Structure and dynamics of central European amphibian populations: A comparison between *Triturus dobrogicus* (Amphibia, Urodela) and *Pelobates fuscus* (Amphibia, Anura)

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Abstract During a long-term study of the amphibian fauna on an artificial island near Vienna (Austria), one isolated site was completely encircled with a permanent drift fence and pitfall traps. Eleven amphibian species occurred at the study site. For the Common Spadefoot Toad (*Pelobates fuscus*) and for the Danube Crested Newt (*Triturus dobrogicus*) individuals could be recognized by photographing the highly variable dorsal/ventral patterns. Daily patrols of the drift fence, for 6 years since 1986, enabled us to monitor the demography and dynamics of these two species. For *T. dobrogicus*, the adult part of the censused population decreased from 207 to 87 individuals during the first 2 years of investigation and then remained stable. *Pelobates fuscus* showed a constant decrease over 6 years, from 626 to 62 individuals. Juveniles were produced annually; a massive increase in this age class was observed for both species during the period of investigation. *Triturus dobrogicus* showed higher adult survival than *P. fuscus*. The constancy of several population parameters of both species may reflect the stability of the cultured parkland habitat in which the study site is located.

Key words: amphibians, long-term study, *Pelobates fuscus*, population biology, *Triturus dobrogicus*.

INTRODUCTION

Worldwide declines in amphibian populations have attracted wide attention (e.g. Barinaga 1990; Wake 1991; Pechmann & Wilbur 1994). Different regions and taxa seem not to be affected to the same extent (Blaustein & Wake 1990). Substantial variation in demography and size of breeding aggregations of amphibians has been observed in many species all over the world. To distinguish between natural fluctuations and declines due to anthropogenic causes numerous long-term studies are necessary (Pechmann *et al.* 1991). Documentation of the natural variability of the number of breeding individuals can help to identify factors regulating populations (Semlitsch 1983). In Europe, amphibian populations are increasingly endangered by loss of breeding ponds and decreasing suitability of the terrestrial habitat (Beebee 1975; Feldmann 1978).

Pond-breeding amphibians are very suitable for population studies (Hairston 1987). The adult part of the population can be censused easily during their breeding migration using the drift fence and pitfall-trap technique (e.g. Shoop 1965; Gibbons & Semlitsch 1982; Verrell & Halliday 1985). We report on a long-term study focusing on the population dynamics and survival ability of the Danube Crested Newt (*Triturus dobrogicus*) and the Common Spadefoot Toad (*Pelobates fuscus*) in a man-made environment. We also discuss the observation period necessary to gather sufficient and reliable data to reflect dynamic processes in population biology.

METHODS

The study site ('Endelteich') is located at the edge of Vienna (Austria) on an artificial island, bordered by the River Danube and a floodable watercourse ('New Danube'). Providing a recreation area for the Viennese, this island, in combination with its water canal, was created

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to prevent floods in the Vienna area. The pond has a surface area of approximately 1500 m² and a maximum depth of 0.6 m. Reed (*Phragmites australis*) and cat-tail (*Typha latifolia, Typha angustifolia*) cover the water zone. Several species of *Salix* dominate the edge of the pond. A drift fence with pitfall traps was used to monitor amphibian populations at this site. The permanent fence, made of solid plastic 70 cm high and buried 30 cm into the ground, completely encircled the pond. For *T. dobrogicus* and *P. fuscus*, the fence achieved an almost complete census of migrating individuals (Arntzen *et al.* in press). The pitfall traps (10 L buckets), placed at approximately 5 m intervals alternately on either side of the fence, have been patrolled daily since 1986, with the exception of 1988. Visits were skipped only on days following night temperatures below freezing.

Eleven species of amphibians occurred at the pond (Endel 1989). The weight, length, sex, and reproductive condition of every animal collected were noted. *Triturus dobrogicus* has been the dominant urodele species since 1991. Among anurans, *P. fuscus* has shown the highest annual number of censused individuals throughout the study period. Photographs of the belly pattern of *T. dobrogicus* (since 1987) and of the dorsal pattern of *P. fuscus* (since 1986) were used for recognition of individuals of these two species. Individuals showing secondary sex characters were classed as adults. Subadults of *T. dobrogicus* were in their second year of life and were not yet mature during the reproductive period. At our study site, both sexes of *T. dobrogicus* and female *P. fuscus* reached sexual maturity at the age of 2 years. Male *P. fuscus* exhibited secondary sex characters after their first winter. Juveniles hatched in the year of their registration. The juvenile cohort of one reproductive period was defined as recruitment for that year. After processing, all amphibians were immediately released at the collecting site on the opposite side of the fence to their capture. Data presented here cover the period from 1986 to 1992. From April 1988 to December 1988 the fence was removed and only irregular visits to the site were undertaken (Endel 1989). The evaluation of data on *P. fuscus* from 1992 is still in process.

