Tying ecology and genetics of hemiclonally reproducing waterfrogs (*Rana*, Anura)

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Hybridogenesis is a hemiclonal mode of reproduction occurring in several species complexes with various effects on the ecology and genetics of the involved species. The complexity of these systems is illustrated with the example of Western Palearctic waterfrogs. Deviations from original models of hybridogenesis are discussed, proofs for recombination between the parental genomes of the hybrid are reviewed, and the sex ratio disturbance found in many populations is explained. The review shows that benefits deriving from hybridogenesis, such as increased genetic variability and colonization ability, seem to be primarily directed toward *R. ridibunda*, but also have an impact on the other parental species. It is concluded that, due to mating possibilities and fertilization success, regions with mixed populations of two (or more) parental species and their hybridogenetic associate might be especially of interest in investigating recombination patterns and relating these to the population dynamics of the parental species.

Introduction

Hybridogenesis is a hemiclonal mode of reproduction that has been observed in several species complexes from a range of different taxa: *Bacillus* (Mantovani & Scali 1992), *Poeciliopsis* (Schultz 1966), *Rana* (Berger 1973a), *Trophidophoxinellus* (Carmona *et al.* 1997). Such systems seem to be highly complex and interesting for evolutionary ecology due to the various impacts hybridogenesis has on the ecology and genetics of the involved species (e.g. Beukeboom & Vrijenhoek 1998). The interest in hybridogenetic systems, especially in hybridogenetic waterfrogs, is illustrated by the recent accumulation of evolutionary ecology studies on those frogs (e.g. Hellriegel & Reyer 2000, Pagano *et al.* 2001, Som 2001, Vorburger 2001, Altwegg 2002, Vorburger & Reyer 2003).

The initial step for the establishment of a hybridogenetic system is usually the hybridization of two parental species PI and PII, each submitting one set of chromosomes to the hybrid H (Fig. 1). Results from crossing experiments (Berger 1973b) suggested that the genome of one parental species (i.e. PI) is excluded from the gametes of the hybrid. The remaining parental genome (i.e. PII) subsequently undergoes endoreduplication and, since incompatibilities of non-sister chromosomes are avoided, leads to a
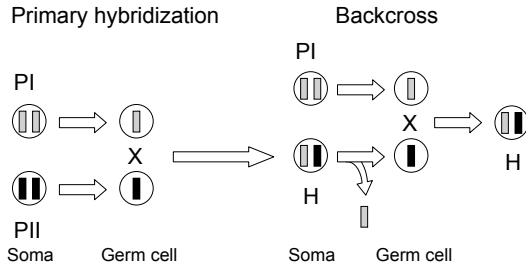
Primary hybridization   Backcross

Fig. 1. The hybridogenetic reproduction model (R-hybridogenesis *sensu* Polls Pelaz 1994) as proposed by Schultz (1969) and Tunner (1973). The genomes of different species are marked in grey (PI) and black (PII). PI = *R. lessonae*, *R. perezi*, *R. bergeri* (grey); PII = *R. ridibunda*; (black), H = *R.* kl. *esculenta*, *R.* kl. *grafi*, BR-hybrid. Hybridogenetic systems originate from matings between PI and PII or, alternatively, by matings between a hybridogen of an existing system with another PI species (Arano *et al.* 1994). The hybrid H is rarely infertile (exceptions reported from the Danube Delta, Günther *et al.* 1991), as the primary gametes of the hybridogen contain sister chromatid-derived copies of each PII chromosome due to the exclusion of the PI genome and the subsequent endoreduplication of the PII genome (Tunner & Heppich-Tunner 1991). Therefore, hybridogenetic gametogenesis has been assumed to represent a reproductive mode without genetic recombination between the two parental genomes.

fully fertile hybridogen. The hybrid itself reproductively mimics the parental species, whose genome is kept and endoreduplicated (Schultz 1969, Tunner 1973). In allopatry to that parental species, the hybridogens' lineage is maintained by backcrosses of the hybridogen with the sympatric parental species PI (Fig. 1).

