August		September		Total	
	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	%N	%B
Arachnida*	-	-	-	-	2.44	0.03	3.95	38.99	5.05	31.66	3.53	5.73	2.39	10.30
Araneae	15.79	32.12	2.40	0.58	9.76	14.22	6.58	6.47	4.04	0.71	9.41	17.60	7.37	6.51
Onyscidae	3.95	17.07	4.00	2.64	1.22	5.38	2.63	9.56	5.05	10.87	3.53	17.43	3.50	5.13
Homoptera	2.63	0.32	-	-	3.66	0.40	7.89	0.72	15.15	2.86	22.35	2.46	8.29	1.40
Heteroptera	1.32	0.29	2.40	0.99	7.32	10.49	6.58	9.32	7.07	4.30	1.18	0.08	4.24	5.78
Lepidoptera larvae	31.58	24.26	33.60	49.00	24.39	34.06	7.89	8.08	6.06	12.83	3.53	13.57	18.60	27.90
Lepidoptera adult	3.95	2.08	1.60	0.88	3.66	1.97	-	-	-	-	2.35	1.97	1.84	0.46
Carabidae larvae	30.26	20.58	43.20	37.76	18.29	13.30	32.89	18.18	12.12	9.61	2.35	0.53	24.13	26.42
Scarabeidae	-	-	-	-	3.66	10.87	-	-	3.03	3.88	3.53	2.25	1.66	2.23
Curculionidae	-	-	2.00	1.84	1.22	1.04	5.26	2.84	14.14	15.14	12.94	17.25	6.08	5.65
Other Coleoptera	2.64	2.60	0.80	5.28	10.98	7.06	10.53	4.26	10.10	5.41	21.18	20.23	8.94	7.12
Formicidae	3.95	0.36	0.80	0.04	10.98	0.72	10.53	0.46	14.14	1.36	8.24	0.30	7.73	0.61
Other Insecta	3.95	0.29	8.80	0.98	2.44	0.44	5.26	0.41	4.04	1.36	5.88	0.60	5.34	0.49
Vegetal (%P)	7.14		0.00		8.00		8.70		12.90		3.13		5.88	
Prey length (mm)	9.79+0.62 ^a		10.62+0.44 ^a		9.06+0.65 ^a		8.58+0.82 ^b		7.27+0.53 ^b		7.24+0.81 ^b		8.88+0.27	
Prey biomass (mg)	10.03+1.70 ^a		10.88+0.80 ^a		10.81+0.99 ^a		13.08+3.37 ^a		8.55+1.43 ^b		7.92+1.37 ^b		10.22+0.79	
No. prey	76		125		82		7		99		85		543	
No. faeces	28		31		21		23		31		32		170	

for its OTU and month in order to get a better estimate of the importance of that OTU.

Dietary data were computed on a monthly basis, and summarized as percentages of both numeric frequency and estimated biomass. For vegetal remains, only occurrence was recorded. Differences in dietary composition were analysed with the *G*-test, whereas prey sizes and masses were analysed with the Kruskal-Wallis test, with the Dunn test for *a posteriori* comparisons between pairs of months (Zar, 1996). Nonparametric tests were applied because of the non-normal distribution of prey sizes and biomasses (Shapiro-Wilk test). All tests were carried out by using the JMP statistical package (SAS Institute, 1994).

A total of 170 faecal pellets was collected during the study period, containing a total of 543 identified animal prey, all arthropods (Table 1). Vegetal remains were found in 10 scats, but the nature of the records (dry leaves and debris) suggests that they were ingested accidentally. Five groups, Araneae (spiders), Homoptera (leafhoppers), Lepidoptera larvae (caterpillars), Carabidae (ground beetles) larvae, and Formicidae (ants), comprised roughly two-thirds of the diet in terms of numeric frequency; especially noteworthy was the predominance of the larvae of Lepidoptera and Carabidae, representing more than 40% of the prey identified. Two of these prey-categories – beetles and ants – also formed two of the three major prey items in other previously studied continental desert-lizard systems (Pianka, 1986), and specifically in other palearctic gecko species (Szczerbak & Golubev, 1996). Biomass

data gave a slightly different picture: although the larvae of Lepidoptera and Carabidae persisted as the dominant groups, they were followed by non-Araneae Arachnida (solpugids and scorpions), Araneae, and Onyscidae (woodlice), the three non-Hexapoda groups. These five groups constituted more than 75% of the biomass consumed by the Moorish gecko in our study area (Table 1).

