HERPETOZOA 10 (3/4): 139 - 148
Wien, 30. Dezember 1997

REVIEW

The Water Frogs (*Rana esculenta* complex) of the Neusiedlersee region (Austria, Hungary)
(Anura: Ranidae)

Die Wasserfrösche (*Rana esculenta* Komplex) der Region Neusiedlersee (Österreich, Ungarn)
(Anura: Ranidae)

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KURZFASSUNG

Die Region Neusiedlersee im Grenzgebiet von Österreich und Ungarn ist der Lebensraum einer einzigartigen Wasserfroschfauna. *Rana lessonae* CAMERANO, 1882 (Kleiner Wasserfrosch) bildet zusammen mit *R. esculenta* LINNAEUS, 1758 (Teichfrosch) eine individuenreiche Mischpopulation. Die Teichfrösche, einst aus Kreuzungen der Art *R. ridibunda* PALLAS, 1771 mit *R. lessonae* entstanden, sind zu 97% Weibchen. Bei *R. lessonae* ist das Geschlechterverhältnis ausgeglichen. Die *R. lessonae* - Männchen verpaaren sich sowohl mit den arteigenen Weibchen als auch mit den hybriden *R. esculenta* - Weibchen. Eine im Organismenreich äußerst seltene Art der Fortpflanzung (Hybridogenese) garantiert, daß aus Paarungen zwischen *R. lessonae* - Männchen und den hybriden *R. esculenta* - Weibchen immer nur *R. esculenta* - Phänotypen resultieren. Die gegenwärtige Verteilung der beiden Wasserfroschtaxa in der Seeregion und die ausgedehnten jährlichen Wanderungen der Art *R. lessonae* stehen offensichtlich im Zusammenhang mit der Entstehungsgeschichte des Sees sowie mit den speziellen ökologischen Verhältnissen im Süden der Seeregion.

ABSTRACT

The Neusiedlersee region situated at the border of Austria and Hungary is the habitat of a unique Water Frog fauna composed of *Rana lessonae* CAMERANO, 1882 and *R. esculenta* LINNAEUS, 1758. *Rana esculenta* is a hybrid that originally arose from crosses between *R. ridibunda* PALLAS, 1771 and *R. lessonae*. Around Neusiedlersee, *R. lessonae* males and females are about equally common while the females of the hybrid account for 97% of the *R. esculenta* specimens. Successful mating occurs between *R. lessonae* males with conspecific females and beween female *R. esculenta* and male *R. lessonae*. An aberrant type of klonal reproduction (hybridogenesis) guarantees that mating between *R. lessonae* males and *R. esculenta* females results exclusively in *R. esculenta* progeny. The present distribution of Water Frogs in the lake region (*R. esculenta* predominating in the northern part) is apparently a consequence of the geological formation of the region and its ecology. An extended yearly migration of *R. lessonae* to more northern breeding areas results in the persistence of female *R. esculenta*.

KEY WORDS

Anura, Ranidae, *Rana esculenta, Rana lessonae*, hybridogenesis, unisexuality, migration; Neusiedlersee region, Austria, Hungary

Topography of the Neusiedlersee region

The heart of the Neusiedlersee region, which is situated on the edge of the Small Hungarian Plain, approximately 50 km southeast of Vienna, includes the lake Neusiedlersee, (over 300 km²; about half of it covered by the reed *Phragmites communis*), and the Seewinkel lowland (about 400 km²) (figs. 1, 2).

The Neusiedlersee is a slightly saline, shallow lake (maximum depth 1.80 m), 114 m above sea level. Together with its extended reed belt, the lake is certainly one of Europe's most remarkable wetlands. In the south and on the western shore, the reed belt is up to five km wide and offers numerous breeding sites to a unique bird and Water Frog fauna.

