HERPETOLOGICAL JOURNAL, Vol. 14, pp. 1-7 (2004)

BIAS IN ESTIMATION OF NEWT POPULATION SIZE: A FIELD STUDY AT FIVE PONDS USING DRIFT FENCES, PITFALLS AND FUNNEL TRAPS

KLAUS WEDDELING, MONIKA HACHTEL, ULRICH SANDER AND DAVID TARKHNISHVILI

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Sektion Herpetologie, Adenauerallee 160, D-53113 Bonn, Germany

Drift fences are frequently used to sample amphibians for population studies. Thus, some researchers do not mark animals, but use capture rates at the drift fence as an indicator of population size. Other workers use mark-recapture techniques to estimate population sizes. These approaches require different amounts of effort and lead to different results. Our study compares several estimates of population size for alpine newts (*Triturus alpestris*) and smooth newts (*Triturus vulgaris*) in five breeding ponds surrounded by permanent drift fences and pitfall traps. The estimates based on mark-recapture techniques (Petersen method) do not vary substantially between the two modes of recapture applied (funnel traps, and drift fences with pitfall traps). These estimates give even better results than simple counts if a substantial part of the newt populations remain within the drift fences throughout the year. While unrecognized trespass by newts appears to be a rare event, some newts may leave a pond for a short time even during the breeding season. This is an important source of bias for population estimates in studies based on counts at drift fences when animals are not marked.

Key words: capture methods, mark-recapture, *Triturus alpestris, Triturus vulgaris*

INTRODUCTION

A common approach for estimating population sizes of newts at the breeding pond involves the use of mark-recapture methods. This approach has been regarded as the most precise among indirect methods (Caughley, 1977). The Petersen method (Petersen 1896) or its modifications (e.g. Bailey, 1952) are most often used for newts, as these methods require group marking – rather than individual marking – of animals (Blab & Blab, 1981; Glandt, 1978; Arntzen & Teunis, 1993; Donnelly & Guyer, 1994; Wenzel *et al.*, 1995; Diaz-Paniagua, 1998). One obvious problem associated with group marking in conjunction with the Petersen method is that it only allows the population size to be estimated at one point in time (Caughley, 1977). Some newts leave a pond before breeding is over, and the number of animals found in the pond – even during the peak of reproductive activity – may represent only a part of the reproductive population (Schoorl & Zuiderwijk, 1981; Tarkhnishvili, 1986). Another difficulty is that the Petersen method requires a high proportion of recaptures to attain acceptable estimate errors (Caughley, 1977). Estimates based on marking with individual codes (Seber, 1973) are sometimes more accurate. However, individual marking of a few hundred animals often needs amputation of several toes and one or two fingers, especially in studies where populations in several neighbouring ponds are analysed and movement between ponds is of interest. Due to the rapid regeneration of toes in newts (Henle *et al.*, 1997), a complete amputation at the base of a toe is necessary in order to recognize marked animals for a few months after marking. Complete amputation of more than two fingers may potentially affect survival or reproductive functions of newts and, in our opinion, should be done only if individual tracking of animals is essential.

Other methods such as direct counts of newts at night (Cooke, 1995), or even observations of the number of animals surfacing for air (Andreas, 1982) can provide estimates of relative abundance, but their use is rather limited by the type and size of the breeding pond and species-specific habitat preferences (Wenzel *et al.*, 1995).

Since the 1960s, drift fences have been regularly used in population studies of pond-breeding amphibians (Shoop, 1965; Gibbons & Bennet, 1974; Gill, 1978; Verrell & Halliday, 1985; Dodd, 1991; Dodd & Scott, 1994; Kogoj, 1997; Kneitz, 1998; Baker, 1999). Because it is often assumed that drift fences with pitfall traps will catch all individuals entering a pond, some researchers make direct counts of individuals rather than estimating population size. One problem concerning this approach is that breeding animals may stay in or at the pond throughout the year (Gibbons & Bennett, 1974; Baker, 1999). Trespass is also a problem when animals cross the fence (Dodd, 1991; Verrell & Halliday, 1985; Jahn & Jahn, 1997). It was shown that the number of newts (*Notophthalmus, Triturus*) caught in pitfall traps may represent as little as 15% of the population, with mean values varying between 50 and 70% (Dodd, 1991; Baker, 1999), while in other studies up to 95% of the population could be captured (Gill, 1978). These studies show that this type of census represents a sample that has an unknown estimation error. Additionally, most drift fence

