Reproductive ecology of *Bombina variegata*: characterisation of spawning ponds

Jonas Barandun, Heinz-Ulrich Reyer*

Zoological Institute, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Abstract. The use of spawning sites by *Bombina variegata* was analysed in a dynamic habitat containing a variety of different ponds. Cool or shadowy as well as permanent ponds were not used for spawning at all. Among the ephemeral ponds that were used, egg numbers increased with water temperature, both when compared among ponds and between different areas within ponds. Egg numbers were also higher in ponds of intermediate duration than in those persisting for shorter or longer periods. Ponds of intermediate duration with moderate predator densities and with larvae of competing anuran species (*Hyla arborea, Bufo calamita*) were used more often than short-lived ponds with no predators and competitors. This pattern of spawn deposition can be interpreted as an attempt to select sites allowing rapid larval development (warm water) and to avoid sites with high numbers of newts and invertebrate predators (permanent ponds). The selection critera seem to be adaptive, because pond duration and desiccation are more important for larval survival than predators and competitors. Yet, optimal reproductive conditions remain highly unpredictable for *Bombina variegata*, as the characteristics and dynamics of spawning ponds are mainly determined by climatic conditions. Consequently, survival chances of tadpoles can change within a few days or weeks, depending on rainfall and evaporation.

Introduction

The choice of a spawning pond by anurans has a strong influence on offspring survival. In most species, highest mortality occurs before metamorphosis. But mortality rates differ dramatically among spawning sites depending on predation rate, risk of desiccation, feeding conditions, and larval density (Smith, 1983; Banks and Beebee, 1987). Rapid larval development is advantageous because it reduces the exposure to these risks of mortality. Development is enhanced by high temperature, low larval density, and sufficient food supply (Pawlowska-Indyk, 1980; Riis, 1991). In order to maximize their reproductive success, adult anurans are consequently expected to avoid short-lived as well as cool ponds or ponds with high densities of predators or competing anuran larvae (Smith, 1983; Banks and Beebee, 1987).

---

*Corresponding author.

Permanent ponds or lakes are generally cool and characterized by high diversity and abundance of predators which can eat large numbers of tadpoles. Thus, larval mortality is usually high in permanent ponds (Licht, 1974). This high mortality rate may be the reason why few anuran species regularly spawn in permanent ponds or lakes (Duellman and Trueb, 1986). Competition may affect growth and survival in both durable and temporary ponds, but is more persistent under stable conditions. When exposed to sunshine, temporary ponds are warm and highly productive which favours quick development (Williams, 1987). But temporary ponds pose the risk of desiccation. Thus, ponds which offer better conditions in terms of temperature, productivity, and predation are usually worse in terms of desiccation risk, and vice versa (Smith, 1983). This poses a dilemma for the selection of optimal spawning sites: the animals are forced to trade-off the advantages of rapid development and low predation risk with high desiccation risk.

In this article, we investigate whether there are reasons to assume that individuals choose a pond based on factors related to the dilemma described above. Under the assumption that these qualities are assessed, we hypothesize that ponds with high densities of predators or competitors as well as cool and ephemeral ponds are avoided.

The yellow-bellied toad *Bombina variegata* is a suitable model organism to study spawning site selection under conflicting and unpredictable conditions. The animal is known to spawn in small, sunny, temporary ponds, nowadays mostly in agricultural or industrial habitats (Bauer, 1987). But a wide range of pond types is used for spawning, ranging from newly created wheel depressions to vegetated persistent ponds.

Methods

Study site

The study area is located north-east of Zürich, Switzerland, in a military training area for armoured vehicles. About one third of the area is a closed mixed forest with little herbaceous vegetation. The remaining open area is a scarcely vegetated sheep pasture on clay. The study was restricted to a ca. 10 ha area with the highest density of both ponds and toads. All existing ponds are artificial, created when vehicles compress the soil. Vehicle activity changed the shape of ponds mainly during winter and early spring every year. During the annual sampling period from April to September, single ponds were disturbed occasionally. At 18 sites, ponds have existed since at least 1989, although their shapes have repeatedly changed.

