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Taxonomic reassessment of Middle Eastern water frogs: Bioacoustic variation among populations considered as *Rana ridibunda*, *R. bedriagae* or *R. levantina*

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Abstract

Temporal characteristics of advertisement calls of water frogs of 10 localities in Turkey, Syria, Israel and Egypt were compared with those of *Rana ridibunda* in Kazakhstan, Armenia and Greece (Thrace) as reference populations. These study sites include the type localities of *R. ridibunda*, *R. r. caralitana*, *R. esculenta* var. *bedriagae* und *R. levantina*. The temperature-dependent as well as the temperature-independent call parameters clearly revealed two species. *R. ridibunda* is represented by the three reference populations and, in addition, a population in central Turkey. The other populations (in Turkey, Syria, Israel and Egypt) represent *R. bedriagae*. *R. bedriagae* is the oldest available name for water frogs of these regions and was given priority over *R. r. caralitana* and *R. levantina*.

Key words: *Rana ridibunda* – *Rana bedriagae* – advertisement calls – call analysis – bioacoustic method – allopatric variation

Introduction

Bioacoustic analyses have shown that the water frogs (genus *Rana*) in Israel differ markedly from those in southern Yugoslavia and northern Greece with respect to the structure of advertisement calls, whereas the latter two populations have identical advertisement calls (Nevo and Schneider 1983; Kuhn and Schneider 1984; Schneider and Sofianidou 1985). Until recently (Günther 1990, 1991) the water frogs in these three regions were considered a single species, the lake frog, *Rana ridibunda*. The very different call structure observed in Israel, however, suggested that these frogs should be separated from the others, at least as a distinct subspecies (Schneider and Sofianidou 1985).

Subsequent bioacoustic studies of water frogs at two sites in Turkey, namely Izmir and Dalaman (Joermann et al. 1988), and in the Nile delta (Akef and Schneider 1989) corroborated the inference that the Middle East is inhabited by a form of water frog other than *R. ridibunda*, for all these frogs have the same advertisement call.

Comparisons of allozymes of water frogs in Israel and northern Greece not only confirmed this view but also led to the conclusion that the two groups of frogs are of different species, which began to split in the Pleistocene (Nevo and Filippucci 1988; Sinsch and Eblenkamp 1994). Surprisingly, neither of the two species is the typical *R. ridibunda*. The distinction has been established by studies of the advertisement calls of the water frogs of Armenia and of Atyrau (formerly Guryev) in western Kazakhstan: neither the water frogs in Israel nor those in northern Greece have advertisement calls consistent with those of *R. ridibunda* in the type locality (Schneider and Sinsch 1992). As a result of these findings, the species found in the Middle East was described as *R. levantina* (Schneider et al. 1992), and the one living in the main region of Greece was called *R. balcanica* (Schneider et al. 1993).

Further investigations have now been undertaken to clarify certain remaining problems. Camerano (1882) had described the water frogs of Damascus, Syria, as *Rana esculenta* var. *bedriagae*, and those of Lake Beyşehir in southern Turkey were described by Arikan (1988) as *R. ridibunda caralitana*. An analysis of their advertisement calls was desirable, in order to determine the systematic position of these two taxa. Furthermore, it was not known whether *R. ridibunda* is also present in Turkey. Given that this species is a native of Armenia, it seemed likely

to inhabit Turkey as well. To provide a good basis for comparison, the advertisement calls of water frogs of Birket Ata (Israel), the type locality of *R. levantina*, were analysed. Other advertisement calls included in this study, in addition to those of frogs of Damascus (Schneider 1997) were recorded from populations in the southern coastal region of Turkey and in the interior of the country, in Lake Beyşehir and at Gülşehir on the Kizilirmak River. These findings were evaluated with reference to previous studies of water-frog calls in Israel (Nevo and Schneider 1983), Turkey (Joermann et al. 1988) and Egypt (Akef and Schneider 1989). The results obtained from these bioacoustic data are presented here.

Materials and methods

The regions sampled for advertisement calls of water frogs are in the Middle Eastern states Turkey, Syria, Israel and Egypt and include the type localities of *Rana ridibunda caralitana* Arikan, 1988, *Rana esculenta* var. *bedriagae* Camerano, 1882 and *Rana levantina* Schneider et al. 1992 (Fig. 1). In several regions we pooled records obtained from local

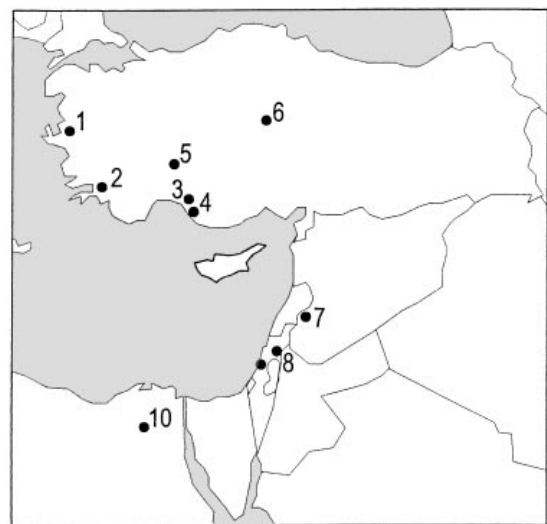


Fig. 1. Map of localities. Turkey: Izmir (1); Dalaman (2); Karpuz Çay (3); Alanya (4); Lake Beyşehir (5); Gülşehir (6); Syria: Damascus (7); Israel: Jordan Valley (8); Birket Ata (9); Egypt: Cairo (10). Further information on localities is given in the appendix

populations within a radius of about 30 km because we consider them as interacting parts of the same metapopulation (Sjögren 1991; Tunner 1992). Moreover, we used series of the advertisement calls of lake frogs *Rana ridibunda* Pallas 1771 from another three sites (including the type locality) as an outgroup for the evaluation of interpopulational variation and taxonomic decisions. Details on the localities and the numbers of call series are listed in the appendix.

