

Habitat isolation and habitat quality – consequences for populations of the *Rana esculenta/lessonae*-complex

(Amphibia, Anura, Ranidae)

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The influence of habitat quality and habitat isolation on populations of *Rana esculenta/lessonae* was studied in two areas in southern Bavaria. In area A there was a high density of ponds and a large frog population. In area B pond and population density were low. In area A the size of the stocks and the reproduction rate depended on characteristics of the ponds (sun, depth, vegetation). The highest stock sizes were found in two types of sunny ponds with rich vegetation and it was only in these ponds that a high reproductive success was reached. A cluster analysis was made to decide which types of ponds the frogs preferred, whether these types also exist in area B, and whether the number of frogs in the ponds of area B correspond to the habitat quality. Only parts of area B were inhabited by frogs. The size of the stocks was correlated to the number, size and distance of the neighbouring ones. The percentage of preferred types of ponds was lower in area B than in A, and additionally most of the ponds in area B had lower stock sizes than the habitat quality would lead to expect. In area B the highest frog population was found in the part with the highest density of ponds. It is the isolation of the habitats and not the habitat quality alone which seems to limit the population in area B. The ratio of *R. esculenta* to *R. lessonae* was higher in area B than in area A. The low percentage of *R. lessonae* in B is a possible explanation for the low reproductive success in this area. In both areas the ratio of *R. esculenta* was higher among juveniles than among the adults of a pond. A different preferred habitat type of *R. esculenta* and *R. lessonae* is discussed to compensate the higher number of metamorphosing *R. esculenta*. Ponds of different types show a different ratio of *R. esculenta* to *R. lessonae*, the highest percentage of *R. esculenta* being found in ponds with sparse vegetation.

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1. Introduction

The degree of isolation of animal populations plays an important role in evolutionary history. Size and distribution of habitats determine whether a species will colonise an area and whether neighbouring stocks of a species share a common gene pool.

For a population the probability of becoming extinct rises with the decreasing size of the population and increasing isolation. Reasons for extinction may be a low degree of heterozygosity and polymorphism but there is also a greater risk of extinction caused by stochastic events (Gilpin 1987, Hanski & Gilpin 1991, Loeschke 1988, Nunney & Campbell 1993, Torbjörn 1991). Additionally population survival is strongly influenced by habitat quality (Mühlenberg et al. 1991, Hanski 1991).

This paper reviews the results of a study of the influence of habitat isolation, habitat quality and species composition on mixed populations of *Rana kl. esculenta* (Linnaeus, 1758) and *Rana lessonae* (Camerano, 1882).

Isolation of habitats seems to cause the extinction of *Rana lessonae* in ponds on the northern periphery of its geographical range in Sweden (Sjogren 1991, 1994). Blab (1986) mentions that these species became extinct in still existing habitats after a large number of ponds had been destroyed. He also states that of all amphibian species in central Europe *Rana kl. esculenta* and *Rana lessonae* have the highest requirements with regard to the habitat structure of reproduction habitats. For reproduction both depend on permanent ponds with rich vegetation and little shade (Blab 1986). Furthermore reproductive success is influenced by the species composition and the genetic structure of mixed *Rana kl. esculenta-lessonae* populations (Günther 1983).

The present study, however, is the first that considers the interaction of these different factors that influence the development of *Rana kl. esculenta-lessonae* populations.

2. Methods

2.1. The *Rana kl. esculenta/Rana lessonae*-complex

Rana kl. esculenta is a hybrid of the species *Rana lessonae* and *Rana ridibundia* (Pallas, 1771) and it is distributed throughout Central and Eastern Europe. *Rana ridibundia* (from now on referred to as *R.r.*) and *R. lessonae* (from now on: *R.l.*) prefer different habitats. *R.r.* is found in lakes or ox-bows and *R.l.* in small ponds. Both species live ashore during summer. *R.l.* hibernates on land and *R.r.* at the bottom of lakes and rivers (Blab & Vogel 1989).

In most regions the hybrid *Rana kl. esculenta* (from now on: *R.c.*) lives sympatrically with one of its parental species and can be found in many kinds of waters (Wijnands 1977, Heym 1974). It hibernates on land or in water, depending on the area and the type of habitat. For successful reproduction *R.c.* depends on mates of the parental species. In areas where *R.c.* lives together with the other (*R.r.*) and clonally area), it excludes the parental *R.l.* genome prior to meiosis, reduplicates the other (*R.r.*) and clonally transmits it to eggs and sperm cells. *R.c.* has to mate with *R.l.* to regain the lost *R.l.* genome. Mating between *R.c.* and *R.c.* occurs, but results in very little offspring. *R.c.* seem to prefer *R.l.* mates (Abt & Reyer 1993). For a review of this complex genetic situation see Günther (1983, 1990), Günther & Pflömer (1988), Berger (1983) and Eikhorst (1988).