In addition to numerous canals, ponds, and other artificial wetlands, all inhabited by Water Frogs, some 70 natural shallow saline lakelets (rarely more than 50 cm deep) are scattered across the Seewinkel lowland. Many of these lakelets dry up during the summer. They are of great im-

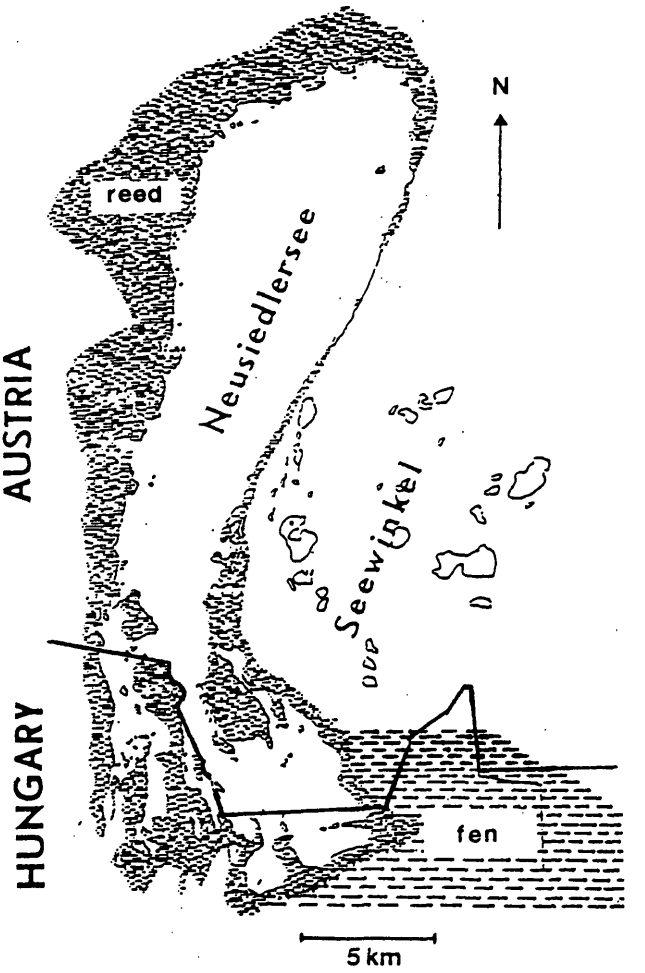

Fig. 1: The Neusiedlersee with the reed belt and the Seewinkel lowland and its saline lakelets. In the south the drained fen.

Abb. 1: Der Neusiedlersee mit dem Schilfgürtel und der Seewinkel mit den Salzlacken sowie dem trockengelegten Moor im Süden.

portance as resting places for migrating birds, but Water Frogs avoid them, apparently because of high salinity, which increases as the lakelets dry up. The southern part of the Seewinkel, called "Hanság", extends into Hungary. Most of the Hanság, once an extended fen, has been drained.

The Neusiedlersee region is inhabited by 12 amphibian species belonging to six families: *Triturus dobrogicus* (KIRITZESCU, 1903) and *T. vulgaris* (LINNAEUS, 1758) - Salamandridae, *Bombina bombina* (LINNAEUS, 1761) - Discoglossidae, *Pelobates fuscus* (LAURENTI, 1768) - Pelobatidae, *Bufo bufo* (LINNAEUS, 758), and *B. viridis* LAURENTI, 1768 - Bufonidae, *Hyla arborea* (LINNAEUS, 1758) - Hylidae, *Rana arvalis* NILSSON, 1842, *R. dalmatina* BONAPARTE, 1840, *R. lessonae* CAMERANO, 1882, *R. ridibunda* PALLAS, 1771, and the hybrid

Fig. 2: The southern part of the lake, with the reed islands.
Abb. 2: Der Südteil des Neusiedlersees mit ausgedehnten Schilfinseln (Photo: LÖFFLER).

taxon *R. esculenta* LINNAEUS, 1758 - Ranidae. The River Frog *R. ridibunda* does not live in the Neusiedlersee proper (for the occasional occurence of juvenile *R. ridibunda* in the lake, see TUNNER 1978), but has recently been identified in the southeastern part of the Seewinkel (TUNNER, unpublished). We suppose an immigration into the Seewinkel lowland from Hungary during recent years.

