HERPETOLOGICAL JOURNAL, Vol. 7, pp. 163-168 (1997)

EFFECTS OF LARVAL HISTORY AND MICROTAGS ON GROWTH AND SURVIVAL OF NATTERJACK (*BUFO CALAMITA*) METAMORPHS

ULRICH SINSCH

Institut für Biologie, Universität Koblenz-Landau, Rheinau 1, D-56075 Koblenz, Germany

The metamorphic success of larval cohorts and the post-metamorphic growth of toadlets were studied in a large metapopulation of natterjack toads (*Bufo calamita*) in the Rhinelands, Germany. Larval density was greater in the cohorts studied in 1991 than in those studied in 1992 and metamorphs were smaller in 1991 than in 1992, indicating short-term carry-over effects. Metamorphic success and average snout-vent length were larger in the cohort originating from the early breeding period than in those from the main breeding period in the previous year. The further terrestrial development of three metamorph cohorts was followed until adulthood using commercial fish marks (microtags) for batch-tagging. Microtags are small pieces of wire which are injected below the skin. Their presence is determined using a hand-wand metal detector. The short- and long-term effects of this new marking technique on growth and survival of almost 2000 free-ranging toadlets are reported. The results obtained indicate that microtagging is a useful and harmless technique for the study of metamorphs.

INTRODUCTION

Studies on the ecology and behaviour of free-ranging anuran metamorphs are severely limited whenever the identification or tracing of recaptured individuals or cohorts is required. For example, carry-over effects of larval history on the early terrestrial stage of life history have been demonstrated experimentally in natterjack toads *Bufo calamita* (e.g. Golay & Durrer, 1995; Golay, 1996), but their significance for survival in the field remains to be evaluated. Any attempt to do this requires an adequate tagging method for metamorphs. Presently, the size of metamorphs (mostly < 10 mm SVL, snout-vent length) impedes the application of most techniques available for adults (Sinsch, 1992*a*; Richards *et al*., 1994). The only exception I am aware of is toe-clipping for individuals or batch-tagging of *Rana* and *Bufo* metamorphs (e.g. Blair, 1953; Dole, 1971; Breden, 1987; Berven & Grudzien, 1990; Reading *et al*., 1991; Tejedo *et al*., 1997). However, its usefulness is controversial as regeneration and accidental toe loss may interfere with the permanency and the individuality of the mark, and the removal of up to four toes may influence survival and thus interfere with conservation measures (e.g. Clarke, 1972; Golay & Durrer, 1994). Therefore, in a pilot project on the recruitment of natterjack metamorphs from different larval cohorts and their postmetamorphic dispersal, a new tagging method based on commercial fish marks (microtags) was tested (Sinsch, 1992*a,b*). Microtags consist of small pieces of wire which are injected below the skin and allow for batch recognition.This paper reports on (1) differential metamorphic success of larval cohorts during the prolonged breeding period, and on (2) the short- and long-term effects of the new marking technique on the growth and survival of almost 2000 toadlets tagged in 1991 and 1992. Results obtained indicate that microtagging is a useful and harmless technique for the identification of anuran metamorphs in long-term ecological studies.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in St. Augustin near Siegburg (northern Rhineland, Germany) at altitudes between 52 and 58 m. An area of about 4 km² inhabited by several thousands of natterjack toads (*Bufo calamita*) has been monitored regularly since 1986. Capture and release of the metamorphs was performed in an area with six ponds labeled as breeding area III in other papers dealing with this natterjack metapopulation (Sinsch 1988*a,b*; 1992*a,b*; Sinsch & Seidel, 1995).

LARVAL DENSITY

Tadpole density was studied in two ponds from which metamorphs were recruited for tagging. Fluctuations of density were monitored weekly in one pond during the breeding period of 1992, whereas in 1991 larval density in another pond was determined only on two occasions. To estimate the numbers of tadpoles, all those captured during a one-hour-census were stained for 15 minutes in a 0.005% solution of neutral red (method adapted from Viertel, 1980) and immediately released again at three localities in their native pond. Control experiments showed that this procedure does not cause any mortality during a period of 48 hr following staining. One day after staining, another one-hour census was performed to determine the tadpole numbers and the corresponding standard deviation using the method of Rüst (1969). The fluctuations in water volume were measured using a permanent grid (1 m x 1 m) to estimate the surface area and the corresponding depth at any point of the grid (Wenzel, 1993). Finally,

mean larval density was calculated as the number of tadpoles per litre of water volume.