Correspondence: D. Tarkhnishvili, Department of Ecology, Tbilisi State University, 0128, 1 Chavachavadze Ave., Tbilisi, Georgia. *E-mail:* t@gol.ge

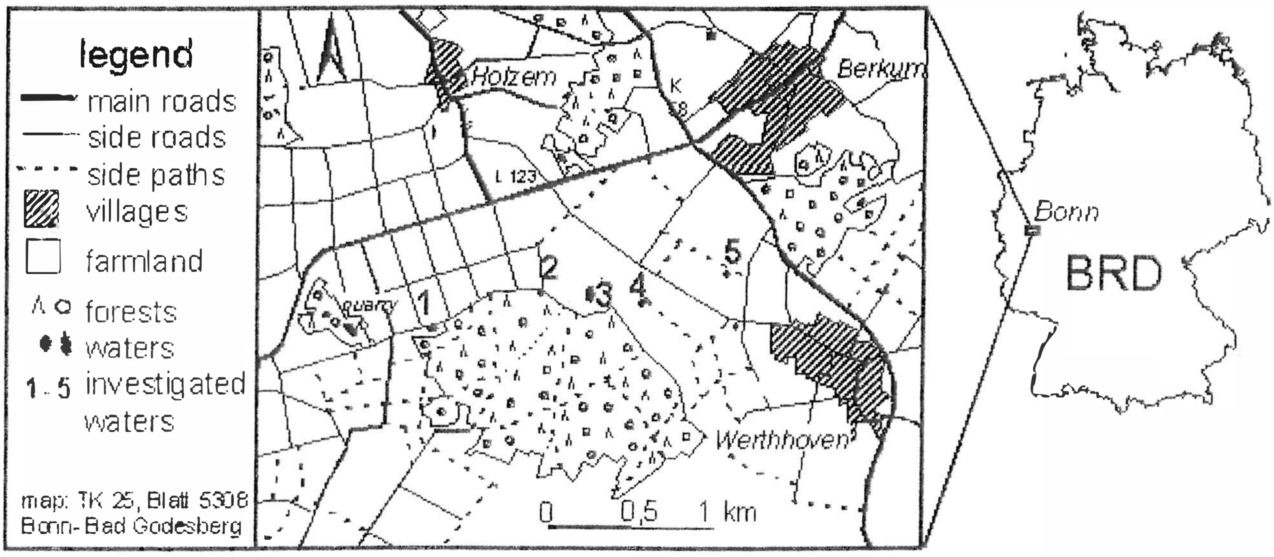

FIG. 1. Study area with position of study ponds.

studies were based on a single pond, and it is likely that the type of pond and surrounding habitat, along with fence construction and distance between fence and water may affect the quality of population size estimates.

The problem that some newts may not leave the water or the shoreline at all, can be compensated for by marking all animals entering the pond. Then, the proportion of unmarked newts caught in the water by dip-netting or funnel trapping represents how many individuals were already at the pond before pitfall trapping commenced (Verrell & Halliday, 1985; Baker, 1999). Unfortunately, some field researchers omit this procedure (e.g. Kogoj, 1997; Kneitz, 1998). Sometimes newts temporarily leave the pond during the breeding season. As a result, the same individual may fall in a pitfall trap more than once. Marking of newts that appear into pitfall traps helps to avoid the risk that the same specimen is counted several times.

Our study was designed to estimate reproductive population numbers of smooth newts (*Triturus vulgaris*) and alpine newts (*T. alpestris*), in five ponds near Bonn, Germany, using standard methods, i.e. toe-clipping, drift fences with pitfalls, and funnel trapping. The main objective of this paper is to evaluate the degree of bias associated with these methods. We did this by comparing several different methods frequently applied in field surveys of pond-breeding amphibians.