2.2. Conception of the study

The study was conducted in two areas characterised by different densities of ponds (Tab. 1). In the first area the pond density was high and the influence of habitat isolation was assumed to be low. Here I determined habitat criteria of main importance for population size and reproductive success. In the second area, pond density was low. Here the influence of habitat isolation on the frog population was investigated. I used the important habitat criteria determined in the first area to decide whether there were less frogs in the isolated ponds of the second area than the habitat structure would lead to expect. I determined the species composition in both areas and in ponds of different habitat structure.

Tab. 1. Comparison of areas A and B.

	area A	area B
size	38 km ²	200 km ²
number of ponds	36	42
ponds/km ²	1	0.21
additional ponds (see 2.7)	30	21
geography	moraines of the last ice age	moraines of the older ice ages and glacial gravel fields
elevation above sea level	418-565	413-550 m

2.3. Areas

The investigation was performed in the south-eastern part of Upper Bavaria, Germany, from April to September 1988. A mixed population of *R.c.* and *R.l.* exists in this region. Table 1 shows a comparison of both study areas. Area A is located about six kilometres to the west of area B. There is no big difference in climate but agriculture is more intensive in B than in A (higher percentage of fields and fewer meadows and pastures). In both areas most ponds are small and rarely exceed 1000 m².

2.4. Population data

The numbers of adult and subadult frogs in each pond were counted at least four times between May and June 1988. On warm and sunny days most of the animals sat ashore facilitating counting. Adults and subadults were distinguished by means of their size. The variable used to describe the stock size of a pond is the median of the counted adult frogs (FR, AD). I also determined the total number of frogs (adults and subadults).

In order to determine the reproductive success, I estimated the number of metamorphosed juveniles in a pond in August. Since it was difficult to determine the exact numbers, I used a very rough classification:

no juveniles seen = no reproduction success (REPR -)
 less than 30 juveniles counted = little reproductive success (REPR +)
 more than 30 juveniles counted = high reproductive success (REPR ++)

From May to July I estimated the ratio of adult *R.l.* to *R.c.*. Since *R.l.* and *R.c.* look very similar, 486 individuals were caught in both areas and determined on the basis of biometrical characteristics. Triploid *R.c.* which would have complicated the genetic situation and which are difficult to determine on the basis of biometrical characteristics did not exist in the area (Zahn 1990). In ponds with high reproductive success (REPR (++)) I also estimated the *R.c.* ratio of the metamorphosed juveniles.

2.5. Characteristics of the ponds

Area A has 36 ponds and area B 42 (Tab. 1). Six of the ponds in area A and nine of area B are periodic water bodies. In order to characterise the habitat structure I determined the following variables at all the ponds in both areas:

- surface (m²)
- length (m) and proportion (%) of sunny, partly shaded and shaded shoreline
- mean shading (%) during the day (estimate)
- area (m²) and proportion (%) of the pond covered with reeds (differentiated into sunny, partly shaded and shaded)
- area (m²) and proportion (%) of the pond covered with webbed leaf vegetation and webbed vegetation
- area (m²) and proportion (%) of the pond covered with submerged vegetation
- mean and maximum depth (cm)
- occurrence of fish, special features (e.g. inflow, runoff)

The shading of a pond was estimated. Areas defined as being "sunny" were shaded less than 50 % of the day, areas defined as being "partly shaded" were shaded 50-90 % of the day and areas defined as being "shaded" were shaded more than 90 % of the day.

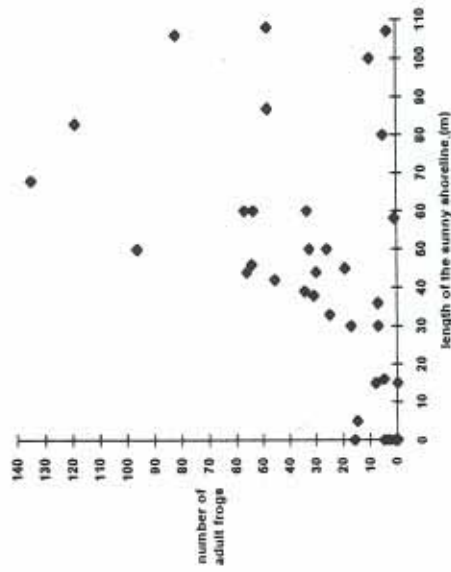


Fig. 1. Influence of the factor "sun" on stock size (Spearman's rank correlation coefficient, $r=0.59$).

