

The reproductive dynamics of temperate amphibians: a review

Tibor HARTEL¹, István SAS²,
Angelo P. PERNETTA³ and Ioana Cristina GELTSCH⁴

1. Mircea Eliade College, 1 Decembrie 1918 street, no.31, 545400 Sighișoara. E-mail: asobeka@yahoo.com
2. University of Oradea, Faculty of Sciences, Department of Biology, Universitatii str.1, Oradea 410087, Romania
3. Centre for Ecology and Hydrology, FBA East Stoke, Wareham, Dorset BH20 6BB, UK
4. Heisterbachstrasse 21, 531273 Bonn - Deutschland

Abstract. The annual life cycle of pond breeding amphibians is characterized by periodical migrations between three critical habitats: breeding, post breeding - feeding - and hibernating. The breeding season starts with the migration of the reproductive adults toward the breeding site and is characterized by intense manifestations in behavior and development of secondary sexual characters. Time spent in the water is strongly influenced by the outcome of success in courtship, insemination and/or fertilization. The aim of this review is to summarize some major findings of the main research directions regarding the reproductive dynamics of temperate (and especially European) amphibians. These are presented in detail for the most studied European species: *Triturus vulgaris*, *Bufo bufo*, *B. calamita* and *Rana temporaria*.

Key words: urodelans, anurans, sperm competition, explosive breeding, prolonged breeding

Introduction

Although many amphibian species are entirely aquatic or have completely terrestrial life stages (Duellman & Trueb 1986) the “typical” amphibian breeding pattern involves an aquatic phase. Pond breeding amphibians are characterized by a complex life cycle, having multiple developmental stages: egg, larvae, and post-metamorphic terrestrial or aquatic stages. The life of adults is characterized by periodical migrations between three critical habitats: breeding, summering (feeding) and hibernating. The breeding season starts with the migration of all

reproductive adults towards the breeding site and is characterized by intense manifestations in behavior (courtship and competition for mates, vocalization in anurans, egg deposition), physiology and morphology (development of secondary sexual characters in particular in males). The time spent in the water (breeding habitat) is strongly influenced by an individual’s success in courtship, insemination and/or fertilization.

The reproductive dynamics of different amphibian species have been well studied in Europe and elsewhere for a number of years. Therefore, the aim of this review is to summarize

some major findings of this research with respect to the reproductive dynamics of amphibians. Due to space restrictions many very interesting papers are not cited in this review, and therefore, in particular we focus on the most studied temperate (and European) amphibians. The main breeding systems are presented in detail in the case of the most studied species from Europe (*Triturus vulgaris*, *Bufo bufo*, *B. calamita*, *Rana temporaria*).

Under "reproductive dynamics" we consider all the events in the breeding area (terrestrial and aquatic), during the breeding season of amphibians, that are related to the probability of being a parent and influence the duration and intensity of the breeding period. These include a wide range of behavioral patterns, together with morphological and physiological changes in individuals during the reproductive stage.

The reproductive dynamics of pond breeding urodelans

Large inter- and intraspecific variations are found in the intensity and duration of breeding seasons and its annual occurrence in urodelans (Duellman & Trueb 1986). Much of this variation is caused by environmental factors such as the latitudinal and altitudinal variation of climate. In high latitudes reproduction tends to be seasonal, occurring in spring, whilst in lower latitudes reproduction may occur throughout the year (Halliday 1998). In high altitude *Triturus alpestris*

populations the cycle is biannual (Vilter & Vilter 1963). Table 1 presents the variation in three aspects of the reproductive system within European urodelans.

Typically, there is a variation in male and female arrival times at a breeding site. In the case of many North American species (*Taricha torosa*, *T. granulosa*, *Notophthalmus viridescens*, *Ambystoma talpoideum*, *Ambystoma tigrinum*, *Ambystoma jeffersonianum*) males arrive at the ponds before females (Halliday 1998, Gill 1978, Semlitsch *et al.* 1993, Douglas 1979, Scott 1993), whereas in the case of *Triturus* species in Europe, males and females arrive simultaneously at the breeding pond (Verrell & Halliday 1985, Halliday 1998).

The early migration of the males in the breeding ponds may expose them to death caused by low temperatures. Douglas (1979) argues that the advantages conferred to early migrating males, which arrive in the ponds before females, may counterbalance the risks of late arrival. The early arrival of the males in some species results in large male agglomerations and a sex ratio that is strongly male biased in the beginning of the reproduction period. The result of this is a large competition between the males for the females that begins as soon as females arrive. This competition leads to sexual selection. Such selection affects some morphological, behavioral and physiological traits that increase the competitive ability: body size, secondary sexual characters, breeding behavior *etc.*

(Douglas 1979, Green 1991, Halliday 1998, Baker & Halliday 2000, Denöel et al. 2001).

An early assumption of Halliday (1977) confirmed by experimental studies (e.g. Green 1991, Gabor & Halliday 1996), was that in some *Triturus* species the crest size is one of the principal morphological traits by which females choose the males. Other morphological characters (such as male body size) seems to be less important in influencing paternity in *T. alpestris*. Males of this species have a relatively simple courtship behaviour (compared with other species such as *T. cristatus* and *T. vulgaris*), that relies primarily on chemical communication (Garner & Schmidt 2003). In the case of urodelans that lack secondary sexual characters amplexus is used to immobilize the females before reproduction (*Euproctus* sp., *Pleurodeles* sp., *Salamandra* sp., *Ambystoma* sp., *Notophthalmus* sp., *Taricha* sp.) (ex. Steward 1969, Douglas 1979, Halliday 1998, Gabor et al. 2000). In these species the body size of the males is the principal trait affecting their reproductive success, with larger males having greater reproductive success. Male body size is often positively related to testis size - a factor that influences the amount of sperm transferred.

Intensity of sexual selection is often influenced by the environmental factors, with temperature thought to be the most important (see below). In *Ambystoma jeffersonianum* (North America), immigration into the breeding pond and egg deposition

intensity are hampered by low temperatures. The consequence of this is a longer immigration period that counterbalances emigration from the pond. This results in decreased competition between males for females and males emigrating soon after reproduction. In optimal temperature conditions the sex ratio is male biased in the pond at the beginning of the breeding period. This leads to intense male-male competition when females arrive. In these conditions males stays for a longer period of time in the breeding pond to increase the mating frequencies (Douglas 1979). Late reproduction may result in increased larval density, of resulting in the depletion of food and hindered larval development. This could delay the period of metamorphosis and cause massive larval mortality in late breeders if the pond has short hydroperiod (Morin et al. 1990).