TAGGING PROCEDURE

In this study, natterjack metamorphs were batch-marked with sequentially coded microtags. Microtags (standard CWT 10-99K FFTEN30) are pieces of wire 1.1 mm long with a diameter of 0.25 mm (mass: < 1 mg) which were injected below the skin using modified syringes (single shot fish I.D. tag injectors). The presence and position of a microtag in a toadlet were detected using a hand-wand style metal detector (S/N35). This equipment was manufactured by Northwest Marine Technology, Inc., Shaw Island, Washington, USA. In this study, microtags served exclusively as batch marks because individual recognition would have required the surgical removal of the microtags.

In 1991, the pond in which larval density had been monitored, was surrounded completely with a drift fence seven days before the onset of metamorphosis. Traps integrated into the fence and the area within the fence were checked daily for metamorphs. A total of 710 metamorphs which emerged from the spawn strings of the early breeding period were batch-tagged immediately after leaving the pond, between 5-24 July. The microtags were placed between cranium and skin and the metamorphs were kept in the laboratory with unlimited food supply (*Drosophila*) until release. The toadlets of the first cohort were released on 27 July, within their natal area. Another 263 metamorphs which emerged from the spawn strings of the main breeding period were provided with tags injected into the abdominal region (28 July - 7 August). They were also kept in the laboratory with unlimited food supply and released on 9 August.

In 1992, the pond studied in the previous year had been destroyed and another pond (150 m distant) was chosen for the monitoring of larval density and recruitment of metamorphs. Again, a drift fence was used to assess the number of emerging metamorphs. A total of 841 metamorphs from the spawn strings of the early breeding period were batch-tagged in the same way as the toadlets of the early cohort of 1991, when they emerged from the pond, between 30 June and 8 July. The survival of these toadlets during the first 48 hr after tagging was recorded in the laboratory (with unlimited food supply) and compared with that of a control group

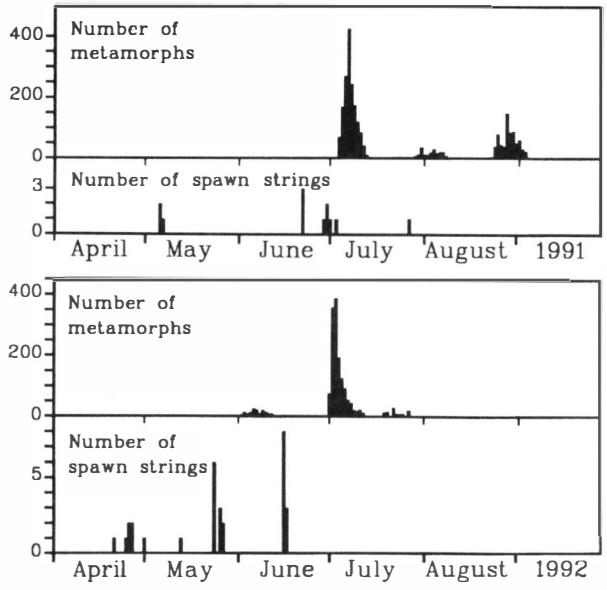

FIG. 1. Time course of spawning and metamorphosis in two permanent ponds of breeding area III. Further data are given in Table 1.

of 845 metamorphs of the same cohort without further treatment. These metamorphs were released in the vicinity of their natal pond on 10 July.

MONITORING OF METAMORPHS IN THE FIELD

Following the release of microtagged toadlets on 27 July 1991, their growth and dispersal were monitored by checking potential daytime shelters (e.g. below stones, planks or in burrows) mainly within their natal area, but also within a radius of 2 km around. Nine censuses were performed, each lasting 6-9 person-hours, on 6, 13, 20/21, 27/28 August; 2, 12, 19, 27 September and 14 October. Capture site, SVL (to the nearest 0.5 mm) and presence of microtag were recorded for each individual captured. Toadlets from the first cohort could not be confused with those of the second cohort because of the size and the position of the tag. Growth and dispersal of the group released on 10 July, 1992, were monitored by the same procedure as in 1991, in 9 censuses on 14, 23, 29 July; 5, 15, 19, 25 August; 3, 9 September.

