WATER FROGS (RANA ESCULENTA COMPLEX) OF THE BORNHOLM ISLAND, DENMARK*

Article *in* Zoologica Poloniae · January 1994

CITATIONS
7

READS
254

1 author:

Mariusz Rybacki
Kazimierz Wielki University in Bydgoszcz
43 PUBLICATIONS **622** CITATIONS

SEE PROFILE

Zoologica Poloniae (1994) 39/3-4: 331-344

WATER FROGS (*RANA ESCULENTA* COMPLEX) OF THE BORNHOLM ISLAND, DENMARK*

MARIUSZ RYBACKI

Research Center for Agricultural and Forest Environment, Polish Academy of Sciences, Bukowska 19, 60-809 Poznań, Poland

Abstract. 12 water frog populations on the Bornholm Island (Denmark) were studied: 7 mixed *Rana ridibunda-R. esculenta* and 5 pure *R. esculenta*. Four genetic forms in these populations were found: *R. ridibunda* species and three forms of *R. esculenta* hybrid - diploids RL and triploids RLL and RRL. RRL (40%) and RL (35%) individuals were the most numerous. In *ridibunda-esculenta* populations *ridibunda* females clearly outnumbered males (sex ratio 3:1). In some of them only *ridibunda* females were found - *esc-rid* ♀ population. A similar population type was found on the Wolin Island (north-western Poland) where *ridibunda* localities closest to the Bornholm are located. This can be related to the early Holocene land connections between both islands.

INTRODUCTION

Water frogs inhabiting Central Europe include three forms: species *Rana lessonae* CAM., *Rana ridibunda* PALL. and their hybridogenetic hybrid *Rana esculenta* L. (BERGER, 1988). The sympatric range of these forms spreads from Belgium to the Don river (GÜNTHER, 1990). However, distribution of the representatives of this group is different on the northern fringes of their range - in Fennoscandia and Denmark. In Scandinavian countries water frogs live only in Sweden where isolated localities of R. *lessonae* (central Sweden - Uppland) and *R. esculenta* (southern Sweden, mainly Skane) are distributed (EBENDAL, 1979; SJÖGREN, 1991). In Finnland only two sites of *R. ridibunda* were known, however, this species (probably introduced) became extinct around 1960 (TERHIVUO, 1993).

---

* II International Symposium on Ecology and Genetics of European Water Frogs, 18-25 September 1994, Wrocław, Poland.

The Danish islands are inhabited by numerous populations of *R. esculenta*, no R. *lessonae* was found there and the only locality of *R. ridibunda* (together with *R. esculenta*) is the Bornholm Island located about 140 km east of Copenhagen (KNUDSEN and SCHEEL, 1975; FOG, 1994). The species was found there in 1949 (LARSEN, 1950). This was later confirmed by morphological and serological studies (KAURI, 1954; LARSEN, 1954; KNUDSEN and SCHEEL, 1975; VAHL, 1985). It is the north-westernmost locality of *R. ridibunda* in Europe.

The Bornholm Island is a very interesting area with respect to water frogs studies. This is mainly due to its isolated location (40 km away from mainland) in the peripheral zone of water frog distribution and to its geological history. About 10000 years ago the island was connected by a land strip with the area on which the Wolin and Uznam islands are located (AARIS-SÖRENSEN, 1988). Bornholm has an isolated population of *R. ridibunda*. The nearest localities of this species are situated in northern Poland about 100 km away (RYBACKI and BERGER, 1994).

The results of studies presented in this paper are an introduction to a comprehensive work on water frog populations of the Bornholm Island including their structures, reproduction, origin and relations with the populations of the neighbouring areas: southern Sweden, Denmark, northern Germany and Poland (RYBACKI, in preparation).

MATERIALS AND METHODS

The study on the Bornholm Island was carried out from 17 to 22 August 1992. The material included 203 adult and subadult (body length ≥ 50 mm) specimens originating from 12 localities (fig. 1):

1. Ankermyr (1.5 km W Allinge) - small, forest pond
2. Krakken (2 km N Tejn) - large, deep clay-pit
3. Bromme (3.5 km SW Gudhjem) - small, shallow (< 1m) field pond
4. Korsmyr (4.5 km SW Gudhjem) - deep, artificial lake
5. Rø Plantage (6 km SW Gudhjem) - small, shallow swamp in the Rø Plantage forest
6. Ypnestedgård (3 km NE Østermarie) - small, shallow (c. 1.2 m) garden pond
7. Sorthat (3 km N Rønne) - large, deep kaolin mine
8. Bastemose (5.5 km N Åkirkeby) - large swamp
9. Vandttappergård (4 km NW Neksø) - two small, shallow (0.8 - 1.0 m) field ponds
10. Smålyngen (5 km SE Åkirkeby) - shallow (c. 1 m) sandstone mine
11. Snogebaek (3.5 km SW Neksø) - small fish pond
12. Dueodde (7 km SW Neksø) - deep gravel-pit in the forest

Additional studies were carried out at further 4 localities registering frogs with binoculars: Rønne (kaolin mine), Nylars (field ponds) and Gadeby, Neksø (sandstone mines). These data are not included in the tables.