Synchronous arrival of males and females into the breeding pond has also been reported in urodelans (see below). At least two selective forces can result in such synchronisation: (i) a decrease in the quality of the breeding ponds (high risk of total reproductive failure caused by pond desiccation) and (ii) the social behavior of reproductive adults, especially those linked with sperm competition. Both will be mentioned below. In the first case environmental conditions (external factors) select for synchronisation. Synchronisation of sexes is advantageous especially when the drying out of the pond is unpredictable. This was observed in the case

of North American species, *Notophthalmus perstriatus* by Dodd (1993). Breeding in synchronization with ponds filling, in conjunction with morpho-physiological adaptations such as the ability to accelerate larval development, may increase the chances of metamorphosis. There is strong evidence to show that sperm competition may be a decisive factor in modulating sexual behavior (causing synchronization), and the reproductive dynamics of urodelans belonging to the *Triturus* genera. Synchronization of sexes has been observed in *Triturus vulgaris* populations both in permanent (Verrell & Halliday 1985) and temporary ponds (Hartel 2001, Hartel *unpublished data*). This can be explained through the reproductive dynamics and sperm storage mode of *T. vulgaris* (Verrell & Halliday 1985, Sever *et al.* 1999, 2001). Verrell & Halliday (1985) found that females of *T. vulgaris* arrive at the breeding pond in larger numbers than males at the beginning of reproduction period. The egg laying period in *T. vulgaris* can last three months (Baker 1992). The main cause of the long duration of the egg laying period is the way in which eggs are deposited: females deposit each egg individually, packed in the leaves of vegetation. This egg wrapping behavior is characteristic of the females of the *Triturus* genera (*Triturus vulgaris*, *T. marmoratus*, *T. helveticus*, *T. alpestris*, *T. cristatus* etc.), and has a role in protecting eggs from both predators and UV-B radiation (Miaud 1995, Jacob *et al.* 1998, Marco *et al.* 2001). During the early breeding period

females mate with several males over a short period. The competitive interactions between males to obtain females are rare at the beginning of the breeding season, when the secondary sexual characters are not developed, but increase in intensity as the secondary sexual characters become more pronounced (Verrell & McGabe 1988). As the egg deposition begins, the females remain receptive only to males with well developed secondary sexual characters (especially large crests) (Green 1991, Gabor & Halliday 1997). Evidence shows that there is a last male advantage in *T. vulgaris*, with the probability of the last male siring a clutch being higher than that of the early males. Sever *et al.* (1999, 2001) firstly recognized that the mode of egg laying and the structure of the spermathecae results in sperm storage that allows sperm competition to occur (fig.1) and therefore may be responsible for the breeding phenology described above for *T. vulgaris*. It has been shown that sperm tend to fill the first tubules of the spermathecae (in the case of *T. vulgaris* the posterior tubules) situated far from the oviduct. These tubules are filled with sperm originating from different males, as the female pairs with them. The structure of the spermathecae make it possible for sperm coming from the last (more "fit") male to be closest to the oviduct and thus to fecund eggs. Thus, the last male (having well developed sexual characters), has a higher probability of siring young than the first males (with less developed sexual characters). Another

cause of multiple mating of females during a breeding season may be the replacement of deteriorated sperm, which is absorbed by the spermathecae (spermiophagy; Sever et al.

1999). Moreover, multiple mating may be the consequence of low fertilization rates in eggs in *Triturus* (Halliday 1998).

Table no.1 Comparison of the reproductive systems of European urodelans

Group	Sexual dimorphism	Courtship/ Amplexus	Fertilization, egg deposition
Hynobiidae	Loosely distinguishable	Courtship	External fertilization, after the eggs are deposited in the water
Salamandridae	Loosely distinguishable in <i>Salamandra</i> , <i>Chioglossa</i> , <i>Salamandrina</i> , <i>Pleurodeles</i> .	Amplexus	Internal fertilization (spermatheca) - live born young (<i>Salamandra</i>)
	Well developed in <i>Triturus</i> (males: crests, size)	Courtship	- eggs laid in the water (<i>Triturus</i> , <i>Chioglossa</i> , <i>Pleurodeles</i> , <i>Salamandrina</i>)
Plethodontidae	Loosely distinguishable	Amplexus	Internal fertilization, eggs laid in terrestrial habitats
Proteidae	Males have an enlarged cloaca during the breeding season	Courtship	Internal fertilization, eggs laid in the water

Few studies have attempted to explain the role of environmental conditions in modulating egg deposition rate in *T. vulgaris*. Experimental studies have shown that females that reproduce in temporary ponds (and probably metamorphosed in these ponds) lays fewer eggs than those depositing in permanent ponds. Analysis of the ovaries shows that females depositing in temporary ponds do not deposit all the eggs, the

egg laying process stops at a certain moment (Cogălniceanu 1999). A new short egg deposition period could be triggered by injecting human chorionic gonadotropin (HCG). Experimental studies show that females have a higher susceptibility towards HCG during the early period of the egg deposition (Hartel & Cogălniceanu 2005). The parameters describing egg deposition differed between newts originating from highly unpredictable

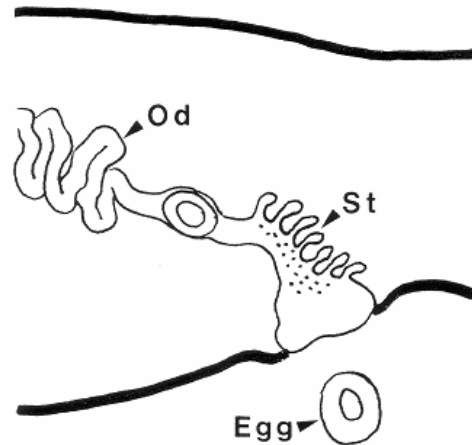
environments (flooded areas, temporary ponds) and more stable environments (permanent ponds). In temporary ponds with a high risk of desiccation the end of oviposition is probably triggered by a decrease in hormones induced by environmental factors (Hartel & Cogălniceanu 2005). Recent field observations show that female *T. vulgaris* arrive in the ponds and deposit even after a short (up to two weeks) desiccation period in May (Hartel *personal observations*). The long egg deposition period in newts (lasting from April to the second part of June in the Târnava Mare Valley) probably

allow a temporary cessation of egg laying if the pond desiccates.