In the open area, 44 to 46 ponds were studied in each year of the study. Fifteen other temporary ponds were situated in the forest. The forest ponds were all completely shaded, small and without vegetation; eight of these only rarely dried out. Adults and subadults were regularly found in the forest ponds but no calling, mating, nor spawn was ever recorded. These ponds were not included in the analyses. Ephemeral rain puddles which dried out within two days after rain had stopped were also not included in the analyses, because no adequate habitat measures could be taken.

Since pond dynamics depended mainly on human activities, rainfall and evaporation, ecological differences within ponds between spawning periods were as large as between ponds within periods. Therefore, we treated ponds as independent, even when they were used in more than one spawning period. This results in a total of 302 ponds for which data are available. For some of them the data set on reproduction and pond characteristics is not complete. Therefore, sample sizes can differ between analyses.

Description of pond characteristics

Data were collected from 28 April to 6 September 1991 and from 5 May to 16 September 1992. During periods of potential reproduction (i.e., after significant rainfall) activities and numbers of adult anurans (*Bombina variegata, Hyla arborea* and *Bufo calamita*) were recorded twice a week; presence and numbers of new eggs were noted daily. Both in 1991 and 1992, there were four separate spawning phases. In 1991: 19-24 May, 3-10 June, 16-30 June, 25-31 July. In 1992: 7-9 June, 24-29 June, 10-13 July, 22-25 July. For both years combined, these phases can be grouped into five non-overlapping seasonal periods: 19-24 May, 3-10 June, 16-30 June, 10-13 July and 22-31 July. Tadpole numbers were recorded in four categories of 0, <100, 100-1000, >1000. In addition to adult and juvenile anurans, we measured the following six pond characteristics during each spawning period:

(1) Surface area of ponds was calculated from measurements with a tape measure 1-3 days after maximal filling. Areas ranged from 0.1 (a small wheel depression) to about 50 m^2, but varied daily in several ponds as a consequence of desiccation. Consequently, the size data are only approximate.

(2) Pond duration was measured by the number of days each pond contained water, starting from the beginning of a spawning period. In some cases, this represents an overestimate with respect to larval survival, because in irregularly shaped ponds, desiccation was a gradual process with large parts of ponds drying long before the whole pond was dry. However, only the day a pond was completely dry could be taken as an operational measure for desiccation. With tadpole development taking up to 60 days, a pond duration of 70 days was taken as the maximum necessary durability for successful development.

(3) Maximum pond temperatures were measured on sunny days, in 1991 on 31 May, 23 June, and 29 July, in 1992 on 26 June and 30 July.

(4) Vegetation cover was estimated as the percentage of the surface area covered by emergent plants, mainly *Glyceria* sp., *Alisma plantago-aquatica* and *Sparganium erctum.* In most ponds, vegetation cover changed markedly over the sesaon.

(5) Adult newts (*Triturus alpestris*, *T. vulgaris*) were predators on eggs and small tadpoles. The presence of newts was recorded by dipnet sampling and visually during every visit; their abundance per pond was estimated in three categories: none (never

observed), few (1-2 individuals or single times), many (several individuals and regularly noted).

(6) Predators on tadpoles were mainly invertebrates (*Libellulidae, Aeschnidae, Dytiscidae, Hydrophilidae, Notonectidae, Nepidae*) (Engelhardt, 1989). The presence and abundance of invertebrates was recorded in the same way as described for newts.

Statistics

We used univariate statistics to relate numbers of *Bombina variegata* eggs per pond (dependent variable) to five pond characteristics (independent variables) that are most relevant for larval performance: pond duration, water temperature and numbers of adult newts, predacious insects and other anurans, respectively. In order to test for interactions among these five and three additional independent variables (seasonal period, surface area and vegetation cover) and for reducing the eight, potentially correlating variables to a smaller number of independent composite factors, we performed a principal component analysis (PCA) with subsequent varimax rotation. A lowest eigenvalue of 1 was used for determining the number of principal components (PCs) to be extracted; loadings $< |0.450|$ between original variables and PCs were ignored ("zero loadings") and only loadings $\geqslant |0.550|$ were used for interpreting the resulting factors (Aspey and Blankenship, 1977). Normal distribution of original variables, a precondition for most multivariate techniques, did not exist in any of the eight independent variables (all $P < 0.05$; Lilliefors-modification of the Kolmogorov-Smirnov-test). But PCAs are quite robust against deviations from the assumption of normality (Balthazart, 1973; Aspey and Blankenship, 1977) and neither data transformation nor use of Spearman, rather than Peason correlations changed the outcome of our PCA. Therefore, we used factor scores from the PCA based on untransformed data. We related the scores to egg occurrence (yes or no) by means of a discriminant analysis and to egg number (log-transformed) by means of a multiple regression analysis.