Survival rates were calculated as the number of individuals in the current year that had been recorded in the previous year divided by the number of individuals in the previous year. The probability of surviving a certain number of reproductive years is based on the formula $lx = e^{-\alpha x}$ (where lx = proportion to survive x years, α = annual death rate [= 1-survival rate]; see Hairston 1987).

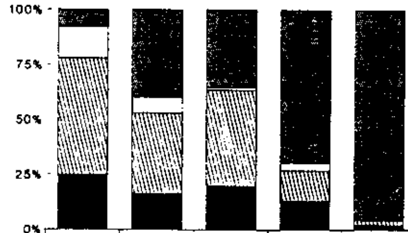
RESULTS

The number of adults of *T. dobrogicus* censused decreased from 210 individuals in 1987 to 87 in 1989 (Fig. 1). From 1989 to 1992 the number remained stable, with between 81 and 89 newts. The sex ratio varied between 1:1 and 1:1.2 in favour of males. Recruitment increased dramatically from 52 (1986) to 818 (1991) individuals. Since 1989 more than two-thirds of the censused individuals have been juveniles. The number of subadult *T. dobrogicus* almost equalled the number of adults in 1992.

In *P. fuscus*, there was a continuous decrease in the number of adults censused (Fig. 1). The number of adult individuals registered in 1991 was less than one-tenth of the number censused in 1986. The sex ratio was biased towards males when adult numbers were high. In 1990 the sex ratio was almost even and in 1991 the number of females exceeded the number of males for the first time. Few subadult *P. fuscus* were recorded between 1989 and 1991. Numbers of juveniles were high, especially during the last 2 years of the study. In 1991, 96% of all recorded individuals were recruits.

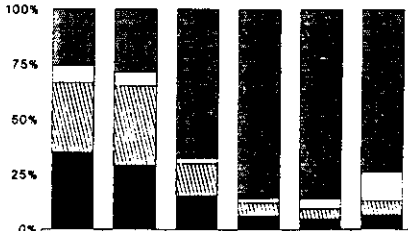
We are able to trace the history of some individuals back to their first year of life (Table 1). In 1992, individuals of *T. dobrogicus* born in every study year except 1987 were registered. One female, registered in 1987 as juvenile and in 1989 as adult, was not recorded in 1990 but returned the following year. In fact, disregarding

(a)



	1986	1987	1989	1990	1991
Juveniles	63	442	147	242	1365
Subadults	116	81	5	12	2
Males	427	406	182	48	30
Females	199	179	82	45	32

(b)



	1986	1987	1989	1990	1991	1992
Juveniles	52	93	194	614	818	457
Subadults	16	19	7	14	42	80
Males	64	116	43	43	44	41
Females	71	94	44	44	45	40

Fig. 1. Dynamics of the (a) *P. fuscus* (1986–91) and (b) *T. dobrogicus* (1986–92) populations. No data were collected in 1988. *Triturus dobrogicus* was not recognized individually in 1986; the given data are number of captures.

subadults, females occasionally skipped a period of reproduction (unpubl. data). Males visited the pond annually without exception. Only one juvenile born in 1986 was registered again as an adult in 1989, but this single animal survived until 1992. Twelve newts collected in 1992 (14.8% of the adult population) had been registered as adults at the beginning of the study in 1987. They were therefore at least 7 years old. In 1992, the average age was 3.25 years for females, and 3.32 years for males.

Pelobates fuscus marked as juveniles in 1986 first appeared at the pond in 1987. The last time an individual from the 1986 juvenile cohort was captured was in 1990 (Table 1). However, in 1992 6.6% of the adult population were known to have been adult since 1986 and were therefore at least 7 years old. In 1991, the mean age of females was 2.63 years and that of males 3.31 years.

Annual survival rates of adult *T. dobrogicus* varied between 0.341 and 0.535 (Table 2). Although survival rates did not differ significantly between the sexes, the weighted mean over the study period was biased towards males. The survival rates of male *P. fuscus* (0.132–0.496) exceeded those of females in two out of three year-to-year censuses. The male-biased sex ratio in 1986 and 1987 can be explained by higher male survival. A change in the sex ratio of *P. fuscus* between 1989 and 1990 coincides with higher female survival. Mean adult survival rates over the whole study period were used to estimate the probability of survival for a certain number of reproductive years (Fig. 2). For example, at a probability level of 1%, female *P. fuscus* survive 6.4 reproductive years and males 7.4 reproductive years. For *T. dobrogicus* the survival times are longer: 7.3 years for females and 8.4 years for males.