The reproductive dynamic of anurans

Wells (1977) distinguishes two breeding systems in anurans: *explosive breeding* and *prolonged breeding* systems. These two categories represent two ends of a continuum, ranging from Reproduction occurring during a single night in some species to the reproduction covering several months in other species (Wells 1977).

Figure no.1
The structure of the spermathecae in *Triturus v. vulgaris*.
Ov = oviduct, St = spermathecae.
After Sever et al. (1999).



1. Explosive breeding

Explosive breeding is characterized by a large agglomeration in and/or near the breeding sites and a short breeding period (days to weeks). Explosive breeding is characteristic of many anurans from the temperate

region: *Bufo*idae, *Rana*idae, *Pelobatidae* (Van Gelder & Hoedemaekers 1971, Oldham 1974, Gittins et al. 1980, Elmberg 1990, Kusano & Fukuyama 1989).

The males of many explosive breeder species form a chorus at the breeding site. Wells (1977) proposed a

speculative hypothesis regarding the role of chorus in the female's attraction. He suggested that the calls are largely overlapping due to the high density of males, which results in reduced female attraction to the calls of individual males. Another possibility is that the chorus made by several males attracts the females to the reproduction site, and after the female arrival the male-male competition will decide the reproductive potential of individual males. In other species with explosive breeding system the male vocalization does not appear to be important in female attraction to individual males (Oldham 1974).

The pre-reproductive period (the period between the first chorus and the first egg mass [Hartel 2005]) is relatively short in explosive breeders in Europe. Strömberg (1988), in a seven year study of a Swedish population of *Rana dalmatina*, found an average of one day between the first call and the first egg mass. He found that in two years the first egg mass appeared four and 11 days before the first chorus. Elmberg (1990) found an average pre-spawning period of 5.4 days in *R. temporaria* during a 10 year study (Sweden). Figure 2 shows our results gathered over 10 years in the Târnava Mare Valley, for *R. dalmatina*, *R. temporaria* and *B. bufo*. These examples show that the egg deposition period begins soon after, or in some cases even before, the chorus activity of males, suggesting that it plays an insignificant role in female attraction to the breeding ponds. In all three

species, the vocalization of males is relatively silent. It was showed that in *R. temporaria* the calling behaviour depends on the energy reserves that remain after the hibernation period and so calling may be completely absent if the energy reserves have depleted after a very long winter (Elmberg 1990, Elmberg & Lundberg 1991). We hypothesize that male vocalization in such circumstances (when the breeding activity of the males is limited by the low energy reserves after hibernation) may be a "sign" of male fitness and increase the mating probability of the calling male. This could lead to sexual selection if the female approaching a calling male is not "caught" by a "silent" satellite male.

The males of many explosive breeders have indiscriminate pairing behaviour during the breeding season. Typical examples are the common toad and the common frog, in which males may grab any object in the water that are of similar size to a female, females belonging to other species or even conspecific males (Wells 1977, Reading 1984). In the case of pairing with conspecific males, male vocalizations have a role in intraspecific recognition, resulting in release of the clasped male (release calls) (Di Tada *et al.* 2001).

Territoriality could be present in some explosive breeders (*B. americanus*, *R. temporaria*, *R. dalmatina*) (Licht 1976, Elmberg 1986, Lode & Lesbarreres 2004). An interesting topic of research could be the effect of male density on their territorial behaviour.

It was reported that male common toads at low densities show a behaviour similar to territoriality, and

with increasing male density they begin an active search for females (Wells 1977).

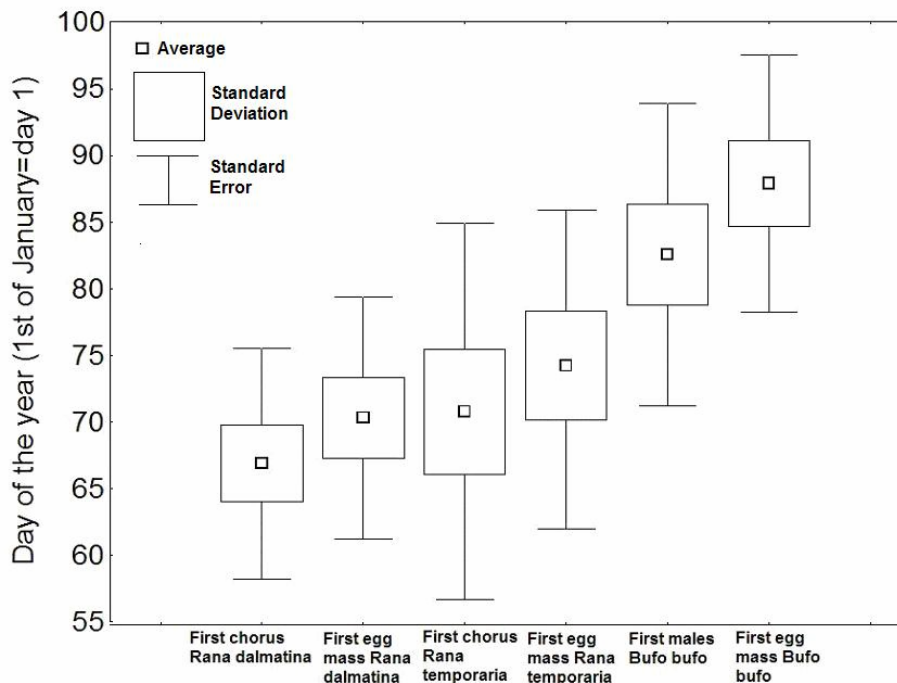


Figure no.2 The variation in the beginning of chorusing and egg deposition periods in three anurans from the middle section of Tárnava Mare Valley.