The calls were recorded with a condenser microphone (Sennheiser, Type MKH 415 T) and a portable tape recorder (Stellavox SP 8, Uher report 4000 S), and the corresponding water temperature, with an electrical thermometer (Technoterm 1500). Oscillograms (Tektronix Oscilloscope 502 A, Toennies Recordine camera) and sonagrams (Medav Mosip Signal Processing System) were prepared for evaluation. Each call series was characterized by nine parameters: 1. duration of pulse groups (ms); 2. interval between pulse groups (ms); 3. period of pulse groups (ms); 4. call duration (ms); 5. intercall interval (ms); 6. call period (ms); 7. number of pulse groups/call (N); 8. pulses/pulse group (N); 9. pulse groups/s (Hz). Intercall interval and call period were not measured in the data sets from localities 1 and 2. The arithmetic means of these call parameters were calculated for each series and used for further analyses. Thus, the basic data set describing the advertisement calls of each population consisted of 10 variables (9 call parameters and the corresponding temperature) with N (the number of call series) observations.

At the level of local populations (localities 5, 6, 7, 9) or metapopulations (localities 1, 2, 3, 4, 8, 10), the four temperature-dependent call parameters (pulse group duration, pulse group interval, pulse group period, pulse groups per second; Schneider and Sinsch 1992) were plotted against water temperature in order to detect potential differences in the type of dependence. The small range of temperatures and/or the low number of call series recorded at some localities impeded a statistical comparison of regression lines. In contrast, the five temperature-independent call parameters (pulses per pulse group, pulse groups per call, call duration, intercall interval, call period; Schneider and Sinsch 1992) were statistically compared by means of a one-way ANOVA for each variable. Grouping of populations was determined by a multiple range test using the least square deviation method with a confidence interval of 99%. Discriminant functions (procedure: forward selection, F-to-enter: 4.0) that represent the best subset of these five parameters were also calculated to test for a grouping of populations. Taxonomic decisions were based on the grouping obtained by the three methods of interpopulational comparison.

At the level of species, a principal-component analysis was performed on the matrix of the linear correlation coefficients of all individual variables in order to reduce the amount of information to statistically unrelated factors. The first principal component (PC1) derived from advertisement call data represents the amount of variance caused by temperature, the following ones (PC2/PC3) temperature-independent sources of variation. The influence of temperature on PC1 was assessed by linear correlation and regression analysis for each species, and slopes and intercepts of regression lines were tested for species-specific differences, using the conditional sum of squares. Finally, the five temperature-independent variables entered into a discriminant analysis to quantify the bioacoustic segregation of the taxa.

Results

The temperature dependence of four call parameters – pulse group duration, pulse group interval, pulse group period and pulse groups per second – was confirmed in the Middle Eastern water frog populations (Fig. 2A–D). The individual data separated despite a partial overlap into two clusters with a different degree of temperature dependence: one cluster consisted of the three reference populations of *R. ridibunda* and that from Gülşehir (Fig. 2A), the other one included the remaining populations from Turkey, Syria, Israel and Egypt. The *R. ridibunda* cluster was characterized by a smaller range of temperature (12.0–25.5°C) in which frogs called, and a steeper temperature dependence of the parameters pulse group duration, pulse group interval, and pulse group period. The frogs grouped in

the second cluster called over a considerably larger temperature range (14.0–33.5°C).

Among the five temperature-independent advertisement call parameters, pulses per pulse group ($p < 0.01$) and pulse groups per call ($p < 0.05$) significantly separated the studied populations into the same two groups as delimited above (Fig. 3A, B; Multiple Range Test). No consistent grouping of populations was obtained by analysing call duration, intercall interval and call period, but intercall intervals and call periods were significantly longer in the populations from Gülşehir and the reference populations from Kazakhstan and Thrace (Greece) (Fig. 3C,D,E; $p < 0.05$, Multiple Range Test).

The discriminant analysis revealed that only three of the temperature-independent call variables significantly contributed to distinction among the populations: pulses per pulse group, pulse groups per call, and call duration (Table 1). The three significant canonical variables (discriminant functions) derived explained the total variance of the data set. Remarkably, the calls of the frogs from Gülşehir were never confounded with those of any other populations from Turkey, but exclusively with those of the *R. ridibunda* reference populations. The discriminant plot of the individual scores confirmed the grouping of populations into two clusters (Fig. 3F): one cluster which consisted of the three *R. ridibunda* reference populations plus that from Gülşehir, Turkey, and a second one which was formed by all coastal and the highland population of Beyşehir, Turkey, together with the populations studied in Syria, Israel and Egypt. Therefore, we conclude that only two water frog species instead of four taxa (*R. ridibunda ridibunda*, *R. r. caralitana*, *R. esculenta* var. *bedriagae*, *R. levantina*) are represented in the analysed data set. According to the covariance with the reference populations, one species is identified as *R. r. ridibunda*, whereas the second species includes the populations from the type localities of *R. esculenta caralitana*, *R. r. var. bedriagae*, and *R. levantina*. For further analysis at the species level, we use the two population groups thus delimited as taxonomic units and refer to them as *R. ridibunda* and *R. bedriagae*, respectively.

