

The Effect of Assortative Mating on the Coexistence of a Hybridogenetic Waterfrog and Its Sexual Host

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ABSTRACT: In central Europe, the hybridogenetic waterfrog *Rana esculenta*, a hybrid between *Rana ridibunda* and *Rana lessonae*, lives in sympatry with one of its parental species, the poolfrog *Rana lessonae*. As *R. esculenta* has to backcross constantly with *R. lessonae* in order to produce viable offspring, this coexistence is obligatory for *R. esculenta*. Since *R. esculenta* has a higher primary fitness than *R. lessonae*, a mechanism is required that prevents the hybrid from driving the parental species, and hence itself, to extinction. Here, we present an analytical model and a computer simulation that investigate whether assortative mating can operate as such a control mechanism. Our results show that assortative mating is very effective in regulating coexistence in such a hybrid-host system. This is particularly true when choice is affected by the proportion of the two male types in the population. Furthermore, we could show that even if the species composition in a mixed hybrid-host population may be largely influenced by differences in life-history parameters, assortative mating still plays a very important role by stabilizing coexistence. Thus, mating behavior turns out to be more important for the population dynamics of hybridogenetic waterfrog systems than previously assumed.

Keywords: population dynamics, female choice, assortative mating, ecological modeling, *Rana lessonae*, *Rana esculenta*.

For more than a decade, biologists have emphasized the close link between adaptive variation in the behavior of individuals, its effects on birth rates, death rates, immigration and emigration, and the resulting dynamics of populations and communities. Although intuitively ob-

vious, the link is supported by surprisingly little empirical data (for recent reviews, see Clemmons and Buchholz 1997; Caro 1998). Even most models are restricted to a few behaviors only, such as space use, diet selection, and defense against predators (reviewed by Sutherland 1996; Fryxell and Lundberg 1998). Investigations on the effects of mate choice, parental care, and other social behaviors on population dynamics are extremely scarce, and some scientists even question their value (see Berger 1996, and literature therein).

There are several obvious reasons for this gap (see Anholt 1997). First, the time span between the observed behavior, its lifetime fitness consequences, and the ecological impact can be extremely long and usually exceeds the short-term funding of research projects. Second, the possible interactions and trade-offs between behavioral and demographic variables are enormously complex so that the observed covariation between behavior and population dynamics may be due to a chain of indirect causes and/or several unmeasured causal variables. Third, the proximate behavioral effects may be weak or the effect on population dynamics may remain cryptic. Fourth, ecologically realistic experiments that manipulate behavior are not easy.

Although these points more or less apply to all studies linking behavior to population dynamics, difficulties increase as the behavior and its consequences get more complex. This may explain why, even among the few existing studies in this field, those on social behavior are underrepresented; most investigations focus on behaviors with easy to measure short-term effects, like food intake or predator avoidance, which then are used as assumed or proven correlates of lifetime fitness (Sutherland 1996; Clemmons and Buchholz 1997; Caro 1998; Fryxell and Lundberg 1998).

Because the link between behavior and population dynamics is complex, systems that include heritable variation in behavior that has direct and pronounced fitness consequences and relatively fast dynamics may provide considerable insight (Anholt 1997). Unusual mating systems, especially hemiclonally reproducing hybrid vertebrate sys-

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tems, may provide the same kind of insight that rare mutations and unusual diseases have in unraveling the action of genes or the physiology of healthy organisms (Vrijenhoek 1989). However, results from studies of most sexual “host-parasite” systems as in *Poeciliopsis* fish or in stick insects of the genus *Bacillus*, are restricted in their portability because the involved hybrids are unisexual. The frog mating system analyzed in this study is the only system known so far where the hybrids are bisexual, which allows us to study intra- and intersexual interactions combined with intra- and interspecific interactions.

Hemiclonal Hybridogenetic Waterfrogs

The system encompasses the waterfrog *Rana esculenta* (*E*), originally a hybrid between the poolfrog *Rana lessonae* (*L*) and the lakefrog *Rana ridibunda* (*R*). During gametogenesis, the hybrid eliminates the *L* genome from the germ line premeiotically, duplicates the remaining *R* genome, and, after a normal meiosis, transmits a clonal haploid set to eggs and sperm (Graf and Müller 1979; Tunner and Heppich 1981). Matings within *R. esculenta* result in inviable offspring, probably due to high amounts of homozygote recessive lethal factors inherent in the clonal *R* genomes (Berger 1976; Graf and Müller 1979; Uzzell et al. 1980). Sexual (i.e., recombined) *R* genomes are usually not available because *R. ridibunda* has been absent from most parts of Central Europe, probably since the last glacial period. Therefore, the waterfrog *R. esculenta* can only persist when it “borrows” the premeiotically excluded *L* genome every generation anew.

This “hemiclonal hybridogenesis” (Schultz 1969) requires that *R. esculenta* live in sympatry and mate with *R. lessonae*, the other parental species. In such mixed *L-E* populations, all four mating combinations (table 1) can occur, but there is a conflict over mating between the hybrid and the parental species: while, for *R. esculenta*, mating with *R. lessonae* is the only way to produce viable offspring, *R. lessonae* should avoid these matings as the resulting hybrids will exclude their *L* genome in the next generation. Both, the parental species and the hybrid, therefore, have a direct genetic benefit from choosing the appropriate partner, which is in both cases *R. lessonae*.

Several factors complicate this forced coexistence and the resulting conflict: First, only one of the four possible mating combinations shown in table 1 produces *L* offspring, whereas two combinations produce *E* offspring. Second, *E* females are larger than *L* females and have larger clutch sizes, both absolutely and per gram of body mass (Berger and Uzzell 1980; Reyer et al. 1999). Third, *E* males, which are larger than *L* males, may have higher success in competition for mates. Fourth, in addition to the first three factors, which favor production of hybrid eggs, hy-

Table 1: Possible mating combinations and the resulting offspring in mixed *Rana lessonae*/*Rana esculenta* populations

	Male <i>Rana lessonae</i> (<i>LL</i>)	Male <i>Rana esculenta</i> (<i>RL/LR</i>)
Female <i>R. lessonae</i> (<i>LL</i>)	<i>R. lessonae</i> (<i>LL</i>)	<i>R. esculenta</i> (<i>LR</i>)
Female <i>R. esculenta</i> (<i>RL/LR</i>)	<i>R. esculenta</i> (<i>RL</i>)	(<i>R. ridibunda</i> [<i>RR</i>]) not viable

Note: The first letter of the genotype refers to the genome of the mother, the second to the genotype of the father.

brid tadpoles also can be more successful than those of the parental species. This seems the case in harsh environmental conditions such as gravel pits and highly disturbed areas, although in other habitats the reverse seems to hold true. (Semlitsch and Reyer 1992; Semlitsch 1993; Semlitsch et al. 1997).