Rana ridibunda, R. lessonae, and *R. esculenta* are referred as "Water Frogs" because they are bound to a relatively aquatic life. The most common amphibian taxon in the Neusiedlersee region is the hybrid *R. esculenta*.

Reproduction in Water Frogs

Among the three morphologically well defined Central European Water Frog taxa, *R. lessonae, R. ridibunda* and *R. esculenta* (fig. 3), only *R. lessonae* and *R. ridibunda* are species with phylogenies tracing back to the late Tertiary (UZZELL 1982). *Rana esculenta* is not a species in the conventional zoological sense, because it originally arose - and occasionally still arises - as a result of hybridization of the two species *R. ridibunda* and *R. lessonae* (BERGER 1968; TUNNER 1970; GÜNTHER 1973; UZZELL & al. 1975).

Each somatic cell of diploid *R. esculenta* contains a chromosome set from both *R. ridibunda* and *R. lessonae*. Thus, one cannot really speak of *R. esculenta* genetic material. It is not known when and where in Europe the first hybridization occurred that led to the creation of the hybrid taxon *R. esculenta*.

The hybrid nature of *R. esculenta* does not mean that recent hybrids are the result of crosses between *R. ridibunda* and *R. lessonae*. Although the area of sympatry of the two species is large in Central Europe, *R. ridibunda* and *R. lessonae* have strongly divergent environmental requirements; syntopic existence of both species is, therefore, very rare.

Rana esculenta is not, however, what one could call a stabilized hybrid. A stabilized hybrid taxon should have a hybrid origin, but a reproduction indepentent of both of its parental species. For instance, approximately 30 reptile species of hybrid