While current literature provides many interesting insights in either the ecology or the genetics of hemiclonally reproducing waterfrogs, an overall view is lacking perhaps due to the fact that hybridogenetic systems appear highly complex. Here, I will illustrate the complexity of these systems, discuss deviations from original models of hybridogenesis, and attempt to tie the ecology and genetics of this species group with the aim to stress important issues for future research.

Deviations from the common model of hybridogenesis

Currently, several hybridogenetic modes in waterfrogs have been described in regard to the

exclusion of parental species genomes (Polls Pelaz 1994). The most common model seems to be R-hybridogenesis (Fig. 1) as proposed by Schultz (1969) and Tunner (1973). However, flowcytometric analyses have shown the occurrence of gametes of both parental species in the germ cell lineage of the same individual (Vinogradov *et al.* 1991). Those results support the R+-Anti-R hybridogenetic mode (*sensu* Polls Pelaz 1994), defined by the random exclusion of either the PI or the PII genome. Further deviations from R-hybridogenesis have been reported, as exchange of alleles between the two parental species is appreciable (Table 1).

The detection of PII (*R. ridibunda*) alleles in PI gene pools (e.g. Mezhzherin & Morozov-Leonov 1997, Pagano & Schmeller 1999) and non-hybrid offspring from matings of hybrids also suggest that parental genomes recombine during hybridogenetic gametogenesis (Vorburger 2001). Opportunity for recombination might be given due to gradual elimination of a parental genome, as supported by the occurrence of aneuploid oogonia with predominating chromosomes of *R. ridibunda* (Tunner & Heppich-Tunner 1991) and nucleus like bodies (NLB), containing fragments of one parental species, observed in the cytoplasm of gonial cells (Ogielska 1994).

The cytological processes during hybridogenetic gametogenesis are hardly understood and recombination in hybridogenetic gametogenesis remains controversial; particularly, because recombination events have not been reported in experimental crosses so far. However, the mediation of geneflow between two parental species via the hybridogens has been evidenced in natural populations (Table 1). The reason for the discrepancy appears to lie in the low probability of detecting recombined genotypes. For instance, if only 1 in 1000 hybrids recombines the parental genomes in a fraction of its gametes, to detect recombination (i) this one hybrid has to be backcrossed with the parental species, (ii) the gametes containing the recombined genomes have to be reproductively successful, and (iii) all offspring (several hundreds to thousands) have to be genetically analyzed.

Such a huge experimental crossing combined with genetic analysis has not yet been undertaken. In contrast, it can be assumed that in natu-

ral populations copies of recombined genomes are generated by normal Mendelian segregation once they have re-entered the gene pool of the respective parental species. Hence, many copies of a recombined genome, and therefore a high number of recombined genotypes, are present and are more likely to be detected than in experimental conditions.

Consequences of recombination

Studies assessing the effects of gene exchange on the ecology and genetics of parental species are not yet available. Gene exchange, however, might break up coevolved gene complexes resulting in disturbed epistasis (Mayr 1963), as *R. ridibunda* belongs to a phylogenetically different sister species group than any of the other parental species (Plötner 1998, Plötner & Ohst 2001). Newly originated parental genotypes carrying alleles of the opposite parental species may therefore be unviable and may not reproduce (Mayr 1963, Tregenza & Wedell 2000). However, the diploid chromosomal system may provide a field of recombination (Carson 1975), where only a fraction of the whole chromosome "field" is amenable to exchange between spe-

cies. Hence, if recombination between species genomes occurs outside balanced gene blocks, newly originating (parental) genotypes should be viable (Ortíz-Barrientos *et al.* 2002), and are likely to gain fitness due to increased genetic variability relative to their sympatric conspecifics (Lerner 1954).