MATERIAL AND METHODS

STUDY PONDS

The five study ponds are situated in an agricultural landscape about 15 km south of Bonn, Northrhine-Westfalia, Germany, on the western side of the river Rhine. The ponds are located 275-1800 m from each other (Fig. 1). Ponds 3 and 5 are natural, whereas ponds 1, 2 and 4 were created artificially in 1988. Ponds 1 and 2 lie at the margin of a mixed forest. Ponds 3, 4 and 5 are surrounded by cereal fields and grassland; their distance from forest ranges from 150 to 700 m. Pond 3 is considerably larger than the other four ponds (Table 1). Pond 5 is ephemeral and regularly dries up for 1-1.5 months during the summer. Ponds 3 and 4 dried out occasionally in late summer for shorter time periods, but did not do so during the reported study. All ponds are surrounded by willow (*Salix* spp.), bramble shrubbery (*Rubus fruticosus*), reedmace (*Typha latifolia*) and sedges (*Carex* spp.). The waterbodies are partly covered by duckweed (*Lemna*, *Spirodela*) and broad-leaved pondweed (*Potamogeton natans*).

In addition to alpine and smooth newts, the common toad (*Bufo bufo*), agile frog (*Rana dalmatina*), common frog (*R. temporaria*) and green frogs (*R.* kl. *esculenta* complex) reproduce in the ponds. In ponds 2 and 3, great crested newts (*Triturus cristatus*) are also present.

TABLE 1. Characteristics of study ponds during the study year. SM, maximum surface area (m^2); DM, maximum depth (m); SF, size of terrestrial fringe inside the fence (m); ** dry up occasionally in late summer.

Pond	SM	DM	origin	status	setting	SF
1	50	1.2	artificial	permanent	forest/arable	0.5-1.5
2	45	1.5	artificial	permanent	forest/arable	1.5-2.0
3	400	1.7	natural	permanent**	arable	0-4.5
4	45	1.0	artificial	permanent**	arable	2.0-3.0
5	150	1.6	natural	temporary	meadow/arable	0-3.0

Small-bodied newts start the breeding migration in February and leave the ponds before the end of June.

DRIFT FENCES, FUNNEL TRAPS AND TOE-CLIPPING

From June 2000 to December 2001, all study ponds were surrounded by permanent drift fences made from a dense, green, non-transparent polyethylene or metallic fabric. The fence (height 45 cm) was embedded 5-10 cm deep into the soil. A U-shape profile at the top prevented newts from climbing over the fence. The distance between the pond margin and the fence ranged from 0 to 4.5 m depending on pond topography and changes in water level throughout the year (Table 1, following Schäfer, 1993). Paired pitfall traps on opposite sides of the fence consisted of plastic buckets (depth 46 cm, volume 23 l) set at intervals of 3-8 m. The rims of the buckets with their U-shape profile reduced the number of newts leaving the pitfalls. The bottoms of the buckets were covered with water to prevent desiccation. Pitfall traps both at the outer and the inner side of a fence were checked daily from the end of January until the end of November 2001. Unmarked individuals caught in pitfall traps were marked by toe-clipping (pond-specific marking) and released on the opposite side of the drift fence. Funnel trapping was used for two weeks between 28 April and 13 May (peak of breeding activity). The funnel traps were made of green coarse plastic fabric with a mesh size of approx. 2 mm. The size of the box-shaped traps was about 40 × 40 × 80 cm and the top was kept above the water level so that captured newts could breath. Newts entered the traps through two funnel-shaped entrances with a minimum aperture diameter of 5 cm. A maximum of eight funnel traps was used simultaneously in one pond. Every day during a two-week period the traps were checked, and marked and non-marked newts were counted and released. Non-marked animals were released again unmarked.

DATA ANALYSIS

We used four different approaches to interpret our data and compared the resulting estimates of population size. The first 'naive' approach assumed that any newt would be caught on a single occasion by a pitfall trap on the way to the pond during immigration and on a single occasion – if it survives – when it leaves a breeding site. According to this approach, the population size is equal to the total number of newts that fall into the outer pitfall traps, irrespective of marking. These results equal those one would obtain without marking animals. The second approach considered that the same animal could fall in to an outer pitfall trap several times. In this case the population size equals the cumulative number of unmarked newts in outer pitfall traps. The third approach is based on mark-recapture techniques and took into consideration the proportion of marked newts among those emigrating from the pond and caught in inner pitfall traps. Using also the total number of animals marked when entering the pond, one can calculate the total number of newts in the pond using the Petersen method. The fourth approach estimates the proportion of marked newts among those caught in funnel traps in water. The third and the fourth approaches assume that trap catches accurately reflect the proportion of both the number of marked and unmarked newts in the pond.