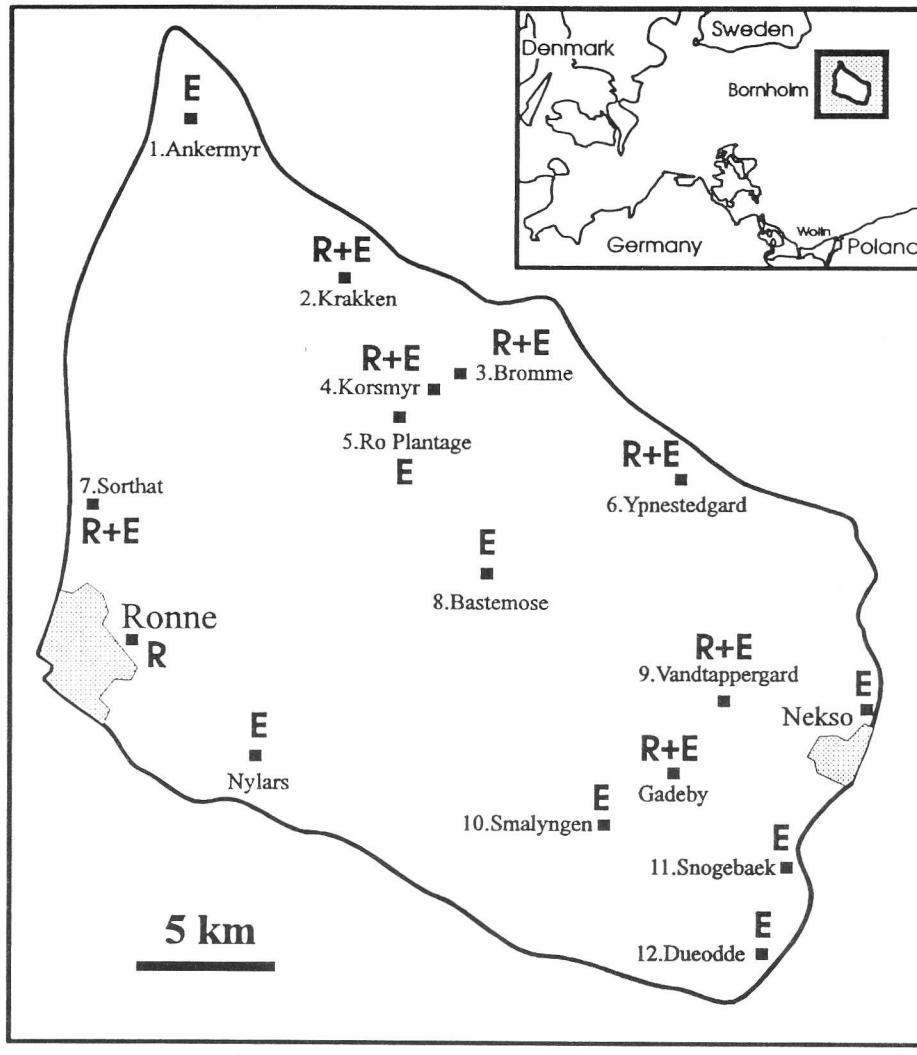

Fig. 1. Distribution of localities and types of water frog populations on Bornholm. R - *R. ridibunda*, E - *R. esculenta*. Numbers of localities (1-12) as in tab. 1. At localities without numbers only observations of frogs were done

For morphological analysis 4 measurements were used: body length measured from the end of snout to anus, length of tibia (T), length of the first toe of hind limb (digitus primus - DP) and length of internal metatarsal tubercle (callus internus - CI) (BERGER, 1966). Always a right limb was measured. From these measurements two indices most often used in water frogs biometrics were calculated: relation DP/CI and T/CI (BERGER, 1966; GÜNTHER, 1975). When determining the genotype the shape of callus internus was considered (BERGER and TRUSZKOWSKI, 1980; GÜNTHER, 1990).

Ploidy of the specimens was determinated based on their erythrocyte size (GÜNTHER, 1977). Blood of all the specimens was used for dry blood smears and then, under 750x magnification the length and width of 10 erythrocytes was measured and their surface area was calculated.

RESULTS

Phenotypic composition of population. Two forms of the frogs were found on the study area: *R. esculenta* i *R. ridibunda* (tab. 1, fig. 1). The individuals with *esculenta* phenotype (N = 171) constituted 84% caught frogs and oc-

Table 1

Genomic composition and sex ratio of water frog populations from Bornholm. Genomes: L - *lessonae*, R - *ridibunda*; 3n? - undetermined triploids. Numbers of localities as in fig. 1.