The presence of microtagged natterjacks was monitored during 50-70 night and day censuses per year in the period from April to September during the years 1991 - 1994. The night censuses began about 30 min

TABLE 1. Metamorphic success of natterjack tadpoles and size of metamorphs originating from spawn strings of different temporal breeding assemblages. Size is presented as mean SVL ± SE.

Cohort	1991			1992		
	Spawn strings	Metamorphs number	Metamorphs SVL (mm)	Spawn strings	Metamorphs number	Metamorphs SVL (mm)
Early breeding period	3	1626	8.6±0.03	16	1568	9.4±0.02
Main breeding period	8	263	8.3±0.06	11	118	9.3±0.07
Late breeding period	1	695	8.3±0.03	/	/	/

after sunset and lasted about 2-4 person-hours each, depending on general reproductive activity (Sinsch & Seidel, 1995). The day censuses in the years 1993 and 1994 consisted of searches in potential shelters and lasted about 3 person-hours each.

RESULTS

METAMORPHIC SUCCESS OF LARVAL COHORTS

In 1991, the number of spawn strings laid into the monitored pond varied considerably among the early, main and late breeding periods (Fig. 1, Table 1). The density of tadpoles hatching from the spawn strings of the early breeding period was estimated at 8.5 per litre on 6 June , whereas density of the second larval cohort was 4.3 per litre on 18 July. The recruitment of metamorphs was higher from spawn of the early breeding period than from that of the main breeding period (Table 1). The largest 710 metamorphs of the first cohort, and all 263 metamorphs of the second cohort, were batch-tagged, but at distinct parts of the body to distinguish between the two groups.

In 1992, there was little difference between the number of spawn strings laid during the early and main breeding period (Fig. 1, Table 1). The density of tadpoles was low during the whole breeding period ,ranging from 0.1 to 3.9 per litre (Table 2). However, metamorphic success differed dramatically among the larval cohorts (Table 1): the cohort resulting from the early spawning period produced far more metamorphs than the second cohort. Due to substantial post-tagging mortality in 1991, the 1568 metamorphs of the first cohort were randomly allocated to an untreated control group ($N = 845$) and a batch-tagged experimental group ($N = 841$) to check for treatment effects. Because of the low number of metamorphs recruited from spawn laid during the main breeding period, no further metamorphs were marked in 1992.

TABLE 2. Estimates of the number of natterjack tadpoles in the study pond during 1992 and the corresponding tadpole density per litre water. Estimates are given as means ± standard deviation except for the estimates in early May which are based on one sample.

Date	Number of tadpoles (N)	Density of tadpoles (N/l)
18 May	1220	0.4
25 May	633	0.6
31 May	332±7	0.2
17 June	11 117±2550	3.9
29 June	8824±763	1.9
8 July	3460±536	0.4
15 July	504±51	0.2
21 July	4074±14	0.7
28 July	141±14	0.1

TABLE 3. Mortality in tagged and untagged metamorphs during 48 hr following capture.

Temporal population	Tagged toadlets	Control toadlets
Early cohort 1991	14.8% (105 out of 710)	/
Main cohort 1991	4.6% (12 out of 263)	/
Early cohort 1992	0% (0 out of 841)	1.8% (10 out of 845)

SIZE AT METAMORPHOSIS

The average snout-vent-length of the metamorphs was significantly lower in 1991 than in 1992 (Table 1, ANOVA, $P < 0.001$). Within one year, metamorphs of the early cohort tended to be larger at metamorphosis than those of the later, but only in 1992 was the difference significant (ANOVA, $P < 0.01$).

MORTALITY RATES OF RECENTLY METAMORPHOSED TOADLETS

The mortality rate of microtagged metamorphs during the first 48 hr following treatment varied among the years and ranged from 0% to 14.8% (Table 3). The post-metamorphic mortality of untreated metamorphs was in the same range as that of the microtagged individuals when tested in 1992. No further mortality was observed between the third day following tagging and the day of release.