Given these advantages for *R. esculenta*, one would expect that they increase their relative abundance in mixed populations and eventually eliminate *R. lessonae* from common breeding areas. In isolated populations with no migration between ponds, this would lead to an overshoot-collapse pattern because *R. esculenta*, as a sexual hybrid, is unable to persist without the presence of its sexual host *R. lessonae*. Long-term coexistence of the two species could be promoted by superior larval or adult survival in *R. lessonae* (see the fourth factor, above) and/or by mechanisms enhancing matings that increase initial production of *L* tadpoles (see the first three factors). The influence of dispersal and differences in tadpole performance on the coexistence of *R. lessonae* and *R. esculenta* is studied in detail by B. Hellriegel and H.-U. Reyer (unpublished manuscript).

Here, we focus on the effectiveness of female choice as a possible mechanism for coexistence using a deterministic population dynamics model. Mate choice does, indeed, occur in this group. While males do not discriminate between *L* and *E* females, females of both species preferred *L* males in binary choice experiments (Abt and Reyer 1993; Engeler 1994) and exerted cryptic choice by altering their clutch size in response to the genotype of the amplexing male (Reyer et al. 1999). But when exposed to groups of interacting males (i.e., the realistic situation), their preference is partly overrun by male-male competition and the mating pattern is strongly influenced by the *L* : *E* ratios among males (Bergen et al. 1997). Such differences in *L* : *E* ratios do occur in mixed populations with the proportion of *R. lessonae* varying widely from 5% to 95% (Berger 1977; Blankenhorn 1977). Therefore, we also use the model to estimate the

importance of female choice for the relative abundance of the two genotypes and test whether several stable equilibria between the two species are possible.

The Models

In an earlier attempt to model the population dynamics of the L - E system, Graf (1986) excluded all $L_{\varphi} \times E_{\delta}$ matings from his model as these matings were considered to be extremely scarce. But recent field studies by G. Abt (personal communication) have shown that such matings do occur in a nonnegligible frequency. In a first step, we, therefore, expanded the existing analytical model of Graf to include the $L_{\varphi} \times E_{\delta}$ mating combination. The resulting model with nonoverlapping generations allows us to find an analytical solution for the species frequencies when both species co-occur.

Analytical Model with Nonoverlapping Generations

The possible matings and their associated fitness components are listed in table 2. Female fecundities and offspring viabilities are relative values compared to the values from $E_{\varphi} \times L_{\delta}$ matings.

The frequencies of the four possible mating combinations can be derived as follows: Let $P(t)$ be the frequency of L and $Q(t)$ be the frequency of E genotypes at time t (assuming even sex ratios within species). We introduce the factor a , which describes the preference of E females for E males relative to their preference for L males, and the factor b , which describes the preference of L females for E males relative to their preference for L males. According to the definition of b , the ratio of L_{φ} mating with L_{δ} versus L_{φ} mating with E_{δ} equals $1 : b$, if males of both species are equally frequent. Since this is not always the case (see the introductory paragraphs), we have to correct the $1 : b$ ratio by the actual frequencies of the male genotypes. Thus, the corrected ratio of $L_{\varphi} \times L_{\delta}$ matings versus $L_{\varphi} \times E_{\delta}$ matings equals $1 * P(t) : b * Q(t)$. The fraction of L_{φ} mating with L_{δ} now calculates as $[1 * P(t)]/[P(t) + bQ(t)]$ and the fraction of L_{φ} mating with E_{δ} is $bQ(t)/[P(t) + bQ(t)]$.

The frequency of $L \times L$ matings compared to all possible mating combinations is thus the frequency of L_{φ} times the fraction of L_{δ} that mate with L_{δ} , or

$$f(L \times L) = \frac{P^2(t)}{P(t) + bQ(t)}.$$

The other mating frequencies are derived similarly:

Table 2: Matings and associated fitness components (after Graf 1986)

Mating ♀ × ♂	$L \times L$	$L \times E$	$E \times L$	$E \times E$
Genotype of offspring	L	E	E	R
Female fecundity	F_1	F_2	1	F_3
Offspring viability	V_1	V_2	1	0

Note: L and E females can adjust the number of eggs released during a mating depending on the male species they mate with (Reyer et al. 1999). We therefore used different parameters (F_1 , F_2 , 1, F_3) for the L and E females' fecundity.

$$f(L \times E) = \frac{P(t)bQ(t)}{P(t) + bQ(t)},$$

$$f(E \times L) = \frac{Q(t)P(t)}{P(t) + aQ(t)},$$

$$f(E \times E) = \frac{aQ^2(t)}{P(t) + aQ(t)}.$$

As $E \times E$ matings do not produce viable offspring, the genotype frequencies at time $t + 1$ will be

$$P(t + 1) = \frac{1}{\bar{W}} \left[\frac{P^2(t)F_1V_1}{P(t) + bQ(t)} \right], \quad (1a)$$

$$Q(t + 1) = \frac{1}{\bar{W}} \left[\frac{P(t)Q(t)bF_2V_2}{P(t) + bQ(t)} + \frac{P(t)Q(t)}{P(t) + aQ(t)} \right], \quad (1b)$$

where \bar{W} is the average mixed-population fitness.

By introducing $u(t) = P(t)/Q(t)$ and replacing F_1V_1 by W_1 and F_2V_2 by W_2 , we can combine equations (1a) and (1b) into

$$u(t + 1) = u(t)W_1 \left[\frac{u(t) + a}{u(t)(bW_2 + 1) + b(aW_2 + 1)} \right]. \quad (2)$$

It is easy to verify that, by setting b to 0, equation (2) can be transformed into the equation for the $L : E$ ratio used by Graf: namely,

$$u(t + 1) = u(t)W_1 + aW_1. \quad (3)$$

We did not find a closed form for $u(t)$ of equation (2), but a numerical solution for equation (2) (J. Lane, personal communication) is

$$u(t) = u_0 \left(\frac{W_1}{bW_2 + 1} \right)^t + \frac{W_1(a-b)}{(bW_2 + 1)^2} \times \sum_{i=1}^t \frac{u(t-i)(bW_2 + 1)[W_1/(bW_2 + 1)]^{(i-1)}}{u(t-i)(bW_2 + 1) + b(aW_2 + 1)}. \quad (4)$$

Under equilibrium conditions, $u(t+1) = u(t)$ and u_{eq} can be calculated from equation (2) as

$$u_{\text{eq}} = \frac{aW_1 - abW_2 - b}{1 + bW_2 - W_1}. \quad (5)$$

Expanding Graf's (1986) model with the $L_\varphi \times E_\delta$ mating combination increased the complexity of the model considerably. Whereas Graf's model consists of a linear difference equation (eq. [3]), the equation in the expanded model now becomes nonlinear, and one cannot expect to find a closed-form solution for $u(t)$ in equation (2) (D. Rusin, personal communication).