Locality	N	RLL		RL		RRL		3n?	RR	
		♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♂♂	♀♀	♂♂
1.Ankermyr	29	–	1	4	1	10	12	1	–	–
2.Krakken	7	–	–	–	–	1	1	–	1	4
3.Bromme	7	–	1	2	–	–	1	–	2	1
4.Korsmyr	20	1	–	6	–	6	2	1	2	2
5.Rø Plantage	7	–	1	3	–	2	1	–	–	–
6.Ypnestedgård	11	–	–	–	3	–	–	–	8	–
7.Sorthat	2	–	–	–	–	–	–	–	–	2
8.Bastemose	2	–	1	–	1	–	–	–	–	–
9.Vandtappergård	40	–	2	11	2	8	8	1	8	–
10.Smålyngen	31	–	2	–	–	12	15	–	2	–
11.Snogebaek	33	–	7	16	10	–	–	–	–	–
12.Ducodde	14	–	1	10	2	1	–	–	–	–
Total	203	1	16	52	19	40	40	3	23	9

curred at all investigated localities (in Sorthat they were observed with binoculars). At 5 localities (Ankermyr, Rø Plantage, Bastemose, Snogebaek, Dueodde) only the *esculenta* form was noted while on the remaining ones both forms were present.

Individuals of both forms were observed also in Gadeby. In Nylars only *R. esculenta*, and in Rønne only *R. ridibunda* were noted.

Ploidy. In the studied material 100 triploid individuals were found (49%), all belonging to *esculenta* phenotype. Triploid individuals occurred at 10 localities (tab. 1) and their percentage ranged 14% in Dueodde to 94% in Smålyngen. Erythrocyte size of triploids ranged from 394.6 μm^2 to 451.9 μm^2 ($\bar{x}$ = 425.8 μm^2, SD = 14.0) while that of diploid *R. esculenta* varied from 277.3 μm^2 to 334.1 μm^2 ($\bar{x}$ = 310.63 μm^2, SD = 14.79). Triploid individuals erythrocytes were on average by 37% larger. The erythrocytes of *R. ridibunda* were similar in size to diploid ones of *R. esculenta*: range 272.2-346.6 μm^2, $\bar{x}$ = 305.49 μm^2, SD = 18.08.

Morphology. Based on the value of biometrical indices DP/CI and T/CI and cytometric measurements the studied frogs were divided into 4 groups with different genotypes (tab. 2, fig. 2). Among individuals of *R. esculenta* three groups were distinguished: two triploid types (genotypes RLL and RRL) with opposing features and diploid genotype RL with intermediate characters. The fourth group comprised *R. ridibunda* (RR).

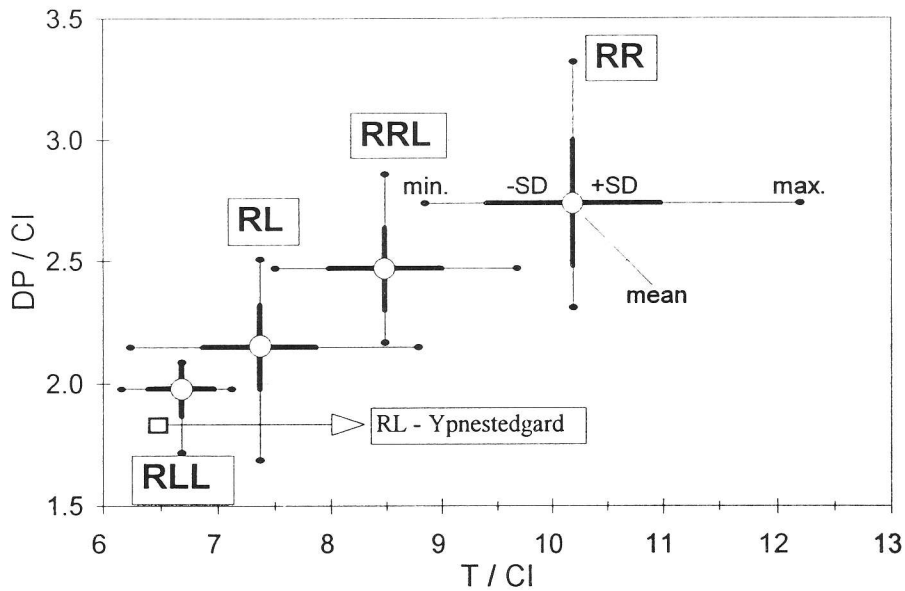

Fig. 2. Comparison of biometrical indices DP/CI and T/CI of water frogs from Bornholm (for details see tab. 2). Genomes: L - *lessonae*, R - *ridibunda*. Square indicates atypical RL-individuals from Ypnestedgård.