We used the Petersen method (Bailey, 1952; Caughley, 1977) for estimation of population size with mark-recapture techniques: $N = M(n+1)/(m+1)$, where N is the population size; M the number of marked animals; n the number of newts caught during the second trapping session (either in pitfall traps when newts left the pond or in funnel traps); and m the number of recaptured newts. Standard errors (SE) and confidence intervals were calculated as recommended by Caughley (1977). It is important to note that recruitment or immigration between two capture sessions leads to an overestimation of the population size, but mortality and emigration do not bias the estimate (Caughley, 1977). Therefore, mortality of newts during the breeding season should not be a problem. In order to meet assumptions of the index, we defined the period of "second capture session" after immigration to the pond was completely – or almost completely – over.

Baker (1999) stressed that the use of different capture techniques between the first and second capture sessions may potentially bias the population estimates. Use of pitfall trap recaptures (instead of funnel trapping) may help to avoid this source of error. On the other hand, there is a risk that newts that were inside the fences before the reproductive season started might show a preference to remain there also after completion of the breeding period. In this respect, recapture in funnel traps may provide a better estimate.

Significance of differences in 'temporary' terrestrial activity between sexes was tested with 2 x 2 contingency tables (χ^2 test; Sokal & Rohlf, 1995).

RESULTS

POPULATION ESTIMATE BASED ON PITFALL TRAPPING

Due to terrestrial activity, the total number of animals in pitfall traps on the outer side of the fence ("first approach") was always much higher than the results obtained by counting only marked individuals ("second approach"). In different ponds, 10-529 individuals of *T. vulgaris* and 43-2249 individuals of *T. alpestris* were caught on the outer side of drift fences more than once (compare N and N_1 in Table 2). The bias was highest in small artificial ponds 1, 2 and 4 and higher in *T. alpestris* than in *T. vulgaris*. Marked differences between sexes were recorded in 'temporary' terrestrial activity: analysis in 2 x 2 contingency tables showed significantly higher activity of female *T. vulgaris* in small ponds which provide little shelter inside the fence (Table 3). In *T. alpestris*, only at pond 3 did terrestrial activity significantly differ between sexes.

TABLE 2. Number of newts estimated from captures in pitfall traps. N, total number of captures on the outer side of a drift fence; N_1, total number of unmarked newts caught on the outer side of a drift fence; M, number of newts marked prior to the second capture session (2 June for *T. vulgaris* and 15 May for *T. alpestris*); n, number of newts captured on the inner side of the drift fence during the second session, with the number of recaptures (m); N_2, population estimate (Petersen method) calculated from recapture rates in inner pitfall traps, with the standard error (SE).

	Pond	1	2	3	4	5
T. alpestris, males	N	2041	1021	622	158	62
	N_1	949	600	575	89	49
	M	942	599	571	88	42
	n (m)	76 (72)	20 (16)	208 (184)	40 (37)	26 (15)
	N_2(SE)	994 (26)	740 (76)	645 (16)	95 (4)	71 (11)
T. alpestris, females	N	2095	1018	696	358	110
	N_1	938	584	614	185	80
	M	932	579	606	184	75
	n (m)	113 (106)	27 (22)	221 (186)	97 (87)	35 (21)
	N_2(SE)	993 (24)	705 (61)	719 (21)	205 (7)	123 (16)
T. vulgaris, males	N	332	558	1704	518	47
	N_1	254	478	1640	332	43
	M	254	478	1627	326	41
	n (m)	25 (16)	24 (19)	477 (381)	62 (51)	13 (7)
	N_2(SE)	388 (54)	598 (58)	2031 (46)	395 (23)	72 (16)
T. vulgaris, females	N	366	697	2555	794	75
	N_1	241	530	2442	451	69
	M	241	528	2423	443	63
	n (m)	46 (38)	23 (21)	772 (683)	81 (73)	19 (14)
	N_2(SE)	290 (19)	576 (35)	2738 (36)	491 (18)	84 (11)

The number estimated by the Petersen method, taking into consideration the proportion of unmarked newts among those leaving the pond ("third approach"), was always higher than the total number of newts marked at the fence. The standard error of an estimate was usually (except for pond 5) lower than 10% of the population size. The number of unmarked newts among those migrating from a breeding site reached 5-40% (usually 10-20%) in different ponds. In particular, pond 5 showed high proportions of unmarked individuals. There were unmarked newts leaving the pond during the breeding season (before mid-May). Their number varied from just a few individuals to up to 90 newts per species and sex. For *T. alpestris*, this number was especially high in ponds 1 and 2 (153-159 specimens of each sex); for *T. vulgaris* in ponds 2 and 3 there were 98-112 specimens, respectively (not shown in Table 2).