A principal-component analysis run on the data set detected three principal components with an eigenvalue > 1 which together explained 89.3% of the total variation. PC1 had an eigenvalue of 5.3 and alone explained 58.8% of the total variation. This canonical variable significantly correlated with temperature ($p < 0.001$; Fig. 4A), but slopes and intercepts of the species-specific regression lines significantly differed between the taxa ($p < 0.01$). The call parameter pulse group period exemplifies this difference between the two species (Fig. 4B). Its correlation with temperature is highly significant in the two species ($p < 0.001$), but slopes and intercepts varied ($p < 0.01$). PC2 (eigenvalue 1.71) and PC3 (eigenvalue 1.03) accounted for 19.0% and 11.5% of the total variance, respectively. The range of temperature-independent variability of the advertisement calls completely overlaps in the two species, but the range of variation is smaller in *R. bedriagae* than in *R. ridibunda* (Fig. 5A). Discriminant analysis based on the five temperature-independent call parameters yields a reliable distinction at the 95% level of correct assignment of calls to species (Fig. 5B, Table 2).

Discussion

The advertisement calls compared here were recorded from water frog populations within a large region, extending from western and southern Turkey through Syria and Israel to Egypt. Bioacoustic analysis of these calls has revealed that some of the

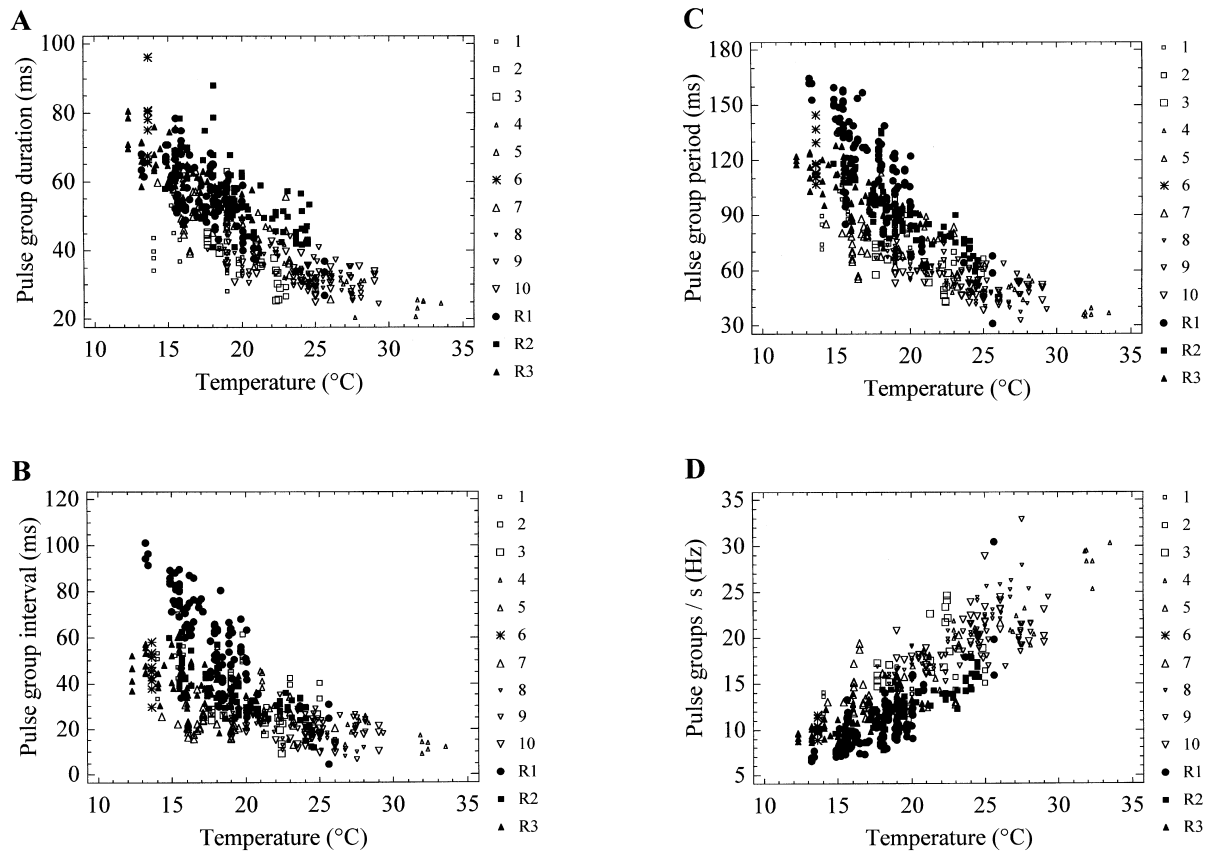


Fig. 2. Variation of the temperature-dependent advertisement call parameters among geographically distant water frog populations including three reference populations (R1–R3) of *R. ridibunda*. (A) Pulse group duration; (B) Pulse group interval; (C) Pulse group period; (D) Pulse groups per second. Each symbol represents the mean of three calls of a single call series. Details on localities are given in Fig. 1 and the appendix