Table 2

Comparison of biometrical indices DP/CI and T/CI of water frogs from Bornholm. Genomes: L - *lessonae*, R - *ridibunda*; DP - length of digitus primus, CI - length of callus internus, T - length of tibia, V - coefficient of variability

Genotype	N	DP / CI			T / CI		
		Min–Max	$\bar{x}$±SD	V (%)	Min–Max	$\bar{x}$±SD	V (%)
RLL	17	1.72–2.09	1.98±0.11	5.6	6.16–7.12	6.68±0.29	4.3
RL	71	1.69–2.51	2.15±0.17	7.9	6.24–8.79	7.37±0.50	6.8
RRL	80	2.17–2.86	2.47±0.17	6.9	7.50–9.68	8.49±0.51	6.0
RR	32	2.31–3.32	2.74±0.26	9.5	8.85–12.20	10.19±0.79	7.7

Triploids of the first triploid type - RLL (two *lessonae* and one *ridibunda* genomes) - were morphologically similar to R. *lessonae*. They had low values of both biometrical indices (DP/CI - $\bar{x}$ = 1.98; T/CI - $\bar{x}$ = 6.68), short tibia and large, symmetrical and high callus internus. Triploids of RRL type (two *ridibunda* and one *lessonae* genomes) had features similar to *R. ridibunda*: high values of the indices (DP/CI - $\bar{x}$ = 2.47; T/CI - $\bar{x}$ = 8.49), long tibia and small, low callus internus. Among triploids three individuals were found whose features were not characteristic of any type and therefore they were marked as "3n?" (tab. 1).

The features of RL diploids were intermediate. In this group 58% individuals (from Dueodde and Snogebaek mainly) had a relatively large and high callus internus. In Ypnestedgård all the three RL individuals had metatarsal tubercles of the shape typical for RLL triploids and short tibia. The values of their indices were exceptionally low, lower than in many RLL individuals: DP/CI 1.69-1.93 ($\bar{x}$ = 1.83), T/CI 6.24-6.73, ($\bar{x}$ = 6.51). The features of these individuals made the ranges of the RL and RLL specimens indices overlap almost completely (fig. 2). These two groups of individuals were the most similar to each other.

The value ranges of other neighbouring groups (RL - RRL, RRL - RR) overlap partially but the division between each genotype can be separated considering ploidy criterion. The ranges of groups of the same ploidy usually are not connected.

In *R. ridibunda* values of biometrical indices were the highest: DP/CI - $\bar{x}$ = 2.74, T/CI - $\bar{x}$ = 10.19. Among them the highest dispersion of features was observed (highest values of variability coefficient - tab. 2), resulting in division of these individuals into two groups (fig. 3). In the first group called "Ypnestedgård" (including also 6 of 8 *ridibunda* individuals from this popu-

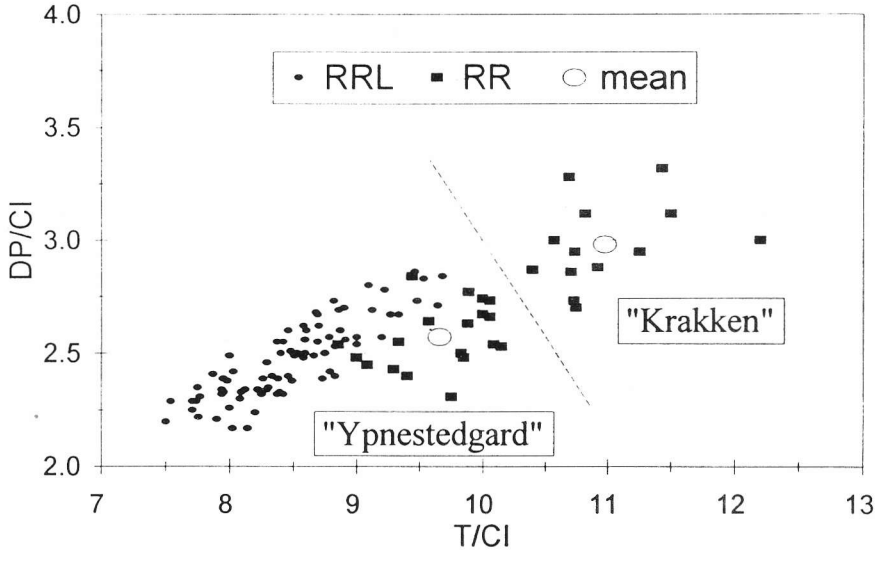

Fig. 3. Comparison of biometrical indices DP/CI and T/CI of two groups of *R. ridibunda* ("Ypnestedgård" and "Krakken") and RRL individuals from Bornholm. Genomes: L - *lessonae*, R - *ridibunda*

lation) the ranges of index values (DP/CI 2.31-2.84, $\bar{x}$ = 2.57; T/CI 8.85-10.15, $\bar{x}$ = 9.66) greatly overlap with those characterising RRL triploids. The second group called "Krakken" (including also all *ridibunda* from this population) includes individuals with clearly higher index values: DP/CI 2.70-3.30, $\bar{x}$ = 2.98; T/CI 10.40-12.20, $\bar{x}$ = 10.98. Both groups differ mostly with respect to the T/CI index - the ranges of its values do not overlap. Differences of the means are statistically significant ($p < 0.01$) for both indices.