Our field and laboratory data indicate that L_φ do not produce more surviving offspring per capita than E_φ . We, therefore, assume that W_1 and W_2 are <1 and consequently $W_1 < bW_2 + 1$, which means that the first term in equation (4) tends toward 0 with $t \rightarrow \infty$. If $b = a$ (no difference in mate preference between L and E females), the second term in equation (4) becomes 0 and $u(t)$ tends to 0 with $t \rightarrow \infty$ (pure E population with subsequent crash). If $b > a$ (L_φ show less preference for L_δ than E_φ), the second term becomes negative and $u(t)$ tends to 0 even faster. Only if $b < a$ (L_φ show a higher preference for L_δ than E_φ), $u(t)$ can be different from 0. Analysis of equation (5) for the equilibrium value u_{eq} reveals the following: if W_1 and W_2 have similar magnitudes, the value for b has to be <1 . Otherwise, the term for u_{eq} would become negative. A value for $b < 1$ means that L females should prefer L males over E males, which supports the theory outlined in the introduction. Equation (4) shows that a difference in male preference between L_φ and E_φ is required to achieve long-term coexistence, regardless of differences in fertility or fitness of the offspring. If the females of the two species do not differ in their male preference ($a = b$), the L to E ratio in the population would calculate as

$$u(t) = u_0 \left(\frac{W_1}{bW_2 + 1} \right)^t.$$

Depending on the reproductive success of $L \times L$ matings (W_1), $L_\varphi \times E_\delta$ matings (W_2) and the E to L male preference of L females (b), $u(t)$ tends to 0 or ∞ for $t \rightarrow \infty$. Only if $W_1 = bW_2 + 1$, then $u(t) = u_0$ for all t (unstable neutral equilibrium).

A Simulation Model with Overlapping Generations

The analytical model from the previous section allows us to formulate conditions that hinder coexistence. However, it is much more difficult to deduct from equations (1)–(5) the exact parameter space of a , b , W_1 , W_2 , and u_0 in which the two species actually can co-occur. A computer simulation (iteration of eq. [2] over many generations) would easily yield the necessary information. But since the analytical model assumes nonoverlapping generations, it lacks certain dynamics of real waterfrog systems. The time delay between offspring production and sexual maturity of the offspring, for example, may act as a buffer against single directional impacts on mixed adult populations. We, therefore, decided to expand the approach of the analytical model by building a more realistic computer simulation with overlapping generations and absolute population sizes.

For this purpose, the life history of waterfrogs can be described by a simplified life cycle featuring two major parts with different dynamics: the subadult stage from egg deposition until sexual maturity and the adult stage. *Rana esculenta* and *Rana lessonae* gather at the breeding sites for reproduction during the mating season, every year. Every female is assumed to lay eggs once per year. Males may mate with several females within one breeding season. The resulting tadpoles remain in the ponds until late autumn. Metamorphs surviving the first winter enter the juvenile stage. Juveniles do not take part in breeding due to their small size and the resulting disadvantages in competition for mates. The juvenile stage lasts 1 yr. Juveniles surviving the next winter then join the adult population. The whole subadult stage from hatching of the tadpoles to the joining of the adult population, therefore, lasts 2 yr. In nature, few *R. lessonae* adults mature after one winter, and *R. esculenta* females never mature before two winters (Berger and Uzzell 1980).

This simplified waterfrog life cycle incorporates three different survival rates: a density-dependent survival for tadpoles that depends on the maximum number of tadpoles that the pond can sustain, a density-independent high mortality rate for metamorphs and a density-independent, relatively low survival rate for adults and juveniles. In the absence of empirical data, we assume for convenience that tadpoles, metamorphs, juveniles, and adults of both species and both sexes have identical survival rates. Differences in survival will clearly affect the outcome of the model (see B. Hellriegel and H.-U. Reyer, unpublished manuscript), but our purpose here is to investigate the effect of mate choice on stability. In the model, all mating combinations produce offspring with an equal sex ratio, and tadpole viability does not differ

between the different mating combinations except that $E \times E$ matings produce no offspring (see table 1).

Model Equations

Female Preference and Resulting Mating Combinations. The observed number of matings with the preferred species depends on female (but not male) preference and also on the proportion of available males of both species (Abt and Reyer 1993; Engeler 1994; Bergen et al. 1997; see introductory paragraphs). Thus, the fraction of L females mating with L males at time t is calculated as

$$fLL(t) = \frac{p_L L_\delta(t)}{p_L L_\delta(t) + (1 - p_L) E_\delta(t)},$$

$$p_L \in [0.05, 0.95], \quad (6a)$$

and similarly, the fraction of E females mating with L males as

$$fEL(t) = \frac{p_E L_\delta(t)}{p_E L_\delta(t) + (1 - p_E) E_\delta(t)},$$

$$p_E \in [0.05, 0.95]. \quad (6b)$$

Here, $L_\delta(t)$ is the absolute number of L males, and $E_\delta(t)$ is the absolute number of E males in the mixed population. The preferences for L males of $L(p_L)$ and $E(p_E)$ females are defined as the fraction of females that mate with L males if given a free choice from an equal number of E and L males. The fractions of L and E females that mate with E males equal $1 - fLL(t)$ and $1 - fLE(t)$ and the preferences of L and E females for E males equal $1 - p_L$ and $1 - p_E$, respectively. When p_L or $p_E = 0.5$, no choice is being exercised, and the fraction of females mating with L males equals the fraction of L males in the male population ($fLL(t)$ or $fEL(t) = L_\delta(t)/[L_\delta(t) + E_\delta(t)]$).