Table 1. Number of juvenile *T. dobrogicus* and *P. fuscus* that had been registered as juveniles during the period of investigation and were still present in the last study year

Study year	1986	1987	1989	1990	1991
T. dobrogicus					
1987	19*	—	—	—	—
1989	1	7	—	—	—
1990	1	0	14	—	—
1991	1	1	6	42	—
1992	1	0	4	9	80
P. fuscus					
1987	10	—	—	—	
1989	4	30	—	—	
1990	4	12	12	—	
1991	0	5	9	2	

*Subadults registered in 1987 (and juvenile in 1986) are listed, even though individual recognition was not done in 1986.

Table 2. Year-to-year survival rates of male and female *T. dobrogicus* and *P. fuscus*

	T. dobrogicus		*P. fuscus*	
	Females	Males	Females	Males
1986–87	—	—	0.379	0.496
1989–90	0.341	0.465	0.185	0.132
1990–91	0.364	0.535	0.200	0.292
1991–92	0.400	0.341	—	—
Weighted mean	0.367	0.450	0.308	0.381
Paired *t*-test	$P>0.05$, NS		$P>0.05$, NS	

DISCUSSION

The size of the adult part of amphibian populations tends to remain more constant than the annually produced recruitment (Hairston 1987; see Pechmann & Wilbur 1994). Despite this general pattern, many previous long-term studies on amphibians revealed fluctuations in the adult population size of several orders of magnitude (Tilley 1980; Semlitsch 1983; Berven 1990; Pechmann *et al.* 1991). The 'Endelteich' pond, formed in 1979, is one of the last refuges for the amphibian fauna that occurred in the formerly extensive floodlands of this region prior to the construction of the Danube Island in 1978. Early in the study, the site may have been overpopulated; this may account for the observed decrease in numbers of both species in 1986/87. After higher numbers in the first 2 years of the study, the numbers of adult *T. dobrogicus* fluctuated less than 10% during the following 4 years. Hairston (1987) concluded that fluctuations in salamander numbers were minor compared to other groups of animals of approximately the same size. In fact, then numbers of adult *T. dobrogicus* remained more constant than those of *P. fuscus*.

A dramatic short-term population decrease does not necessarily indicate severe population threat or extinction. Bannikov (1948; after Pechmann & Wilbur 1994) monitored a *Rana temporaria* population over 7 years and

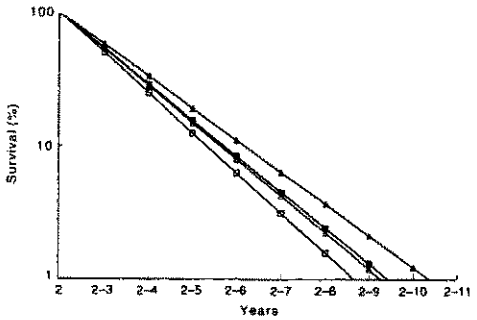


Fig. 2. Probability that female and male *T. dobrogicus* and *P. fuscus* will survive a certain number of reproductive years. Note that the y-axis has a logarithmic scale. (■) *P. fuscus* males; (□) *P. fuscus* females; (▲) *T. dobrogicus* males; (△) *T. dobrogicus* females.

observed a 97% decrease in the first 4 years, followed by a 44-fold increase. Berven (1990) reported fluctuation by a factor of 10 for a breeding population of *Rana sylvatica* during a 7 year period. Our data showed fluctuation of a similar order of magnitude but his population varied by a factor of 10 between 2 years. In our study, the number of adult *P. fuscus* decreased continuously from 626 to 62 individuals over the whole period of investigation. Pechmann *et al.* (1991) recorded an increase in numbers of *Pseudacris ornata* in South Carolina over 4 years, followed by a constant decrease over 7 years, but to a much greater extent (30-fold).

The adult population of *T. dobrogicus* (81–210 individuals) lies within the range of *Triturus cristatus* populations in Sweden (Hagström 1979; Hedlund 1990) and France (Arntzen & Teunis 1993). For *P. fuscus*, the population size in 1986 and 1987 is within the upper range reported by other studies; most of the reported estimates do not exceed 50–60 adults (see Nöllert 1990). Sex ratios biased in favour of males are common for *P. fuscus* (Nöllert 1990). In three of five study years, the number of male *T. dobrogicus* slightly exceeded that of the females; summing up the years of investigation, the sex ratio was almost equal. For *T. cristatus*, sex ratios favouring females (Verrell & Halliday 1985) and favouring males (Hagström 1979) are known, as well as equality between the sexes (Glandt 1978).