Further details of the tests are given with the respective results. All statistical tests were performed with Systat for Windows, Version 5.0 (Systat, Inc.) and a significance level of $P = 0.05$ was used throughout.

Results

Eggs were laid between 19 May and 31 July. Within this time span, spawning activity was not uniformly distributed, but occurred in distinct periods, synchronized with heavy rainfall (Barandun and Reyer, in press). We recorded spawning activity for 302 ponds. In 197 (= 65%) of them we never found eggs, in the others, densities ranged from 0.1 to 61 eggs/m^2 pond surface. Spawning is likely to be influenced by a combination of different ecological variables, rather than by single pond qualities. Nevertheless, knowledge of univariate relationships (1) helps to illustrate the data distribution and to interpret results from subsequent multivariate analyses (2).

1) Analyses based on single ecological variables

In fig. 1a-e, the number of eggs (dependent variable) per pond is plotted against the five pond characteristics (independent variables) that are most important for larval perfomance: (a) pond duration (representing risk of desiccation), (b) water temperature (influencing speed of development), (c) newt and (d) invertebrate densities (affecting predation) and (e) number of other larval anurans (representing competition for food). Relationships between the dependent and each independent variable were tested with regression analyses.

(a) Pond duration (fig. 1a): The duration of the monitored ponds varied from three days to perennial. Within the same pond, dessication rate varied during the season, depending on weather and vegetation. There was no linear relationship between egg number and pond duration ($P = 0.543$, $r^2 = 0.001$), but a tendency for ponds of intermediate duration to contain the highest number ($P = 0.008$, $r^2 = 0.034$; 2nd degree polynomial regression). While the low egg number in durable ponds may reflect active avoidance as a response to higher predation pressure in these ponds (see below), the low number in ponds of very short duration does not seem to result from avoidance, because in seven cases, toads spawned in almost dry ponds. A more likely explanation is that short-term ponds cannot be used as frequently for spawning as more durable ones. Thus, the decrease in egg numbers at the right end of the distribution curve seems to indicate an adaptive response, the decrease at the left end a constraint.

(b) Temperature (fig. 1b): Water temperature varied markedly, both within and among ponds. On sunny days, temperature could increase by more than 10°C within two hours in open shallow parts, but remained almost constant at the bottom or in vegetation. Spawning ponds were on average warmer ($\bar{x} \pm s$: 31.9 ± 2.3°C) than ponds which were not used (30.5 ± 2.4) and there was a significant positive relationship between egg number and water temperature ($P = 0.003$, $r^2 = 0.030$). The importance of warm water for spawning is also supported by two other observations: First, none of the shadowy, cool ponds in the forest was ever used for reproduction. Second, in 16 cases where the spatial distribution of spawn was recorded in thermally heterogeneous ponds, eggs were found 13 times in the warmer and only 3 times in the cooler parts. This is significantly different from an equal distribution ($P = 0.011$, Binomial test, one-tailed).

(c, d) Predators (fig. 1c, d): Newts and invertebrate larvae of the first seasonal generation occurred in ponds until about mid-June. The second invertebrate larval generation did not become dangerous for tadpoles before the end of July. So, eggs and tadpoles were likely to be safe from aquatic predators from late June to late July, but not from predation