Several studies have compared the fitness of hybrids and sympatric parental species, but fewer have focused on the fitness of parental genotypes, in regard to individual genotype and amount of recombination. Hotz and Semlitsch (2000) compared the fitness of *R. lessonae* tadpoles according to their *ldh*-b genotype, and found a better performance of ee as compared with bb genotypes in three life-history traits. Unfortunately, that study focused only on a single allozyme locus for identification of different *R. lessonae* genotypes, but did not take into account genomic introgression. Other fitness studies, comparing hybrids and sympatric parental species (e.g. Neveu 1991, Semlitsch 1993a, 1993b, 1993c, Hotz *et al.* 1999, Plénet *et al.* 2000, Thurnheer & Reyer 2000, Holenweg Peter 2002b, Altwegg & Reyer 2003, Anholt 2003) have produced contradicting results and do not allow conclusion of a general superiority of the hybrid genotype.

Table 1. Review of current data on recombination in the western Palearctic waterfrog complex. N_{loci} = the number of analyzed loci in the study, I = relative frequency of foreign alleles, $F_{genotype}$ = relative frequency of recombined genotypes of the whole taxon sample in a study, regardless of the number of loci affected.

Taxon	Origin	N_{loci}	I (%)	$F_{genotype}$ (%)	Reference
R. kl. *esculenta*	Poland	5	1.2	3.7	Uzzell & Berger 1975
R. lessonae			2.2	4.5	
R. ridibunda			7.8	15.6	
R. kl. *esculenta*	Eastern Germany	1	–	5.7	Günther & Hähnel 1976
R. lessonae			0.9	1.9	
R. ridibunda			9.7	19.4	
R. kl. *esculenta*	Eastern Germany	1	3.1	6.2	Günther & Koref-Santibanez 1983
R. lessonae			2.2	4.3	
R. ridibunda			4.0	7.9	
R. kl. *esculenta*	Eastern Germany	5	3.3	6.5	Plötner & Klinkhardt 1992
R. kl. *esculenta*	Western Germany	7	13.0	82.7	Schröer 1997
R. lessonae			12.5	87.9	
R. ridibunda			13.6	85.8	
R. kl. *esculenta*	Central France	3	5.8	34.8	Pagano & Schmeller 1999
R. lessonae			2.1	12.5	
R. ridibunda	Southern France	8	6.2	61	Schmeller 1999
R. kl. *grafi*			0.6	3.5	
R. perezi			2.9	22	

The inconsistent results could, however, be the outcome of differential performance of parental species due to their genotype and the level of adaptation to the current environment, as none of the latter studies took the genetics of the parental species into account. A preliminary study on fluctuating asymmetry (FA) in *R. perezi* and *R. ridibunda* revealed a trend of lower FA of recombined as compared with unrecombined genotypes (Wöste 2000), suggesting a higher fitness of at least some of the recombined individuals. Hence, future research needs to focus on the genotype–environment interactions in waterfrog species to reveal a clear image of parental performance in particular. Results are likely to be highly interesting, as *R. ridibunda* and other species of the *R. ridibunda*-species group have been repeatedly introduced to various European countries (Anholt 2003, Pagano *et al*. 2003, Zeisset & Beebee 2003, and sources cited therein).

However, the ability of the *R. ridibunda* genome to initiate hybridogenesis in interspecies hybrids varies geographically (Hotz *et al*. 1985), which may account for the low number of foreign alleles in *R*. kl. *esculenta* from Switzerland (< 5%, Vorburger 2001), and the lack of reports of recombined genotypes of *R. ridibunda* and *R. lessonae* in Switzerland. Recombined parental genomes, however, may only be introduced in the parental gene pool if the hybrid shows hybridogenetic gametogenesis. In the case of sterility of hybrid individuals, recombination between its two parental genomes is meaningless, as the genomes are trapped in the hybrid and cannot return to the gene pool of the parental species. Hence, regional differences in the ability of the *R. ridibunda* genome to induce hybridogenesis will most likely lead to different effects on the gene pools of sympatric waterfrog species.