GROWTH OF METAMORPHS

The growth of microtagged toadlets, i.e. the increase of SVL, following release in the field was compared with that of untagged individuals captured simultaneously (Fig. 2). In 1991, only the fate of tagged toadlets

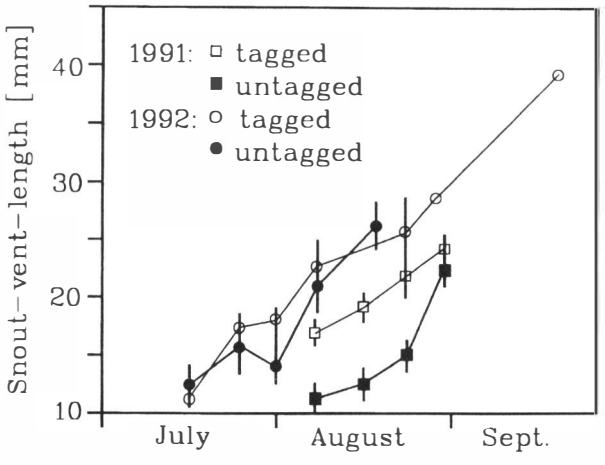

FIG. 2. Growth of tagged and untagged metamorphs of the early cohort in the year of release. Data are given as means with the corresponding 95% confidence interval. The number of observations per mean ranged between 13 and 446 in the control group and 1 and 36 in the experimental group.

TABLE 4. Recaptures of microtagged individuals as reproductive adults.

Origin	Initial no. in 1991-2	No. found 1993	No. found 1994
Early cohort 1991	605	5(0.8%)	1(0.2%)
Main cohort 1991	251	4(1.6%)	1(0.4%)
Early cohort 1992	841	/	/

pertaining to the early cohort was followed. At the date of release, they were significantly larger than the untagged toadlets of the same cohort which were found in the field (ANOVA, $P< 0.001$). This difference is an experimental artefact due to (1) the selection of the larger metamorphs for tagging and (2) their prolonged stay under laboratory conditions (unlimited food supply and higher temperatures than in the field). However, the mean growth rate during the first month after release was identical in the two groups: 0.32 mm increase of SVL per day.

In 1992, tagged metamorphs were released after two days in the laboratory and size differences between these and untagged individuals remained insignificant until mid-July (ANOVA, $P> 0.05$). The mean growth rate during this period was 0.39 mm increase of SVL per day. The massive appearance of new metamorphs from neighbouring ponds in mid-July rendered the mean size of the untagged toadlets meaningless for comparison after this time with the few recaptured tagged individuals, which continued to grow at about the same rate as before.

Survival Rates of Microtagged Metamorphs to Adulthood

The numbers of microtagged individuals which were recaptured as breeding adults in 1993 and in 1994 are summarized in Table 4. All recaptured individuals were males advertising at the ponds of the breeding area from which they originated. Despite thorough censuses in neighbouring breeding areas over a radius of 2 km, neither microtagged females nor additional males advertising in other than their natal site were found. Moreover, all microtagged adults originated from the two cohorts marked in 1991, whereas no individual of the 1992 cohort was recaptured later than October 1992.

DISCUSSION

In this study, microtags have been used for the first time to permanently tag toadlets of 6-11.5 mm SVL and to follow their fate until adulthood in the field. As there has been no previous experience with the short-term and/or long-term effects of this method in toads, a critical evaluation of tagging as a potential additional source of juvenile mortality is neccessary before assessing the significance of carry-over effects from larval history on the fitness of adults.

Effects of Microtags

Severe short-term effects should result in an increased mortality within two days after handling. Yet mortality rates in tagged and untagged metamorphs of 1992 were at the same low level, indicating that the treatment did not directly affect survival. Still, mortality of tagged metamorphs was substantial in the 1991 cohorts (no data were collected on untreated controls). Two factors probably increased mortality over the level found in 1992: (1) the skill of placing the microtags without harming the toadlets certainly improved in the course of the study; (2) larval density in the pond of origin was much higher in 1991 than in 1992, a factor shown to correlate with postmetamorphic mortality in *Bufo bufo* (Goater, 1994) and *Bufo calamita* (Golay, 1996). Moreover, the time immediately following metamorphosis is a period of high natural mortality because metamorphs are more vulnerable to desiccation (unfavourable surface/volume-ratio), to predation and to intraspecific competition (high densities occur in the vicinity of ponds) than are larger juveniles and adults (Licht, 1974; Cohen & Alford, 1993).