nine call parameters examined are correlated with the ambient temperature. The same applies to the advertisement calls of the frogs, *R. ridibunda*, of Atyrau (Kazakhstan), Armenia and Thrace (Greece), included in the analysis as an outgroup. On the basis of both temperature-dependent and temperature-independent parameters, the populations formed two groups with almost no overlap. These two groups represent two species. One group comprises the outgroup populations, those of Atyrau (Kazakhstan), Armenia and Thrace, which belong to *R. ridibunda*. It also includes the frogs of the Kizilirmak River at Gülşehir, which have advertisement calls identical to that of *R. ridibunda* and hence should be assigned to that species. The existence of *R. ridibunda* in Turkey has thus been reliably documented for one locality. Beerli et al. (1994) carried out allozyme investigations for water frogs of many localities in the eastern Mediterranean region. Four of these (each represented by 5–16 individual frogs) were in Turkey at Ezine, Selçuk, Akçapınar and Marmaris, all directly on the Aegean coast and thus in the extreme west of the country. The results of the allozyme electrophoresis confirmed those of previous bioacoustic analyses (Joermann et al. 1988; Schneider and Sinsch 1992) showing that the water frogs living there are not identical to *R. ridibunda*. Although the database was so sparse, Beerli (unpublished data) suggested that all of Anatolia is inhabited by this other species. Our demonstration of *R. ridibunda* at Gülşehir refutes this suggestion.

The water frogs forming the second group, according to the structure of the advertisement call, are also a distinct species.

This group includes the populations in western Turkey, Israel and Egypt, the calls of which were analysed long ago (Nevo and Schneider 1983; Schneider and Sofianidou 1985; Joermann et al. 1988; Akef and Schneider 1989). It was clear at the time that these frogs were different from *R. ridibunda*, and it was upon them that the description of *R. levantina* was based (Schneider and Sinsch 1992; Schneider et al. 1992). Now that the advertisement calls of water frog populations of southern Turkey, Damascus and Birket Ata (Israel) have been analysed, these have been shown to belong to the same group. Although some of the populations in this group are widely separated geographically, the advertisement calls of each of them are indistinguishable. Such consistency is especially remarkable in view of the fact that over large parts of the region inhabited by these populations, only the one water frog species is present. These results show quite clearly, yet again, that the advertisement calls are distinguishing and unmistakable species characters.

Bioacoustic variation and allopatry

As a consequence of our bioacoustic research on water frogs, doubts have been raised about the reliability of taxonomic conclusions based on mating calls: 'Mating calls are a very powerful way to distinguish between sympatric anuran species but they do not provide good data to build phylogenies. The reason for this is simple: precisely because mating calls are important for discriminating between species they will tend to be dissimilar in sympatry, and not so dissimilar in allopatry.

