

Mate choice and fitness in a hybrid frog: *Rana esculenta* females prefer *Rana lessonae* males over their own

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Summary. The evolution and maintenance of female choice based on purely genetic differences is still a controversial issue, not only for theoretical reasons, but also because of the practical difficulty of demonstrating the fitness consequences of preferences and heritability of and genetic variability in the chosen traits. We argue that hybrid systems (broadly defined) offer suitable models for studying mate choice according to genetic differences. We present such a study for European waterfrogs of the “hybridogenetic” *Rana lessonae*/*Rana esculenta* complex (L/E complex). *R. esculenta*, originally a hybrid between *R. lessonae* and *R. ridibunda*, eliminates the L genome premeiotically and only produces eggs and sperm containing only the *R. ridibunda* (R) genome. Consequently, the hybrid will only persist when it lives and mates with *R. lessonae* in mixed populations where it can regain the lost L genome. In such mixed populations, there is strong selection against E × E matings, because these will produce no viable offspring. We tested whether females of the hybrid *R. esculenta* do indeed avoid their own *R. esculenta* males and choose males of the parental species *R. lessonae* instead. Eleven E females were offered a simultaneous choice between one L and one E male. Females exhibited a significant preference for L males that was determined by the type of male, rather than by its size or activity. This choice is in the direction predicted from genetics. The question of why L males “agree” to mate with E females, but L females only rarely mate with E males, is answered by a sexual asymmetry in the cost/benefit ratios of mating with the wrong type and the right size. Our results are consistent with the mating pattern found in natural populations, but further studies are needed to show that female choice really causes this pattern.

Introduction

Mate choice

In many species of animals, males and females do not mate randomly, but according to certain traits such as size, activity, calls or colour patterns. Since Darwin (1871) such non-randomness has been explained through competition (usually among males) and mate choice (usually by females). The adaptive significance of female choice is fairly obvious in cases where selection of mates is based on territory quality, parental care, costs of searching, disease or parasite transmission and other factors which directly affect the females’ survival and/or reproductive success. However, choice in the absence of such obvious benefits is more difficult to understand, because the alternative, choice for purely genetic benefits, poses a number of theoretical and practical problems (for review see Bradbury and Anderson 1987; Harvey and Bradbury 1991; Maynard Smith 1991; Kirkpatrick and Ryan 1991; Ryan 1991). On the theoretical level, the biggest challenge is to explain how sufficient genetic variation in male traits can be maintained to keep female choice advantageous. On the practical level, it is often difficult to measure the fitness consequences of the preference and to demonstrate the heritability of and genetic variability in the chosen trait. Consequently, empirical evidence for genetic benefits resulting from mate choice is rare (Kirkpatrick and Ryan 1991).

We feel that studying hybrid systems can help to close this gap. Here the term hybridization is very broadly defined. It refers not only to the interbreeding of individuals from two different species, but also to breeding between individuals of different subspecies, geographical races, ecotypes, populations and other forms, which are distinguishable on the basis of one or more heritable traits (cf. Harrison 1990, p. 70).

Traditionally, hybrid systems have been considered within the framework of speciation. Studies have concentrated on analysing (genetic) *trait differences among species* and the – usually negative – fitness consequences

of hybridization, but have neglected mating discrimination within hybrid zones (for review see Barton and Hewitt 1985, 1989; Hewitt 1988; Harrison 1990). On the other hand, studies on sexual selection have focused on measuring *mate choice within species*, but usually with little knowledge about the genetic background and adaptive advantage of the preferred traits. We believe that this dichotomy is neither justified nor useful. The biological function of choosing genetically compatible mates remains the same, no matter whether the potential mates belong to the same or to different species. Putting different labels on two points in a continuum of genetic similarity is arbitrary and misleading, especially as our opinion of genetic similarity depends on the number of alleles investigated (see Grafen 1990 for a similar argument with respect to kin recognition). Recently, a few studies have indicated that female choice within species can have important consequences for the formation, maintenance and breakdown of reproductive isolation between species (Wilson and Hedrick 1982; Phelan and Baker 1987; Lande and Kirkpatrick 1988; Grant and Grant 1992). Thus, incorporating concepts from sexual selection into studies of hybrid zones may help to solve some ongoing debates about the routes to speciation (e.g. allopatric vs. sympatric speciation).