Sublethal effects of the tagging procedure could influence growth and reduce the probability of long-term survival. Mean growth rates of natterjack juveniles during their first summer of life in the field did not significantly differ between tagged and untagged individuals, and the increase in overall size ranged from 2.4 to 3.4-fold. These values closely correspond to those measured in *Bufo bufo* (2.0-2.8; Goater, 1994), in *Bufo calamita* (1.5-2.2; Golay, 1996), in *Bufo fowleri* (3.4; Labanick & Schlueter, 1976), and in *Bufo hemiophrys* (2.2; Breckenridge & Tester, 1961). An experimental analysis of growth in *Bufo bufo* metamorphs suggests that a size increase of about a factor of three indicates *ad libitum* feeding conditions (Goater, 1994). Thus, the growth of the tagged natterjack toadlets in the study area was probably neither influenced by tagging nor limited by the availability of food.

Finally, long-term survival of tagged individuals could have been modified by other effects than growth retardation. Such effects, if they exist, would be difficult to detect as local environmental factors are the main determinants of survival. Comparisons among different study areas or even among different species can only yield ideas about the order of magnitude of survival. There have been few attempts to estimate the rates of survival between metamorphosis and adulthood by toe-clipping: in *Bufo bufo* Reading *et al.* (1991) found 0.6% survival of males and 0.1% survival of females out of 5158 toadlets marked in 1984, and 0.2% male and 0% female out of 2101 toadlets marked in 1985 at the same site. In *Bufo fowleri,* Breden (1987) found 0.4% unsexed adults out of 8539 toadlets and in *Bufo valliceps,* Blair (1953) found 5.6% males and 1.4% females out of 357 toadlets. The survival rates es-

timated from the recaptures of microtagged *Bufo calamita* as breeding adults (this study) were in the same range: 0.8% as males from 605 toadlets, 1.6% as males from 263 toadlets and 0% out of 841 toadlets, but no female from any of the three cohorts of metamorphs. These rates are still two or three times higher than those found in the same species marked by toe-clipping in Spain: Tejedo *et al.* (1997) recaptured only seven adults (0.3%) out of 2500 toadlets marked in 1992 after two years, and another seven after three years. The exceptionally high survival rate in *Bufo valliceps* is due to the fact that they attain sexual maturity within one year, whereas in the *Bufo* species studied here males need at least two years, and females three or more years (Hemelaar & Van Gelder, 1980; Gittins *et al.*, 1985; Reading, 1991).

The sex-specific difference in the duration of the juvenile stage probably accounts for generally lower recapture rates of females. In the study population, there is no indication that females suffer a significantly higher mortality than males and the failure to recapture microtagged females may more probably be due to the fact that the vagility of females is far larger than that of males (Sinsch, 1992*b*; Sinsch & Seidel, 1995). The monitored area was probably too small to adequately cover their range of activity. Thus, the number of the 1991 metamorphs reaching adulthood was probably greater than suggested by the recaptures in 1993 and 1994, and it seems reasonable to assume that approximately the same numbers of immature females and males survive from year to year. Furthermore, an unknown, but probably very small, proportion of individuals may have joined breeding assemblages at sites which have not been intensely monitored. Based on these assumptions, an overall survival rate of 2-3% in the 1991 metamorphs until 1993 seems realistic. This estimate agrees remarkably well with the corresponding survival rates averaging 2% (range: 0.3-6.0%) determined in the Woolmer natterjack population over 15 years (Banks & Beebee, 1988; Banks *et al.*, 1993). Survival rates of this magnitude imply annual mortality rates in the range of 80-85%, lower than larval mortality (e.g. Kadel, 1975; Banks & Beebee, 1988).