The impact of hybridogenesis on the sex ratio

Hybridogenesis may have an impact on the sex ratio, if combined with the mating behavior in waterfrog assemblages. Generally, it is assumed that female choice plays the predominant role in waterfrog mating systems (Abt & Reyer 1993, Hellriegel & Reyer 2000, Roesli & Reyer 2000).

However, male choice is not negligible, as males prefer to mate with larger females (Blankenhorn 1974, 1977, Lada *et al*. 1995). Large females produce more eggs and thus contribute more to the fitness of the male than do small females (Dyson *et al*. 1992).

Accordingly, in mixed waterfrog assemblages large females of *R. ridibunda* and hybrids are likely to experience mating attempts by conspecific and heterospecific males. In some cases, female mating preferences can either be overrun by male-male competition (Bergen *et al*. 1997, Engeler & Reyer 2001) or hampered by an overlap in courtship-call characters and morphology (Lodé 2001). Hybridization would be favored in such contexts and thus reinforce the hybridogenetic process (Lodé & Pagano 2000).

Cryptic female choice restores female mating preferences only incompletely, as females have to release some eggs to trick the undesired male (Reyer *et al*. 1999). Therefore, matings leading to hybrids usually consist of male PI and female PII or H and it can be deduced that in the hybridogen the *R. ridibunda* genome is most likely linked with the X-chromosome, whereas the Y-chromosome is linked with the PI genome. As the latter genome is preferentially excluded, the relative number of X-chromosomes linked to the PII genome is increased leading to a skew in the sex ratio favoring females.

Moreover, there is evidence to suggest that *R. ridibunda* propagates from hybrid × hybrid crosses and reaches maturity (Hotz *et al*. 1992, Guex *et al*. 2002), which will further skew the sex ratio in favor of female *R. ridibunda*. Females of both *R. ridibunda* and the hybrid generally exceed the number of conspecific males (e.g. Berger *et al*. 1988, Neveu 1991, Holenweg Peter 2002a), and sex ratio disturbances in waterfrogs have been reported to various degrees (Berger 1971, Rybacki & Berger 2001, Schmeller *et al*. unpubl. data).

In that respect, hybridogenesis functions similarly to sex chromosome meiotic drive, and the "hybridogenesis-gene" can be thought of as a meiotic distorter (*see* also Joly 2001). Following the drive/distorter-hypothesis, *R. ridibunda* may have a greater intrinsic rate of increase and might be capable of rebounding faster from population declines in the presence of hybridogens (but *see*

Jaenike 2001), due to the increased availability of females and multiple matings by males. The female bias may also lead to a rapid increase in population size in newly colonized habitats and might be seen as a new mechanism of species replacement (Vorburger & Reyer 2003). It has also been argued, however, that strong sex chromosome meiotic drive may lead to the extinction of a population, as many females go unmated (Hamilton 1967). This is unlikely to be the case for *R. ridibunda*, as sex chromosome meiotic drive does not seem to occur in this species itself, but only in the hybridogenetic associate (Schmeller *et al.* 2001). For instance, waterfrog assemblages in high-oxygen habitats are rarely mixed, usually consisting only of *R. ridibunda* (Pagano *et al.* 2001), supporting the species replacement mechanism at least in optimal habitats for *R. ridibunda*.

Tying the ecology and genetics

The benefits deriving from hybridogenesis seem to be primarily directed toward *R. ridibunda*, and due to mating possibilities and fertilization success might be especially pronounced in regions with mixed populations of two (or more) parental species and their hybridogenetic associate. From the genetic point of view, hybridogenesis increases the probability that a recombined *R. ridibunda* hemigenome will re-enter the *R. ridibunda* gene pool, as the meiotic distorter generally drives out the PI genome. The probability of hemigenome return is further increased by the mating behavior of male waterfrogs, preferring larger females, and overlaps in call structure and morphology in sympatric waterfrog species (Lodé & Pagano 2000), increasing the likelihood of hybrid × hybrid crosses or crosses between hybrids and *R. ridibunda*. From an ecological point of view, the high availability of *R. ridibunda* gametes in waterfrog assemblages could strengthen its colonization success and competitiveness (e.g. Vorburger & Reyer 2003). Future ecological genetic analyses may assess if regional recombination patterns affect the gene pools of the parental species, if the increased diversity enhances the performance of the parental species, and how sex ratio disturbance and increased genetic diversity interact in parental species.