In case of both biometrical indices a pronounced gradient of their values was observed correlated with *lessonae* (L) and *ridibunda* (R) genome dosage effect: RLL - RL - RRL -RR. Also body size increased in accordance with this gradient. RLL triploids were the smallest and *R. ridibunda* the largest (tab. 3). RRL triploids which were smaller then RL individuals constituted an exception. This was due to considerable differences in the frequency distribution of both forms in each size class (tab. 3). Most RRL females (74%) were in three size classes: 50-59 mm, 60-69 mm, 70-79 mm while the same classes included only 44% of RL females. The same was true of males. Within the size range of 50-69 mm there were 70% RRL and 58% RL males.

Within each genotype females were larger than males. The largest caught male was *R. ridibunda* 90.5 mm long. The largest males of three forms of *R. esculenta* reached the length of 82-83 mm. The largest females reached from 99 mm (*R. ridibunda*) to 106 mm (RRL) body length.

Table 3
Length of body (in mm) of water frogs from Bornholm. Genomes: L - *lessonae*, R - *ridibunda*.

Genotype and sex	N	Min–Max ($\bar{x}$)	Frequency (%) in size classes (mm)					
			50–59	60–69	70–79	80–89	90–99	100–109
RLL ♀♀	1	86.5						
RLL ♂♂	16	51.0–82.0 (67.71)	12	44	38	6	0	0
RL ♀♀	52	52.5–100.0 (77.37)	13	23	8	37	17	2
RL ♂♂	19	51.5–83.0 (68.31)	26	32	21	21	0	0
RRL ♀♀	39	54.0–106.0 (71.94)	20	26	28	13	8	5
RRL ♂♂	41	51.5–82.0 (65.24)	38	32	25	5	0	0
RR ♀♀	23	55.0–99.0 (77.85)	13	26	9	17	35	0
RR ♂♂	9	58.0–90.5 (73.61)	23	33	0	33	11	0

Differences in body colour were also related to genome composition of the individuals. The colour of the dorsal part was the darkest in *ridibunda*, most often it was brown, less frequently olive-brown or olive-green. None of the individuals of *R. ridibunda* was green. Hybrid individuals were generally green with various intensity while RRL triploids were mostly dark green and RLL ones light green, however opposite cases were also noted. Among 171 individuals of the *esculenta* phenotype only 4 (2%) had dark colour: one

green-brown RLL and one brown RL in Bastemose, and two olive-brown RL in Ypnestedgård.

Genomic composition of populations. The investigated water frog populations were characterized by a large diversity of genetic forms (tab. 1). The greatest diversity was found in Korsmyr, Vandtappergård and Bromme where all 4 genotypes were observed. RRL triploids (N = 80 - 39% all frogs) noted in 8 populations were the most numerous. Their number was the highest in Smålyngen (87%) and in Ankermyr (76%). In the remaining populations their percentage ranged from 7% (Dueodde) to 40% (Korsmyr and Vandtappergård). In contrast RLL triploids were the least numerous (N = 17 - 8%). Although they were found in 9 populations, only in Snogebaek (21%), Bromme and Krakken (14%) their proportion exceeded 10%. RL individuals (N = 71 - 35%) appeared at most localities, and were most numerous in Dueodde (86%) and Snogebaek (79%). This form was not observed in Smålyngen despite the large number of caught frogs (N = 31). *R. ridibunda* (N = 32 - 16%) appeared at 7 localities always together with hybrids. This species predominated in Ypnestedgård (73%) and Krakken (71%), and in the remaining populations its percentage varied from 6% (Smålyngen) to 43% (Bromme).

Sex ratio. Normal sex ratio (1:1) was found only in the RRL genotype (tab. 1). Only in Korsmyr females of this form predominated significantly (sex ratio 3:1). RLL triploids included almost only males (1:16). Sex ratios among diploid *R. esculenta* and *R. ridibunda* were very similar. In both groups females predominanted, in RL at the ratio of 2.7:1 and in *ridibunda* 2.5:1. The only locality where males predomonated among RL individuals was Ypnestedgård, no female being found there. In other populations there were either only females (Korsmyr) or they clearly outnumbered males (Vandtappergård and Dueodde - 5:1, Ankermyr 4:1). The lowest bias in the sex ratio of RL form was noted in Snogebaek (1.6:1).

Populations of *R. ridibunda* can be classified into those where only females were found (Ypnestedgård, Vandtappergård, Smålyngen) and those where individuals of both sexes were present (Bromme, Korsmyr, Krakken). Krakken was the only locality where more males than females of this species were caught.