Numbers of Tadpoles, Juveniles, and Adults. *Rana lessonae* tadpoles can only originate from $L \times L$ matings; thus, the number of tadpoles is the result of the number of L females times the fraction of females that mate with L males and their fecundity, or

$$L_{\text{tad}}(t) = L_\varphi(t) fLL(t) L_{\text{eggs}}. \quad (7)$$

Rana esculenta tadpoles originate from $E_\varphi \times L_\delta$ matings as well as from $L_\varphi \times E_\delta$ males matings; thus,

$$E_{\text{tad}}(t) = fEL(t) E_\varphi(t) E_{\text{eggs}} + [1 - fLL(t)] L_\varphi(t) L_{\text{eggs}}. \quad (8)$$

Here $L_\varphi(t)$ and $E_\varphi(t)$ is the absolute number of L and E females and L_{eggs} and E_{eggs} , the average fecundity (absolute

number of eggs) per female. One-year-old juveniles that do not take part in the breeding consist of last year's tadpoles that survived the larval period, metamorphosis, and the first winter; therefore,

$$L_{\text{juv}}(t) = s_{\text{met}} \times s_{\text{tad}}(t-1) \times L_{\text{tad}}(t-1), L_{\text{juv}}(0) = 0, \quad (9a)$$

$$E_{\text{juv}}(t) = s_{\text{met}} \times s_{\text{tad}}(t-1) \times E_{\text{tad}}(t-1), E_{\text{juv}}(0) = 0. \quad (9b)$$

Here, s_{met} is the survival rate of metamorphs through the first winter. The survival rate of tadpoles $s_{\text{tad}}(t)$, consists of a constant intrinsic high survival rate for low tadpole densities ($s_{\text{tad}}(t) = 0.8$) and a density-dependent survival rate, if tadpole densities get higher. The maximum number of tadpoles that can reach metamorphosis in the pond is limited by T_{max} :

$$s_{\text{tad}}(t) = 0.8 \text{ for } L_{\text{tad}}(t) + E_{\text{tad}}(t) < 1.25 T_{\text{max}},$$

$$\text{else } s_{\text{tad}}(t) = \frac{T_{\text{max}}}{L_{\text{tad}}(t) + E_{\text{tad}}(t)}. \quad (10)$$

The density-dependent part of equation (10) only applies for the situation where the sum of the hatched tadpoles exceeds $1.25 T_{\text{max}}$. This guarantees that $s_{\text{tad}}(t)$ can never exceed 0.8. Therefore, the male breeding population in the next year consists of the adult males surviving from the present year, joined by the male half of this year's juveniles that survive the next winter.

$$L_\delta(t+1) = s_a [L_\delta(t) + \frac{1}{2} L_{\text{juv}}(t)], \quad (11a)$$

$$E_\delta(t+1) = s_a [E_\delta(t) + \frac{1}{2} E_{\text{juv}}(t)], \quad (11b)$$

and for females,

$$L_\varphi(t+1) = s_a [L_\varphi(t) + \frac{1}{2} L_{\text{juv}}(t)], \quad (11c)$$

$$E_\varphi(t+1) = s_a [E_\varphi(t) + \frac{1}{2} E_{\text{juv}}(t)]. \quad (11d)$$

Here, s_a is the survival rate of adults.

Model Implementation

The fraction values for $L_{\text{tad}}(t)$, $E_{\text{tad}}(t)$, $L_{\text{juv}}(t)$, $E_{\text{juv}}(t)$, $L_\varphi(t)$, $L_\delta(t)$, $E_\varphi(t)$, and $E_\delta(t)$ were truncated to the next lower integer value. The parameter values used in the simulation model are listed in table 3. Values for fecundity and survival are within the range of published values (Berger and

Table 3: Parameter values used in the model

Parameter	Definition	Value
L_{eggs}	Fecundity <i>Rana lessonae</i> females	182–1,000 eggs
E_{eggs}	Fecundity <i>Rana esculenta</i> females	1,000–1,820 eggs
s_a	Survival rate for adults	.83
s_{met}	Survival rate for metamorphs	.02
T_{max}	Maximum number of surviving tadpoles in pond	5,000 tadpoles
P_L, P_E	Female preference	.05–.95
$L_{\varphi}(0), L_{\sigma}(0), E_{\varphi}(0), E_{\sigma}(0)$	Starting populations	25

Uzzell 1980; Berven 1990; Neveu 1991) or are derived from ongoing field studies near Zürich (G. Abt and A.-K. Holenweg, personal communication; B. R. Anholt, unpublished data). The simulation was programmed in Borland Pascal 7.0 on a Pentium 233.

Model Analysis

Our first test focused on whether female choice can compensate for the hybrid's primary demographic superiority due to higher fecundity of *R. esculenta* females. We varied the relative fitnesses of females using $L : E$ clutch size ratios between 0.1 and 1.0 in steps of 0.1. These ratios represent absolute clutch sizes between 182 : 1,818 and 1,000 : 1,000. Figure 1A–1C shows selected cases only with $L : E$ clutch size ratio of 0.2 (333 : 1,667), 0.5 (667 : 1,333), and 1.0 (1,000 : 1,000).

For each clutch size ratio, we tested which combinations of *R. esculenta* and *R. lessonae* female preference for L males resulted in long-term population stability. For this test, we varied preferences from 0.05 to 0.95 in steps of 0.05. Starting with a population of 25 males and 25 females for each of the two species, population development was simulated for 200 breeding cycles. All populations either reached a stable equilibrium (stable absolute subpopulation sizes) or crashed within 200 cycles. Where population development led to a stable equilibrium, we noted the final percentage of *R. lessonae* in the mixed population. A population crash was defined as a situation where stability could not be achieved and both species went extinct within 200 cycles.

Equations (7) and (8) model tadpole production for conditions where female mate preferences are modified by the relative abundance of males of the two taxa (see eq. [6a] and [6b]). To test the effect of this frequency dependence on the dynamics of the L - E system, we compared the results with those from simulations where mate choice

was independent of male genotype ratios. For this second model, we replaced the male frequency-dependent terms $fLL(t)$ and $fEL(t)$ in equations (7) and (8) with p_L and p_E . By this replacement, equations (7) and (8) now become independent of the relative abundance of males. We, therefore, assumed that males are always present (due to the 1 : 1 sex ratio in the offspring) and can mate several times as long as females of the same species persist. When the *R. lessonae* subpopulation went to extinction, $E_{\text{tad}}(t)$ was set to 0.

Sensitivity to Variation in Different Model Parameters

In order to estimate the importance of differences in life-history parameters between the two species, we ran several sensitivity analyses. Starting from a parameter set that best matched data from our field studies and literature (see fig. 2) and that produced a stable coexistence in the first test, we varied each of the main model parameters over its whole range, leaving the other parameters on their initial values and plotted the resulting species composition after 200 generations.