Intraspecific density-dependent factors, like cannibalism on the larval stage by adults (Dolmen & Koksvik 1983) and oophagy (Avery 1968), are considered to be regulators of population size. In the present study a large number of adults coincided with low juvenile recruitment. In a study of the colonization of a newly created pond by newts, Arntzen and Teunis (1993) observed little or no recruitment when adult numbers peaked. In permanent ponds, predators play a more important role for amphibians than in ephemeral ponds (Smith 1983). Semlitsch (1983), working on *Ambystoma tigrinum* at an ephemeral breeding site, judged density-independent factors, mainly caused by annual variation in climatic conditions, to be the reason for massive population fluctuations.

Although juveniles of both species showed massive fluctuations, they did not follow a pattern of episodic recruitment (see Corn & Fogleman 1984 for *Rana pipiens*; Semlitsch 1983 for *Ambystoma tigrinum*). Juveniles were recorded in each breeding season. In 1991, recruitment from four out of five previous study years was observed for both species. In *T. dobrogicus*, a rising number of juveniles was followed by an increase in the number of subadults in the subsequent year. However, focusing on 1989 and particularly 1990, this increase had no influence on the number of adults in 1991 and 1992, when these cohorts reached maturity. The large number of juvenile *P. fuscus* also did not result in an increase in the number of adults.

The terrestrial habitat of our study site is characterized by very compressed soil. No fallen logs or stubs and almost no leaf litter are found on the uniform surface. *Pelobates fuscus* prefers loose-packed sand for hibernation (Nöllert 1990). For both species, but especially for *P. fuscus*, terrestrial hibernation sites seem to be limited, probably resulting in high juvenile mortality.

The stability of a breeding population greatly depends on survival and longevity of adult animals. Hairston (1987) listed six studies reporting 21 estimates of annual adult survival for 11 species of tailed amphibians in Europe and North America. The rate ranged from 0.238 for male *Desmognathus fuscus* (Danstedt 1975) to 0.91 for male *Taricha rivularis* (Twitty 1966). Eighty per cent of the rates for females and 77% of the rates for males were higher than the year-to-year survival of *T. dobrogicus* at our study site. Arntzen and Teunis (1993) compared five published rates of yearly survival for the very closely related species *T. cristatus* with their own results and all six ratios exceeded the estimations of our study. To our knowledge, no survival data are available for *T. dobrogicus*; however, average adult longevity at our site seems to be rather low. Surprisingly, the higher survival rate for males did not result in a male-biased sex ratio or a male-biased longevity. Because males and females mature at the same age, a possible explanation is sex-dependant survival in the juvenile and/or subadult stage. *Pelobates fuscus* had, on average, lower survival rates than *T. dobrogicus*, coinciding with the population decline. Similar rates are known for *R. sylvatica* at an isolated breeding site, where $24.0 \pm 11.6\%$ of the males and $21.6 \pm 8.4\%$ of the females were recorded in the following year (Berven 1990). We have no explanation for the female-biased survival in our population between 1990 and 1991, which led to an even sex ratio of *P. fuscus*. Although we assume that our pond is isolated from other breeding sites, some males might have emigrated, in search for other habitats.

Our estimates of the probability of survival for a certain number of reproductive years assume equal annual survival rates over all adult age-classes. More study years are necessary to compare abiotic factors, like weather parameters, with the annual variation in survival. Calculating mean generation times would provide a further population parameter but would need to incorporate age-specific reproduction rates, which cannot be estimated by using the drift-fence method without dissecting females of known age.

Observed variability may be misleading, because variability increases with the duration of a study (Pechmann & Wilbur 1994). However, the adult part of the *T. dobrogicus* population showed a surprising constancy. Fluctuations in the adult census of *T. dobrogicus* were less than 10% over 4 years. Comparable long-term studies on amphibians (e.g. Semlitsch 1983; Semlitsch 1987; Berven & Grudzien 1990; Pechmann *et al.* 1991) reported variations which greatly exceeded 10%, even over period of only 2 years. Constancy of several population parameters of both species may reflect the specific stability of the cultured parkland habitat. The numbers of adult *P. fuscus* constantly decreased over 6 years. The water level of the study pond is held constant by irregular water donations. The terrestrial habitat is a regularly treated parkland. Census data for the coming years will give further information on whether a stable equilibrium has already been reached in this 'undynamic' habitat or whether the unusual constancy is just a result of an insufficient study duration.

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