Among newts entering a pond, there were many returning individuals that had been previously marked and released, especially in small ponds 1, 2 and 4 (difference between N and N_1 in Table 2).

RECAPTURING BY FUNNEL TRAPS

The number estimated by the Petersen method, if funnel trapping was applied during the second capture session, showed figures similar to those obtained via recapturing by pitfall traps, with comparable values of standard error (Table 4). Differences between these two estimates were never significant: 95% confidence limits of both estimates overlapped for each individual pond.

TABLE 3. Intersexual differences in 'temporary' terrestrial activity: results from several 2 x 2 contingency tables testing differences between sexes in proportions of (N-N_1) and N_2 from Table 2. (M=male, F= Female)

Pond	1	2	3	4	5
T. alpestris	M ~ F	M ~ F	M < F	M ~ F	M ~ F
	χ^2=0.9123	χ^2=0.8350	χ^2=5.5827	χ^2=0.6315	χ^2=0.6232
	P>0.05	P>0.05	P<0.05	P>0.05	P>0.05
T. vulgaris	M < F	M < F	M ~ F	M < F	M ~ F
	χ^2=22.1689	χ^2=28.1416	χ^2=2.8894	χ^2=12.1496	χ^2=0.1433
	P<0.01	P<0.01	P>0.05	P<0.01	P>0.05

TABLE 4. Number of newts marked at drift fences and proportion of non-marked individuals in funnel traps. M, number of newts marked at the fences prior to funnel trapping (28 April); n, number of newts captured in funnel traps, with the number of recaptures (m); N_3, population estimate (Petersen method) calculated from recapture rates in funnel traps, with the standard error (SE).

	Pond	1	2	3	4	5
T. alpestris, males	M	914	591	568	88	39
	n (m)	88 (84)	191 (176)	59 (53)	74 (73)	88 (39)
	N_3(SE)	957 (22)	641 (13)	631 (27)	89 (1)	87 (10)
T. alpestris, females	M	906	567	579	168	72
	n (m)	110 (108)	87 (84)	99 (88)	130 (129)	132 (98)
	N_3(SE)	923 (12)	587 (12)	651 (23)	169 (1)	97 (5)
T. vulgaris, males	M	248	469	1615	313	39
	n (m)	44 (35)	70 (62)	207 (165)	47 (47)	60 (31)
	N_3(SE)	310 (23)	529 (22)	2023 (70)	313 (0)	74 (9)
T. vulgaris, females	M	232	495	2383	407	53
	n (m)	15 (14)	18 (15)	151 (135)	54 (53)	40 (22)
	N_3(SE)	247 (15)	588 (57)	2663 (74)	415 (8)	94 (13)

The proportion of unmarked newts in funnel traps was thus comparable with the proportion of unmarked animals at drift fences during migration from the pond.

DISCUSSION

The fact that part of the reproductive population remains at the breeding site throughout the year can bias the estimate of population size when using only drift fences (see introduction). However, it is not clear how to separate this factor from trespass, another potential source of error. Dodd (1991) assumed that newts crawled under the fence using holes produced by plant roots, but he did not provide conclusive evidence of trespass: moreover, his experiments showed that at laboratory newts at least could not climb over or under the fence. Verrell & Halliday (1985) assumed climbing to be a potential source of error and refrained for this reason from estimating the population size of smooth newts. Data presented here demonstrate that the proportion of newts that were not marked at drift fences is high in areas with plenty of terrestrial refugia within the fence (Pond 5), moderate at the large deep site (Pond 3), but quite low at small ponds 1 and 4 with small distances between fence and water edge. Moreover, the proportion of non-marked alpine newts was less than that of smooth newts. As our fence construction was standardized, the effectiveness of a fence depends on the species-specific migration activity and the likelihood of a newt staying in its immediate surroundings. Trespass itself appears to be a relatively unimportant source of bias, estimated in the range of 0.7-3.4%. This is the lowest proportion of unmarked newts in small ponds where there is an absence of refugia between the water line and the fence (e.g. females of *T. alpestris* in small ponds).