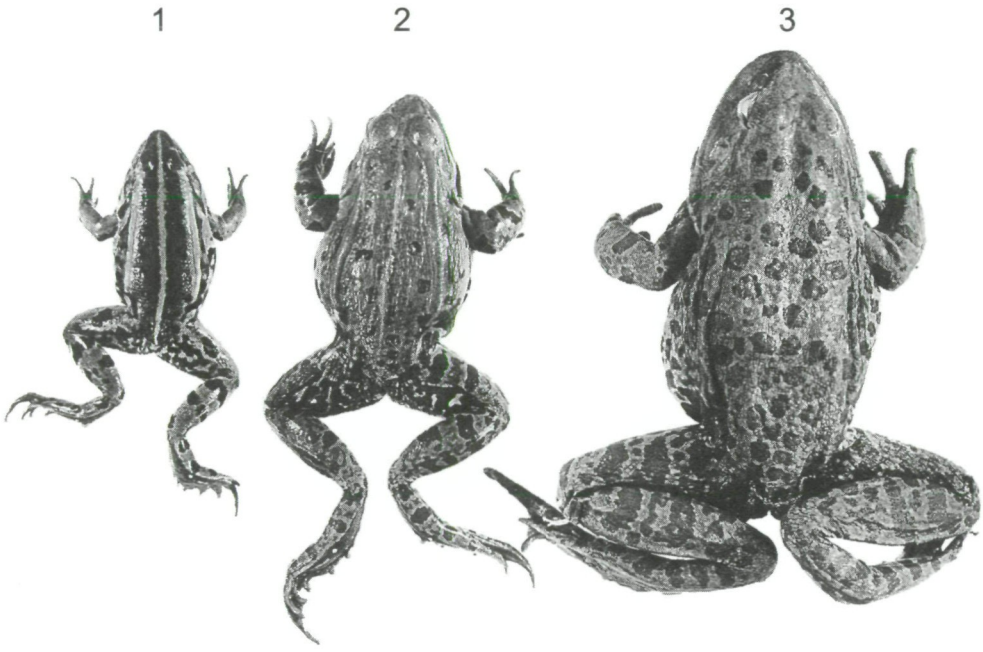

Fig. 3: The three water frog taxa found in the Neusiedlersee region: *Rana lessonae* (1), the hybrid *R. esculenta* (2), and *R. ridibunda* (3). The last species has been recently identified in the southeastern part of the Seewinkel lowland.
Abb. 3: Die drei Wasserfrosch-Taxa, die im Neusiedlerseegebiet vorkommen: *R. lessonae* (1), die hybride *R. esculenta* (2) und *R. ridibunda* (3).
Das erst kürzlich belegte Vorkommen von *R. ridibunda* ist auf die südöstliche Region des Seewinkels beschränkt.

origin reproduce by parthenogenesis and, thus, are independent of their parents. In *R. esculenta* mating between hybrids (*R. esculenta* x *R. esculenta*) usually leads to an inviable progeny (BERGER 1968; BLANKENHORN 1971; TUNNER 1979).

How then does *R. esculenta* arise? The majority of diploid hybrids are the result of "backcrossing" of the hybrid *R. esculenta* with *R. lessonae*. This means: In mixed *R. esculenta* + *R. lessonae* populations hybrids usually transmit unrecombined *ridibunda* chromosomes to functional gametes (fig. 4). This has been proven repeatedly by genetic and cytological analysis of progeny from defined crossings (reviewed by BERGER 1977; GRAF & POLLS PELAZ 1989). For example: We crossed *R. esculenta* from Neusiedlersee with *R. lessonae* from various geographic areas and obtained hundreds of frogs that were not only phenotypically very similar to their *esculenta* parent, but also genotypically; i.e., they received 50% of their genetic material from *R. lessonae* and 50% from *R. ridibunda* which came from the clonally inherited *ridibunda* genome of their *esculenta* parent. In other words, we received genetic F1-hybrids, although they resulted from backcrosses. Consequently, when we crossed two *R. esculenta* from Neusiedlersee, we obtained *R. ridibunda* (TUNNER 1979). Functional germ cells of the hybrid taxon, therefore, contain genomes of *R. ridibunda*. With respect to the production of germ cells leading to viable offspring, the hybrid *R. esculenta* is a *R. ridibunda*.

The mode of reproduction in which a hybrid taxon transmits the genome of the non syntopic parent, while the other genome is introduced each generation by the syntopic parent, is called hybridogenesis (SCHULTZ 1969; TUNNER 1974). Aside from European Water Frogs, only two other hy-