2.6. Neighbouring ponds

Neighbouring ponds were defined as all the ponds within the radius of two kilometres of a given pond. To investigate the influence of the neighbouring stocks on the number of frogs in a given pond, I determined the following variables for every pond:

- number and size of the neighbouring ponds
- number and size of the frog stocks in neighbouring ponds
- reproductive success in neighbouring ponds

For each pond the probability of immigrating frogs was assumed to rise with the size of the neighbouring stocks and according to proximity. To accommodate this assumption, I calculated a new variable (N.AD):

N.AD = sum of all adult frogs of neighbouring ponds, whereby the number of frogs of each pond (FR.AD) is divided by the logarithm (log) of the distance to the focus pond. The logarithm was chosen to avoid overestimation of the influence of nearby stocks.

$$N.AD = \sum \frac{\text{number of adult frogs in the neighbouring pond}}{\text{logarithm of the distance to the focus pond}}$$

2.7. Additionally studied neighbouring ponds

In order to examine the influence of neighbouring stocks on the stocks in ponds situated at the edge of the study areas, I investigated additional waters in a two kilometre wide belt encircling each area to determine all the neighbouring stocks. I found 30 ponds in the belt around area A and 21 in the belt around B (Tab. 1). The only data taken from the ponds outside the study areas consisted of the number of frogs, their reproductive success and the distance from the focus ponds in the study areas.

2.8. Statistics

For purposes of statistical analysis Spearman's rank correlation coefficient (two tailed signif.), the chi-square test and the U-test (two tailed signif.) were used (Zafel 1992). To group the ponds into certain types a cluster analysis was made.

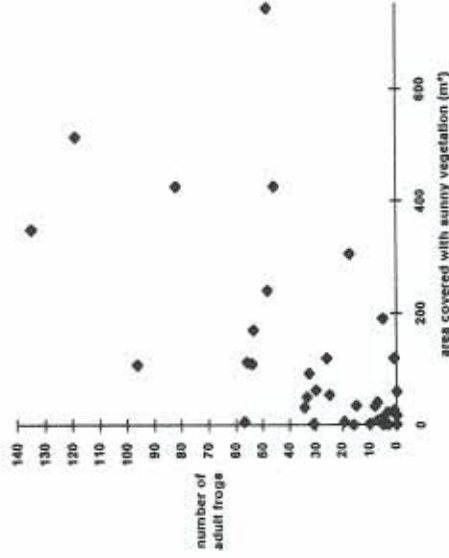


Fig. 2. Influence of the factor "vegetation" on stock size (Spearman's rank correlation coefficient, $r=0.55$).

3. Results

3.1. Area A (high pond density)

3.1.1. Population size and ratio of R.e. and R.J.

With the exception of one totally shaded periodic water body, I found frogs in all the ponds of area A with a total number of about 1130 adult frogs being counted altogether. The median stock size was much higher than in area B. (Tab. 2). R.J. and R.e. occurred in mixed stocks wherever either of them are able to prevail. 363 adult frogs altogether were caught and determined, whereby the overall ratio of R.e. was 55%. In seven cases it was possible to compare the R.e./R.J.-ratio of adult and juvenile frogs. In every case, the percentage of R.e. was higher in the sample of juveniles than in the sample of adults (Fig. 3).

3.1.2. Habitat features and stock size

In area A there was no correlation between the stock size of a pond and the number and distances of neighbouring stocks (N.AD). It would seem that the size of a stock was regulated by the features of its habitat as the number of adult frogs was significantly correlated to decreasing degree of shade, increasing depth and increasing vegetation cover of a pond (Tab. 3).

Fig. 1 shows that the factor "sun" determines the maximum possible size of the stocks, but sunny ponds with rather few frogs were also observed. Therefore this factor (as well as depth) can be regarded as necessary but not sufficient for high population density. Contrary to this, increasing vegetation cover of the ponds (in most cases connected with little shade) results in increasing frog stocks (Fig. 2).