In explosive breeders there is a strongly male biased sex ratio in the breeding population (Wells 1977, Davies & Halliday, 1979, Gittins *et al.* 1980). Reading (1991) assumed that in the common toad the sex ratio after metamorphosis is equal, and it may be distorted by environmental factors such as temperature. The sex ratio may be male-biased for several reasons: (i) Males breed yearly but the females do

not, because the eggs are energetically more costly to produce than sperm (Reading 1988, Halliday 1994). (ii) Males reach sexual maturity at 2 - 3 years whilst the females are not sexually mature until their fourth year. Both males and females may have a minimal body length at which they reach sexual maturity, and the males are typically smaller than females at sexual maturity (Reading 1991).

However the body size at which sexual maturity is reached is not fixed and could vary between populations (Reading 1988). (iii) The males reach breeding ponds earlier and spend more time there than females (Davies & Halliday 1979, Gittins et al. 1980, Loman & Madsen 1986). (iv) Winter mortality may be higher in females than in males (Kuhn 1994, Reading 2001). Only a few studies examine some of the above presented hypotheses (i-iv) and not all confirm those assumed by Reading (see above) for the common toad. Elmberg (1991) found that females of *R. temporaria* breeds annually even in high altitude mountains, suggesting that the male biased sex ratio in the breeding population is not caused by the differences of the breeding frequencies of the two sexes.

Pairs of explosive breeders may be formed randomly or nonrandomly. It could be a large intraspecific and inter populational variation in the amplexant male-female size correlations. In common toads (*Bufo bufo*) the correlation between the SVL (snout-vent length) of the amplexant adult common toads was found to be positive and significant in English populations (Gittins et al. 1980, Reading & Clarke 1983), but not in a Swedish population (Loman & Madsen 1986). These differences could be explained by the fact that females only stay in the water for a short period of time in the Swedish population, and for a longer period in the populations from England (Loman & Madsen 1986). Similarly, Hartel &

Demeter (2005) found no significant correlation between the body length of paired males and females in a Romanian common toad population. Moreover no significant difference between the SVL of paired and unpaired males was found (Hartel & Demeter 2005). Davies & Halliday (1979) found that the largest male common toads are stronger than the smaller ones and this can result in larger males having more opportunities to obtain females by takeovers. Studies regarding male mate choice in *B. bufo* shows contradictory results: no preference for larger females (Marco & Lizana 2002) or the presence of mate choice (Arntzen 1999). Hettyei *et al.* (2005) found that male *R. dalmatina* does not show preference for larger females during the breeding season. From the previously cited studies, it can be concluded that sexual selection may be under the influence of some localised (maybe demographic) factors and more studies should be conducted to find out what circumstances influence the male mating behaviour in explosive breeders.

There is no general finding about the relationship between the arrival time (early or late in breeding season) and the size of male toads. Some studies suggest that larger (older) males arrive earlier (Loman & Madsen 1986) whereas others report an earlier migration of smaller males (Gittins *et al.* 1980). Individual body size (Davies & Halliday 1979) and previous experience (Reading 2001) seem to be important determinants of the male mating success in the common toad.

Males may temporarily retreat from the breeding pond to search for potential mates on the surrounding terrestrial habitats. Populational differences were found regarding this behaviour of males: 29% in England (Reading & Clarke 1983) and 2% in Sweden (Loman & Madsen 1986). These examples regarding the common toad shows that the breeding system of explosive breeders may be flexible. Further long-term studies examining the yearly, age and population size specific variation in the reproductive strategies used by males from the same population are required.

It is not known, how male density influences the mate choice behaviour of females. If several males clasp a single female (as Fig. 3 shows in *Bufo bufo*), the female could be seriously injured and even killed. It has been shown that an increased frequency of takeovers may cause a reduction in the number of offspring (Halliday 1998). It could be expected that reproductive females avoid areas with large male densities in the case of common toad. Studies that examine the behaviour of the females when the males are present in different densities are scarce. Generally, larger males may have larger reproductive success if the male density is high (these being at a size advantage). A further question is to what extent the large males contribute to an increase in the offsprings fitness. Only one study is available for *B. bufo* in this respect. Semlitsch (1994) found that the fitness of offspring of larger males is not

greater than that of small males. If so, the "sexual selection" observed in the common toads resulted only from the male size (and thus the powerfullness) of males and has no role in transmitting "good" genes.

The male biased sex ratio in the breeding population and the advantages of larger males in pairings (takeovers) does not allow all males to breed. Multiple paternity may be a common phenomenon in explosive breeding anurans but studies that examine this are scarce (Laurila & Seppa 1998, Lode & Lesbarreres 2004, Vieites et al. 2004). Recent studies shows that the fertilization success of "satellite males" (i.e. those that fail to pair due to sexual selection) could be high (D'Orgeix & Turner 1995, Laurila & Seppa 1998, Lode & Lesbarreres 2004). A recent study of a montane population of *R. temporaria* has shown explosive breeding amphibians to utilise a behaviour previously unknown in vertebrates with external fertilization (Vieites et al. 2004): egg cluth piracy was first reported in a. "Pirate" males search for freshly laid clutches, and clasp them in the same manner as would be used on a female, and successfully fertilize the eggs. The fertilization by satellite males may act against sexual selection (Vieites et al. 2004). These data show that the explosive breeding system, although of short duration, could be very efficient and could assure high genetic variation in offspring. Similar behaviour of *R. temporaria* males was observed in the Ciuc basin recently (Demeter & Benkő 2007).



Figure no.3 Several males clasping a female (above) may result in injuries that lead to death of the female (below). This occurs frequently in *Bufo bufo* (Photo T. Hartel, Şercheş pond, Sighişoara)

2. Prolonged breeding

Prolonged breeding is characterized by extended breeding periods. Contrary to many explosive breeder species, prolonged breeder males use vocalization efficiently to delimit territories and attract females to a breeding site. Females are able to detect and select males on the basis of vocalization. It was assumed that clasping different objects and individuals from other species by prolonged breeder males (see Anexes 1, 2 și 3 from Wells 1977) is rare (Wells 1977, but see Fig. 4) and the direct competition between them happens only occasionally. In *Bombina variegata* however, direct competition was observed frequently (Hartel *personal observations*).