However, dietary composition was not constant over time, as there were significant changes over the study period ($G = 251.17$, $df = 50$, $P < 0.0001$). Lepidoptera and Carabidae larvae were the main groups, along with Araneae, during the first half the study period. From July onwards, these decreased in numerical importance, and were surpassed by Homoptera, several types of Coleoptera, and Formicidae. A notable dietary component was non-Araneae Arachnida, comprised exclusively of *Buthus occitanus* (Scorpionida) and *Glubia dorsalis* (Soliphuga). Despite their low number, this group represented an important source of biomass in July and August, when other prey were scarce (Sánchez-Piñero 1994). In spring, the Moorish gecko preys on less sclerotised, and hence highly profitable (e.g. Karasov, 1990) groups such as larvae, but in summer, shifts to species adapted to the harsh conditions of drought and food scarcity. This change proved noteworthy also in terms of prey size and biomass: there was a significant change in prey length ($H = 58.55$, $df = 5$, $P < 0.0001$) and prey mass ($H = 28.50$, $df = 5$, $P < 0.0001$, Kruskal-Wallis test) during the active period, with geckos feeding more on longer and heavier prey

during the spring than during the summer (Table 1). Most of the prey (80.1%) were 2-12 mm body length, although some reached considerable size, e.g. a potentially dangerous scorpion measuring about 42 mm was consumed.

Like other temperate zone gekkonids (Marquet, Bozinovic, Medel, Werner & Jaksic, 1990; Valakos & Polymeni, 1990; Perry & Brandeis, 1992; Saenz, 1996; Szczerbak & Golubev, 1996), as well as those from tropical zones (Avery, 1981; Bauer & deVaney, 1987), the Moorish gecko feeds almost exclusively on arthropods. Neither the present study nor previous work in Mediterranean peninsulas (Valverde, 1967; Martínez-Rica, 1974; Gil *et al.*, 1994; Capula & Luiselli, 1994) and islands (Salvador, 1978; Seva, 1988; Gil *et al.*, 1993) indicate clear specificity for any arthropod group, but within each zone, there are usually about two dominant groups in the diet, usually Coleoptera and Araneae. In this sense, the main difference displayed by our data is the relative importance of Carabidae larvae, which were the basic elements of the diet for most of the study period. Only in the Chafarinas Islands (Gil *et al.*, 1993) did Coleoptera larvae reach relatively high values (but only 7.0% in frequency, and sample size was smaller). The greatest differences appear when our results are compared with those of Capula & Luiselli (1994) in Rome, where the two main groups are reportedly Araneae and Diptera. In fact, two flying groups, Diptera and adult Lepidoptera, represent some 36.1% of prey for the Moorish gecko diet in Rome. By contrast, in our study only 20 prey (3.7%) can be considered flying groups (adult Lepidoptera, Diptera, Formicidae winged and Neuroptera), and the most important dietary groups live mainly on low shrubs and the ground (Sánchez-Piñero, 1994; Hódar *et al.*, 1996).

The Moorish gecko has been considered a hunter almost exclusively linked to rock walls and cliffs, in contrast to the geographically proximate *H. turcicus*, which hunts mainly on bare ground (Salvador, 1978; Mellado *et al.*, 1975; Seva, 1988; but see Sáenz, 1996). However, this vision of the Moorish gecko, and in general of most Mediterranean rupicolous geckos, as primarily sit-and-wait foragers restricted to cliffs, walls and rocks, is currently under discussion (Perry & Brandeis, 1992; Gil *et al.*, 1993; Werner, Bouskila, Davies & Werner, 1997). Most of these conclusions are supported exclusively by dietary data or, sometimes, by data from only one of the microhabitats presumably used by the gecko (Gil *et al.*, 1994), despite the fact that the microhabitat seems to determine food acquisition (e.g. Sáenz, 1996). Sample sites in some of these studies are in or near human habitation (Martínez-Rica, 1974; Capula & Luiselli, 1994; Gil *et al.*, 1994), with artificial lights illuminating the walls and attracting prey for geckos (Capula & Luiselli, 1994; Gil *et al.*, 1994; Pérez-Mellado, 1994). Furthermore, other factors apart from prey availability are important in determining the diet of the gecko, and most of these factors may change between localities.