Tab. 2. Comparison of the frog populations in both areas.

	area A	area B
median stock size (adults) of ponds with adult frogs (area A: N=35, area B: N=17)	28	5
maximum stock size (adults) of ponds with adult frogs (area A: N=32, area B: N=17)	135	25
R.e. ratio of all adult frogs caught (area A: N=363, area B: N=123)	55%	71%
mean N.AD (neighbouring frogs)	270	11
percentage of ponds with reproductive success	42%	10%

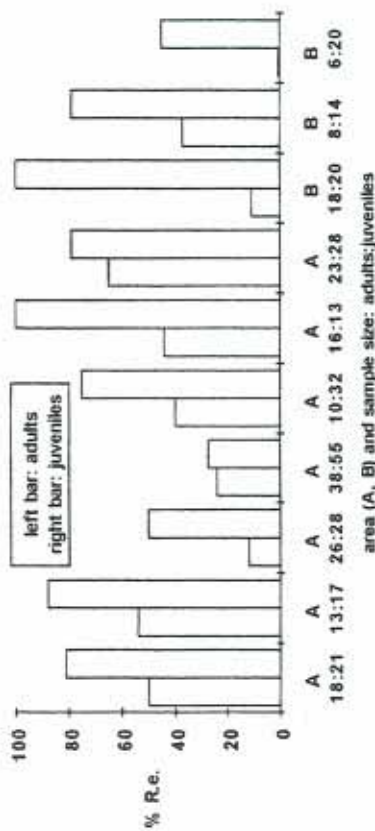


Fig. 3. Comparison of the *R.e.* ratio in adults and juveniles (10 ponds: A: pond of area A; B: pond of area B. The mean percentage of *R.e.* in these ponds was 34 amongst the adults (N=176) and 64 amongst the juveniles (N=249).

Reeds seem to be less important for the frogs ($r < 0.37$, not significant) than webbed leaf and submerged vegetation (Tab. 3), but does not seem to be without influence for there is a more increased correlation between vegetation and stock size if reed vegetation is included (Tab. 3).

Stocks (FR, AD) were significantly smaller in periodic ponds (mean 2, N=6) than in permanent ponds (mean 37, N=30; U-test, $p < 0.01$).

15 ponds with fish (different species of Cyprinidae) had significantly more adult frogs (mean 46) than 21 ponds without fish (mean 21; U-test, $p = 0.01$).

3.1.3. Frog reproduction in area A

In 50 non periodic ponds inhabited by adult frogs, including those in the two-kilometre-wide belt encircling the area, frog reproduction was potentially possible; however I found metamorphosed juveniles (indicating reproduction) only in 21 of them (42%). High reproductive success (REPR++) was only achieved in 11 ponds (22%).

Ponds with low or high reproductive success (REPR+/++) had significantly more frogs, a longer stretch of sunny shoreline and more vegetation (U-test, $p = 0.05$) than the ponds without reproductive success in area A. Ponds with high reproductive success (REPR++) featured in particular less mean shade (U-test, $p = 0.02$) and rich vegetation with a higher percentage of submerged and webbed leaf vegetation ($p < 0.01$) than ponds with no reproduction (REPR-). Tab. 4 shows the differences between ponds with high and no reproductive success (REPR++ and -). In shaded or periodic ponds, spawn or tadpoles were not found at any time.

Tab. 3. Significant correlations (r) between stock size and features of the ponds in area A (Spearman's rank correlation coefficient, $p < 0.05$).

features of the ponds	number of adult frogs (FR, AD)	total number of frogs (adult + subadult)
mean shade of the ponds	-0.57	-0.59
length of sunny shoreline	0.59	0.53
mean depth	0.57	0.50
area covered with vegetation: m ² (sum of sunny reed, webbed and submerged vegetation)	0.55	0.57
area covered with webbed and submerged vegetation, m ² (without reed)	0.47	0.50

The same factors that correlate with the number of frogs are also important for successful reproduction.

However the high reproductive success of a pond is not just the result of high stock size as proved by the fact that up to 100 adult frogs were counted in ponds in which frog reproduction was not observed. In those cases there was only very little vegetation in the pond. On the other hand, three of the ponds with high reproductive success (REPR++) were inhabited by no more than 35 adult frogs.

3.2. Area B (low pond density)

In area B I studied the influence of the habitat isolation on the frog population. Compared with area A, area B displayed significantly fewer ponds/km², fewer ponds with reproductive success, a higher ratio of *R.e.* (chi-square; $p < 0.05$) and lower stock sizes (U-test, $p < 0.01$; tabs. 1, 2).

3.2.1. Population size and ratio of *R.e.* and *R.I.*

Frogs were found in only 20 of the 42 ponds within the area and in 14 of the 21 ponds in the two-kilometre-wide belt surrounding area B. The stocks were mostly small (Tab. 2) and occurred only in the southern part of the area. Three ponds were only inhabited by a few subadult frogs, which had probably immigrated. A sample of 123 frogs featured 71% *R.e.* Only 13 ponds were inhabited by mixed stocks of *R.e.* and *R.I.*, and in the other waters only *R.e.* was found.

In three cases I caught enough adult and juvenile frogs to compare the ratio of *R.e.* to *R.I.* in both age groups whereby the percentage of *R.e.* among the juveniles was in all cases higher than among the adults (Fig. 3). The mean percentage of *R.e.* was 34 amongst the adults (N=32) and 64 amongst the juveniles (N=54).