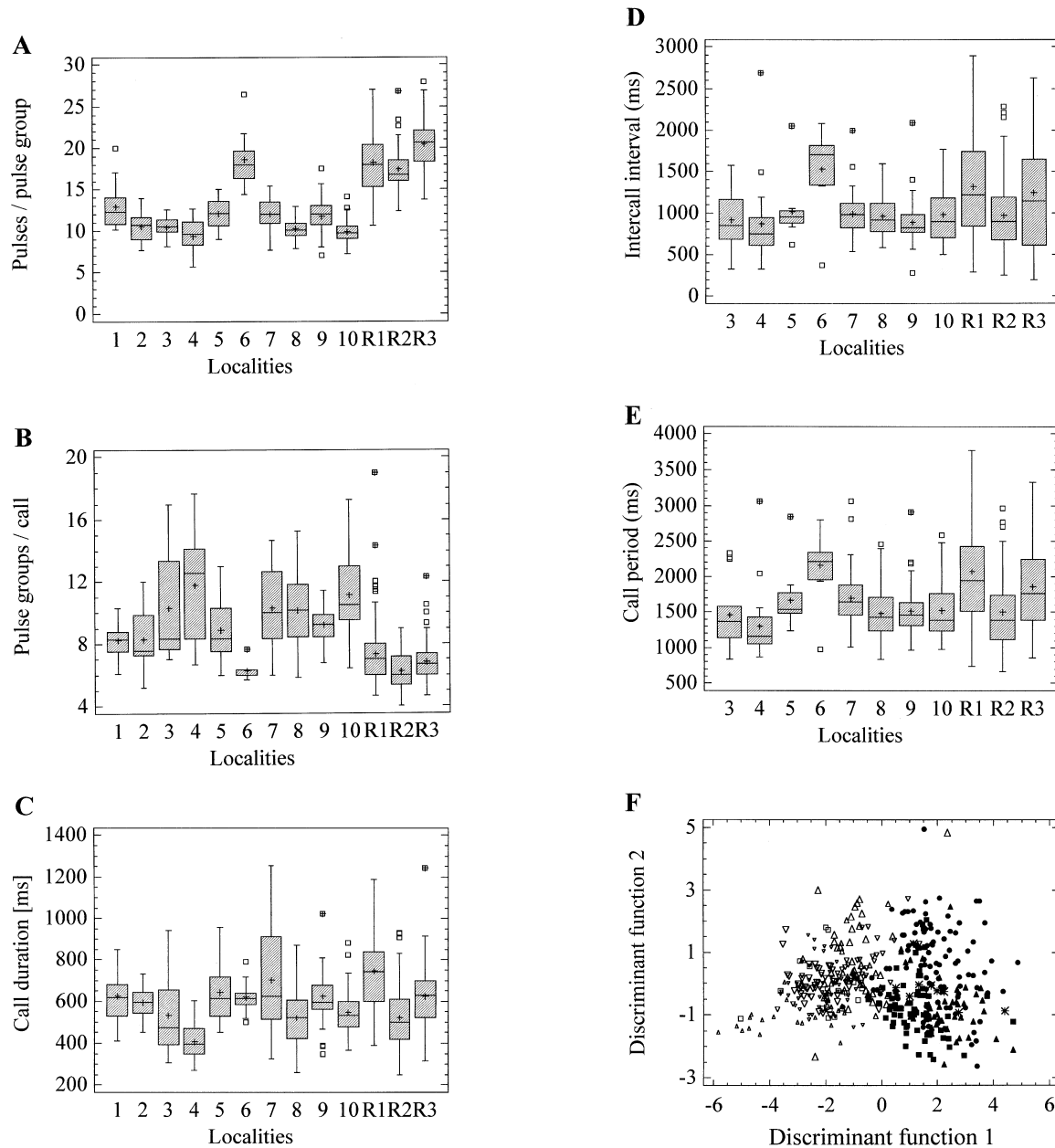


Fig. 3. Box-and-whisker plots of the temperature-independent advertisement call parameters among Middle Eastern water frog populations including three reference populations (R1-R3) of *R. ridibunda*. (A) Pulses per pulse group; (B) Pulse groups per call; (C) Call duration; (D) Intercall interval; (E) Call period; (F) Discriminant plot (based on the five call parameters A-E, Table 1). The central box covers the middle 50% of the data; the sides of the box are the lower and upper quartiles, the horizontal line drawn through the box is the median, + is the arithmetic mean. The whiskers indicate the range of the data; single symbols are outliers. Details on localities are given in Fig. 1 and the appendix

Indeed, acoustic data and enzyme data yield incompatible answers regarding the phylogeny of water frogs' (Hotz, in Arntzen and Bauer 1996). Furthermore, Ohler (1997) writes: 'The synonymy on the basis of mating calls of *Rana shqiperic* with *Rana lessonae* (Sinsch and Schneider 1996) is rather doubtful (allopatric populations), as the species has clearly been defined on a number of biochemical and developmental characters'. However, data supporting these objections have never been presented. Moreover, severe errors in these statements render them personal prejudices rather than serious criticism.

Firstly, the term allopatry always refers to the lack of coexistence between related species or subspecies in a certain geographical area, not to populations of the same species (e.g.

Schaefer 1992; Begon et al. 1996). Taking this into consideration as well as the distribution of water frogs in Europe (Gasc et al. 1997) and Middle East it is obvious that allopatry is not relevant: (1) In large areas of its range of distribution, *Rana lessonae* occurs in sympatry with *R. balcanica*, *R. bergeri*, *R. esculenta*, and *R. ridibunda*. In fact, it is hard to identify areas where this species does not coexist with another water frog species or hybrid. (2) *Rana ridibunda* shares wide areas of its range with *R. balcanica*, *R. bedriagae*, *R. esculenta*, *R. lessonae* and *R. perezi*. According to Hotz (in Arntzen and Bauer 1996), considerable variations should be expected among the advertisement calls given by *R. ridibunda* in regions where it occurs alone and in areas of sympatry with another water frog species.

Table 1. Discriminant functions based on three temperature-independent call variables to distinguish among 13 water frog populations including three reference populations (R1-R3) of *R. ridibunda*. (A) Statistical significance; (B) Unstandardized coefficients of the discriminant functions. (C) Classification success

(A)							
Discriminant function	Eigenvalue	Relative percentage	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	Statistical significance
1	3.18	86.7	0.8724	0.1558	944.5	36	p < 0.0001
2	0.36	9.7	0.5131	0.6520	217.3	22	p < 0.0001
3	0.13	3.5	0.3393	0.8849	62.1	10	p < 0.0001

(B)			
Call parameter	Discriminant function 1	Discriminant function 2	Discriminant function 3
pulses/pulse group	0.288	-0.224	0.176
pulse groups/call	-0.291	-0.306	0.440
call duration	0.003	0.007	-0.001
constant	-3.643	1.498	-6.711

(C)													
Actual group	Pred. group										R1	R2	R3
	1	2	3	4	5	6	7	8	9	10			
1 Izmir, Turkey	5 28%	4 22%	1 6%	0	2 11%	0	2 11%	0	1 6%	0	2 11%	0	1 6%
2 Dalaman, Turkey	2 12%	10 62%	0	0	1 6%	0	0	1 6%	1 6%	1 6%	0	0	0
3 Karpuz Çay, Turkey	1 6%	3 19%	0	2 12%	0	0	2 12%	5 31%	2 12%	0	0	0	0
4 Alanya, Turkey	0	3 14%	1 5%	14 64%	0	0	0	4 18%	0	0	0	0	0
5 Beysehir, Turkey	2 17%	3 25%	1 8%	0	1 8%	0	2 17%	0	0 8%	0	0	2 17%	0
6 Gülsehir, Turkey	0	0	0	0	0	4 44%	0	0	0	0	1 11%	2 22%	2 22%
7 Damascus, Syria	7 18%	3 8%	1 3%	1 3%	2 5%	0	14 36%	4 10%	2 5%	3 8%	1 3%	1 3%	0
8 Jordan Valley Israel	2 4%	10 20%	2 4%	9 18%	0	0	2 4%	12 24%	4 8%	10 20%	0	0	0
9 Birket Ata Israel	7 16%	4 9%	0	2 5%	5 11%	0	5 12%	5 12%	10 23%	2 5%	2 5%	1 2%	0
10 Cairo, Egypt	1 3%	6 16%	3 8%	4 11%	0	0	0	12 32%	0	12 32%	0	0	0
R1 Atyrau, Kazakhstan	11 10%	0	0	1 1%	0	9 8%	4 3%	1 1%	1 1%	0	49 45%	9 8%	25 23%
R2 Yerevan, Armenia	5 7%	0	0	0	0	7 9%	0	0	0	0	7 9%	45 59%	12 16%
R3 Thrace, Greece	2 3%	0	0	0	0	5 7%	0	0	0	0	9 13%	10 15%	41 61%