It is known that reptile species tend to forage actively when food availability is low, despite their usual sit-and-wait foraging strategy (Ananjeva & Tsellarius, 1986; Pianka, 1986). For instance, Gil *et al.* (1993) suggest that the Moorish gecko behaves as a sit-and-wait predator in the Iberian peninsula and as an active forager in Mediterranean islands, but these researchers attribute this change to reduced predation risk, rather than to reduced prey availability. We do not believe that this assumption applies to our zone, in which nocturnal and potential predators for the Moorish gecko are varied (e.g. false smooth snake *Coronella girondica*, little owl *Athene noctua*, fox *Vulpes vulpes*, hedgehog *Erinaceus europaeus*). The Moorish geckos in the study area use silt walls as diurnal retreats and at night forage on the ground far from the walls (pers. obs.), and dietary analysis indicates predation mainly upon ground-dwelling arthropods, as observed in other rupicolous geckos inhabiting arid zones in the Mediterranean region (Perry, 1981; Perry & Brandeis, 1992). Consequently, we suggest that in these arid natural habitats of south-east Spain, the species forages widely on the ground, as previously proposed for other gekkonids from arid habitats (Werner *et al.*, 1997). Although foraging widely is energetically expensive, species that engage in this mode of feeding appear to capture more prey per unit of time than do sit-and-wait species (Pianka, 1986). The narrow activity period and the low food availability of an arid zone may force Moorish geckos to forage actively on the ground instead of waiting on the silt cliffs, where food availability is relatively lower, and their main prey are rare or absent (Sánchez-Piñero, 1994). This contrasts with previously accepted ideas on the feeding habits of the Moorish gecko and Gekkonidae in general, and stresses the necessity for more detailed works on this group (Werner *et al.*, 1997).

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BOOK REVIEWS

Homeostasis in Desert Reptiles. S. D. Bradshaw. (1997). xii + 213 pp. Springer-Verlag. Berlin, Heidelberg, New York. £77.00 (cloth).

This small-format hardback is one of 15 titles in the *Adaptations of Desert Organisms* series edited by J. L. Cloudsley-Thompson. The book is divided into an introduction; four distinct chapters dealing in turn with osmotic anatomy, water and electrolyte homeostasis, action and hormonal control of excretory organs, and thermal homeostasis; a conclusion and an exhaustive reference list.

The introduction deals primarily with the process of "adaptation", and its various meanings and applications, and the concept of the *milieu intérieur*, or internal environment. In reviewing the history of homeostasis theory, Bradshaw justifies his use of comparative methodology to examine a set of four specific propositions in the remainder of the book.

In the first chapter, the evidence for homeostasis from a comparative analysis of the literature leads to the conclusion that the data available are crude and demonstrate a lack of homogeneity in the *milieu intérieur* between reptile groups. However, different stable states exist in each taxon and the next three chapters set out to review and explain what is known of the mechanisms by which homeostasis is achieved.

The second chapter deals at some length with water and electrolyte balance. It begins with a brief consideration of the general principles by which homeostasis is maintained, and a description of regulatory responses and the role of stress. The structures of the kidney, cloaca and salt-secreting glands are then considered in turn, followed by more specific discussion of osmoregulation in different taxonomic groups: crocodilians and chelonians, lizards and snakes respectively. The majority of this chapter is taken up with specific examples of saurian osmoregulation, clearly the best-studied group of reptiles with regard to this aspect of physiology.

Chapter Three focuses on activity and the hormonal control of the excretory organs. The function and control of the reptilian kidney, the cloacal-colonic complex and cephalic salt-secreting glands (involving a mixture of pituitary and adrenal hormones) are discussed in some detail.

Thermal homeostasis is the subject of Chapter Four. This is probably the most interesting chapter for general herpetologists and even herpetoculturists. Detailed discussion of both physiological and behavioural mechanisms by which thermoregulation is achieved, and its role in the maintenance of the *milieu intérieur*, includes detailed discussion of metabolic heat production, panting and evaporative heat loss, and the roles of the pineal eye and photoperiod.

The concluding chapter is thorough but surprisingly brief given the depth and extent of the preceding chapters. It summarizes the individual conclusions of the earlier chapters and considers the apparent variation in homeostatic condition and control both within reptile groups and in comparison with the other vertebrates. The chapter ends with a brief consideration of the taxonomic confusion that continues to surround the reptiles, particularly from a cladistic stand point. Finally, the author suggests that future clarification of the phylogenetic relationships between the reptile taxa will throw important light upon, and perhaps lend significance to, studies of the unique physiological and behavioural attributes exhibited by this fascinating order of animals.