Ecology. In 1988 about 1780 water reservoirs were registered on the Bornholm Island, of which 62% were small ponds, below 0.05 ha (Fog, 1988). Most of them were artificial reservoirs which are usually colonised by water frogs. This phenomenon is particularly clear in new ponds made within the project of Hyla arborea protection. In 1989-93 286 such ponds were made generally in agrocenoses (Hansen, 1993). These ponds of the area not exceeding 0.01 ha with poor vegetation are occupied by relatively large populations, mainly of *R. esculenta*. Example of such reservoirs are field ponds in Nylars and Vandtappergård, used as watering troughs for farm animals. In both ponds, constructed in 1990, during the investigations (1992) almost devoid of water plants, from 30 to 50 adult frogs were observed and in Vandtappergård also newly metamorphosed froglets.

Water frogs inhabit also most clay, kaolin, sandstone and (less frequently) granite mines numerous on the island and often filled with water. In this type of reservoirs, usually deep ones, individuals of *R. ridibunda* were most often observed (Krakken, Sorthat, Safirsøen, Rønne, Smålyngen, Gadeby). This species also lived and reproduced in small, shallow ponds, less than 1.2 m deep (Ypnestedgård, Vandtappergård,).

DISCUSSION

Populations with high proportion of triploid individuals are mostly known from the areas of northern Germany (GÜNTHER, 1975, 1991; EIKHORST, 1984; BERGER and GÜNTHER, 1988), southern Sweden (EBENDAL, 1979; EBENDAL and UZZELL, 1982) and Denmark (FOG, 1994) but, in contrast to Bornholm, among triploids RLL individuals predominate there. Populations where among triploids only RRL individuals were found are known from the Wolin Island and the coast of the Dzwina Strait in north-western Poland (RYBACKI, this volume), i.e. from the areas neighbouring with the Bornholm Island. In these populations, however, the percentage of RRL form is much lower (mean 12%) with clear domination of males over females (1:3).

The diversity among *R. ridibunda* individuals is very interesting. Based on the presented results it can be concluded that populations of this species on the Bornholm Island are not uniform and consist of two groups of individuals different with respect to sex ratio and also morphology and ecology.

In three populations - Ypnestedgård, Vandtappergård, Smålyngen - among adult *R. ridibunda* only females were found (N = 18). This fact was confirmed by the analysis of sex ratio among newly metamorphosed individuals of this species (RYBACKI, unpublished). In Ypnestedgård among 12 froglets and tadpoles before metemorphosis there were only females, however, in two neighbouring ponds located about 500 m away sex ratio was normal (N = 6). In turn in Vandtappergård in the sample of 34 froglets there were 28 females and 6 males.

The phenomenon of unisexuality in parental species of hybrid *R. esculenta* is very rare. It was described only in *R. ridibunda* in two different population types. In Switzerland (BEERLI, 1986; HOTZ et al., 1991) in mixed R. *lessonae-R. esculenta* populations only females of the *ridibunda* phenotype were found originating from esc x esc crosses. In north-western Poland on the Wolin Island in some *R. ridibunda-R. esculenta* populations also only females of this species were noted (RYBACKI, 1994). In other populations of this island, as on the Bornholm, there were individuals of both sexes with clear predomination of females. As indicated by the studies on the reproduction of these populations, females of *R. ridibunda* originate from *rid* ♀ x *esc* ♂ crosses (RYBACKI, unpublished).

It seems possible that on the Bornholm some females of *R. ridibunda* may also originate from *esc* x *esc* or *rid* x *esc* crosses. Several facts can support this suggestion. Among *R. ridibunda* bred in laboratory from *esc* x *esc*

crosses there were almost exclusively females (BERGER, 1971; TUNNER, 1980). This results from the fact that haploid gametes produced by RL and RRL individuals in the majority of Central European populations generally contain R genome and that these gametes transferred to progeny by hybrid males determine female sex (BERGER and GÜNTHER, 1988; BERGER, 1987; GÜNTHER, 1991). However, since *ridibunda* individuals from such crosses have very low viability (BERGER, 1988), it seems more probable that the origin of females of this species in some Bornholm populations is related rather to the reproduction model found on the Wolin Island. This is confirmed by preliminary results of the studies on reproduction of the population from Ypnestedgård (RYBACKI, unpublished). This populations has an unusual structure (tab. 1). Beside females *R. ridibunda* only RL males with morphological features very atypical for this form were found (fig. 2). One of these males was crossed with several females to determine gamete production. This male transferred to progeny mainly gametes with R genome determining female sex and single gametes with L genome determining male sex. Probably the population from Vandtappergård reproduces in a similar way. This type of reproduction enables maintenance of females of *R. ridibunda* in these populations.

A population with the same structure as that in Ypnestedgård has not been described yet. It shows some similarities with the already mentioned populations from the Wolin Island, where in the *ridibunda* phenotype there are also only females but among *esculenta* individuals are both males and females. *Esculenta* males from these populations, described as *esc-rid* ♀ (*R. esculenta* predominates) also produce gametes with genomes of both parental species (RYBACKI, unpublished).