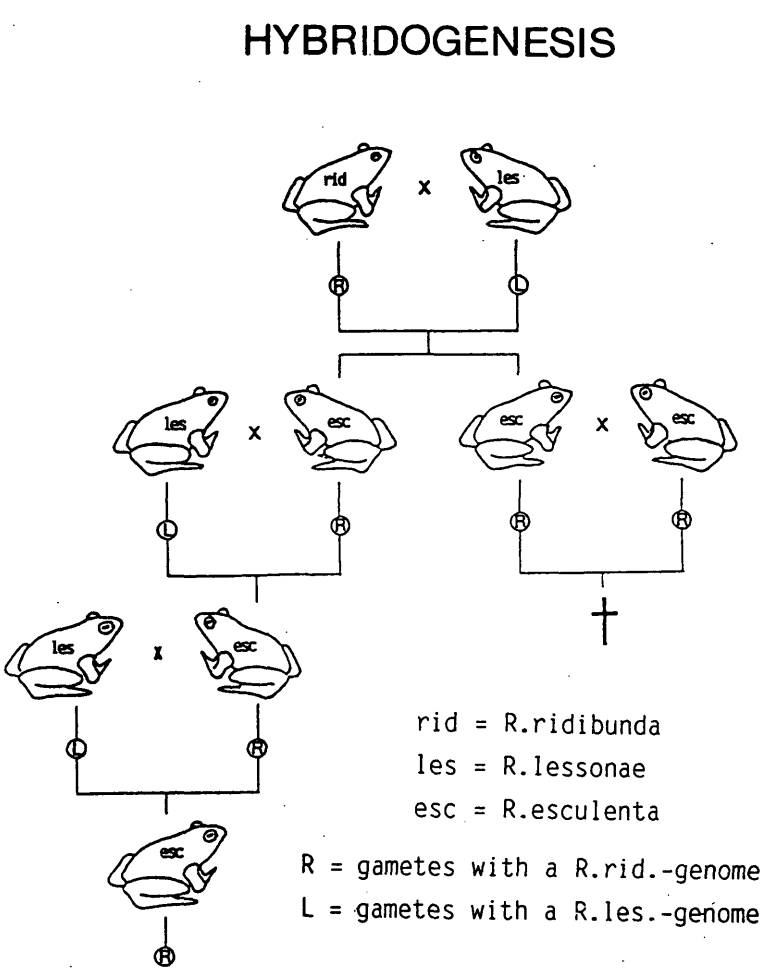

Fig. 4: Diagram of the hybridogenetic reproduction. The hybrid *R. esculenta* originally arose from crosses between the species *R. lessonae* and *R. ridibunda*. Hybrids, as a rule, only pass on the *ridibunda* chromosomes to their offspring. Consequently, matings (backcrosses) of the hybrid *R. esculenta* with *R. lessonae* result in true *R. esculenta* (F1-hybrids). Crosses between two *R. esculenta* result in *R. ridibunda*. *R. ridibunda*, however, that result fom homotypic *esculenta* matings, usually die before reaching sexual maturity.

Abb. 4: Schema der hybridogenetischen Fortpflanzung: Die Entstehung der hybriden *R. esculenta* geht auf Kreuzungen zwischen den beiden Arten *R. ridibunda* und *R. lessonae* zurück. Die Hybriden vererben in der Regel ausschließlich die Chromosomen der Elternart *R. ridibunda*. Das hat zur Folge, daß aus Rückkreuzungen der Hybriden mit *R. lessonae* wieder typische *R. esculenta* - Indiviuen (F1-Hybriden) entstehen. Folglich resultiert aus Kreuzungen zwischen zwei *R. esculenta R. ridibunda*. Diese, aus homotypischen Hybridpaarungen entstandenen *ridibunda* - Individuen, sterben allerdings in der Regel noch bevor sie die Geschlechtsreife erreichen.

bridogenetic taxa are known so far: A fish of the genus *Poeciliopsis* (SCHULTZ 1969), and a stick-insect (Phasmatodea) (MANTOVANI & SCALI 1990). The chromosomal drive mechanism that leads to the hybridogenetic pattern of inheritance involves the elimination of one parental genome and duplication of the other during gametogenesis (TUNNER & HEPPICH-TUNNER 1991). Since the perpetuation of a hybridogenetic

taxon depends upon the reproduction of another species, hybridogenesis is a unique mode of sexual parasitism. *Rana esculenta* parasitizes upon the reproduction of *R. lessonae*. If there were no *R. lessonae* to mate with, *R. esculenta* of the Neusiedlersee would become extinct.

The unique status of the Water Frog population of the Neusiedlersee

The Water Frog populations of the Neusiedlersee region differ from *R. lessonae* + *R. esculenta* populations of other geographic regions in several ways. First, *R. esculenta* are very common throughout the lake region whereas *R. lessonae* seems to be rare in most parts of the area. For example, among more than 1000 frogs from 30 sites along the Neusiedlersee and the Seewinkel lowland, approximately 5% were *R. lessonae* (TUNNER 1970, 1974; TUNNER & DOBROWSKY 1976; KNOFLACHER 1975; KRATCHOVIL 1976; GRILLITSCH & GRILLITSCH 1984). At some sites where *R. esculenta* and other amphibian species were common, *R. lessonae* seemed to be entirely absent. For instance, *R. lessonae* was not represented among 224 Water Frogs caught at one locality (KNOFLACHER 1975).