Acknowledgements

References

Abt, G. & Reyer, H.-U. 1993: Mate choice and fitness in a hybrid frog: *Rana esculenta* females prefer *Rana lessonae* males over their own. — *Behav. Ecol. Sociobiol.* 32: 221–228.

Altwegg, R. 2002: Trait-mediated indirect effects and complex life-cycles in two European frogs. — *Evol. Ecol. Res.* 4: 519–536.

Altwegg, R. & Reyer, H.-U. 2003: Patterns of natural selection in size at metamorphosis in water frogs. — *Evolution* 57: 872–882.

Anholt, B. R. 2003: Overwinter survival of *Rana lessonae* and its hemiclonal associate *Rana esculenta*. — *Ecology* 84: 391–397.

Arano, B., Llorente, G. A., Herrero, P. & Sanchîz, B. 1994: Current studies on Iberian water frogs. — *Zool. Pol.* 39: 365–375.

Bergen, K., Semlitsch, R. D. & Reyer, H.-U. 1997: Hybrid female matings are directly related to the availability of *Rana lessonae* and *Rana esculenta* males in experimental populations. — *Copeia* 1997: 275–283.

Berger, L. 1971: Sex ratio in the F1 progeny within forms of *Rana esculenta* complex. — *Genet. Pol.* 12: 87–101.

Berger, L. 1973a: Systematics and hybridization in European green frogs of *Rana esculenta* complex. — *J. Herpet.* 7: 1–10.

Berger, L. 1973b: Some characteristics of backcrosses within forms of *Rana esculenta* complex. — *Genet. Pol.* 14: 413–430.

Berger, L., Uzzell, T. & Hotz, H. 1988: Sex determination and sex ratios in western Palearctic water frogs: XX and XY female hybrids in the Pannonian Basin? — *Proc. Acad. Nat. Sci. USA* 140: 220–239.

Beukeboom, L. W. & Vrijenhoek, R. C. 1998: Evolutionary genetics and ecology of sperm-dependent parthenogenesis. — *J. Evol. Biol.* 11: 755–782.

Blankenhorn, H. 1974: *Soziale Organisation einer Mischpopulation von Rana lessonae Camerano und Rana esculenta Linnaeus.* — Ph.D. thesis. University Zurich-Irchel, Zurich.

Blankenhorn, H. J. 1977: Reproduction and mating behavior in *Rana lessonae-Rana esculenta* mixed populations. — In: Taylor, D. H. & Guttman, S. I. (eds.), *The reproductive biology of amphibians*: 389–410. Plenum Press, New York and London.

Carmona, J. A., Sanjur, O. I., Doadrio, I., Machordom, A. & Vrijenhoek, R. C. 1997: Hybridogenetic reproduction and maternal ancestry of polyploid Iberian fish: The *Trophidophoxinellus alburnoides* complex. — *Genetics* 146: 983–993.

Carson, H. L. 1975: The genetics of speciation at the diploid level. — *Am. Nat.* 109: 83–92.

Dyson, M. L., Passmore, N. I., Bishop, P. J. & Henzi, S. P. 1992: Male behavior and correlates of mating success in a natural population of African painted reed frogs (*Hyperolius marmoratus*). — *Herpetologica* 48: 236–246.