In contrast, the reasons for the absence of any recapture of adults originating from the microtagged early cohort of 1992 are completely obscure. Similar disappearences of cohorts have also been noticed in the Woolmer population (Beebee, personal communication). Yet, the 1992 generation of toadlets was not lost completely, as evidenced by a number of untagged juveniles captured in 1993 before the emergence of new metamorphs. The origin of these juveniles, i.e. breeding pond and tadpole cohort, is unknown because the 1992 generation of this area included metamorphs originating from the early, main and late tadpole cohort. A contribution of tagging to the cohort disappearence cannot be excluded, but does not seem probable. Still, the available data do not indicate any adverse effect of microtagging on the short- or long-term survival of juveniles. In conclusion, microtags have proved to be a useful tool to study small-sized anurans.

CARRY-OVER EFFECTS

As observed from experimental plots (Golay & Durrer, 1995), the size of metamorphs in the field was inversely related to the density the tadpoles experienced before metamorphosis. However, the average SVL obtained under field conditions was up to 4 mm lower than under experimental conditions, indicating that food availability in the natural ponds was far from optimal (Banks & Beebee, 1988). Mortality within four weeks after metamorphosis was also demonstrated to be higher in metamorphs raised in high tadpole densities than in those originating from low density conditions (Golay, 1996). Remarkably, even optimal food supply after metamorphosis did not compensate for this carry-over effect on post-metamorphic mortality, but only reduced mortality from about 50% to 35% (Golay, 1996). Consequently, in 1991 a substantial contribution of a carry-over effect resulting from high larval density to post-metamorphic mortality seems probable. The data presented here are in agreement with the hypothesis that the larval history influences important life history parameters during the early terrestrial stage of life.

In contrast, there was no indication of effects on the probability of long-term survival during the terrestrial stage. Larval history was apparently more favourable in 1992, but survival to adulthood was certainly lower than in the two 1991 cohorts. Even comparing only the fate of first and the second 1991 cohort, the significantly larger toadlets of the early breeding period apparently did not perform better than the smaller ones of the main breeding period. This is remarkable not only because of the size difference at metamorphosis, but also because the first cohort was fed far longer in the laboratory and had a longer feeding period in the field before hibernating. Effects of body size on toadlet survival over winter were also absent in the Woolmer population (Denton & Beebee, 1996). In conclusion, it seems doubtful that carry-over effects from the aquatic life history stage have long-term consequences for the performance of toads during the juvenile stage or even for the fitness of adults.

ACKNOWLEDGEMENTS

The permissions for field studies and handling of the toads were issued by the Regierungspräsident Köln, Untere Natur- und Landschaftsschutzbehörde Siegburg, and Umweltamt St. Augustin. I am grateful for the technical assistance of W. Jagla, A. Schmoll, D. Seidel and S. Wenzel. This paper benefited from the comments of T. J. C. Beebee and M. Tejedo on an earlier version. The financial support by the Deutsche Forschungsgemeinschaft (grants: Si 391/1-1, 1-2, 1-3, 1-4) is gratefully acknowledged.

REFERENCES

Banks, B. & Beebee, T. J. C. (1988). Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *Journal of Animal Ecology* **57**, 475-492.

Banks, B., Beebee, T. J. C. & Denton, J. (1993). Long-term management of a natterjack toad (*Bufo calamita*) population in southern Britain. *Amphibia-Reptilia* **14**, 155-168.

Berven, K. A. & Grudzien, T. A. (1990). Dispersal in the wood frog (*Rana sylvatica*). Implications for genetic population structure. *Evolution* **44**, 2047-2056.

Blair, W. F. (1953). Growth, dispersal and age at sexual maturity of the Mexican toad (*Bufo valliceps* Wiegmann). *Copeia* **1953**, 208-212.

Breckenridge, W. J. & Tester, J. R. (1961). Growth, local movements and hibernation of the Manitoba toad, *Bufo hemiophrys*. *Ecology* **42**, 637-646.

Breden, F. (1987). The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* **1987**, 386-395.

Clarke, R. D. (1972). The effect of toe-clipping on survival in Fowler's toad (*Bufo woodhousei fowleri*). *Copeia* **1972**, 182-185.

Cohen M. P. & Alford, R. A. (1993). Growth, survival and activity patterns of recently metamorphosed *Bufo marinus*. *Wildlife Research* **20**, 1-13.