Conversely, studying hybrid systems with usually more pronounced and often phenotypically detectable genetic differences among their members may help to address some poorly understood issues in sexual selection, including mate choice by genetic compatibility. As mating with the wrong genotype usually has pronounced negative effects on fitness, we can expect strong direct selection for female choice. Such direct selection is not only easier to demonstrate than indirect selection through runaway or good-genes processes; it also may be more important in nature than previously thought (Kirkpatrick and Ryan 1991).

In this paper we use European waterfrogs of the hybrid complex *Rana lessonae*/*Rana esculenta* (L/E complex) as a model system for studying female choice by genetic compatibility. The usual genetic and reproductive system of this complex has been reviewed by Berger (1977, 1983) Graf and Polls Pelaz (1989) and Günther (1990), but a brief outline is necessary to understand our approach.

The L/E complex as a model for studying female choice by genetic compatibility

R. esculenta (genotype *LR*) is an interspecific hybrid which was originally produced through matings between *R. lessonae* (*LL*) and *R. ridibunda* (*RR*)¹. In Switzerland and many other areas of central Europe, *R. ridibunda* does not occur, and only *R. lessonae* and *R. esculenta* occur sympatrically (Berger 1968; Blankenhorn et al. 1971; Günther 1973). These two types differ in average size, some allometric features and several allozyme patterns. During the breeding season, males can also be distinguished by body coloration, calls and probably also by other behaviour (see Günther 1990 for the most comprehensive recent review). Differences in chemical cues are also likely, but nothing is known about their nature or relevance.

The hybrid, *R. esculenta*, has a reproductive mode known as “hybridogenesis” (Schultz 1969; Tunner 1973, 1974): prior to meiosis, it excludes one of its parental genomes (*L*), reduplicates the other (*R*) and clonally transmits it to eggs and sperm cells. Consequently, the hybrid can only persist through sexual parasitism on the parental species: *R. esculenta* must occur and mate with *R. lessonae*, their sexual host, to regain the lost *L* genome.

In mixed L/E populations four different mating combinations are possible (Fig. 1): *L* × *L*, *L* × *E*, *E* × *L*, *E* × *E*, with the first letter denoting the female, the second the male. The two heterotypic matings *L* × *E* and *E* × *L* produce progeny with the genotype *LR* and, thus, “recreate” the hybrid *R. esculenta*. The homotypical mating *L* × *L* produces offspring with the genotype *LL*, thus maintaining the parental species *R. lessonae*. The other homotypical mating (*E* × *E*) results in *RR* progeny, but usually not in sexually mature *R. ridibunda* adults. The offspring usually die during the larval stage, both under laboratory (Berger 1976, 1977) and more natural conditions (Semlitsch and Reyer 1992). This is attributed to an accumulation of lethal factors on the clonally trans-

¹ Throughout this paper, a single capital letter in Roman type denotes a phenotype while one or two capital letters in italics denote a genotype. Thus, *R. lessonae* can be referred to by either *L* or *LL*, *R. esculenta* by either *E* or *LR*, and *R. ridibunda* by either *R* or *RR*