Engeler, B. & Reyer, H.-U. 2001: Choosy females and indiscriminate males: mate choice in mixed populations of sexual and hybridogenetic water frogs (*Rana lessonae*, *R. esculenta*). — *Behav. Ecol.* 12: 600–606.

Guex, G. D., Hotz, H. & Semlitsch, R. D. 2002: Deleterious alleles and differential viability in progeny of natural hemiclonal frogs. — *Evolution* 56: 1036–1044.

Günther, R. & Hähnel, S. 1976: Untersuchungen über den Genfluß zwischen *Rana ridibunda* und *Rana lessonae* sowie die Rekombinationsrate bei der Bastardform *R. esculenta* (Anura, Ranidae). — *Zool. Anz.* 197: 23–28.

Günther, R. & Koref-Santibanez, S. 1983: Die LDH-B-Isoenzyme von Wasserfröschen (Anura, Ranidae) aus verschiedenen Teilen Europas und Mittelasiens. — *Zool. Anz.* 210: 369–374.

Günther, R., Plötner, J. & Tetzlaff, I. 1991: Some features of frogs *Rana-Esculenta* synklepton of the Danube Delta. — *Salamandra* 27: 246–265.

Hamilton, W. D. 1967: Extraordinary sex ratios. — *Science* 156: 477–488.

Hellriegel, B. & Reyer, H.-U. 2000: Factors influencing the composition of mixed populations of a hemiclonal hybrid and its sexual host. — *J. Evol. Biol.* 13: 908–918.

Holenweg Peter, A.-K. 2002a: Species and sex ratio differences in mixed populations of hybridogenetic water frogs: The influence of pond features. — *Ecoscience* 9: 1–11.

Holenweg Peter, A.-K. 2002b: Survival in adults of the water frog *Rana lessonae* and its hybridogenetic associate *Rana esculenta*. — *Can. J. Zool.-Rev. Can. Zool.* 79: 652–661.

Hotz, H., Beerli, P. & Spolsky, C. 1992: Mitochondrial DNA reveals formation of nonhybrid frogs by natural matings between hemiclonal hybrids. — *Mol. Biol. Evol.* 9: 610–620.

Hotz, H., Mancino, G., Bucci-Innocenti, S., Ragghianti, M., Berger, L. & Uzzell, T. 1985: *Rana ridibunda* varies geographically in inducing clonal gametogenesis in interspecies hybrids. — *J. Exp. Zool.* 236: 199–210.

Hotz, H. & Semlitsch, R. D. 2000: Differential performance among ldh-b genotypes in *Rana lessonae* tadpoles. — *Evolution* 54: 1750–1759.

Hotz, H., Semlitsch, R. D., Gutmann, E., Guex, G. D. & Beerli, P. 1999: Spontaneous heterosis in larval life-history traits of hemiclonal frog hybrids. — *Proc. Natl. Acad. Sci. USA* 96: 2171–2176.

Jaenike, J. 2001: Sex chromosome meiotic drive. — *Annu. Rev. Ecol. Syst.* 32: 25–49.

Joly, P. 2001: The future of the selfish hemiclone: a Neodarwinian approach to water frog evolution. — *Mitt. Mus. Nat.kd. Berl., Zool. Reihe* 77: 31–38.

Lada, G. A., Borkin, L. J. & Vinogradov, A. E. 1995: Distribution, population systems and reproductive behavior of green frogs (hybridogenetic *Rana esculenta* complex) in the Central Chernozem Territory of Russia. — *Rus. J. Herp.* 2: 46–57.

Lerner, I. M. 1954: *Genetic homeostasis*. — J. Wiley and Sons, New York.

Lodé, T. 2001: Character convergence in advertisement call and mate choice in two genetically distinct water frog hybridogenetic lineages (*Rana* kl *esculenta*, *Rana* kl *grafi*). — *J. Zool. Syst. Evol. Res.* 39: 91–96.

Lodé, T. & Pagano, A. 2000: Variations in call and morphology in male water frogs: taxonomic and evolutionary implications. — *C.R. Acad. Sci. Paris, Sciences de la vie* 323: 995–1001.