It appears that the presence of newts at a pond before migration starts does not strongly bias population estimates by mark-recapture, even if recaptures are done by drift fences. The majority of newts which remain in water throughout winter, however, leave the pond area after the breeding season. This is supported by a good correspondence between estimates based on recapturing in water and in terrestrial habitats.

This correspondence between estimates obtained from funnel trap and pitfall trap recaptures shows that the time between marking and recapture (and, consequently, mortality between two capture sessions) does not significantly bias the estimate. In fact, mode and time of recapture can be planned dependently on the activity period and peculiarities of an individual pond.

Although the majority of authors (Gibbons & Bennett, 1974; Verrell & Halliday, 1985; Dodd, 1991; Baker, 1999) combined drift fence methods with group marking of migrating newts, no results were reported about terrestrial movements during the breeding season. Our data suggest that such movement may be considerable for the populations we studied. During rainy days, some newts (occasionally almost the entire population, as *T. alpestris* in pond 1) leave a pond for one or several days, travel a short distance, but then return to a pond before the end of the reproductive season. In alpine newts this behaviour is more common than in smooth newts, although intersexual differences occur mainly in smooth newts, where females show significantly higher terrestrial activity. Terrestrial movements are less often recorded at large ponds, but this may be due to more options for moving unnoticed within the fence than at small ponds.

Some publications describe the population size of newts only on the basis of data obtained from drift fences in combination with pitfall traps, without marking animals or taking into consideration the proportion of marked animals at the breeding sites, e.g. Blab & Blab, 1981; Schäfer, 1993; Kogoj, 1997; Kneitz, 1998. We assume that such estimates are strongly biased because part of the population is unaccounted-for. In addition to this, they can give a strong overestimation of population size due to individuals entering the pond more than once during a breeding season (e.g. Kogoj, 1997). Forcing animals to stay inside the fence by keeping them always on the inner side is no solution to the problem because it strongly influences reproductive behaviour of newts and biases observations of movements between ponds and terrestrial habitat.

ACKNOWLEDGEMENTS

We thank Gregor Bosbach, Ruth Rottscheidt, Peter Schmidt and Meike Thomas for helping us during the field work. Stefanie Specht drew the map of the study area. We thank Wolfgang Böhme for leading the project 'Development of amphibian habitats in an agricultural landscape' and Bradley Sinclair for helpful comments on translation problems. Permissions for catching and marking amphibians were granted by the local administration for nature conservation (Untere Landschaftsbehörde, Rhein-Sieg-Kreis, NRW). This project is financially supported as a 'testing and development project' by the Federal Agency for Nature Conservation (BfN) and the Federal Environment Ministry (BMU).

REFERENCES

Andreas, A. (1982). Eine Methode der quantitativen Bestandsaufnahme von Molch-Populationen in Gewässern. *Abh. Ber. Naturk. Museum Mauritanium Altenburg*, **1982**, 93-97.

Arntzen, J. W. & Teunis, S. F. M. (1993). A six year study on the population dynamics of the crested newt (*Triturus cristatus*) following the colonization of a newly created pond. *Herpetological Journal* **3**, 99-110.

Bailey, N. T. J. (1952). Improvements in the interpretation of recapture data. *Journal of Animal Ecology* **21**, 120-127.

Baker, J. M. R. (1999). Abundance and survival rates of great crested newt (*Triturus cristatus*) at a pond in central England: monitoring individuals. *Herpetological Journal* **9**, 1-8.

Blab, J. & Blab, L. (1981). Quantitative Analysen zur Phänologie, Erfassbarkeit und Populationsdynamik von Molchbeständen des Kottenforstes bei Bonn. *Salamandra* **1981**, 147-172.

Caughley, G. (1977). *Analysis of vertebrate populations*. Wiley: Interscience Publication.

Cooke, A. S. (1995). A comparison of survey methods for crested newts (*Triturus cristatus*) and night counts at a secure site, 1983-1993. *Herpetological Journal* **5**, 221-228.