3.2.2. Correlation between stock size and neighbouring stocks

In area B, the main factor determining the size of a frog stock seemed to be the number and size of the neighbouring stocks and their distance from the given stock. The number of adult frogs in a pond was significantly correlated to the N,AD variable representing distances and sizes of the neighbouring stocks within the radius of 2 km (Tab. 5 and Fig. 4). If the subadult frogs are added to the number of adults, the correlation to N,AD becomes more significant. The highest correlation coefficient was calculated after exclusion of periodic ponds and ponds with a mean shade of more than 70% from the analyses (these ponds being suboptimal for frogs according to the observations made in area A).

Generally the habitat structure had less influence in area B than in A. Contrary to area A, shade, depth and vegetation were not significantly correlated to the numbers of frogs in the ponds.

Tab. 4. Significant differences in area A (U-test, $p < 0.05$) between ponds with high reproduction and without reproduction (REPR++; n=9; REPR-; n=23).

variable	ponds without reproductive success		ponds with high reproductive success	
	mean	std. div.	mean	std. div.
number of adult frogs	17	23.7	63	41.0
adult frogs per m ² of the pond	0.24	0.5	0.46	0.5
length of sunny shoreline (m)	34	32.1	62	25.5
percentage of sunny shoreline (%)	53	41.3	84	23.3
mean shade of the pond (%)	35	37.1	3	6.5
mean depth (cm)	34	29.4	67	26.9
webbed leaf vegetation (m ²)	1	3.9	130	193.4
webbed leaf vegetation (%)	1	2.3	29	37.0
submerged vegetation (m ²)	8	22.1	67	108.4
total vegetation (m ²)	42	52.3	281	164.2
total vegetation (%)	30	36.3	91	7.4

3.2.3. Reproduction

In two ponds of area B reproduction was successful and three other ponds with frog reproduction were found in the two-kilometre-wide belt surrounding the area. Therefore I found metamorphosed juveniles only in five of the 31 ponds (=16 %) supportive of frog reproduction, being non-periodic and featuring adult frogs.

3.3. The influence of pond type on stock size and species composition

3.3.1. Stock sizes in different types of ponds

To answer the question of whether the number of frogs in the ponds in area B (low pond density) was indeed smaller than would be expected from the habitat quality, a cluster analysis was made. I grouped the ponds of both areas into types that differ in habitat structure. The stock sizes of each pond type in area A were then determined and compared to the stock sizes of the same type in area B (as shown in 3.1.2., the stock size in area A was correlated to features of the habitat).

The variables used for the cluster analysis included the ratio of sunny shoreline (%), depth (m) and ratio (%) of the types reed, submerged vegetation and webbed leaf vegetation. The ratio of the shoreline, respectively the vegetation was used to group the ponds into different "morphological" types irrespective of their size. The variables were standardised (mean=0, variance=1) to avoid varying importance of the pond features employed in the analyses.

The cluster analyses resulted in four groups of ponds characterised by the following features (Tab. 11 shows the ratio of the different types in both areas):

Cluster 1: sunny, shallow to deep; sparse or no vegetation (=type 1: sunny-bare).

Cluster 2: sunny; shallow; rich vegetation (dominated by reed). It consisted of a "permanent" and a "periodic" group (= type 2: sunny-vertical vegetation).

Cluster 3: sunny; mostly deep; rich vegetation whereby submerged and webbed leaf vegetation are dominant (= type 3: sunny-horizontal vegetation).

Cluster 4: shaded; mostly shallow; sparse vegetation. It consisted of a "permanent" and a "periodic" group (= type 4: shaded-bare).

Tab. 5. Significant correlations (Spearman's rank correlation coefficient) between stock size and neighbouring stocks (N,AD), in area B.

N,AD correlated to:	R (p<0.05)	N
number of adults	0.73	42
number of adults + subadults	0.77	42
number of adults + subadults (suboptimal ponds excluded)	0.82	28

Tab. 6. Stock sizes of different pond types (clusters) in area A.

pond type (Cluster)	mean	std. div.	adult frogs		
			min.	max.	N
1	24.5	18.0	3.5	57.0	8
2 perman.	39.3	13.1	25.0	56.0	6
2 period	2.0	2.0	0.0	5.0	3
3	63.7	43.3	5.0	135.0	10
4 perman	8.5	6.1	0.0	16.0	6
4 period.	1.3	1.5	0.0	3.0	3