Mantovani, B. & Scali, V. 1992: Hybridogenesis and androgenesis in the stick insect *Bacillus rossius-grandii benazzii* (Insecta, Phasmoidea). — *Evolution* 46: 783–796.

Mayr, E. 1963: *Animal species and evolution*. — Belknab Press, Cambridge.

Mezhzherin, S. V. & Morozov-Leonov, S. Y. 1997: Gene introgression in hybrid populations of green frogs of *Rana esculenta* L, 1758 complex (Amphibia, Ranidae) from the Dnepr basin. — *Genetika* 3: 358–364.

Neveu, A. 1991: Demographic structures of green frogs adult populations of the *Esculenta* complex. — *Bull. Franc. Pech. Piscicult.* 321: 55–71.

Ogielska, M. 1994: Nucleus-like bodies in gonial cells of *Rana esculenta* (Amphibia, Anura) tadpoles — a putative way of chromosome elimination. — *Zool. Pol.* 39: 461–474.

Ortíz-Barrientos, D., Reiland, J., Hey, J. & Noor, M. A. F. 2002: Recombination and the divergence of hybridizing species. — *Genetica* 116: 167–178.

Pagano, A., Crochet, P. A., Graf, J.-D., Joly, P. & Lodé, T. 2001: Distribution and habitat use of water frog hybrid complexes in France. — *Glob. Ecol. Biogeogr.* 10: 433–441.

Pagano, A., Dubois, A., Lesbarrerès, D. & Lodé, T. 2003: Frog alien species: a way for genetic invasion? — *C.R. Acad. Sci. Paris, Sciences de la vie* 326: 85–92.

Pagano, A. & Schmeller, D. 1999: Is recombination less negligible than previously described in hybridogenetic water frogs? — In: Miaud, C. & Guyétant, R. (eds.), *9th O.G. Meeting — Current studies in Herpetology*: 351–356. Le Bourget du lac (SEH), Chambéry.

Plénet, S., Pagano, A., Joly, P. & Fouillet, P. 2000: Variation of plastic responses to oxygen availability within the hybridogenetic *Rana esculenta* complex. — *J. Evol. Biol.* 13: 20–28.

Plötner, J. 1998: Genetic diversity in mitochondrial 12S rDNA of western Palearctic water frogs (Anura, Ranidae) and implications for their systematics. — *J. Zool. Syst. Evol. Res.* 36: 191–201.

Plötner, J. & Klinkhardt, M. 1992: Investigations on the genetic structure and the morphometry of a pure hybrid population of *Rana* kl *esculenta* (Anura, Ranidae) in North Germany. — *Zool. Anz.* 229: 163–184.

Plötner, J. & Ohst, T. 2001: New hypotheses on the systematics of the Western Palearctic water frog complex (Anura, Ranidae). — *Mitt. Mus. Nat.kd. Berl., Zool. Reihe* 77: 5–22.

Polls Pelaz, M. 1994: Modes of gametogenesis among kleptons of the hybridogenetic water frog complex: an evolutionary synthesis. — *Zool. Pol.* 39: 123–138.

Reyer, H.-U., Frei, G. & Som, C. 1999: Cryptic female choice: Frogs reduce clutch size when amplexed by undesired males. — *Proc. R. Soc. Lond. B* 266: 2101–2107.

Roesli, M. & Reyer, H.-U. 2000: Male vocalisation and female choice in the hybridogenetic *Rana lessonae/R. esculenta* complex. — *Anim. Behav.* 60: 745–755.

Rybacki, M. & Berger, L. 2001: Types of water frog populations (*Rana esculenta* complex) in Poland. — *Mitt. Mus. Nat.kd. Berl., Zool. Reihe* 77: 51–58.