Using GÜNTHER'S (1975) terminology the Ypnestedgård population can be described as *rid* ♀-*esc* ♂ (*R. ridibunda* females predominate), however, this requires further confirmation by collecting greater number of *R. esculenta*. Nevertheless it is noteworthy that Ypnestedgård is the only population where such a great proportion of RL males was found. The mean sex ratio within this genotype for all populations is 2.7:1 (tab. 1).

The structure of Vandtappergård population (tab. 1) resembles very much that of *esc-rid* ♀ populations from the Wolin Island (RYBACKI, this volume): a clear prevalence of *esculenta* form (80% and 72% respectively), high proportion of RRL triploids (40% and 19%), identical sex ratio among RRL individuals (1:1). The only difference between these populations is the sex ratio in RL form - in Vandtappergård females predominate(5.5:1), and on the Wolin males (1:17). Since basic structure of both populations (predomination of *esculenta* form and absence of *ridibunda* males) is the same, the Vandtapperård population can also be included in the *esc-rid* ♀ type.

Another criterion used in dividing *R. ridibunda* individuals from the Bornholm into two groups was their morphology (fig. 3). However, it turned out that morphological features were only partially related to structures of the populations. In both groups there were specimens from populations with normal sex ratio and from those where only females were noted. However, it was

found that "Krakken" group consisted mostly of individuals with characteristics typical for *R. ridibunda* (only 6 females from unisexual populations) while "Ypnestedgård" group displayed mainly atypical features (12 females from unisexual populations). This is indicated by different sex ratios ("Krakken" 1.6:1, "Ypnestedgård" 3.7:1) and biometrical indices. A comparison of the values of these indices indicates that although individuals of the "Krakken" group are morphologically very close to those from Central Europe, individuals from the "Ypnestedgård" group are considerably different from them. GÜNTHER (1990) and BERGER (1966) give the following mean values for *R. ridibunda* from eastern Germany and Poland: DP/CI-3.05, 3.16 and T/CI-10.27, 10.82 respectively. In the "Ypnestedgård" group these values are 2.57 and 9.66 and in the "Krakken" group 2.98 and 10.98.

Another difference between the populations of *R. ridibunda* from the Bornholm is their ecology. Populations consisting only of females of this form inhabit water reservoirs not typical for this species - small and shallow (0.8-1.2 m) ponds (Ypnestedgård, Vandtappergård) and equally shallow sandpits (Smålyngen) near which there are no large and deep reservoirs. This is strange since in Central Europe *R. ridibunda* generally lives in large, deep, sufficiently oxygenated waters where it also hibernates (RYBACKI and BERGER, 1994). This is related to considerable susceptibility of this species to oxygen deficiency (TUNNER and NOPP, 1979). Perhaps a part of individuals of *R. ridibunda* from the Bornholm has a higher tolerance to lower level of oxygen in water and is able to hibernate in small ponds which in turn, due to mild winters (the Bornholm Island is located in the zone of temperate, warm oceanic climate), are not covered with thick ice which often happens in Central Europe.

At the present stage of investigations it is impossible to definitely state that two different forms of *R. ridibunda* occur on the Bornholm Island although some facts would indicate this. Atypical features of populations of this form can be related to their location on the periphery of the species distribution range (fringe populations). Verification of this hypothesis requires further research, first of all analysis of mitochondrial DNA and studies on the of reproduction of this species.

CONCLUSIONS

The Bornholm Island is the north-westernmost locality of *R. ridibunda* in Europe. It is inhabited by mixed *R. ridibunda-R. esculenta* and pure *R. esculenta* populations. Characteristic features of these populations are: high percentage of triploids (particularly of the RRL type) and biased sex ratios in *R. ridibunda*.

The structure of mixed *R. ridibunda-R. esculenta* populations clearly distinguishes them from most populations of this kind from Central Europe. They are most similar to populations inhabiting the Wolin Island (NW Poland). Common features of populations from these islands are: predomination of RRL individuals among triploids, and predomination of females in *R.*

ridibunda. On both islands unisexual populations of *R. ridibunda* were found belonging to the *esc-rid* ♀ type. Also reproduction of these populations has certain common features - RL males were found in them which produced gametes with R genome determining female sex and with L genome determining male sex. These similarities may evidence a relationship between populations of both islands indicated by the geological history of this region.

Pure populations of *R. esculenta* from Bornholm resemble such populations from southern Sweden, Denmark and northern Germany where, in contrast to the Bornholm, RRL triploids predominate.

ACKNOWLEDGEMENTS

I am grateful to Kåre Fog and Finn Hansen for making my trip to Bornholm possible and for invaluable help in field studies. Particularly cordial thanks go to the whole Hansen family for invitation and warm reception.

REFERENCES

Aaris-Sörensen, K., 1988: Danmarks forhistoriske dyreverden. Gydendal.

Beerli, P., 1986: Seefrösche in einer Tümpelfrosch - Wasserfrosch Population in einem antropogen beeinflusten Habitat. Diss. Diplomarbeit Univ. Zürich.