A second notable aspect of the frog population from the lake region is the sex ratio in the hybrids. Out of 1000 adult *R. esculenta* mentioned above, only 3% were males. Further observation and sampling confirmed the rarity of males (TUNNER & HEPPICH-TUNNER 1989; TUNNER 1991).

To gain some insight into sex determination in *R. esculenta*, many laboratory crosses have been perfomed. They did not supply conclusive explanations for the great excess of female hybrids; they did, however, indicate the genetic basis of this phenomenon and the complexity of sex determination in Water Frogs (TUNNER 1980; BERGER & al. 1988). We may conclude: If a hybrid is involved in mating, the regular sex determining mechanism seems to be disturbed.

The reproductive dependence of *R. esculenta* females on males of *R. lessonae* leads to many interesting, and as yet poorly studied biological questions. For instance, how does the population of hybridogenetic females persist? Recruitment of *lessonae* males by the overabundant hybrid females over a longer period of breeding cycles would drastically reduce the number of homospecific matings (*R. lessonae* x *R. lessonae*). As a consequence, both *R. lessonae* and the hybrids might eventually become extinct. Considering the numerous hybrid females, this should have happened already long ago. In addition, male *R. lessonae* seem to prefer to mate with female *R. esculenta* because they are larger than conspecific females (BLANKENHORN 1977) and *R. esculenta* females prefer *R. lessonae* males (ABT & REYER 1993).

Migration in *Rana lessonae*

We noticed early on that *R. lessonae* are more common in some "undisturbed" habitats in the southern area of the Neusiedlersee than they are in the north (TUNNER & DOBROWSKY 1976). This is in agreement with other observations along the southern shore of the lake (KARPATI 1988; TUNNER, unpublished) where numerous amphibian species overwinter in a forested region. In spring and fall mass aggregations of Water Frogs occur in this southern lake area and the share of *R. lessonae* is high in comparison to more northern areas. These observations lead us to suspect that some *R. lessonae* might leave the southern wintering habitats in spring for northern breeding spots, where they primarily mate with hybrids and might then, after mating, return again to the south. Migration to and from these northern areas could take place within the extensive reed belt (where the breeding grounds are located). The hybrid females would not make such vast migrations but

would stay in the northern lake area all over the year. There they have their various summer habitats (shore areas, around dams, along canals) and hibernate. It was in these *R. esculenta* summer habitats and not in the breeding grounds, which are located well within the reed belt and difficult to reach, that most of the Water Frog collections from Neusiedlersee and Seewinkel have been made. Therefore, *R. esculenta* was overrepresented in most samples.

The great relativ abundance of hybrids in the northern habitats, thus, would be the result of the unusual distribution and dynamics of the extended mixed *R. lessonae* + *R. esculenta* population of the Neusiedlersee region, that is the yearly migration of *R. lessonae* from the south to the north. If this regular migration of *R. lessonae* to the northern breeding grounds did not take place, the number of *R. esculenta* should decline seriously in the northern part of the lake.

Initial results of a study in which more than 3000 individuals were marked in order to investigate the migratory paths of *R. lessonae* confirm the hypothesis that the seasonal movements of *R. lessonae* amount to many kilometres. We have shown that this species travels distances of at least 15 km in a few days (TUNNER 1992).

Hybridogenetic reproduction in *R. esculenta* involves the elimination of *lessonae* chromosomes and because of that, the genetic material of *lessonae* gets lost when mating with *R. esculenta*. The question arises, why there does *R. lessonae* undertake such long and energy expending trips from the south to the north when there is no guarantee of successfully reproducing *lessonae* genetic material?

A possible evolutionary explanation of the extensive migration in *R. lessonae* should consider:

i) the geomorphological history of the lake,

ii) the preference for fen (peat) habitats, and

iii) inter / intraspecific interaction among larvae (crowding effect).