Schmeller, D. 1999: *Hemiklonale Vererbung im hybridogenetischen Rana grafi-Komplex (Anura: Ranidae) — Auswirkungen auf die genetische und demographische Struktur von Populationen im Rhonetal, dem Nationalpark Camargue und mediterranen Küstengebieten Frankreichs.* — Ph.D. thesis. Johannes Gutenberg-University, Mainz.

Schmeller, D., Crivelli, A., Pagano, A., Seitz, A. & Veith, M. 2001: Inheritance in the water frog *Rana ridibunda* (Pallas, 1771) — Is it mendelian or hemiclonal? — *Mitt. Mus. Nat.kd. Berl., Zool. Reihe* 77: 39–42.

Schröer, T. 1997: *Untersuchungen zur Populationsgenetik und Ökologie westfälischer Wasserfrösche (Anura: Ranidae).* — Ph.D. thesis. Heinrich Heine-University, Düsseldorf.

Schultz, R. J. 1966: Hybridization experiments with an all-female fish of the genus *Poeciliopsis*. — *Biol. Bull.* 130: 415–429.

Schultz, R. J. 1969: Hybridization, unisexuality and polyploidy in the teleost *Poeciliopsis* (Poecilidae) and other vertebrates. — *Amer. Nat.* 103: 605–619.

Semlitsch, R. D. 1993a: Adaptive genetic variation in growth and development of tadpoles of the hybridogenetic *Rana esculenta* complex. — *Evolution* 47: 1805–1818.

Semlitsch, R. D. 1993b: Asymmetric competition in mixed populations of tadpoles of the hybridogenetic *Rana esculenta* complex. — *Evolution* 47: 510–519.

Semlitsch, R. D. 1993c: Effects of different predators on the survival and development of tadpoles from the hybridogenetic *Rana esculenta* complex. — *Oikos* 67: 40–46.

Som, C. 2001: *Evolutionary perspectives of the hybridogenetic waterfrog Rana esculenta.* — Ph.D. thesis. University Zurich-Irchel, Zurich.

Thurnheer, S. & Reyer, H.-U. 2000: Spatial distribution and survival rate of waterfrog tadpoles in relation to biotic and abiotic factors: a field experiment. — *Amphibia-Reptilia* 22: 21–33.

Tregenza, T. & Wedell, N. 2000: Genetic compatibility, mate choice and patterns of parentage: Invited review. — *Mol. Ecol.* 9: 1013–1027.

Tunner, H. G. 1973: Demonstration of the hybrid origin of the common green frog *Rana esculenta* L. — *Naturwiss.* 60: 481–482.

Tunner, H. G. & Heppich-Tunner, S. 1991: Genome exclusion and two strategies of chromosome duplication in oogenesis of a hybrid frog. — *Naturwiss.* 78: 32–43.

Uzzell, T. & Berger, L. 1975: Electrophoretic phenotypes of *Rana ridibunda*, *Rana lessonae* and their hybridogenetic associate, *Rana esculenta*. — *Proc. Acad. Nat. Sci. USA* 127: 13–24.

Vinogradov, A. E., Borkin, L. J., Günther, R. & Rosanov, J. M. 1991: Two germ cell lineages with genomes of different species in one and the same animal. — *Hereditas* 114: 245–251.

Vorburger, C. 2001: Non-hybrid offspring from matings between hemiclonal hybrid waterfrogs suggest occasional recombination between clonal genomes. — *Ecol. Lett.* 4: 628–636.

Vorburger, C. & Reyer, H.-U. 2003: A genetic mechanism of species replacement in European waterfrogs? — *Cons. Genet.* 4: 141–155.

Wöste, B. 2000: *Fluktuierende Asymmetrie bei Wasserfröschen des PG-Komplexes.* — Master's thesis. Johannes Gutenberg-University, Mainz.

Zeisset, I. & Beebee, T. J. C. 2003: Population genetics of a successful invader: the marsh frog *Rana ridibunda* in Britain. — *Mol. Ecol.* 12: 639–646.