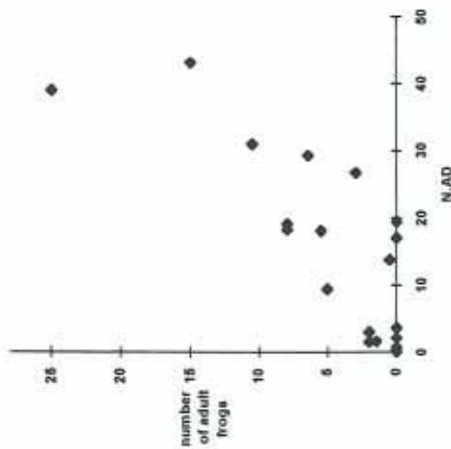


Fig. 4. Influence of the neighbouring stocks on the stock size of the ponds in area B (Spearman's rank correlation coefficient, $r=0.73$).

Starting out with the area A ponds, I looked for differences between the clusters in the number of frogs. The permanent ponds of cluster 2 and the ponds of cluster 3 are characterised by the highest numbers of frogs. Only in ponds of these two types a high reproductive success (REPR++) was observed. Tab. 6 shows the stock sizes of the pond types. Significant differences are shown in tab. 7. The stocks of the different clusters can be described as in tab. 8.

These differences between the stock sizes of the pond types did not occur in area B (low pond density).

As in area A, few frogs were found in the periodic ponds of area B. In the permanent ponds (which are generally more suitable than periodic waters) however, the number of frogs did not depend on the pond type but on the number of frogs in their neighbourhood. The higher the mean value of N,AD (see 2.5.) of a cluster, the higher the mean number of frogs living in this pond type (Tab. 9). Contrary to area A, sunny ponds with horizontal vegetation (cluster 3), and in particular permanent sunny ponds with vertical vegetation (cluster 2), were not characterised by a high number of frogs (Tab. 9). Thus the stocks in the ponds of high habitat quality in area B were much smaller than the findings of area A would have led to expect.

3.3.2. Ratio of *Rana kl. esculenta* to *Rana lessonae*

R.e. and *R.l.* may have different habitat preferences and therefore I looked for differences in the clusters with regard to the ratio of *R.e.* and *R.l.* in area A. Ponds of type 1 (sunny-bare) had a significantly (U-test, $p<0.02$) higher ratio of *R.e.* (85 %) than the types 2 (42 % *R.e.*) and 3 (58 % *R.e.*) with rich vegetation (Tab. 10). It would seem that *R.l.* prefers ponds with rich vegetation (type 2 and 3) and that *R.e.* prefers or tolerates ponds with sparse vegetation (type 1).

Tab. 7. Significant differences of the stock sizes in the four types of ponds in area A (U-test; ns: not significant).

	CL.2	CL.3	CL.4
CL.1	ns	$p=0.01$	$p=0.02$
CL.2		$p=0.02$	$p=0.03$
CL.3			$p<0.01$

3.3.3. Ratio and distribution of the ponds in both areas

The ratio of ponds belonging to each cluster in area A and B differs in some respect (Tab. 11). Type 3 ponds (characterised by a rich vegetation and in area A by the highest numbers of frogs), which were most important for reproduction, were rare in area B. Type 1 (sunny-bare) was more common in area B. This indicates that the mean habitat quality is lower in area B than in area A.

3.4. Change of landscape, decreasing number of ponds and frogs

In both areas there has been an intensification of agriculture during the last 40 years. Comparing topographic maps from 1950 to 1960 with the actual situation revealed a loss in area A of 27 % of the ponds existing 40 years ago and in area B of 56 % of the ponds. The loss was extremely high (75 %) in the northern quarter of area B.

Farmers living in the northern part of area B, where no *R.e.* and *R.L.* were found during the study period, reported that concerts of frogs were common 10 to 20 years ago. Presumably these frogs were *R.e.* and *R.L.* In 1981 I found these species in a pond in the northern half of the area where they are now extinct. The only other possible (calling) species, *Hyla arborea*, was not found in area B. It is likely that area B became less suitable for *R.e.* and *R.L.* with the decreasing number of ponds, and that the number of stocks has been declining over the last years, and may continue to do so.

4. Discussion

4.1. Area A (high pond density)

Shade, depth and vegetation seem to determine the size of the stocks in area A. These findings coincide with descriptions made by Blab (1986) and Dorn & Brandl (1991) of the preferred habitat type of *R.e.* and *R.L.* Frogs depend on vegetation for cover and range of actions and male choruses in particular are formed in areas of webbed leaf vegetation during the mating season. The sun factor may have a direct influence – the animals prefer to sit on sunny parts of the shore (Dorn & Brandl 1991) – as well as an indirect one: sunny ponds generally have richer vegetation (a significant negative correlation between shade and vegetation was found) and a higher water temperature than shaded ponds. The preference of high water temperatures was shown in the case of adult *R.L.* (Sjögren et al. 1988).