Berger, L., 1966: Biometrical studies on the populations of green frogs from the environs of Pozna_. Ann. Zool., 23: 303-324.

Berger, L., 1971: Viability, sex and morphology of F2 generation within forms of *Rana esculenta*-complex. Zool. Pol., 21: 345-393.

Berger, L., 1987: Ewolucja systemów genetycznych u żab zielonych. Kosmos, 36: 395-416.

Berger, L., 1988: On the origin of genetic systems in European water frog hybrids. Zool. Pol., 35: 5-32.

Berger, L., Günther, R., 1988: Genetic composition and reproduction of water frog populations (*Rana* kl. *esculenta* Synklepton) near nature reserve Serrahn, GDR. Arch. Nat. schutz Landsch. forsch., 28: 265-280.

Berger, L., Truszkowski, J., 1980: Viability and inheritance of characters in water frogs (*Rana esculenta* complex) in agrocenoses. Gen. Pol., 21: 309-323.

Ebendal, T., 1979: Distribution, morphology and taxonomy of the Swedish green frogs (*Rana esculenta* complex). Mitt. Zool. Mus. Berlin, 55: 143-152.

Ebendal, T., Uzzell, T., 1982: Ploidy and immunological distance in Swedish water frogs (*Rana esculenta* complex). Amphibia-Reptilia, 3: 125-13.

Eikhorst, R., 1984: Untersuchungen zur Verwandschaft der Grüunfrösche. Diss. Univ. Bremen.

Fog, K., 1988: Løvfrøoer - og andre padder på Bornholm. Bornholms Amtskommune, Teknisk Forvalting.

Fog, K., 1994: Water frogs in Denmark: population types and biology. Zool. Pol. 39(3-4): 305-330.

Günther, R., 1975: Zum natürlichen Vorkommen und zur Morphologie triploider Teichfrösche, "*Rana esculenta*", L., in der DDR (Anura, Ranidae). Mitt. Zool. Mus. Berlin, 51: 145-158.

GÜNTHER, R., 1977: Die Erytrozytengrösse als Kriterium zur Unterscheidung diploider und triploider Teichfrösche, *Rana "esculenta"* L. (Anura). Biol. Zbl., 96: 457-466.

GÜNTHER, R., 1990: Die Wasserfrösche Europas. A. Ziemsen Verlag, Wittenberg Lutherstadt.

GÜNTHER, R., 1991: Europäische Wasserfrösche (Anura, Ranidae) und biologisches Artkonzept. Mitt. Zool. Mus. Berlin, 67: 39-53.

HANSEN, F., 1993: Die Bornholmer Landschaft. Bornholms Amtskommune, Teknisk Forvalting.

HOTZ, H., BEERLI, P., SPOLSKY, Ch., 1992: Mitochondrial DNA reveals formation of nonhybrid frogs by natural matings between hemiclonal hybrids. Mol. Biol. Evol., 9: 610-620.

KAURI H., 1954: Über die systematische Stellung der europäischen grünen Frösche *Rana esculenta* L. und *R. ridibunda* PALL. Lunds Universitets Årsskrift N. F. Avd. 2, Bd. 50 (12): 1-30.

KNUDSEN, K., SCHEEL, J. J., 1975: Contribution to the systematics of European green frogs. Bull. Soc. Zool. France, 100: 677-679.

LARSEN, A., 1950: Latterfrøen, *Rana ridibunda* PALL., ny art for Danmark, fundet på Bornholm. Flora og Fauna, 56: 1-9.

LARSEN, A., 1954: Mere om *Rana ridibunda* og *Rana esculenta* ("De grønne frøer") - en undersøgelse fra Bornholm. Flora og Fauna, 60: 1-10.

RYBACKI, M., 1994: Structure of water frog populations (*Rana esculenta* complex) of the Wolin Island, Poland. Zool. Pol. 39(3-4): 345-364.

RYBACKI, M., BERGER, L., 1994: Distribution and ecology of water frogs in Poland. Zool. Pol. 39(3-4): 293-303.

SJOGREN, P., 1991: Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biol. J. Linnean Soc., 42: 135-147.

TERHIVUO, J., 1993: Provisional atlas and status of populations for the herpetofauna of Finland in 1980-92. Ann. Zool. Fennici, 30: 55-69.

TUNNER, H. G., 1980: Kreuzungsexperimente mit Wasserfröschen aus österreichischen und polnischen Mischpopulationen (*Rana lessonae* + *Rana esculenta*). Eine Analyse biochemischer und morphologischer Merkmale. Z. Zool. Syst. Evol. - Forsch., 18: 257-294

TUNNER, H. G., NOPP, H., 1979: Heterosis in the common European water frog. Naturwissenschaften, 66: 268-269.

VAHL, J., 1985: Naturhistoriske og taxonomiske undersøgelser af en østjysk bestand af grøn frø (*Rana esculenta* -komplexet). Specialerapport ved Institut for Zoologi og Zoofysiologi, Aarhus Universitet, 111 pp., unpublished.