parents

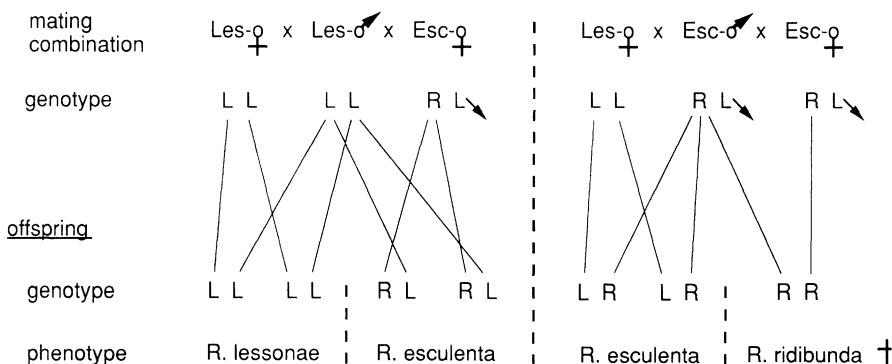


Fig. 1. Offspring genotypes and phenotypes resulting from different L/E mating combinations. Arrows indicate the premeiotic exclusion of the *L* genome in *Rana esculenta* parents. The cross after *R. ridibunda* indicates that larvae of this genotype normally do not survive to maturity. *Les.*, *R. lessonae*; *Esc.*, *R. esculenta*

mitted *R* chromosomes (Berger 1976; Graf and Müller 1979; Uzzell et al. 1980).

Due to these large differences in offspring viability and the resulting "all-or-nothing" fitness consequences, there is a high selective advantage in choosing the correct genotype. Thus, the L/E complex provides an excellent model system to study mate choice based on genetic differences. We therefore tested whether females of the hybrid *R. esculenta* prefer males of the parental species *R. lessonae* over their own *R. esculenta* males, as expected on genetic grounds.

Methods

Animals. In the laboratory, frogs will not show typical reproductive behaviour when taken directly from the field in spring, but they do perform normally when overwintered in captivity (Blankenhorn 1974). In September 1989 55 frogs were caught from a population at Chaltensee (near Zürich, Switzerland) and brought into the laboratory. All frogs were measured [snout-vent length (SVL) in mm] and their belly patterns were photographed for individual recognition. Species were identified electrophoretically by analysing the albumin of the lymph (Vogel 1973).

Frogs were then cooled down to 6° C over 2 weeks and kept at 4–6° C until early February 1990 when the temperature was increased again to 20° C within 8 days. Animals were then placed in four containers, one holding 14–16 females, the other three holding a total of 35 males. Each container had a base of 1 × 1 m, was 50 cm high and covered with a 60 cm high lattice top. The bottom was filled with water up to a level of 12 cm with large stones and pieces of wood offering perches and shelter. The water was changed three times a week and animals were fed ad lib with crickets, earthworms and wax moths.

All containers were in the same room which was lit by mercury vapour lamps. In order to stimulate reproductive activity, day length was increased from 12 to 16 h over 3 weeks (Notter 1974) and tape-recordings of mixed choruses of calling *R. lessonae* and *R. esculenta* males were played several times per day. Choice experiments began when males started calling and females showed obvious signs of being gravid. After completion of the experiments the animals were returned to their pond of origin.

Choice experiments. Tests were done in an aquarium measuring 130 × 50 × 45 cm and filled with water to a level of 7 cm (Fig. 2). The bottom was covered with a grid dividing the width into three sectors of 16.5 cm each and the length into 13 sectors of 10 cm each. Two partitions of plastic coated wire mesh separated a central compartment, consisting of seven 10-cm-wide sectors, from two distal compartments each consisting of three 10-cm-wide sectors.

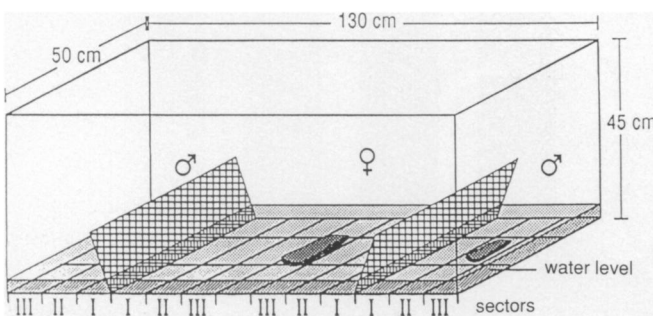


Fig. 2. Experimental tank used for choice experiments with one female compartment in the middle and two male compartments at opposite ends

The partitions were tilted towards the aquarium ends so that females could jump into the males' compartments, but not vice versa.