The reason for the correlation of stock size and depth may be the fact that shallow ponds are often periodic ones and few frogs stay there when they are filled with water. Deeper ponds in the area (maximum 100 cm) also have less reed and a higher ratio of the preferred webbed leaf- and submerged vegetation.

Tab. 8. Description of the stocks of different clusters in area A.

pond type (cluster)	stock size	reproductive success
1: sunny - bare	between long and high	no or little (REPR -/++)
2: sunny - vertical vegetation	permanent stock size between medium and high periodic: no frogs, or low stock size	permanent: no, little or high reproduction (REPR -/+/++) periodic: no reproduction (REPR -)
3: sunny - horizontal vegetation	stock size between high and very high	no, little or high reproduction (REPR -/+/++)
4: shaded - bare	periodic: no frogs or very low stock size permanent: stock size between low and medium	no reproduction (REPR -) no reproduction (REPR -)

The high stock sizes in ponds with fish, that were also found by Dorn & Brandl (1991) may be caused for the following reasons: Ponds with fish are significantly deeper and have a significantly larger proportion of sunny shoreline than ponds without fish, and as already mentioned, depth and sun are correlated positively with stock size (Tab. 3). Fish were not observed to have a negative influence on stock size as mentioned by Hemann & Zucchi (1985), but a negative influence on reproductive success is likely (see below). However, area A did not feature fishponds with large fish populations.

The most important factors for reproduction seem to be sun and vegetation. Sun is important in causing a high water temperature, which in turn accelerates the development of tadpoles (Eikhorst 1984).

Dense vegetation is supposed to be necessary as a cover for the spawn and the tadpoles, which might be more vulnerable in open water. In several ponds without vegetation spawn was found, but in these cases successful reproduction (REPR (+) or (++)) was not observed if fish, which are supposed to be a main predator of the tadpoles, lived in the pond. Additionally the low reproduction rate in ponds with sparse vegetation (type 1) may be also due to the low number of offspring resulting from *R.e.*-*R.e.* matings, which are very likely in such ponds where the percentage of *R.e.* is very high.

Tab. 9. Stock sizes of different pond types (clusters) in area B.

pond type (Cluster)	mean	std. div.	adult frogs			N	mean N/AD
			min.	max.			
1	4.9	7.2	0	25.0	14	15.7	
2 perman.	1.0	2.8	0	8.0	8	5.0	
2 period	1.6	1.9	0	5.0	8	17.1	
3	0.4	0.7	0	1.5	4	0.4	
4 perman	3.5	4.5	0	10.5	6	11.0	
4 period.	0	0	0	0	2	4.7	

Tab. 10. Ratio of *R.e.* in ponds of different types (clusters) in area A.

type	mean % R.e. of the ponds		std. error		N (ponds)		caught frogs	
							total	% R.e.
1:sunny - bare	85.2	17.7	6	87	83			
2:sunny - vertical vegetation	42.0	31.4	8	112	36			
3:sunny - horizontal vegetation	58.1	17.9	9	133	59			
4:shaded - bare	61.6	33.9	7	50	64			

Tab. 11. Ratio of ponds of different types in both areas (2a, 4a: permanent groups; 2b, 4b: periodic groups). The total number of ponds was 36 in area A and 42 in B.

Type	1 sunny - bare	2a sunny - vertical veg.	2b sunny - vertical veg.	3 sunny - horizontal veg.	4a shaded - bare	4b shaded - bare
% in A	22	17	8	28	17	8
% in B	33	19	19	10	14	5

There was no reproductive success in the majority of the ponds inhabited by frogs, meaning that a low number of the habitats, mainly the ponds with high reproductive success (REPR ++), have to support all the other stocks in the area. The number and distribution of such ponds in area A allows a sufficient production of juveniles to populate every pond according to its capacity (habitat quality), meaning that "empty places" e.g. in ponds where reproduction does not take place are quickly filled by immigrating young frogs. The distances between the ponds in area A are short and the exchange of animals is presumably high, meaning that the frogs in this area share a common gene pool. This is suggested by the fluctuating numbers of subadults and the observed migrations of adults and subadults between the ponds of area A (Zahn 1996).