Stability of Equilibria

Finally, we tested the stability of the system and looked for alternate equilibria. We tested female preference combinations that led to a stable equilibrium by either increasing or decreasing one of the L or E subpopulations by 50% after generations 40, 80, 120, and 160. We then recorded the deviations in species composition from the initial stable state.

Results

Female Preference Combinations versus Clutch Size Relations

Random mating (i.e., female preference for L males of 0.5 in both species) produced overshoot-collapse patterns in all clutch size combinations (fig. 1A–1C). *Rana esculenta* first increases at the expense of *Rana lessonae*, but then the sexually dependent hybrid follows its host to extinction. Stable populations are only found when the L preference of *R. lessonae* females is greater than the L preference of *R. esculenta* females. Thus, decreasing the strength of *R. esculenta* L preference allows coexistence over a wider range of *R. lessonae* female preferences. Increasing the clutch size of *R. lessonae* relative to that of *R. esculenta* also increases the range of preference combinations where both taxa can persist.

All clutch size combinations had some female preference combinations that ended in stable equilibria in numbers

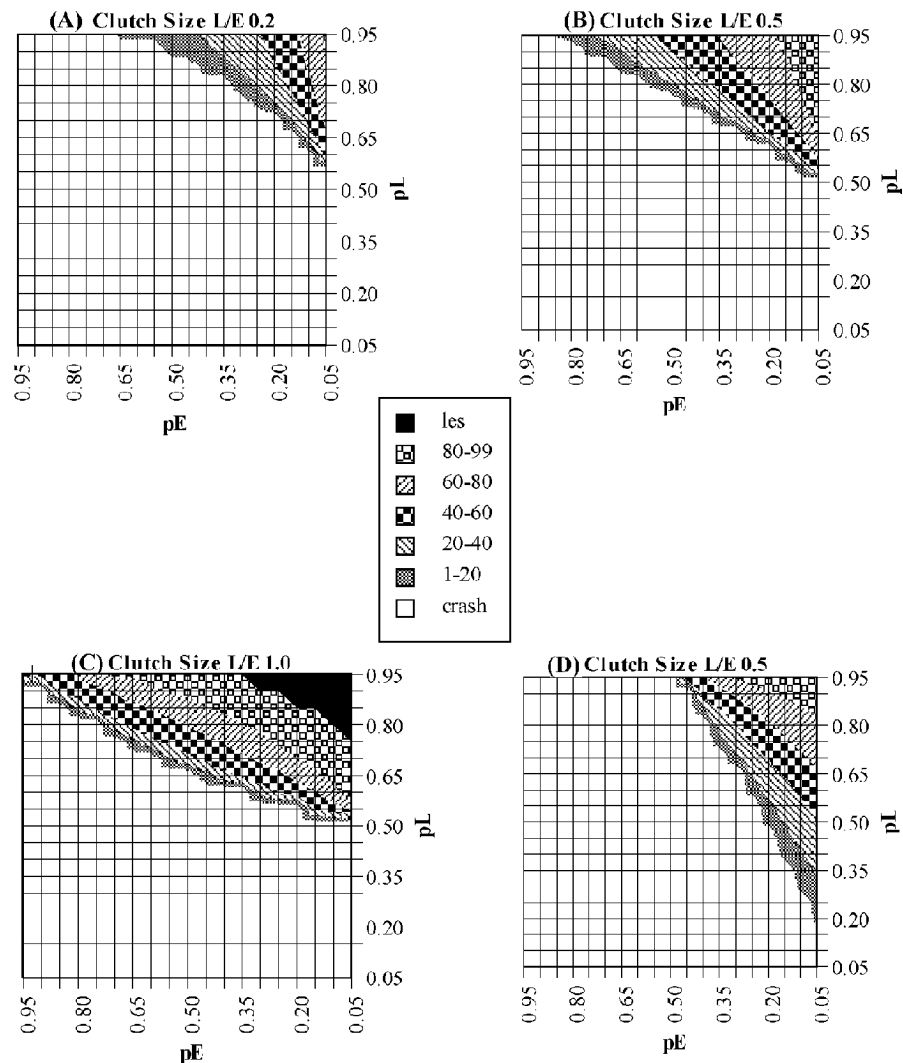


Figure 1: Female preference combinations in relation to clutch size ratios: p_E , preference of *Rana esculenta* females for *Rana lessonae* males; p_L , preference of *R. lessonae* females for *R. lessonae* males. The legend entries show the resulting percentages of *R. lessonae* in the mixed population: *les*, female preference combinations resulting in *R. lessonae* only populations; *crash*, female preference combinations resulting in an overshoot-collapse pattern. A–C, Results for male frequency-dependent mating combinations. D, Results for male frequency-independent mating combinations.

of individuals. When female *R. lessonae* produce half as many eggs as *R. esculenta* (ratio 0.5, fig. 1B; which corresponds to our experimental data), the maximum percentage of *R. lessonae* in the population is <50% when *R. esculenta* females mate with *R. lessonae* males more often than chance. Only relative clutch sizes >0.5 allowed the *R. lessonae* populations to exceed 50% of the total (fig. 1C). When *R. esculenta* females mate randomly ($p_E = 0.5$), the highest proportion of *R. lessonae* was found for equal clutch sizes (ratio = 1.0, fig. 1C), with 98% *R. lessonae* and 2% *R. esculenta*. Under these conditions, the preference of *L* females (p_L) for *L* males had to be at least 0.7 for the

interaction to be stable (fig. 1C). Decreasing the relative clutch size to 0.5 required that this preference be raised to 0.8 to ensure stability (fig. 1B) and for a relative clutch size of 0.2 p_L had to be nearly perfect at 0.9 (fig. 1A).