The geomorphological history of the lake and the preference of *Rana lessonae* for low marshy land

The genesis of the Neusiedlersee probably goes back to the end of the Pleistocene when an ancestral water body was formed in the southeastern part (Hanság) of the present lake region (LÖFFLER 1979). The northern part being of more recent origin should have developed by gradual tectonic depression that allowed a stepwise northward expansion of the lake (LÖFFLER 1974). We suppose that *R. lessonae* invaded the southern part of the "Ur"-Neusiedlersee (first stage of the lake) over the southern edge of the Alps (perhaps also over the Hungarian Lowlands) during the post-glacial climatic improvement. The recent *Sphagnum* peat, almost 1 m thick (BOBEK & al. 1978) and remains of Dryopteridi - Alnetum and Thelypteridi - Alnetum associations (fig. 5) indicate that this southern area of the lake's origin was an extensive fen. We do not know much about the ecology of the Water Frogs, but one thing has been widely observed: *Rana lessonae* prefers marshy and fenny habitats. The filling in of the southern zone of the gradually expanding lake probably produced optimum conditions for *R. lessonae*. To these southern habitat, to which this species is so well adapted, it has remained "faithful" up to now.

Density regulation in Water Frogs

To a greater extent than other European anurans, the tadpoles of Water Frogs are affected by a density regulation mechanism (HEUSSER & BLANKENHORN 1973). If, for instance, one keeps too many water frog tadpoles in too small an amount of water, at least some of them stop feeding, growth is slowed, metamorphosis delayed, and some even die. The reason for this so-called crowding-effect is not completely

Fig. 5: Alnetea glutinosae forest in the southeastern lake region (Hánság); a typical indicator for a fenny and marshy habitat.
Abb. 5: Erlenbruchwald (Alnetea glatinosae) im Hánság; ein Anzeiger für Moorböden (Photo: TUNNER).

understood, but apparently has to do with the excretion of certain Ascomycetes (especially the yeast *Candida humicola*) by larger tadpoles. In higher concentrations, it can inhibit the absorption of nutrients by the intestine walls of smaller tadpoles (STEINWASCHER 1979). Recent investigations have shown that particular physical and chemical characteristics of the habitat are a prerequisite for the effectiveness of these inhibitors (PETRANKA 1989). The movement and exchange of water in the reed belt of the Neusiedlersee (where mating takes place and tadpoles grow up) is extremely low as a result of the strong wind-breaking effect of the dense vegetation (60 to 120 reed stems per m²) (GUNATILAKA 1985). We suspect that the slightly saline and poorly circulating water body in the reeds enhances the crowding-effect and could be the reason for the shift of hypothetic earlier dense breeding areas of *R. lessonae* in the southern region to more northern parts of the lake. The gradual tectonic depression that allowed a stepwise expansion of the lake northwards opened additional habitats that *R. lessonae* apparently used in order to expand its breeding areas. At least a part of the *R. lessonae* population, however, has retained the original southernmost fenny habitat as their hibernaculum to the present time.

When making such considerations also the "catastrophic events" that the lake was subjected to must be mentioned (VARGA & MIKA 1937): Approximately 100-200 times (LÖFFLER, pers. comm.) the shallow Neusiedlersee is supposed to have more or less completely dried up. The lake is deepest in the south (LÖFFLER 1979); thus, minimum water levels and a progressive drying up first had a threatening effect on the frogs in the north and then finally in the south. The particular hydrogeological situation of the shallow Neusiedlersee may have exerted selective pressure on the frogs, to retain the "secure" southern habitat.

ACKNOWLEDGMENTS

We would like to thank H. LÖFFLER (Vienna), F. SCHALLER (Vienna), and TH. UZZELL (Urbana) for critically reading the manuscript. With finacial support by the Austrian Bundesministerium für Wissenschaft und Forschung.

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DATE OF SUBMISSION: July, 8th, 1997 Corresponding editor: Heinz Grillitsch

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