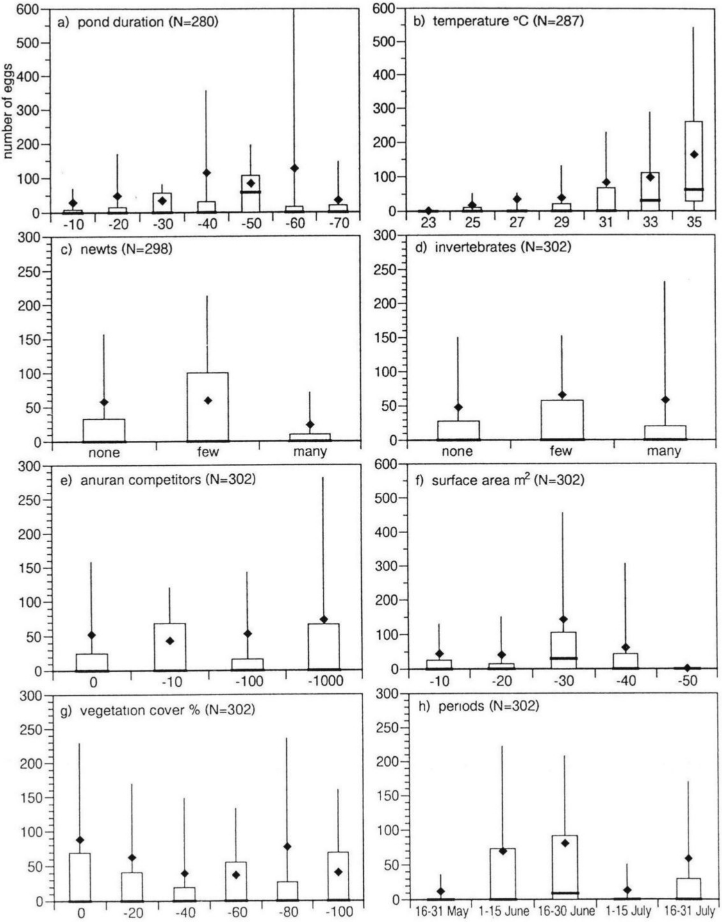

Figure 1. Total number of eggs per pond in relation to seasonal period and seven pond characteristics. Diamonds represent means, solid horizontal lines medians. Vertical lines show 90%, boxes 25-75% ranges. N refers to the number of ponds for which data on the respective variable are available.

by birds (herons, crows, gulls), which also were occasionally observed to eat tadpoles and metamorphs. In one nearly dry pond, a heron took 79 out of 81 large tadpoles within one hour. A single newt or invertebrate predator can also eliminate all eggs or tadpoles from a small pond within a short time. With such dramatic effects of predation on reproductive success, toads could be expected to avoid ponds with predators for spawning. Contrary to this expectation, egg number was not related to aquatic predator density for either newts or invertebrate larvae (ANOVA; both $P > 0.450$, $\mathrm{df} = 2$). Egg number could not be related to terrestrial predation, because the occasional visits of birds to ponds could not reliably be quantified.

(*e*) *Anuran competitors* (*fig. 1e*): Two other anuran species used the studied ponds for spawning: *Bufo calamita* and *Hyla arborea.* Both species started breeding at the end of April, one to three weeks before *Bombina variegata* did, but stopped breeding in early July, while *Bombina* continued until August. Thus, at any one time during the breeding season, *Bombina variegata* adults had the choice to lay their eggs into ponds with or without competition from other tadpoles. Apparently, spawning is not affected by such competition. All three species occurred together in the same pond; their males were observed calling within 30 cm of each other during several hours, and *Bombina* pairs were found to spawn directly beside simultaneously spawning *Bufo calamita* or *Hyla arborea.* There was no significant relationship between *Bombina*-egg number and the combined density of *Bufo*- and *Hyla*-tadpoles (ANOVA; $P = 0.877$, $\mathrm{df} = 4$); eggs were laid into ponds containing up to 100 tadpoles/m^2.

2) *Analyses based on variable combinations*

(*a*) *Relationships among independent variables:* According to the above univariate analyses, pond temperature is the major determinant of egg distribution in *Bombina variegata*; pond duration also seems to exert some influence. However, as mentioned before, a deeper understanding of spawn distribution requires a multivariate approach, because several ecological variables may interact and confound each other's effects. We investigated this interaction by performing a principal component analysis (PCA) on the five variables from the univariate analysis plus three additional pond characteristics (surface area, vegetation cover and period within the season; fig. 1f-h) potentially affecting them and, consequently, providing the toads with cues as to where and when to spawn.