Male Frequency-Dependent versus Frequency-Independent Female Choice

To determine the importance of frequency-dependent female choice for population dynamics, we compared the previous results with the results from a frequency-independent model, that is, one where female preference can

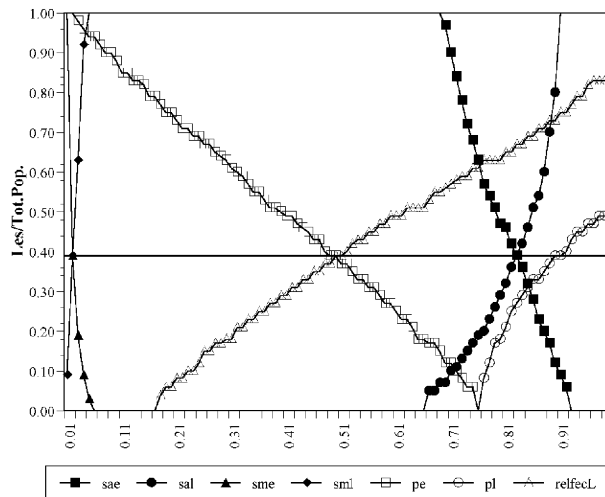


Figure 2: Dependency of species composition on variation in model parameters. The horizontal axis shows the range of parameter variation (0.01–0.99). The horizontal line indicates the starting set of parameters: survival rate E (sae) and L (sal) adults: 0.83, survival rate E (sme) and L metamorphs (sml): 0.02, preference of E females for L males (pe): 0.5, preference of L females for L males (pl): 0.9, L_{φ} fecundity relative to E_{φ} fecundity ($relfecL$): 0.5. The vertical axis shows the resulting fraction of *Rana lessonae* in the mixed population. Each of the parameters was varied separately while leaving the other parameters on the value of the starting set. Where a line reaches $Les/Tot.Pop. = 0$ or $Les/Tot.Pop. = 1$, it continues over the entire domain at $Les/Tot.Pop. = 0$ or 1 (points have not been plotted for clarity).

not be overridden by male composition (fig. 1B vs. 1D). Whereas the frequency-dependent model shows possible stable populations if *R. esculenta* females prefer L males ($p_E > 0.5$), the frequency-independent model only produces stable populations under the unrealistic condition that *R. esculenta* females show a higher preference for E males than for L males ($p_E < 0.5$). Therefore, incorporating frequency dependence into our model of female choice considerably expands the range of female preference combinations leading to population stability.

Sensitivity to Variation in Model Parameters

Figure 2 shows the results of seven different sensitivity tests in one graph. Each of the seven parameters was tested independently over its full range from 0.01 to 0.99 (i.e., over the whole horizontal axis), while the values of the remaining six variables were held constant on the value (horizontal axis), indicated by the intersection between their trajectories and the horizontal starting set line. The steepness of the slopes of the parameter trajectories in figure 2 indicates the sensitivity of the model to variation in the respective parameter. The steeper the slope, the

faster species composition in mixed populations changes with variation of the parameter.

Variation in metamorph survival rate has the largest impact on species composition, followed by the adult survival rates and the selectivity of *R. lessonae* females. One, therefore, might conclude that, based on the direct effect of variation in female preferences on species composition, mate choice plays a minor role in the maintenance of the waterfrog system. But assortative mating may not only have a direct effect on species composition. Interactions between assortative mating and other parameters may be equally or more important than the direct effect alone. We, therefore, further investigated the role of assortative mating for the waterfrog complex by investigating the interaction between female preference and adult survival rate as well as metamorph survival rate. Figure 3A and 3C shows that coexistence is possible with some combinations of adult or metamorph survival rates even when individuals mate randomly. But the parameter space where coexistence is possible under random mating is so small that stochastic minor differences between the two species leads to an L -only population or a population crash. The range of survival rate combinations that allow coexistence expands dramatically if individuals mate selectively (fig. 3B, 3D).

Neutral Equilibria and Stability of the System

All of the investigated clutch size ratios were sensitive to at least one of the four performed stochastic 50% changes in subpopulation size. In all of the cases where populations did not crash during the stability test, population development after disturbance led to equilibria with species compositions different from the situation before the perturbation (fig. 4). None of the combinations of female preference, therefore, resulted in global stability. The magnitude of differences in *R. lessonae* percentages between stable states within one run depended on the combination of adult survival and metamorph survival (fig. 5). Populations with low turnover rates (low metamorph and high adult survival, which correspond to our data of $s_{met} = 0.02$ and $s_a = 0.83$) showed particularly high differences in *R. lessonae* percentages between stable states. All populations with a proportion of $<10\%$ *R. lessonae* crashed if the number of *R. lessonae* individuals was decreased by 50% or, in some cases, if *R. esculenta* individuals were increased by 50%. In almost all cases, decreasing a subpopulation had a greater impact on species composition than increasing the other subpopulation.

Recovery times from the impact were relatively long (between 4 and 22 yr) over all population turnover rates. During this recovery time, populations are particularly susceptible to disturbances. To examine the effect of re-