This is undoubtedly a well researched, comprehensive, but very specialized text. With perhaps the exception of the final chapter on thermoregulation, it is a book that is unlikely to be of great appeal to herpetologists not directly interested in the ecology and physiology of desert reptiles or vertebrate physiology in general. The high price will probably further reduce the incentive to purchase the book. It will, however, make a very important and useful addition to the library of any student of this, or similar, fields of research, and should be available in university libraries for the pleasure and benefit of physiologists and herpetologists alike.

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Gecko Fauna of the USSR and Contiguous Regions. Nikolai N. Szczerbak & Michael L. Golubev. (1996). 233 pp. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA (cloth).

Geckos represent one of the most diverse groups of lizards, numbering about 80 genera and more than 900 species. They are distributed over all temperate and tropical continents (but not the Arctic), and on oceanic islands of both the Old and New Worlds. This book is, in fact, an English translation of the Russian edition (Szczerbak & Golubev, 1986). This translation has appeared after a gap of a decade and this reflects the wide interest of herpetologists in these lizards. Although the authors have taken into account major publications on geckos that have appeared since 1986 (see supplementary literature cited on pp. 227-229), this version is not a significantly revised edition.

The main differences from the Russian version are as follows. Errors in the text have been corrected; new references included; numerous linguistic amendments to the text have been made, relating to the fact that the Russian and English languages are not structurally in-

terchangeable. Colour plates of lizards have undergone significant changes, and many original photographs have been replaced by others.

As in the Russian edition, the information is arranged in species accounts, with several general chapters (materials and methods, and general characterization of phylogeny and zoogeography). Species accounts embrace the families Eublepharidae (3 species of 1 genus) and Gekkonidae (53 species of 8 genera). They consist of a standard narrative: name; type locality; karyotype; synonyms; diagnosis; type specimens; definition; colour and pattern; sexual dimorphism and age variation; distribution; systematics; geographical variation and subspecies; habitats and quantitative data; daily activity cycle; seasonal activity cycle; feeding; reproduction; rate of growth; enemies; behavioural attributes; practical significance and protection. Ecology is described in detail. It is good that concrete facts are given instead of abstract ecological generalizations - this is useful for other investigators.

Shortcomings in the ecological parts relate mainly to methodological errors. For example, route censuses (especially, using electric lamps on cars at night) provide limited information on species abundance, and not exact population numbers. In the tables of food spectra for some species, absolute values of occurrence in lizard stomachs and numbers of prey items are given. Percentages of total prey numbers would seem to be more reasonable. Useful behavioural data are also provided, but these days it is better to provide sonograms of lizard calls than to imitate their calls as "ee-eeek...ee-eeek" (p. 77), "tsok...tsok...tsok" (p. 71), etc. It is known that size distributions of reptiles cannot provide data on their age - determination of the latter requires special techniques, such as skeletochronology. Therefore, data on changes of some morphometric indices with lizard size reflect size variation rather than age variation (e.g., Fig. 25).

I will not repeat criticisms of the systematics and phylogenetics, as expressed by Bauer (1987) and Semenov (1989) in reviews of the Russian edition. However, these criticisms in a large part also apply to the English book. It should be noted, however, that some of these comments may be attributed to any faunistic monograph because they reflect differences in scientific concepts and methodological errors.

Detailed maps with localities and large scale surveys are provided in the book. This approach to the mapping of range, whereby the reader can use comprehensive information on the distribution of each form, is good. It is pity that the rank or type of geographical unit (e.g., city, district, village, etc.) is not given for some localities, nor are collection numbers for museum specimens.

Threats to many species are also discussed (e.g. extinction of *Alsophylax pipiens*), and are useful for the development of programs for their protection. The conservation measures proposed for some species seem to be more important now than in 1986, when the Russian

book appeared. Given the independence today of the former Soviet Republics and the lack of suitable co-ordination between them in the field of nature conservation, territorial conservation measures within a particular Republic attain special value. Recommendations for the inclusion of *Alsophylax pipiens* in the Red Data Book of Russia may serve as an example of this.

Unfortunately, the English edition contains a surprise for any objective zoologist. One of the co-authors, M. L. Golubev, considered a faunistic book on geckos to be a suitable place for the publication of his political views, which occupy about two pages.