For the test a female was placed into the middle of the central compartment and given a simultaneous choice between an *E* and a *L* male, both randomly selected from the stock of males. Each female was tested in three experimental subsets. A subset normally lasted 30 min, but was terminated earlier when a female jumped over the partition into a male's compartment. Within each subset *L* and *E* males were assigned randomly to the left or right side of the tank. If, however, this random assignment had resulted in the same male-side combination during the first two subsets, males were switched for the third subset. Thus a male would be on a particular side either once or twice.

Data analysis. All experiments were video-taped and from the tapes the following variables were measured: (a) "time female" and (b) "time male", i.e. the times (min) a female and a male, respectively, spent in the 10-cm sector closest to the partition; (c) "male activity", measured as the number of gridfield changes; (d) duration of experimental subset, i.e. either 30 min or until a female jumped across the partition. For each of these variables values were summed over all three experimental subsets, resulting in one data set per female. A total of 11 *R. esculenta* females was tested in this way. After each experiment the water was changed.

"Time female" served as our measure of choice and was entered as the dependent variable into a univariate two-way ANCOVA. The independent variables used to explain a potential preference included two main effects and three covariates. The main effects were the type of the male (*L* and *E*) and the frequency (once or twice) the *L* male was caged on the left side. The covariates were "time male", "male activity" and "male size". Male size and male activity were normally distributed; time female and time male were normally distributed only after log-transformation (all $P > 0.10$; Lilliefors modification of the Kolmogorov-Smirnov test). Each female entered the ANCOVA only once, but with two time values, one for the left, the other for the right 10-cm sector of the tank. These time values are independent of each other for the following reason: as the left and right sectors were separated by a 50-cm-long section (which the females also used), the time spent in the left sector is not automatically given by the total observation time minus the time spent in the right sector.

Results

Male characteristics

Among the males used in the experiments *E* males were on average 14% larger than *L* males and about three times as active (both $P < 0.001$, *t*-test with unequal variance), but the two male types did not differ in the time they spent within 10 cm of the partition ($P = 0.706$; Fig. 3a–c).

General female behaviour

During the experiments, most females expressed a clear interest in the males. They spent significantly more time in the two sectors close to the male compartments than expected if their distribution were random (Fig. 4). This is true no matter whether the expectation is calculated on the basis of sector numbers ($0.286 = 2/7$) or on the basis of edge length ($0.565 = 130/230$ cm) (both $P < 0.01$; Wilcoxon test, with pairwise comparison of observed and expected values). Females also moved back and

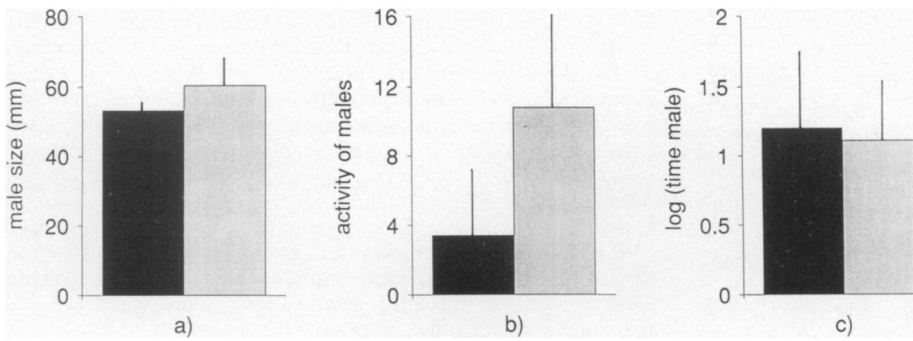


Fig. 3a–c. Differences between L and E males in terms of **a** body size, **b** activity, and **c** time spent close to the partition. Means and standard deviations are shown. *Solid bars*, *R. lessonae* (L); *grey bars*, *R. esculenta* (E)