The PCA reduced the eight, partly correlated original variables to three independent factors, together explaining 72.6% of the total variance (fig. 2). Principal component 1 (PC1) is characterized by high loadings of pond surface and duration and, thus, can be termed "*pond size*". Densities of invertebrate predators and larvae of competing anuran species also correlate with this factor, suggesting that these species prefer larger, more permanent ponds to avoid mortality through complete desiccation. Principal component 2 represents "*seasonality*", as indicated by the high loading of period. Following from the other loadings on PC2 and their signs, increasing factor scores of *seasonality* reflect

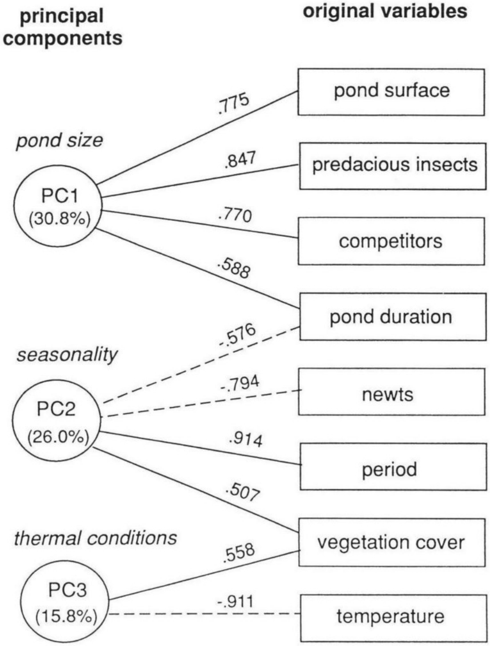

Figure 2. Result from a principal component analyis, based on the eight variables of fig. 1. Names of the three principal components (PCs) are given in italics above the circles, variances explained by the respective PC within the circles. Numbers above the lines connecting PCs and original variables refer to factor loadings. Positive relationships are indicated by solid, negative ones by broken lines.

progressing season, increasing vegetation cover, decreasing newt density and reduced pond duration. Finally, PC3 represents "*thermal conditions*", with high factor scores representing low water temperature and high vegetation cover. Two results of this PCA require special explanations: First, distribution of newts was better explained by *seasonality* than by *pond size*. This is mainly due to their absence from ponds after mid-June. Newts were also highly mobile, often visited ponds only during single nights and, thus, were less restricted to permanent ponds than invertebrate predators. Second, although one would expect that water temperature increases from April to August, pond temperature was not related to *seasonality*. The exlanation probably lies in an opposing (i.e., cooling) effect of vegetation (see PC3) which increases with progressing season (see PC2).

Table 1. Summary statistics of relationships between spawning activity and ecological conditions described by the three principal components (PCs) from fig. 2. Table a) lists statistics from the discriminant analysis based on the occurrence of spawn (yes or no), table b) shows statistics from the multiple regression based on egg numbers. Constants were included in both tests, but omitted from the Tables for reasons of clarity.

a) Variable	df	MS	*F*	*P*
PC1: *pond size*	1	3.24	3.26	0.072
PC2: *seasonality*	1	1.22	1.22	0.271
PC3: *thermal cond.*	1	19.82	21.28	0.000
Wilks' lambda	3, 273		8.78	0.000

b) Variable	Coefficient	*s*	*T*	*P*
PC1: *pond size*	0.10	0.06	1.71	0.089
PC2: *seasonality*	0.05	0.06	0.78	0.435
PC3: *thermal cond.*	–0.26	0.06	–4.50	0.000
	df	MS	*F*	*P*
Regression model	3	6.87	7.78	0.000

(*b*) *Spawning in relation to ecological factors:* The relationship between spawning activity and the three ecological factors extracted by the PCA was tested in two ways: First, a discriminant analysis was used to distinguish between ponds with and without spawn, independent of egg numbers; second, a multiple regression analysis was performed to relate egg numbers to the three PCs. Results of the two analyses are shown in table 1. In both cases, spawning was not significantly related to *pond size* (PC1) and *seasonality* (PC2) but increased with *thermal conditions* (PC3). This supports the dominating effect of temperature found in the univariate analysis. The discriminant function from the first analysis correctly classified about 60% of all ponds, 102 out of 164 without spawn and 66 out of 113 with spawn. This is significantly different from expectation ($\chi^2 = 10.611$, df $= 1$, $P = 0.001$). The discrepancy that egg numbers were related to pond duration in the univariate test, but not to either PC1 or PC2 (also representing pond duration) in this analysis, probably arises from the fact that calculation of principal components assumes a linear relationship which is not true for pond duration (see fig. 1a).