With regard to its scientific value, the book summarizes data on Palaearctic geckos (mainly up to 1986) and can serve as a reference for future studies on this group. Irrespective of differences in taxonomic views on geckos, further studies seem to be impossible without consideration of this book.

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- Semenov, D.V. (1989). N. N. Szczerbak and M. L. Golubev. Geckos of the Fauna of USSR and Contiguous Countries. Kiev, Naukova Dumka, 1986 (Book Review) *Zoologicheskyy Zhurnal* **68**, 155-157 (in Russian).
- Szczerbak, N.N. and Golubev, N.L. (1986). Gekkonid Fauna SSSR i Sopredelnykh Stran [Geckos of the Fauna of USSR and Contiguous Countries]. Kiev, Naukova Dumka Publ., 1986, 232 pp. (in Russian).

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Biology of the Reptilia. Volume 19, Morphology G: Visceral Organs. Carl Gans & Abbot S. Gaunt (Eds.). (1998). xiii+660 pp. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA (cloth).

In this volume the lungs, heart, liver and spleen are treated. Perry gives a wide ranging and well balanced account of the structure and function of the lungs, ranging from gross anatomy to fine structure. A comparative approach to the anatomy goes back to the early nineteenth century and there is now information on representatives of nearly every family of recent reptiles. Perry makes the point that some of the terminology in the older literature has been confusing and he proposes a standard terminology which I hope that future investigators will follow. A distinction is made between phylogenetic and functional influence on lung structure. Avian lungs are kept in view on the grounds that birds and crocodilians are fellow archosaurs. Evidence is presented that testudine lungs

foreshadow the condition of early mammalian lungs. Indeed, there is an outline history of amniote lungs from the earliest times. Amongst other interesting suggestions is the idea that loss of the bronchi in forms which move by sinuous undulation of the body allows shifting of the air between left and right lungs. Non-respiratory functions of lungs are also pointed out.

Wang, Smits and Burggren deal with pulmonary function in reptiles. As these investigations involve experimental procedures, some of which are technically demanding, the taxonomic coverage is less extensive; 90% of the research has been undertaken on less than 1% of the species. The authors sometimes refer to observations on non-reptiles of phenomena which may occur but have yet to be demonstrated in reptiles. Circulation rather than ventilation sets a limit on aerobic activity. The balance between tidal volume and ventilation frequency is usually such as to minimise the energy cost. We learn that cutaneous exchange can be quite important in aquatic reptiles, especially when diving or hibernating, and that loss of carbon dioxide greatly exceeds uptake of oxygen. Evidence suggests that there is no significant difference between diving and non-diving reptiles in respect of lung capacity and blood volume.

Temperature influences gas exchange, lung surfactants and the acid-base balance and viscosity of the blood; this is of particular interest because of the range of temperatures over which many reptiles function. These considerations probably have some bearing on preferred body temperatures. Taken together the chapters on the respiratory system raise the possibility of an integration of pulmonary anatomy, mechanical function, physiology and lifestyle.

This reviewer is one of several who have been waiting for Wallach to find a vehicle for publication of his survey of snake lungs; its thoroughness is awe inspiring. Of 460 genera he lists only 19 which have not been sampled, "most of which are known from the type specimen only". A notable feature is the size of the sample of some species; the variation observed indicates that we should be cautious about drawing inferences from single specimens. There is a mine of information for the systematist. Overall the lungs of snakes have undergone much parallel evolution; *Acrochordus*, the most basal caenophidian, has the most highly derived respiratory system of any snake. However, within lineages recognised on other grounds, the lungs can contribute systematically useful information. The survey of structure and development complements Perry's coverage of other reptiles.

Farrel, Gamperl and the late E. T. B. Francis give a clear and well illustrated account of the three dimensional complexities of the heart of reptiles, based on dissection and serial sections. The four-chambered crocodilian heart is relatively straightforward, complicated only by the communication between pulmonary and systemic circulations via the foramen of Panizza. For other reptiles, the details of the incomplete ven-

tricular septum, the capacities of the chambers and the relationship of the arches to the septum are of importance for an understanding of heart function. The authors point out some differences between reptiles at the ordinal level and indicate that there may be differences at lower taxonomic levels.