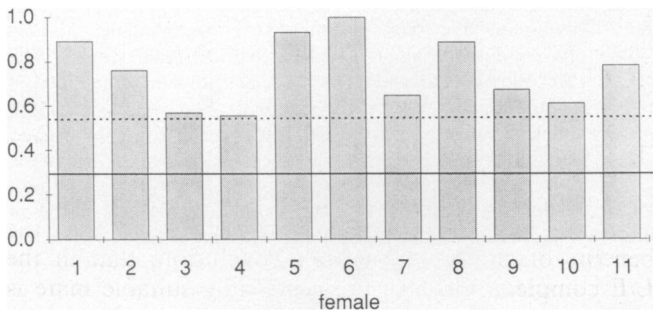


Fig. 4. Proportion of total time which each of the 11 test females spent in the two sectors next to the male compartments (see Fig. 2). Observed values are given by *grey bars*. Values expected from a random distribution are given by two *lines*: the *solid line* shows the expected value calculated from sector numbers, the *broken line* gives the expected value calculated from edge length

forth between the two sides of the tank. The extent of these movements varied individually. Some females changed sides often throughout an experiment; others changed sides only once or twice and then remained on one side, swimming up and down the partition. In no experimental subset did a female stay on one side only. Thus, comparison of the males was always possible. With only one exception, no male called during the experiments. Thus, choice can only have been based on visual, tactile and/or chemical cues, with the latter two being transmitted by water movement through the partition.

Preference for males

When preference was tested by the time females stayed within 10 cm of the partition, the following results were obtained (Table 1). (1) Females spent significantly more time close to L males than to E males, but showed no bias towards a particular side of the tank (Fig. 5). (2) The time a female spent near the partition increased significantly with the time a male was close to that partition, but the two covariates in which E and L males differed significantly (size and activity: Fig. 3) had no influence on the choice.

In 4 of the 11 females this male-directed preference was obvious in any of the three experimental subsets: no matter which side the L-male was on, the female

Table 1. Summary of analysis of variance for the amount of time which E-females stayed close to male compartments [=log (time female)]

	Coefficient	SS	df	F ratio	P
Covariates					
Log (time male)	0.539	1.376	1	8.286	0.012
Male size (SVL)	-0.001	0.347	1	2.086	0.169
Male activity	0.034	0.120	1	0.725	0.417
Main Effects					
Male type		1.597	1	9.615	0.007
Side		0.668	1	4.020	0.063
2-factor interactions					
Male type × side		0.009	4	0.014	0.999
Residual		2.491	15	0.166	
Total		6.417	21		

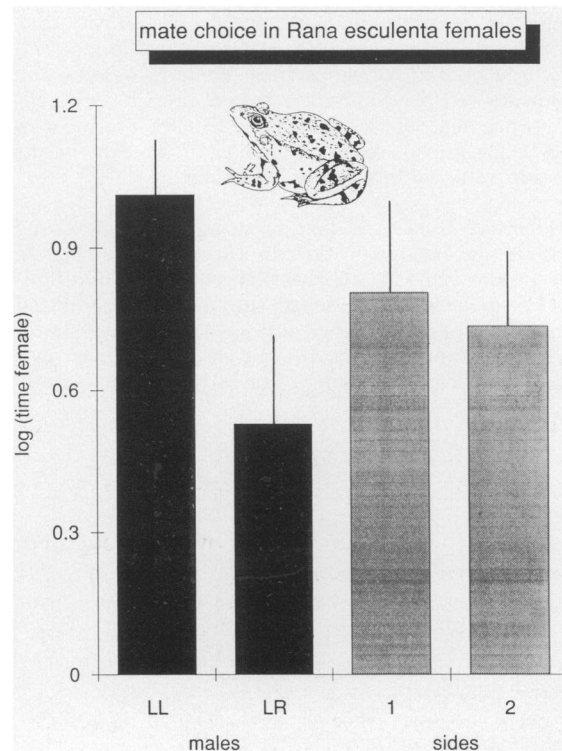


Fig. 5. Amount of time which E females spent with each of the two male types (*black bars*) and on each side of the tank (*grey bars*). Means and standard deviations calculated from log-transformed time data are shown

would spend most of her time on that side (up to 25 out of 30 min). In the other 7 females the preference was less clear, i.e. it was observed only in one or two of the three subsets. An explanation for this difference among females is provided by the following observations.