Discussion

Water temperature turned out to be the major ecological variable affecting selection of spawning sites in *Bombina variegata*. The observed preference for warm ponds, and for warmer parts within a pond, corroborates previous descriptions of typical spawning sites as being sunny (Bauer, 1987; Grossenbacher, 1988). It is also in accordance with preferences for higher water temperatures found in other anurans, e.g., *Bufo bufo* (Kuhn, 1993) and various *Rana* species (Sinsch, 1984; Wollmuth et al., 1987; Sjögren et al., 1988). The adaptive significance of such preference is usually seen in the resulting faster larval development and earlier metamorphosis, allowing the animals to escape the aquatic environment with its high predation and desiccation risks as soon as possible (Smith-Gill and Berven, 1979; Newman, 1980). For *Bombina variegata*, however, this is not sufficient to explain the adults' preference for warm ponds, because successful development of their eggs and larvae was not related to water temperature, but to pond duration (Barandun and Reyer, in press): eggs laid in more durable ponds produced more metamorphs, even though these ponds contained more newts, predacious insects and other anuran species. Thus, in *Bombina variegata*, the well known trade-off between higher desiccation risk in small, ususally predator-free ponds and higher competition and predation risk in durable ponds (Smith, 1983; Woodward, 1983; Semlitsch and Reyer, 1992) is decided for the latter. This result helps to explain why spawning site selection is not affected by densities of competitors and predators. Moreover, choosing small ponds with no or only a few newts and invertebrates is no guarantee to escape predation. The lack of aquatic predators may be compensated by higher predation through birds, particularly at these small ponds (cf. Crump and Vaira, 1991). Avoidance of spawning in ponds with high predator densities has been documented for some other anurans, e.g., for *Hyla chrysoscelis* under experimental conditions (Resetarits and Wilbur, 1989), but the cues used for searching, discriminating, and selecting remain unknown (Ritke and Mumme, 1993).

With the overwhelming importance of pond duration and desiccation for larval development in *Bombina variegata*, it is puzzling that the toads seem to pay only little attention to this factor and, on the other hand, use an environmental cue for egg distribution that is a poor predictor of reproductive success, namely temperature. This discrepancy may arise from both methodological and biological reasons. In terms of method, pond characterisitics were often measured at other than the spawning times. In quickly drying ponds, for instance, size at the time when surface measurements were taken, was often larger than size at the time of spawning. Also, some characteristics were averaged over longer periods and/or different parts of the pond. The finding that egg distribution within ponds was not uniform with respect to temperature, indicates that the pond may not be an adequate unit for characterizing spawning conditions. Spawning site selection within ecologically heterogeneous ponds has also been found in several other amphibians (Howard, 1978; Caldwell, 1986; Wollmuth et al., 1987; Sjögren et al., 1988; Waringer-Löschenkohl, 1988; Warkentin, 1992; Kuhn, 1993).

In terms of biology, pond conditions in our study area are highly unpredictable, because both water temperature and pond duration directly depend on weather conditions. A single heavy rainshower can lower temperatures and extend the duration of a pond by as much as three weeks; a few hot days, causing high evaporation, will result in warm water and can lead to complete desiccation, as seen during the exceptional droughts in July and August of 1991 and 1992 (Barandun and Reyer, in press). Although pond size and time of the season offer some information about pond conditions, these cues are far from being reliable. This is illustrated by the separation of *thermal conditions* (PC3) from most other pond characteristics and by the relatively low component loadings between pond duration and PC1 (*pond size*) and PC2 (*seasonality*), respectively. Under these conditions of unpredictability, spawning in warm ponds of intermediate duration will often result in total reproductive failure. Yet, when synchronized with heavy rainfall (Barandun and Reyer, in press) it will, on average, yield a higher fitness than spawning in cooler, permanent ponds where slow development and high predation rates are guaranteed.

Acknowledgements. We thank the many students and friends for their help in the field and B. Anholt, G. Guex, and R.D. Semlitsch for critical comments on the manuscript.

References

Aspey, W.P., Blankenship, J.E. (1977): Spiders and snails and statistical tails: Application of multivariate analysis to diverse ethological data. In: Quantitative Methods in the Study of Animal Behavior, p. 75-120. Hazlett, B.A., Ed., London, Academic Press.

Balthazart, J. (1973): Analyse factorielle du comportement agonistique ches *Tilapia machrochir* (Boulinger, 1912). Behaviour **46**: 37-72.