The most "typical" and most studied representative of the prolonged breeding system in Central-European anurans is the natterjack toad (*Bufo calamita*). Males of this species form a chorus in the breeding pond to attract females (but also other males). Females arrive at the ponds to breed and emigrate immediately afterwards (Sinsch 1988). The subdivision of the breeding period into two or three seasons seems to be a general feature of the reproductive behaviour of this species: two egg deposition peaks were reported in Sweden (May and July) (Andren & Nilson 1985) and England (April and June) (Denton & Beebee 1993) and three peaks in Germany (April-middle May, the second part of May- first part

of July, and middle July-August) (Sinsch 1988). Vocalization is an important determinant of reproductive success of males in some *B. calamita* populations. Calling males having two times higher reproductive success than silent males (Sinsch 1992). A strong correlation between the amount of male calling and its attractiveness (Denton & Beebee 1993). Females never arrive before chorus formation, and usually only arrive following three to seven days of chorus activity by males (Sinsch 1992). There is evidence that reproductive success may be independent of male calling activity in small, stressed populations (Stevens *et al.* 2003).

Males may use at least two strategies to obtain a mate: the resident males choose a pond and call from it, whereas the switchers move between ponds. The males from the latter category have a higher reproductive success (Denton & Beebee 1993). No correlation was found between the body size of males and their success in finding a mate (Denton & Beebee 1993).

A recapture study conducted in the central part of the Tarnava Mare basin (Hartel *et al.* 2007, Hartel *unpublished data*) on *B. variegata* shows that males of this prolonged breeder also use different strategies to obtain a mate. These strategies seem to be correlated with the female pond preference, that is linked to the temporary pond availability (that ultimately depends on the precipitation). In dry years there are few available ponds for

reproduction and the females tend to be more residential, using the most stable ponds for reproduction. In rainy years, the female yellow bellied toads uses more ponds for reproduction including those with ephemeral characters (Hartel et al. 2007). We have observed that males migrate more frequently between ponds in dry years, whereas the proportion of residents is higher in rainy years. We

suggest this is a strategy to increase the probability to finding a mate: being resident in a period when most of females are searching for new ponds (in rainy years) could be more advantageous than being migrating. However a large percentage of males were found to be migrating in rainy years as well (Hartel, unpublished data).



Figure no.4 A male *Bombina variegata* clasping a female *Hyla arborea*. No interspecific spawning was observed (Photo T. Hartel, Breite, Sighișoara).

The *temporal populations* represent a less studied aspect of prolonged breeders reproductive biology. Such populations were identified by Sinsch (1992, 1997) in a natterjack population from Germany. Genetic studies show that temporal populations within the local *B. calamita* population "behave" as individual populations having their

own gene pools. The persistence of different gene pools of different temporal populations requires the following three conditions (Sinsch 1992, 1997, Sinsch & Seidel 1995): (i) synchronization of breeding by the majority of individuals in successive years, (ii) the reproductive success of individuals within a year should be

limited to one breeding period and (iii) the first breeding adults must originate from the same cohort as their parents (no "gene flow" between cohorts). All three conditions mentioned above were fulfilled by a natterjack population studied in Germany (Sinsh & Seidel 1995, Sinsch 1997). These results shows that the temporal pattern of the breeding activity is genetically determined in that natterjack toad population (Sinsch 1992, 1997). The existence of temporal populations in natterjack toads shows how complex the spatial and temporal interactions between populations can be.

The partition of the breeding season in several cohorts triggered by rainfall is considered an adaptive reproductive strategy in *Bombina variegata* (Barandun 1992, Barandun & Reyer 1997a, b, 1998, Gollmann *et al.* 1998): the reproductive success (i.e. the survival of larvae) could be increased if reproduction starts immediately after the ponds begin filling. This is possible because *B. variegata* females show continuous egg development (Böll 2002). The reproductive phenology of a *Bombina variegata* population was studied by Hartel *et al.* (2007) from 2003 to 2005. They found a considerable variation in the number of ponds available for reproduction, both within season, and throughout the years. In 2003 there were two clearly distinguishable spawning periods: the first spawning period was between 25th of April - 10th of May and the second between 25th of July - 7th of August. In 2004 there were three

loosely distinguishable spawning periods, all covering 42 days: the first spawning period lasts between 18th of April - 6th of May, the second between 20th of June - 6th of July and the third between 21st of July - 8th of July. Observations from 2004 (Hartel *et al.* 2007) and 2006 (Hartel *personal observations*) suggest that the egg deposition periods are not always preceded by an increase in the amount of rainfall and that the egg deposition could be under endocrine control in *B. variegata*.

It should be mentioned that there are species considered "explosive breeders" that have high reproductive success in temporary ponds but have only one breeding season per year (such as *R. temporaria*). In this case physiological adaptations such as quick development of eggs and larvae and phenotypic plasticity of the larvae, have a role in escaping from drying ponds (e.g. Newman 1992, Laurila & Kujasalo 1999).

Conclusions and further research directions

The main research directions on amphibian's reproductive dynamics in Europe have been well established for several years. In both groups emphasis has been made on the role of environmental conditions in determining the intensity of the breeding migration. However, we still lack specific information for a number of species and many interesting research topics are not comprehensively

studied. Considering the wide range of habitat types in Romania we believe that significant contributions can be made from this side of Europe towards identifying the role environmental conditions play in determining intraspecific variation in the reproductive strategies.

The link between the structural complexity of the spermathecae and the breeding phenology and sexual selection in newts is not studied in detail. We lack experimental and field studies examining the environmental control of egg deposition in newts and the hormones involved. As some newt species (such are *T. vulgaris*, *T. cristatus*) have a wide altitudinal distribution in Romania, it is possible that different strategies are used by lowland populations compared to those at higher altitudes.

The energy allocation in eggs (egg number versus clutch size) has not been studied in detail. This would be particularly interesting in the case of the yellow bellied toads that inhabit temporary breeding ponds and reproduce up to three times before the second part of the summer. It can be expected that the allocation index will be larger in the second/third egg laying period. If this occurs (the logic being: larger eggs, larger tadpoles, shorter larval period) it would be beneficial since the winter can cause mass mortality in this species, in the late larval cohorts. We suggest field and laboratory experiments in this direction.

The temporal spacing of the breeding activity in explosive and

prolonged breeders is still not studied. It would be worth studying the course of breeding in altitudinal gradients and hydroperiod gradient in different amphibian species because amphibians may represent interesting and less known adaptations to these gradients.