Diaz-Paniagua, C. (1998). Reproductive dynamics of a population of small marbled newt (*Triturus marmoratus pygmaeus*) in south-western Spain. *Herpetological Journal* **8**, 93-98.

Dodd, C. K. (1991). Drift fence-associated sampling bias of amphibians at Florida Sandhills temporary pond. *Journal of Herpetology* **25**, 296-301.

Dodd, C. K. & Scott, D. E. (1994). Drift fences encircling breeding sites. In: *Measuring and monitoring biological diversity: standard methods for amphibians*. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster (Eds). Washington and London: Smithsonian Institution Press.

Donnelly, M. A. & Guyer, C. (1994). Estimating population size: mark-recapture. In: *Measuring and monitoring biological diversity: standard methods for amphibians*. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster (Eds). Washington and London: Smithsonian Institution Press.

Gibbons, J. W. & Bennett, H. D. (1974). Determination of anuran terrestrial activity patterns by a drift fence method. *Copeia* **1974**, 237-243.

Gill, D. E. (1978). Effective population size and interdemic migration rates in a metapopulation of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Evolution* **32**, 839-849.

Glandt, D. (1978). Notizen zur Populationsökologie einheimischer Molche (Gattung *Triturus*). *Salamandra* **14**, 9-28.

Henle, K., Kuhn, J., Podloucky, R., Schmidt-Loske, K. & Bender, C. (1997). Individualerkennung und Markierung mitteleuropäischer Amphibien und Reptilien: Übersicht und Bewertung der Methoden; Empfehlungen aus Natur- und Tierschutzsicht. *Mertensiella* **7**, 133-184.

Jahn, P. & Jahn, K. (1997). Vergleich quantitativer und halbquantitativer Erfassungsmethoden bei verschiedenen Amphibienarten im Laichgewässer, *Mertensiella* **7**, 61-69.

Kneitz, S. (1998). *Untersuchungen zur Populationsdynamik und zum Ausbreitungsverhalten von Amphibien in der Agrarlandschaft*. Laurenti-Verlag (Bochum).

Kogoj, E. (1997). Populationsdynamik von Amphibien an einem Sekundärgewässer der Wiener Donauinsel (Österreich): Ein Vergleich von zwölf Taxa und neun Untersuchungsjahren (1986-1987, 1989-1995). In: Hödl, W., Jehle, R. and Gollmann, G. (Eds.), *Populationsbiologie von Amphibien. Eine Langzeit-Studie auf der Wiener Donauinsel*. Stapfia (Wien).

Petersen, C. G. J. (1896). The yearly immigration of young plaice into Limfjord from the German sea. *Report of the Danish biological station* **6**, 1-48.

Schäfer, H. J. (1993). *Ausbreitung und Entwicklung von Amphibien-Populationen in der Agrarlandschaft*. Ph. D. thesis, Univ. Bonn, 294 p.

Schoorl, J. & Zuiderwijk, A. (1981). Ecological isolation in *Triturus cristatus* and *Triturus marmoratus* (Amphibia: Salamandridae). *Amphibia-Reptilia* **1981**, 235-252.

Seber, G. A. F. (1973). *The estimation of animal abundance and related parameters*. Griffin: London.

Shoop, C. R. (1965). Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. *Science* **149**, 558-559.

Sokal, R.R. & Rohlf, F. J. (1995). *Biometry (3rd ed.)*. W. H. Freeman and Company, New York.

Tarkhnishvili, D. N. (1986). Analysis and conservation perspective of the banded newt from surroundings of Tbilisi. - *Bulletin of the Academy of Sciences of the Georgian SSR* **12**, 145-147 (in Russian).

Verrell, P. & Halliday, T. (1985). Reproductive dynamics of a population of smooth newt, *Triturus vulgaris*, in southern England. *Herpetologica* **41**, 386-395.

Wenzel, S., Jagla, W. & Henle, K. (1995). Abundanzdynamik und Laichplatzreue von *Triturus cristatus* und *Triturus vulgaris* in zwei Kleingewässern einer Auskiesung bei St. Augustin (Nordrhein-Westfalen). *Salamandra* **31**, 209-230.

Accepted: 27.1.03