In fact, in the contact zone with *R. balcanica* in Greece we showed bioacoustic character displacement in two call features, but the basic structure of the call remained unaltered and species-specific regardless of allopatry (Schneider and Sinsch 1992;

Schneider et al. 1993). This is a reasonable result because of a factor that Hotz (in Arntzen and Bauer 1996) did not consider: the main function of the advertisement call is intraspecific communication and not simply the premating isolation from sym-

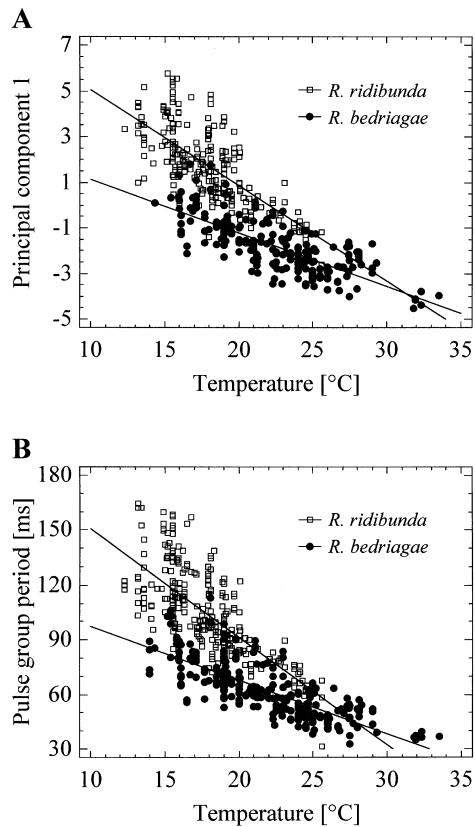


Fig. 4. Advertisement call features of *R. ridibunda* and of *R. bedriagae*. (A) Individual scores of principal component 1 (based on nine call variables) in relation to water temperature. Regression models: $PC1 = 9.15 - 0.42 * \text{temperature}$; $r = -0.710$ (*R. ridibunda*); $PC1 = 3.48 - 0.23 * \text{temperature}$; $r = -0.764$ (*R. bedriagae*). (B) Temperature dependence of the pulse group period. Regression models: $PGP = 210.16 - 5.93 * \text{temperature}$; $r = 0.721$ (*R. ridibunda*); $PGP = 127.0 - 2.95 * \text{temperature}$; $r = 0.778$ (*R. bedriagae*)

patric species. Neighbouring water frog populations are not closed and independent entities but are connected with each other by widely roaming individuals (> 10 km) (Tunner 1992), resulting in large metapopulations with considerable gene flow among local populations. Thus, it is no surprise that selection has favoured the maintenance of a common acoustic signal system within the whole range of distribution. Hotz (in Arntzen and Bauer 1996) and Ohler (1997) ignore existing data proving that sympatry with other related species leads only to minor modifications of call structure, leaving unaltered the species-specific features. With respect to the advertisement calls of frogs, interpopulational variation even over large distances is always smaller than interspecific variation (e.g. Littlejohn 1976; Schneider et al. 1993). Consequently, advertisement calls are perfectly suited for identification in the whole geographic range of a species.

Secondly, allozymes and bioacoustics certainly do give similar answers to the taxonomic questions with regard to water frogs, although homologous protein structures are usually more variable than call structure due to random changes of local gene pools by genetic drift. For instance, the hybrid status of *R. esculenta* is manifested in the call structure as well as in allozyme data. Our bioacoustically determined ranges of distribution among *R. balcanica* and *R. ridibunda* perfectly coincide with that inferred from allozyme data (Sinsch and Eblenkamp 1994;

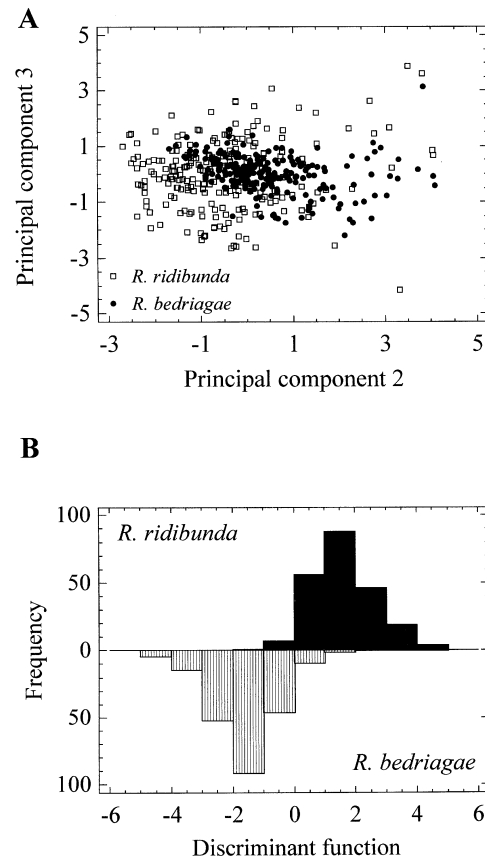


Fig. 5. Advertisement call features of *R. ridibunda* and of *R. bedriagae*. (A) Temperature-independent call variation: PC2 vs. PC3. (B) Frequency histogram (class width: 1 unit) of the discriminant scores (Table 2)