Climate change (including global warming, often associated with long periods of drought or other changes in rainfall patterns) may have a wide range of effects on the breeding phenology of temperate amphibians (i.e. Tryjanovski et al. 2003) and may limit energy intake, affecting both fecundity and fat deposition needed to overwinter, and thus result in decreased reproduction and survivorship potential (Reading, 2007). Further studies should be conducted to find how the phenology of the breeding and habitat use of amphibians in Romania is related to the climatic conditions.

We suggest studying the different aspects of the reproductive dynamic, especially the breeding phenology, correlated with the aquatic habitat and landscape features. Data in this direction are scarce in Europe but recent studies (for example Jacob et al. 2003) suggest that they may be useful in elaborating management plans for amphibians and their habitats.

The above mentioned research directions are relatively easy to conduct in Romania and could significantly contribute to increase of our knowledge on this vertebrata group.

Acknowledgements. We would like to thank Dan Cogălniceanu for comments on an earlier version of the manuscript. Wiley-Liss, Inc. a subsidiary of John Wiley & Sons, Inc. permitted the reprint of the Figure 1.

References

- Andren, C., Nilsson, G. (1985): Breeding pool characteristics and reproduction in an island population of natterjack toads *Bufo calamita* Laur., at the Swedish west coast. *Amphibia-Reptilia* 6: 137-142.
- Arntzen J.W. (1999): Sexual selection and mate choice in the common toad, *Bufo bufo*. *Ethology Ecology & Evolution* 11: 407-414.
- Baker, J.M.R. (1992): Egg production in the smooth newt (*Triturus vulgaris*). *Herpetological Journal* 2: 90-93.
- Baker, J.M.R. and Halliday, T.R. (2000): Variation in dorsal crest morphology and tail height with age in great crested newt (*Triturus cristatus*). *Herpetological Journal* 10: 173-176.
- Barandun, J., and Reyer, H.-U. (1997): Reproductive ecology of *Bombina variegata*: development of eggs and larvae. *Journal of Herpetology* 31: 107-110.
- Barandun, J., and Reyer, H.-U. (1998): Reproductive Ecology of *Bombina variegata*: habitat use. *Copeia* 2: 497-500.
- Böll, S. (2002): Ephemere Laichgewässer: Anpassungsstrategien und physiologische Zwänge der Gelbbauchunke (*Bombina variegata*) in einem Lebensraum mit unvorhersehbarem Austrocknungsrisiko. PhD Thesis, Julius-Maximilians-Universität Würzburg.
- Cogălniceanu, D. (1999): Egg deposition strategies of the Smooth newt (*Triturus vulgaris*) in an unpredictable environment. *Herpetological Journal* 9: 119-123.
- Crump, M. L. (1974): Reproductive strategies in a tropical anuran community. University of Kansas, 68 pp.
- Crump, M. L. (1982): Amphibian reproductive ecology on the community level. Pp. 21-35 in N. J. Scott Jr. ed. *Herpetological communities: a symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists` League*, August 1977, U.S. Fish and Wildlife Service, Wildl. Res. Rep. 13. 239 pp.
- Davies, N.B., and Halliday, T.R. (1979): Competitive mate searching in male common toads *Bufo bufo*. *Animal Behaviour* 27: 1253-1267.
- Demeter, L., Benkő, Z. (2007): Male *Rana temporaria* in amplexus with a clutch. *North - Western Journal of Zoology* 3 (2): 105-108
- Denöel, M., P. Poncin, and Ruwet J.-C. (2001): Alternative mating tactics in the alpine newt *Triturus alpestris alpestris*. *Journal of Herpetology* 35: 62-67.
- Denton, J. S. and Beebee, T. J. C. (1993). Reproductive strategies in a female biased population of natterjack toads *Bufo calamita*. *Animal Behaviour* 46: 1169-1175.
- Di Tada, I.E., Martino, A. and Sinsch, U. (2001): Release vocalizations in neotropical toads (*Bufo*): ecological constraints and phylogenetic implications. *Journal of Zoological Systematics and Evolutionary Research* 39: 13-23.
- Dodd, C.K. Jr. (1993): Cost of Living in Unpredictable Environment: The Ecology of Striped Newts *Notophthalmus perstriatus* during a Prolonged Drought. *Copeia* 3: 605-614.
- D'Orgeix, C.A., Turner, B.J. (1995): Multiple paternity in the red eyed treefrog *Agalychnis callidryas* (Cope). *Molecular Ecology* 4: 505-508.
- Douglas, M. E. (1979): Migration and sexual selection in *Ambystoma jeffersonianum*. *Canadian Journal of Zoology* 57: 2303-2310.
- Douglas, M. E. and Monroe, B.L. (1981): A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). *Copeia* 1981: 460-463.
- Duellman, W.E. (1992): Utódnevelés a békáknál. *Tudomány*: 50-57.
- Duellman, W.E., and Trueb, L. (1986): *The Biology of Amphibians*. Baltimore and London. John Hopkins Press.
- Elmberg, J. (1986): Apparent lack of territoriality during the breeding season in a boreal population of common frogs *Rana temporaria*. *Herpetological Journal* 1: 81-85.
- Elmberg, J. (1987): Random mating in a boreal population of European common frogs *Rana temporaria*. *Holarctic Ecology* 10: 193-195.
- Elmberg, J. (1990): Long - term survival, length of breeding season, and operational sex ratio