Banks, B., Beebee, T.J.C. (1987): Factors influencing breeding site choice by the pioneering amphibian *Bufo calamita*. Holarct. Ecol. **10**: 14-21.

Barandun, J., Reyer, H.-U. (in press): Reproductive ecology of *Bombina variegata*: development of eggs and larvae. J. Herpetol.

Bauer, S. (1987): Verbreitung und Situation der Amphibien und Reptilien in Baden-Württemberg. Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ. **41**: 71-157.

Caldwell, J.P. (1986): Selection of egg deposition sites: a seasonal shift in the southern Leopard frog, *Rana sphenocephala*. Copeia **1986**: 249-253.

Crump, M.L., Vaira, M. (1991). Vulnerability of *Pleurodema borelli* tadpoles to an avian predator: effect of body size and density. Herpetologica **47**: 316-321.

Duellman, W.E., Trueb, L. (1986): Biology of Amphibians. New York, McGraw-Hill.

Engelhardt, W. (1989): Was lebt in Tümpel, Bach und Weiher? Stuttgart, Franckh'sche Verlagshandlung.

Grossenbacher, K. (1988): Verbreitungsatlas der Amphibien der Schweiz. Doc. Faun. Helv., Basel, **7**: 207 p.

Howard, R.D. (1978): The influence of male-defended oviposition sites on early embryo mortality in bullfrogs. Ecology **59**: 789-798.

Kuhn, J. (1993): Fortpflanzungsbiologie der Erdkröte *Bufo b. bufo* (L.) in einer Wildflussaue. Z. Ökologie und Naturschutz **2**: 1-10.

Licht, L.E. (1974): Survival of embryos, tadpoles, and adults of the frogs *Rana pretiosa pretiosa* and *Rana aurora aurora* sympatric in southwestern British Columbia. Can. J. Zool. **52**: 613-627.

Newman, R.A. (1988): Adaptive plasticity in development of *Scaphoipus cochii* tadpoles in desert ponds. Evolution **42**: 774-783.

Pawlowska-Indyk, A. (1980): Effects of temperature on the embryonic development of *Bombina variegata* L. Zool. Pol. **27**: 397-407.

Resetarits, W.J.J., Wilbur, H.M. (1989): Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Evolution **70**: 220-228.

Riis, N. (1991): A field study of survival, growth, biomass and temperature dependence of *Rana dalmatina* and *Rana temporaria* larvae. Amphibia-Reptilia **12**: 229-243.

Ritke, M., Mumme, R.L. (1993): Choice of calling sites and oviposition sites by gray treefrogs (*Hyla chrysoscelis*) — a comment. Ecololgy **74**: 623-626.

Semlitsch, R.D., Reyer, H.-U. (1992): Modification of antipredator behaviour in tadpoles by environmental conditioning. J. Anim. Ecol. **61**: 353-360.

Sinsch, U. (1984): Thermal influences on the habitat preferences and the diurnal activity in three European *Rana* species. Oecologia **64**: 125-131.

Sjögren, P., Elmberg, J., Berglind, S.Å. (1988): Thermal preference in the pools frog *Rana lessonae*: impact on the reproductive behaviour of a northern fringe population. Holarct. Ecol. **11**: 178-184

Smith, D.C. (1983): Factors controlling tadpole populations of the chorous frog (*Pseudacris triseriata*) on Isle Royale, Michigan. Ecology **64**: 905-911.

Smith-Gill, S.J., Berven, K.A. (1979). Predicting amphibian metamorphosis. Am. Nat. **113**: 563-585.

Waringer-Löschenkohl, A. (1988): An experimental study of microhabitat selecion and microhabitat shifts in European tadpoles. Amphibia-Reptilia **9**: 219-236.

Warkentin, K.M. (1992): Microhabitat use and feeding rate variation in Green Frog tadpoles (*Rana clamitans*). Copeia **1992**: 731-741.

Williams, D.D. (1987): The ecology of temporary waters. Portland, Timber Press.

Wollmuth, L.P., Crawshaw, L.I., Forbes, R.B., Grahn, D.A. (1987): Temperature selection during development in a mountain anuran species, *Rana cascadae*. Physiol. Zool. **60**: 472-480.

Woodward, B.D. (1983): Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology **64**: 1549-1555.

Received: May 17, 1996. Accepted: August 5, 1996.