Sofianidou et al. 1994). The same applies to the recognition of *R. epirotica* and *R. bedriagae* as distinct species (Nevo and Schneider 1983; Schneider et al. 1984; Beerli, unpublished data; Sinsch and Eblenkamp 1994). The few cases of disagreement of which we are aware concern the assignation of species status to *R. shqiperica*, *R. cretensis* and *R. cerigensis* (Hotz et al. 1987; Beerli et al. 1994). These descriptions are mainly based on supposedly private alleles identified in allozyme studies on remarkably few animals. If sample sizes of individuals are small, attributes might appear fixed or absent from a population, when in fact they are polymorphic (Sites and Crandall 1997). Doubts about the taxonomic status of *R. shqiperica* arise from the fact that these frogs are bioacoustically indistinguishable from *R. lessonae* (Sinsch and Schneider 1996). The specific differentiation of *R. cretensis* and *R. cerigensis* from *R. bedriagae* is not even supported by a logically consistent application of the phylogenetic or phenetic species concept (Veith 1996). The anecdotal remarks concerning the advertisement calls of these island water frogs which are given in the description are insufficient for a reliable comparison with the calls of *R. bedriagae*. However, the main weakness of these descriptions is the continual disregard of the fact that a proposed new taxon has to be proved to differ significantly from specimens of the type localities of potentially related species: Testona near Torino (topotypical *R. lessonae*) and Petrele, Albania (*R. kurtmuelleri*) in case of *R. shqiperica*, and Damascus (*R. bedriagae*) in case of *R. cretensis* and *R. cerigensis*. Inexplicably, Dubois and

Table 2. Discriminant function based on five temperature-independent call variables to distinguish between *R. ridibunda* and *R. bedriagae*. (A) Statistical significance; (B) Unstandardized coefficients of the discriminant functions; (C) Classification success

(A)						
Eigenvalue	Relative percentage	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	Statistical significance
2.591	100	0.8495	0.2784	554.3	5	p < 0.0001
(B)						
Call parameter	Discriminant function					
Pulses/pulse group	0.286					
Pulse groups/call	-0.256					
call duration	0.0014					
intercall interval	0.0001					
call period	-0.00004					
constant	-2.951					
(C)						
Actual species	Predicted species					
	<i>R. ridibunda</i>	<i>R. bedriagae</i>				
<i>R. ridibunda</i>	213 (96.4%)	8 (3.6%)				
<i>R. bedriagae</i>	11 (5.1%)	206 (94.9%)				

Ohler (1994) failed to criticize this deficiency. In conclusion, the present disagreements are apparently not a matter of incompatibility of allozyme and bioacoustic data, but of the species concept followed.

Taxonomic decisions

The first analysis of the advertisement calls of water frogs in Israel involved animals at several sites, from Dan in the north to Nahal Arugot in the south and Nesher in the west (Nevo and Schneider 1983). In the subsequent description of these frogs as *R. levantina*, Birket Ata was chosen as the type locality; this decision was based on the relatively large size of this body of water, which implies that its frog population will exist there for a long time (Schneider et al. 1992). A comprehensive analysis of the calls of the frogs in the type locality was needed, and the results form part of the database presented here.

For an accurate evaluation of the status of water frogs in the Middle East, it was necessary also to analyse the calls of the frogs of Damascus that Camerano (1882) called *Rana esculenta* var. *bedriagae*. Although Damascus is only 180 km away from Birket Ata, it seemed likely that the prolonged isolation of the water frogs of Damascus would have produced a local form. These frogs do indeed exhibit adaptations to the local conditions in the Barada River. Their territorial behaviour is not very well developed; therefore males that are ready to mate can crowd together within small areas during the pre-spawning and main spawning seasons (Schneider 1997). The Barada River is a mountain stream, flowing at high velocity with little surface vegetation, so that it provides few habitats suitable for frogs. Their low level of territoriality distinguishes the frogs of Damascus from those at Birket Ata, where males calling for a mate establish large territories.

The advertisement calls themselves, however, do not differ in the two localities. Because the name introduced by Camerano (1882) has priority, we designate the water frog species found in the Middle East *Rana bedriagae* Camerano, 1882. As the common name we propose the one we chose previously, the Levantine frog, because it emphasizes its presence in the region called the Levant.

The call analyses also enable an evaluation of frogs of Lake Beyşehir, which Arikan (1988) described as *R. ridibunda caralitana*. These frogs are exceptionally large and have a characteristic marking on the ventral surface. More than half a century ago Kosswig (cf. Bodenheimer 1944) had noticed this. Nevertheless, they are also assignable to *R. bedriagae*, because the temporal characters of the advertisement call are species-specific. They are identical to those of *R. bedriagae* in the type locality. The calls recorded at Lake Beyşehir differ from those of the other Levantine frogs in having a lower dominant frequency, and this difference is secondary. Because these frogs have larger bodies, the vocal apparatus with its vibrating components is also large, which lowers the frequency of the calls. Morphometric data also identify the frogs of Lake Beyşehir as typical *R. bedriagae* (Sinsch and Schneider 1999). Hence there is no justification for classifying them as a separate subspecies.