Hicks surveys the subject of cardiac shunting in reptiles and distinguishes between three kinds of shunt. Such shunting is possible because in crocodilians the foramen of Panizza links left and right aortae and in the others the ventricular septum is incomplete. A right-left shunt puts deoxygenated blood into the systemic circulation; a left-right shunt puts oxygenated blood into the pulmonary circulation. Incomplete partition of the ventricle is presumably primitive but the author presents evidence that shunting is not due to "primitive" inefficiency but is finely regulated in air breathing animals with a metabolic rate which is low overall but can vary greatly both daily and seasonally. They do not have an oxygen requirement such that they need lungs able to accommodate the total circulating volume of blood. Measurement of the volume of blood flowing through right and left aortic arches can indicate overall shunt but measurement of oxygen levels is needed to recognise that shunting occurs in both directions at different phases of the cardiac cycle. This is better understood in crocodilians than in the other groups, most of our knowledge of which is based on *Trachemys* and *Varanus*.

In contrast to the lungs and heart, the liver and the spleen are at the disadvantage that there is no obvious relationship between gross anatomy and function. For such a relationship we have to go to the level of microscopical anatomy and at this level most of these functional considerations apply without reference to taxonomic group. Schaffner starts by telling us that the "reptilian liver is similar in structure and function to that of other vertebrates". Although there is some systematic variation in bile ducts the liver itself has little comparative anatomy; indeed its "shape conforms to the shape of the visceral cavity"; however, its relationship with mesenteries varies. The author points out that knowledge of reptilian livers is very incomplete so that he has to draw on mammals to make points which may be relevant to reptiles. The histology of the liver is described; there are some general differences from mammals as well as some differences between reptilian orders. It is pointed out that the liver may well vary, in these ectothermic animals, in relation to season and temperature but that this aspect has barely been investigated. A special feature of amphibian and reptilian livers is the melanomacrophages; their biochemistry suggests that they are scavengers of free radicals. The section with the best taxonomic coverage is on the pathology of the liver, presumably due mainly to post-mortems in zoos.

Tanaka points out that non-mammalian spleens have been neglected, and like Schaffner, he draws on mammals to make points which may be relevant. Unlike the

other organs the spleen is usually not essential for life, and its functions have parallels in other tissues. In order to recognise evolutionary trends he gives us a survey of the spleen of vertebrates in general, much of which is based on his own investigations. The few studies which have been made indicate that within reptiles there are differences in the blood supply of the spleen and its relationship with other viscera.

Poor editing usually evokes reviewer's comments; good editing all too easily passes unnoticed. I could count the typographical errors on the fingers of one hand. Out of date names are amended. All of the chapters adopt a comparative approach and follow the same systematic framework; it is easy to see which groups have been studied and which not, which aspects require further study and which features may be of systematic interest. There is a thorough index.

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BOOKS RECEIVED

The Reptiles of Virginia. Joseph C. Mitchell. (1994). 352 pp. Smithsonian Institution Press, Washington and London. £19.50 (paper).

A comprehensive catalogue of all the reptiles occurring in Virginia, with additional chapters on physiography and climate, biogeography, habitats, conservation and snakebite.

La Vipère Aspic. Guy Naulleau. (1997). 72 pp. Eveil Nature.

The natural history of the asp viper is described in this short book, based on the author's own extensive field research on the species. French text with colour and black and white photos.

Die Blindwühlen. Werner Himstedt (1996). Die Neue Brehm-Bücheri Bd. 630, Westarp Wissenschaften, Heidelberg. 159 pp.

A comprehensive account of the natural history and biology of the caecilians, fully illustrated with line drawings and photographs.

Die Amphibien und Reptilien Portugals, Madeiras und der Azoren. Rudolf Malkmus. (1995). Die Neue Brehm-Bücheri Bd. 621, Westarp Wissenschaften, Heidelberg. 192 pp.

The reptiles and amphibians in this little-studied region are fully described in this book. Illustrated by colour and black and white photos and distribution maps.

Biologie und Ökologie der Kreuzkröte. Ulrich Sinsch. (1998). Bochum: Laurenti Verlag. 222 pp.

An up-to-date account of the evolution, biogeography, behaviour and ecology of the natterjack toad. Fully illustrated throughout including black-and-white and colour photographs.

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1999)

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. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.
2. Three copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of five words or less, and the name and address of the corresponding author with (if available) an email address. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Keywords, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. Illustrations produced using other types of computer printer are not usually of suitable quality. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.
8. References in the text should be given as in the following examples: "Smith (1964) stated—"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. Articles 'submitted' or 'in prep' may not be cited in the text or reference list. The following examples will serve to illustrate the style and presentation used by the Journal.

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

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

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

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* 216, 995–1002.
9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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