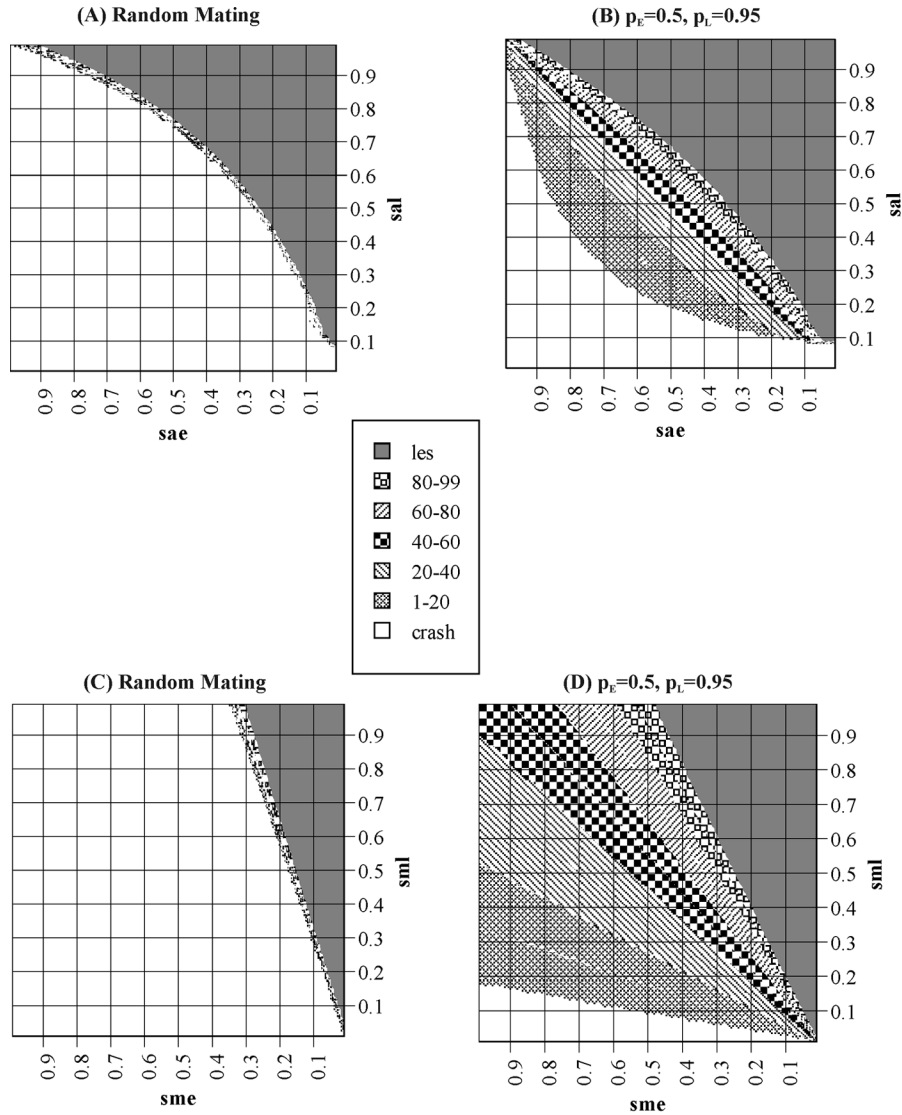


Figure 3: Interaction between assortative mating and survival rates. *A, B*, Interaction with adult survival rates: *sal*, survival rate *L* adults; *sae*, survival rate *E* adults. *C, D*, Interaction with metamorph survival rate: *smi*, survival rate *L* metamorphs; *sme*, survival rate *E* metamorphs. The legend shows the resulting percentage of *Rana lessonae* in the mixed population (see fig. 2). Areas with nonsolid patterns (1%–99% *L*) indicate the parameter space that allows coexistence. *A, C*, Show the case where no choice is exercised ($p_E = p_L = 0.5$). *B, D*, *L* females show a strong preference for *L* males, *E* females show no specific preference. Clutch size ratio *L* : *E* in this example: 0.5.

peated disturbances during the recovery phase, we randomly varied the size of the breeding population between -20% and $+20\%$ for each species independently every year. As illustrated by one specific case (fig. 6), the species composition is now highly variable among years, with the *L* : *E* ratio ranging from 1 : 1 up to approximately 1 : 5. The analytical model with nonoverlapping generations did not show any of these behaviors mentioned in this section because of the lack of carry-over or buffering phenomena due to the complete generation turnover from year to year.

Discussion

Our model shows that assortative mating can be essential for regulating coexistence between the hybridogenetic and the sexual parental species. In our example, assortative mating by itself may not be sufficient to explain the large variations in species composition that we observe in the field. Other life-history parameters can have a larger influence on species composition but only if assortative mating provides the system with the necessary stability.

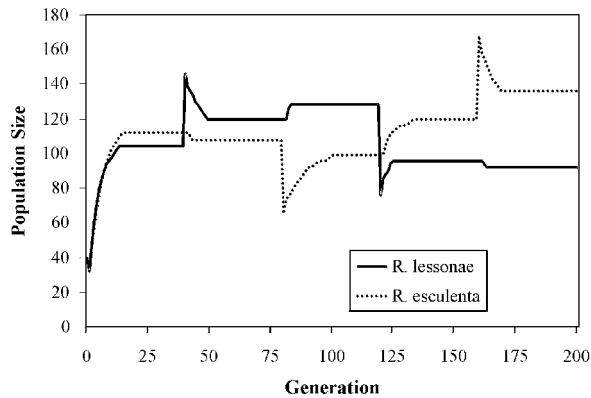


Figure 4: Neutral equilibria of a mixed population with low population turnover rate. Each of the four subpopulation reductions or increments by 50% produced a new species composition. The values for this example are clutch size relation *Les/Esc*: 0.8. Preference of *Rana esculenta* females for *Rana lessonae* males: 0.55. Preference of *R. lessonae* females for *R. lessonae* males: 0.85; survival rate of adults: 0.8; survival rate of metamorphs: 0.02.

Moore and McKay (1971) and Moore (1975) have already shown in their model that assortative mating can stabilize the unisexual : bisexual ratio in the *Poeciliopsis* complex. Schlupp et al. (1994) and Schlupp and Ryan (1997) suggested that mate copying in mollies may operate in a similar manner but did not model this explicitly. But in such unisexual hybrid systems, the all-female hybrids do not have to make a choice between males of a host species and hybrid males because there are no hybrid males. Host-hybrid systems such as the *Rana esculenta* complex where all intra- and interspecific matings are possible show much more complicated dynamics compared to unisexual hybrid systems. Adding male hybrids increases the chances of hybrid offspring production. Furthermore, the selection against heterospecific matings in unisexual hybrid systems is relatively weak, as only males can lose their reproductive investment if they mate with the wrong partner. In the waterfrog system, females of both species can have high fitness losses from mismatings with *R. esculenta* males. Regulating mechanisms in such a hybrid host system, therefore, have to be much more powerful than in unisexual hybrid systems.

The clear fitness advantage for females choosing *Rana lessonae* mates provides the required effective mechanism for stabilizing *R. lessonae* : *R. esculenta* ratios in mixed populations. Stability arises from a reduction in the number of *E* offspring, which normally would swamp and out-compete *L* tadpoles due to the four mechanisms outlined in the introductory paragraphs. Because stable *L* : *E* ratios are possible under all clutch size ratios (fig. 1), genotype

differences in the attractiveness of males seem to be more important for achieving equilibria than differences in female fecundity. This is particularly true when choice is affected by the proportion of the two male types in the population (frequency dependent). Such frequency dependence increases the range where mate choice leads to an equilibrium compared to absolute preferences (cf. fig. 1B and 1D). Absolute preference increases the chance of successful *E* female reproduction when *L* males are scarce, leading to an overshoot-collapse pattern. Moreover, the higher success of frequency-dependent mating allows us to reconcile the clear preferences for *L* males in females exposed to individual *L* and *E* males (Abt and Reyer 1993; Engeler 1994) with the less obvious response in females exposed to several males in different *L* : *E* ratios (Bergen et al. 1997). The frequency-dependent choice may not necessarily be due to male-male competition overrunning female choice, as suggested by Bergen et al. (1997). An alternative explanation is that a female’s costs of choosing varies with the relative frequency of the preferred male type in the population. When the preferred *L* males are rare, encounters with unwanted *E* males increase as well as the associated costs of rejecting them. This relates our specific frequency-dependent choice model for hybrid-