Climate and geographic distribution

According to what is known about the distribution of *R. bedriagae*, the species mainly occupies regions with a mild climate. In contrast, *R. ridibunda* is adapted to a cold climate and therefore occurs at more northern latitudes than *R. bedriagae* and also in regions, where a continental climate prevails as at Atyrau, the type locality of *R. ridibunda*. In view of the ecological potency of *R. ridibunda*, the discovery of this species at Gülşehir in central Anatolia is unsurprising, because the climate here is considerably colder than in the southern coastal regions of Turkey. *R. ridibunda* can be expected to be found in other relatively cold parts of Turkey.

In the case of *Hyla* the situation is comparable. *Hyla savignyi*, a native of Israel, also lives in Armenia, on the plain of the Araks River where it is hot and dry in summer. The cool, rainy northern part of the country is occupied by *Hyla arborea* (Egiasarjan and Andronnikov 1986; Egiasarjan and Schneider 1990, 1991).

In this interpretation of the distribution of *R. bedriagae* and *R. ridibunda*, the frogs of Lake Beyşehir seem to be exceptional; the lake is inhabited by *R. bedriagae* even though the climate is sufficiently inclement that *R. ridibunda* would be expected there.

Zusammenfassung

Taxonomische Neubewertung von Wasserfröschen aus dem Mittleren Osten: Bioakustische Variation bei Populationen, die als Rana ridibunda, R. bedriagae oder R. levantina angesehen werden

Bei Wasserfröschen von zehn Standorten aus der Türkei, Syrien, Israel und Ägypten wurde ein Vergleich der temporalen Parameter der Paarungsrufe durchgeführt. In den Vergleich wurden außerdem die Paarungsrufe von *Rana ridibunda* aus Kasachstan, Armenien und Griechenland (Thrakien) einbezogen. Zu diesen Standorten gehören die Typuslokalitäten von *R. ridibunda*, *R. r. caralitana*, *R. esculenta* var. *bedriagae* und *R. levantina*. Sowohl die temperatur-abhängigen als auch die temperatur-unabhängigen Rufparameter führten zur Aufspaltung in zwei Gruppen, die zwei Arten repräsentieren: *R. ridibunda*, und *R. bedriagae*. *R. ridibunda* ist durch die drei Referenzpopulationen und durch eine Population aus der zentralen Türkei vertreten, *R. bedriagae* durch die anderen untersuchten Populationen aus der Türkei, Syrien, Israel und Ägypten. Da *R. bedriagae* ist der älteste verfügbare Name für Wasserfrösche aus diesen Regionen ist, hat er Priorität über *R. r. caralitana* und *R. levantina*.

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Appendix

Localities where advertisement calls have been recorded

Numbers of localities refer to Fig. 1. Altitude above sea level and the number of call series are also given.

Turkey

Localities 1–4 are situated near the Aegean or Mediterranean coast. The population of Lake Beyşehir (locality 5) is inland and at high altitude. The lake is isolated toward the Mediterranean coast because it is without drainage and the Taurus mountains represent a huge barrier. Locality 6 is at Gülşehir in central Turkey. Here the water frogs live in the Kizilirmak River, which flows into the Black Sea.

Locality 1: Surroundings of Izmir, 10–20 m above sea level. $n = 18$ (Joermann et al. 1988).

Locality 2: Region of Dalaman, 10–20 m above sea level. $n = 16$ (Joermann et al. 1988).

Locality 3: Karpuz Çay (River), ≈ 7 km from the mouth at Hacıobaşı, 10–20 m above sea level, and at Murtici. $n = 16$

Locality 4: Alanya, 10 m above sea level. $n = 22$

Locality 5: Beyşehir, 1116 m above sea level (type locality of *R. ridibunda caralitana*). $n = 12$.

Locality 6: Gülşehir, 815 m above sea-level. $n = 9$.

Syria

The water frogs mainly inhabit the Barada River at Damascus. They are isolated because high mountains and semidesert surround the region.

Locality 7: Barada River at Idaide Al-Wadi, ≈ 12 km west of Damascus,

≈ 800 m above sea level (type locality of *R. bedriagae*). $n = 39$ (Schneider 1997).

Israel

The first analysis was based on calls recorded at various sites in the Jordan valley and at Nesher near Haifa (locality 8). A new sample of call series was collected at Birket Ata near Hadera (locality 9).

Locality 8: Jordan valley: Dan, Tabigha, Nir Dawid, Paza'el, Nahal'Arugot, 100–300 m below sea level. $n = 51$ (Nevo and Schneider 1983).

Locality 9: Birket Ata, ≈ 30 m above sea level (type locality of *R. levantina*). $n = 43$.

Egypt

Locality 10: Surroundings of Cairo: Giza, Al-Kanater, Al-Khairya (Barrage), 50 m above sea level. $n = 38$ (Akef and Schneider 1989).

Reference populations of *Rana ridibunda* for the outgroup comparison

Kazakhstan

(R1) Atyrau (formerly Guryev), 25 m below sea level, (type locality of *R. ridibunda*). $n = 110$ (Schneider and Egiasarjan 1991).

Armenia

(R2) Yerevan, Lake Sevan, 1200 m & 1900 m above sea level. $n = 76$ (Schneider and Egiasarjan 1989)

Greece

(R3) Thrace: Evros delta, Erythropotamos River at Didimotiho, Ardas River at Komara, 5–67 m above sea level. $n = 67$ (Schneider et al. 1993).