- in a boreal population of common frogs, *Rana temporaria* L. Canadian Journal of Zoology 68: 121 - 127.
- Elmberg, J. (1991): Ovarian cyclicity and fecundity in boreal common frogs *Rana temporaria* L. along a climatic gradient. Functional Ecology 5: 340-350.
- Elmberg, J., and Lundberg, P. (1991): Intraspecific variation in calling, time allocation and energy reserves in breeding male common frogs *Rana temporaria*. Annales Zoologici Fennici 28: 23-29.
- Gabor, C.R. and Halliday, T.R. (1996): Sequential mate choice by multiply mating smooth newts: females became more choosy. Behavioural Ecology 8: 162-166.
- Gabor, C.R., Krenz, J.D. and Jaeger, R.D. (2000): Female choice, male interference, and sperm precedence in the red spotted newt. Behavioural Ecology 1: 115-124.
- Garner, T.W.J. and Schmidt, B. (2003): Relatedness, body size and paternity in the alpine newt, *Triturus alpestris*. Proceedings of the Royal Society of London 270: 619-624.
- Gill, D. E. (1978): The metapopulation ecology of the red spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48: 145-166.
- Gittins, S.P., A.G. Parker and F.M. Slater. (1980): Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in Mid-Wales. Journal of Animal Ecology 49: 161-173.
- Gollmann G, Gollmann B., & Baumgartner C. (1998): Oviposition of yellow bellied toads *Bombina variegata* in contrasting water bodies. Pp. 139-145. In: Miaud, C. & Guyetant R. (eds), Le Burget du Lac, SEH.
- Green, A.J. (1991): Large male crests, an honest indicator of condition, are preferred by female smooth newts, *Triturus vulgaris* (Salamandridae) at the spermatophore transfer stage. Animal Behaviour 41: 367-369.
- Halliday, T.R. (1977): The courtship of european newts: an evolutionary perspective. Pp 185-232. In Taylor, D.H. and S.I. Guttman (eds.): The reproductive biology of amphibians. Plenum, New York.
- Halliday, T. (1994): Sex and evolution. Pp. 465-502. In Slater P.J.B. and Halliday T.R. (eds.): Behaviour and Evolution. Cambridge University Press.
- Halliday, T. 1998. Sperm competition in amphibians. Pp 465-502. In Sperm competition and sexual selection, Academic press.
- Hartel, T. (2003a): Data on the activity in the breeding period of the smooth newt (*Triturus vulgaris*) in two temporary ponds in Târnava Mare Valley. Acta Siculica 1: 57-64. (in Romanian with English abstract).
- Hartel, T. (2003b): The breeding biology of the frog *Rana dalmatina* in Tarnava Mare Valley Romania. Russian Journal of Herpetology 10: 169-175.
- Hartel, T. (2004): The long-term trend and the distribution of amphibian populations in a seminatural pond in the middle section of the Târnava-Mare Valley (Romania). Biota - Journal of Biology and Ecology 4/1-2: 25-36.
- Hartel, T. (2005): Aspects of breeding activity of *Rana dalmatina* and *Rana temporaria* reproducing in a seminatural pond. North-Western Journal of Zoology 1: 5-13.
- Hartel, T., Cogălniceanu, D. (2005): Experimental study of the hormonal control of egg deposition in *Triturus vulgaris*. Scientific Annals of the Danube Delta Institute 11: 34 - 38.
- Hartel, T., Demeter, L. (2005): The breeding migration and population characteristics of a common toad (*Bufo bufo*) population in Târnava Valley, Romania. Transylvanian Review of Ecological and Systematical Research 2: 145-154.
- Hartel, T., Nemes, Sz., Mara, Gy. (2007): Breeding phenology and the spatio-temporal dynamic of pond use by a yellow-bellied toad population (*Bombina variegata*): the importance of pond availability and duration. Acta Zoologica Lituanica 17: 56-63.
- Hettyei, A., Török, J., and Hévízi, G. (2005): Male mate choice lacking in the agile frog, *Rana dalmatina*. Copeia 2: 403-408.
- Jacob, C., Hoffmann, O., Braun, C., Crivelli, A.J., and Veith, M. (1998): Characteristics of intra-pool egg deposition of *Triturus marmoratus* (Latreille, 1800) and *T. helveticus* (Razoumowski, 1789). Pp 215-219. In Miaud, C. and R. Guyetant (eds.): Current Studies in Herpetology. Le burget du lac/France - SHE.
- Jacob, C., Poizat, G., Veith, M., Seitz, A., Crivelli, A.J. 2003. Breeding phenology and larval distribution of amphibians in a Mediterranean

- pond network with unpredictable Hydrology. *Hydrobiologia* 499: 51-61.
- Kusano, T. and Fukuyama, K. 1989. Breeding activity of a stream – breeding frog (*Rana* sp.). *Current herpetology in East Asia*: 314-322.
- Laurila, A. and Kujasalo, J. (1999): Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. *Journal of Animal Ecology* 68: 1123-1132.
- Laurila, A., and Seppä P. (1998): Multiple paternity in the common frog (*Rana temporaria*): genetic evidence from tadpole kin groups. *Biological Journal of Linnean Society* 63: 221-232.
- Licht, D.E. (1976): Sexual selection in toads (*Bufo americanus*). *Canadian Journal of Zoology* 54: 1277-1284.
- Lode, T. and Lesbarreres, D. (2004): Multiple paternity in *Rana dalmatina*, a monogamous territorial breeding anuran. *Naturwissenschaften* 91: 44-47.
- Loman, J., and Madsen, T. (1986): Reproductive tactics of large and small male toads *Bufo bufo*. *Oikos* 46: 57-61.
- Marco, A. and Lizana, M. (2002): The absence of species and sex recognition during mate search by male common toads, *Bufo bufo*. *Ethology Ecology and Evolution* 14: 1-8.
- Marco, A., Lizana, M., Alvarez, A., Blaustein, A. (2001): Egg-warpping behaviour protects newt embryos from UV radiation. *Animal Behaviour* 61: 630-644.
- Marsh, D.M. and Trenham, P.C. (2001): Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15: 40-49.
- Miaud, C. (1995): Oviposition site selection in three species of European Newts (Salamandridae) genus *Triturus*. *Amphibian-Reptilia* 16: 265-272.
- Miaud C. and Merila, J. (2001): Local adaptation or environmental induction: causes of population differentiation in alpine amphibians. *Biota* 2: 131-58.
- Miaud, C., Sanui, D., and Avriller, J.-N. (2000): Terrestrial movements of the natterjack toad *Bufo calamita* (Amphibia, Anura) in a semi-arid, agricultural landscape. *Amphibia-Reptilia* 21: 357-369.
- Morin, P.J., Lawler, S. P., and Johnson, E.A. (1990): Ecology and breeding phenology of larval *Hyla andersonii*: the disadvantages of breeding late. *Ecology* 71: 1590-1698.
- Newman R. A. (1992): Adaptive plasticity in amphibian metamorphosis. *BioScience* 42: 671 – 678.
- Oldham, R.S. (1974): Mate attraction by Vocalization in members of the *Rana pipiens* complex. *Copeia* 4: 982-984.
- Reading, C.J. (1984): Interspecific spawning between common frogs (*Rana temporaria*) and common toads (*Bufo bufo*). *Journal of Zoology London* 203: 95-101.
- Reading, C.J. (1988): Growth and age at sexual maturity in common toads (*Bufo bufo*) from two sites in Southern England. *Amphibia-Reptilia* 9: 277-288.
- Reading, C.J. (1991): The relationship between body length, age and sexual maturity in the common toad, *Bufo bufo*. *Holarctic Ecology* 14: 245-249.
- Reading C.J. (1998): The effect of winter temperature on the timing of breeding activity in the common toad, *Bufo bufo*. *Oecologia* 117: 469-475.
- Reading, C. J. (2001): Non-random pairing with respect to past breeding experience in the common toad (*Bufo bufo*). *Journal of Zoology (London)* 255: 511-518.
- Reading, C.J. and Clarke, R.T. (1983). Male breeding behaviour and mate acquisition in the common toad, *Bufo bufo* L. *Journal of Zoology (London)* 201: 237-246.
- Reading, C.J., Loman, J., and Madsen, T. (1991): Breeding pond fidelity in the common toad, *Bufo bufo*. *Journal of Zoology (London)* 225: 201-211.
- Reading, C.J. (2007): Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* 151: 125-131.
- Roberts, W. (1994): Explosive breeding aggregations and parachuting in a neotropical frog *Agalychnis saltator* (Hylidae). *Journal of Herpetology* 28: 193-199.
- Scott, D. E. (1993): Timing of reproduction of paedomorphic and metamorphic *Ambystoma talpoideum*. *American Midland Naturalist* 129: 397-402.
- Semlitsch, R.D. (1994): Evolutionary consequences of non-random mating: do large males increase offspring fitness in the