4.2. Area B (low pond density)

The main factor limiting the number of frogs in area B ponds is the "supply of frogs" from the neighbouring ponds and not the quality of the ponds themselves. More frogs could live in most of the ponds than is actually the case. There was no reproduction in most of the ponds and therefore the stock size mainly depended on immigration. It can be presumed that suboptimal habitat structure (little vegetation) and the high percentage of *R.e.* (low reproductive success of *R.e.* × *R.e.* matings) prevent successful reproduction in many cases. In ponds with only few adults it is uncertain whether they are inhabited by sexually active frogs of both sexes during the mating season and thus in the case of many ponds it may be purely chance which decides whether reproduction occurs; equally the number of ponds in area B where reproduction occurs might differ from year to year.

The combination of great distances between the ponds and low habitat quality limits the distribution of the frog population. The number of offspring produced in the few ponds suitable for reproduction, is not sufficient to populate the isolated ponds in most parts of the area.

The intensive agriculture of area B may intensify the "isolation" effect, devaluing some of the ponds (for example, because of the diffusion of chemicals) and thus causing a lower density of suitable waters. Additionally migration between ponds is more difficult in fields with low cover and a dry micro climate than it is in meadows and forests (Müller & Steinwarz 1987, Blab et al. 1991).

4.2.1. Why were no frogs observed in ponds of high habitat quality

The frog population in area B probably declined over the last 20 years (see section 5). It is not clear why there are no small stocks left in the few ponds of the northern half of high habitat quality (types with rich vegetation 2 and 3; potentially suitable for reproduction). The time of population decline seems to be short for an extinction due to risks of a low population density. Sjögren (1991), for example, could not find any signs of inbreeding depression in isolated populations of *R.l.* A possible explanation for this phenomenon is that changes in pond quality may happen quickly. Most of the ponds in area B were artificial created to raise fish and ducks or as watering places. Depending on the owner's interests times of intensive use of a pond may alternate with those of undisturbed succession. This may cause that the vegetation, a factor of main importance for frog reproduction, may alter totally within a few years. Therefore, it is likely that throughout years varying ponds were suitable for high reproduction for longer or shorter periods. In areas with a high density of ponds the frog population is able to exist if the percentage of ponds suitable for reproduction is not too low, irrespective of alterations within the single ponds (situation in area A). Similar models are discussed by Ebenhard (1991), Olivieri et al. (1990), Hanski (1989, 1991), Hanski & Gilpin (1991) and for a northern population of *R.l.* by Sjögren (1994). However, if many ponds are destroyed, a local decrease of habitat quality can no longer be compensated for by better conditions in the neighbourhood and if local extinction occurs, new immigration is no longer possible.

Assuming that this explanation is correct, ponds which are not populated by frogs but which seemed suitable might have been suboptimal some years ago. Immigration is now unlikely due to the distances of existing stocks.

4.2.2. Ratio of *R.e.* and *R.l.* in area B

A higher percentage of *R.e.* was found in ponds of area B than in ponds of area A. Possible explanations for this difference are the habitat types and the distances between the ponds:

Type 1 ponds (sunny-bare), which showed the highest percentage of *R.e.* in area A (Tab. 10), are more common in area B than in area A. Additionally, *R.l.* seems to be less able to migrate than *R.e.* (Heym 1974). Therefore it can be assumed that the *R.e.* ratio of a stock will increase with the isolation of the pond, if frogs do not reproduce in the pond itself and the habitat is populated by immigrants (as most ponds of B).

4.3. Ratio of *R.e.* and *R.l.* in adults and juveniles

In every case the *R.e.*-ratio of juveniles was higher than the *R.e.*-ratio of adults (Fig. 3). It can be assumed that mechanisms exist to compensate for the higher number of metamorphosing *R.e.*, otherwise a strong sudden shift in the *R.e.*-*R.l.* ratio will occur within a few generations. Obviously this does not happen in areas as A where the ratio of *R.l.* is high. A possible compensating factor is the difference in habitat preference of *R.e.* and *R.l.* (see section 3.3.2.). Most *R.e.* settle in ponds with sparse vegetation where reproduction is low, while *R.l.* prefers ponds with rich vegetation. In ponds with rich vegetation that are suitable for high reproduction, the percentage of *R.e.* therefore may not rise, if lots of young *R.e.* emigrate to other types of ponds.

It would seem that this compensation does not work in area B as the percentage of *R.l.* was also low in the (few) ponds with reproduction belonging to types preferred by *R.l.* Probably the percentage of *R.e.* is still rising in area B. In only one pond considerable reproduction did occur and in this case the ratio of *R.e.* was 11 % amongst the adults. About 50 juveniles metamorphosed of which 20 were caught and all were *R.e.* There seems to be no possibility to compensate for this high percentage of *R.e.* Eventually the fact that *R.e.* females prefer *R.l.* males over their own (Apt & Reyer 1993) accelerates the change of species composition.

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