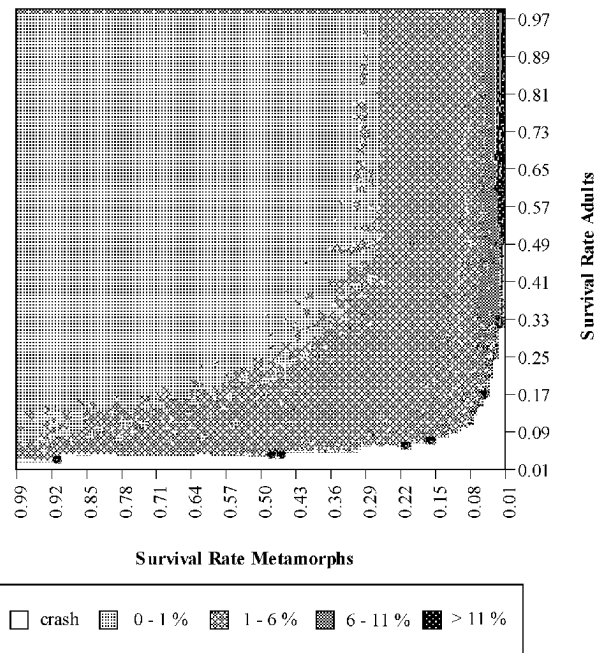


Figure 5: Maximum differences in percentages of *Rana lessonae* between neutral equilibria within one run depending on the combination of survival rates of adults and metamorphs. Clutch size relation *Les/Esc*: 0.8, Preference of *Rana esculenta* females for *R. lessonae* males: 0.55. Preference of *R. lessonae* females for *R. lessonae* males: 0.85.

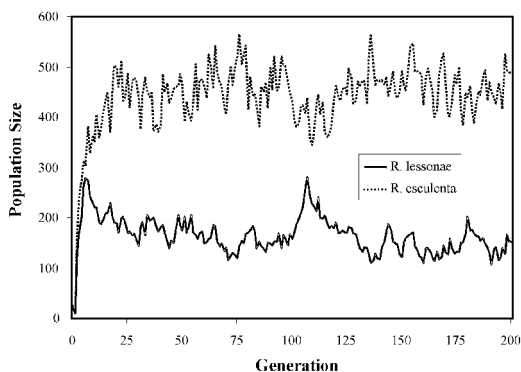


Figure 6: Overall population development if the breeding population varies randomly between -20% and $+20\%$. Relative clutch size relation $L:E$ is 0.5 , preference of L females for L males is 0.85 and the preference of E females for L males is 0.5 .

genetic waterfrogs to the more general case of sequential mate sampling where the costs of choosing increase with every sampling. In such a situation, decreasing the critical quality threshold for accepting a male leads to higher fitness than a best-of- n -males strategy (Real 1990). It could be argued that in the $L:E$ system, with its all-or-nothing fitness consequences of choosing the right male, E males should always be rejected. But the females' options for continuing search until they find a rare L male may be restricted by time because females are capable of ovulating spontaneously and even lay eggs without amplexus (Reyer et al. 1999). Kawecki (1988) described a similar mechanism in his model of the *Poeciliopsis* complex. In his model, subordinate males have to make a trade-off between quick sneaky matings and the more time-consuming correct identification of females. This male strategy works as a density-dependent regulating mechanism: if bisexuals are common in the mixed population, male competition and, therefore, interspecific matings increase, which initiates a shift toward more unisexuals.

In our models, coexistence can only be achieved if L males preference is higher in L females than in E females. The hybrid origin of *R. esculenta* could cause such a difference in preference for L males. If the *Rana ridibunda* genome and its associated preference for conspecifics is still expressed to a nonnegligible extent in *R. esculenta*, we would expect that patterns for L recognition are less well defined in *R. esculenta* than in *R. lessonae*.

Species composition within mixed $L:E$ populations is highly variable, ranging from 5% to 95% *R. lessonae* (Blankenhorn 1974, 1977; Berger 1977; Binkert 1981). Frequency-dependent mate choice will contribute to these differences but does not explain them sufficiently, as shown by figures 4 and 6. When L and E numbers change sto-

chastically, populations return to stability but with species compositions different from those before the impact. Repeated disturbance can increase these differences, which depend on survival rates of juveniles and adults (fig. 5). Repeated disturbance in our model can be used to describe annual variation in breeding population size, which is widespread in anurans (e.g., Meyer et al. 1998). This can be due to migration between neighboring ponds or year-to-year differences in environmental conditions, which may affect species, sexes, and age classes differently. The sensitivity analysis of our model has shown that differences in life-history parameters, such as survival rates of adults or juveniles, have a strong influence on the species composition. This might explain why $L:E$ ratios fluctuate over time within ponds if changing environmental conditions affect the two species differently. Yet, some ponds seem to always have more *R. lessonae* and others more *R. esculenta* (Berger 1977; Hohenweg 1999), which could be explained by the stabilizing effect of assortative mating.

In emphasizing the importance of female choice, be it the direct effect on species composition or its indispensability for the stability of the coexistence, our model differs from previous ones, which identified nearly equal fitness of R and E males (Plötner and Grunwald 1991), differences in habitat preferences (Guex et al. 1993), and relative female fecundity and larval viability (Graf 1986) as the crucial factors stabilizing hybrid:parental ratios. Previous models contained some unrealistic assumptions including discrete rather than overlapping generations and no matings between L females and E males. Any life-history variable that affects birth and death rates, (including starting conditions, dispersal, habitat preference, disturbance, etc.) can modify the ratios (B. Hellriegel and H.-U. Reyer, unpublished manuscript), but assortative mating still seems to be required to provide the system with the necessary stability. Thus, mating behavior turns out to be more important for the populations dynamics of hybridogenetic waterfrog systems than previously assumed. It remains to be seen whether this is also true for other systems where individuals of different clones, populations or species interact reproductively. The analysis of hybrid zones and their long-term stability (Arnold 1997) seems to be an obvious area where similar models could provide some insights as several authors mention assortative mating or asymmetric mating preferences as key factors influencing the structure of hybrid zones (e.g., Howard et al. 1993; Davies et al. 1997; Yoshimura and Starmer 1997).

According to classic ecological theory, most interactions between herbivores and plants, predators and prey, hosts and parasitoids, or interspecific competitors should be unstable or cycling, but in the real world, long-term stability and coexistence occurs in many systems (Begon et al. 1996). It has been suggested recently that this discrepancy

between predicted and observed dynamics may often disappear when we model ecological interactions as the outcome of fitness-enhancing behavior patterns, rather than as (unrealistic) "random collisions" between individuals in the sense of Lotka-Volterra equations (Fryxell and Lundberg 1998). The model presented here strongly supports this contention.

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