- anuran *Bufo bufo*? Behaviour, Ecology and Sociobiology 34: 19-24.
- Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W. (1993): Phenotypic variation in the arrival time of breeding salamanders: individual repeatability and environmental influences. *Journal of Animal Ecology* 62: 334-340.
- Sever, D.M. (2002): Female sperm storage in amphibians. *Journal of Experimental Zoology* 292: 165-179.
- Sever, D.M. and Brizzi, R. (1998). Comparative biology of sperm storage in female salamanders. *Journal of Experimental Zoology* 282: 460-476.
- Sever, D.M., Halliday, T., Waights, V., Brown, J., Davies, H.A., Moriarty, E.C. (1999): Sperm storage in females of the smooth newt (*Triturus v. vulgaris*): I. Ultrastructure of the spermathecae during the breeding season. *Journal of Experimental Zoology* 283: 51-70.
- Sever, D.M., Halliday, T., Moriarty, E. C., and Arano B. (2001): Sperm storage in females of the smooth newt (*Triturus v. vulgaris*): II. Ultrastructure of the spermathecae after the breeding season. *Acta Zoologica* 82: 49-56.
- Sinsch, U. (1988): Temporal spacing of breeding activity in the natterjack toad, *Bufo calamita*. *Oecologia* 76: 399-407.
- Sinsch, U. (1992): Structure and dynamic of a natterjack toad metapopulation (*Bufo calamita*). *Oecologia* 90: 489-499.
- Sinsch, U. (1997): Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. *Oecologia* 112: 42-47.
- Sinsch, U., and Seidel, D. (1995): Dynamics of local and temporary breeding assemblages in a *Bufo calamita* metapopulation. *Australian Journal of Ecology* 20: 351-361.
- Sofianidou Th.S. and Kyriakopoulou-Sklavounou, P. (1983): Studies on the biology of the frog, *Rana dalmatina*, Bonap. during the breeding season in Greece. *Amphibia-Reptilia* 4: 125-136.
- Stevens, V. M., Wesseling, R.A., and Baguette, M. (2003): Demographic processes in a small, isolated population of natterjack toads (*Bufo calamita*) in southern Belgium. *Herpetological Journal* 12: 59-67.
- Steward, J. W. 1969. The tailed amphibians of Europe. David & Charles: Newton Abbot.
- Strömberg G. (1988): A study of the jumping frog (*Rana dalmatina*) in Blekinge, Sweden, 1982-1988. *Memoranda Societatis pro Fauna et Flora Fennica* 64: 107-109.
- Tryjanovski, I.P., Rybacki, M., Sparks, T. (2003): Changes in the first spawning dates of common frogs and toads in western Poland in 1978-2002. *Annales Zoologici Fennici* 40: 459-464.
- Van Gelder, J. J., and Hoedemaekers, H.C.M. (1971): Sound activity and migration during the breeding period of *Rana temporaria*, L., *R. arvalis* Nilsson, *Pelobates fuscus* Laur. and *Rana esculenta* L. *J. Anim. Ecol.* 40: 599 - 568.
- Verrell, P. (1988): Sexual interference in the alpine newt *Triturus alpestris* (Amphibia, Urodela, Salamandridae). *Zool. Sci.* 5: 159-164.
- Verrell, P. and Halliday, T. (1985): Reproductive dynamics of a population of smooth newt, *Triturus vulgaris*, in southern England. *Herpetologica* 41: 386-395.
- Verrell, P. and Krenz, J.D. (1998): Competition for mates in the mole salamander, *Ambystoma talpoideum*: tactics that may maximize male mating success. *Behaviour* 135: 121-138.
- Verrell, P. and McGabe, N. (1988): Field observations on the sexual behaviour of the smooth newt, *Triturus vulgaris vulgaris* (Amphibia: salamandridae). *Journal of Zoology (London)* 214: 533-545.
- Vieites, D.R., Nitero-Roman S., Barluenga, M., Palanca, A., Vences, M., Meyer, A. (2004): Post mating clutch piracy in an amphibian. *Nature* 431: 305-308.
- Virtel, V., and Virtel, A. (1963). Mise en évidence d'un cycle reproducteur biennal chez le Triton alpester de montagne. *C. R. Soc. Biol.* 157: 464-469.
- Wells, K.D. (1977): The social behaviour of anuran amphibians. *Anim. Behav.* 25: 666 - 693.
- Wilbur H. M. (1980): Complex life cycles. *Annual Review of Ecology and Systematics* 11: 67-93.

Submitted: 29 August 2007
/ Accepted: 22 November 2007