Denton, J. S. & Beebee, T. J. C. (1996). Habitat occupancy by juvenile natterjack toads (*Bufo calamita*) on grazed and ungrazed heathland. *Herpetological Journal* **6**, 49-52.

Dole J. W. (1971). Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* **1971**, 221-228.

Gittins, S. P., Kennedy, R. I. & Williams, R. (1985). Aspects of the population age-structure of the common toad (*Bufo bufo*) at Llandrindod Wells Lake, Mid-Wales. *British Journal of Herpetology* **6**, 447-449.

Goater, C. P. (1994). Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology* **75**, 2264-2274.

Golay, N. (1996). Die Kreuzkröte (*Bufo calamita*) Laur. als Pionierart. *PhD Thesis, University of Basel*, 180 pp.

Golay, N. & Durrer, H. (1994). Inflammation due to toe-clipping in natterjack toads *(Bufo calamita*). *Amphibia-Reptilia* **15**, 81-83.

Golay, N. & Durrer, H. (1995). Zur Variabilität der Metamorphosegröße bei Kreuzkröten (*Bufo calamita*). *Zeitschrift für Feldherpetologie* **2**, 3-15.

Hemelaar, A. S. M. & Van Gelder, J. J. (1980). Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Netherlands Journal of Zoology* **30**, 129-135.

Kadel, K. (1975). Freilandstudien zur Überlebensrate von Kreuzkrötenlarven (*Bufo calamita* LAUR.). *Revue Suisse de Zoologie* **82**, 237-244.

Labanick, G. M, & Schlueter, R. A. (1976). Growth rates of recently transformed *Bufo woodhousei fowleri*. *Copeia* **1976**, 824-826.

Licht, L. E. (1974). Survival of embryos, tapoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Canadian Journal of Zoology* **52**, 613-627.

Reading, C. J. (1991). The relationship between body length, age and sexual maturity in the common toad, *Bufo bufo*. *Holarctic Ecolology* **14**, 245-249.

Reading, C. J., Loman, J. & Madsen, T. (1991). Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology* (London) **225**, 201-211.

Richards, S.J., Sinsch. U. & Alford, R. A. (1994). Radio-Tracking. In: *Standard Methods for Measuring Biological Diversity: Amphibians*, 155-158. Donnelly, M., Heyer, W. R., Inger, R. F., & McDiarmid, R. W. (eds.). Smithsonian Institution Press.

Rüst, H. (1969). Schätzung der Amphibienbestände in einem Teich durch ein Wiederfangverfahren. *Vierteljahresschrift der naturforschenden Gesellschaft Zürich* **114**, 279-291.

Sinsch, U. (1988*a*). Temporal spacing of breeding activity in the natterjack toad, *Bufo calamita*. *Oecologia* **76**, 399-407.

Sinsch, U. (1988*b*). Auskiesungen als Sekundärhabitate für bedrohte Amphibien und Reptilien. *Salamandra* **24**, 161-174.

Sinsch, U. (1992*a*). Zwei neue Markierungsmethoden zur individuellen Identifikation von Amphibien in langfristigen Freilanduntersuchungen: erste Erfahrungen bei Kreuzkröten. *Salamandra* **28**, 116-128.

Sinsch, U. (1992*b*).Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). *Oecologia* **90**, 489-499.

Sinsch, U. & Seidel, D. (1995). Dynamics of local and temporal breeding assemblages in a natterjack metapopulation (*Bufo calamita*). *Australian Journal of Ecology* **20**, 451-461.

Tejedo, M., Reques, R. & Esteban, M. (1997). Actual and osteochronological estimated age of natterjack toads (*Bufo calamita*). *Herpetological Journal* **7**, 81-82.

Viertel, B. (1980). Überlebensraten und Mortalität bei Erdkrötenlarven (*Bufo bufo* L.) im Freiland. *Salamandra* **16**, 19-37.

Wenzel, S. (1993). Zeitliche Variabilität des Wachstums und der Metamorphoserate von Kreuzkröten-Kaulquappen im Freiland. *Unpubl. Diplom-thesis, Zoological Institute of the University of Bonn*, 89 pp.

Accepted: 25.6.97