Escape from the test chamber

In 20 out of 33 experimental subsets, females jumped across the partition before the end of the 30-min period. Eight of these jumps were into the compartment of a L male, 12 into that of an E male. The difference is not significant, nor is the difference between jumps to the left ($n=8$) and to the right side ($n=12$) of the tank (both $P=0.54$; binomial test, 2-tailed). Probably these jumps reflect an undirected attempt to escape from the experimental tank rather than an attempt to get into the compartment of a particular male.

The four females that showed an unambiguous preference for L males jumped over the partition significantly later than the other seven females, or did not jump at all ($P=0.046$, Mann-Whitney U -test). The longer a female stayed in her compartment the more pronounced was the preference for L males as expressed by the ratio "time with L"/"time with E" ($r_s=0.718$, $P<0.02$; Spearman rank correlation, two-tailed). These data suggest that E females that did not show an unambiguous preference for L males had a higher tendency to escape from the test chamber and/or a lower interest in the males. The lower this escape tendency (i.e. the higher the male-directed behaviour), the clearer the preference for L over E males.

Discussion

Who chooses, male or female?

The results of our experiments can be summarized as follows: (1) *R. esculenta* females do not associate randomly with L and E males, but exhibit a preference for L males. (2) This preference is in the direction predicted from knowledge of the genetics because only mating with L males will guarantee the E females successful production of viable offspring. (3) The choice is determined by the type of male, rather than by his size or activity.

This explanation of our results by female choice differs from the only two studies that have previously tried to explain non-random mating in L/E populations by mate-choice. After field studies and a series of laboratory experiments with one male and one or two females in the same tank, Blankenhorn (1974, 1977) and Notter (1974) concluded that there is no evidence of females selecting males; rather males were supposed to exhibit a preference for particular females.

We question this conclusion for several reasons. First, their experiments did not control either for male-female

and female-female interactions or for the strength of the stimulus, which can differ with distance between the potential mates (cf. "circle of attraction", Parker 1983; Arak 1988). Second, Blankenhorn and Notter found that sexual activity was high between L males and E females, but almost never occurred between E males and L females, even when the male was smaller than the female (see Fig. 5 in Blankenhorn 1977). Considering that E must mate with L, but L should avoid mating with E, these results contradict the expectations from male choice, but are fully consistent with female choice. Finally, female rather than male choice is also to be expected on more general theoretical grounds. In species like *R. lessonae*, *R. esculenta* and several other anurans, where males provide neither parental care nor resources for the offspring, females should be the choosy sex, because they invest more in eggs than males invest in sperm (Trivers 1972). This choice should be particularly pronounced in lekking species, like our frogs, where competing males are spatially clumped and females incur low searching costs (which potentially could counteract the benefits of choice). Thus, our conclusion, that in the L/E complex choice of the genetically suitable mate is exhibited by females rather than by males, is supported by both theory and previous empirical results.

It should be noted that our conclusion only refers to the choice of the phenotype. We make no inference whether the E females' preference for L males is inherited through the L or the R genome. This question will be addressed by studying mate choice (a) in triploid hybrids of different genetic composition (*LRR* and *LLR*), (b) in areas where the hybrid interbreeds with *R. ridibunda*, the other parental species, and (c) in areas where the two parental species hybridize.

Sexual conflict between hybrid and parental mates

Preferences for genotypes guaranteeing a high fitness have also been demonstrated in other studies. Animals were found to choose mates of (a) the same species (e.g. anurans, reviewed by Blair 1964 and Gerhardt 1988), (b) the same ecotype (e.g. *Gasterosteus aculeatus*, Hay and McPhail 1975), (c) a certain degree of relatedness (e.g. *Bufo americanus*, Waldmann et al. 1992; *Drosophila*, Maynard Smith 1991, p. 150) and (d) a type not carrying lethal alleles (e.g. *t* alleles in mice; Lenington et al. 1992). These preferences guarantee that the offspring produced are fertile (as in a), maintain adaptations to specific environments (b and c in case of inbreeding) and do not suffer from an accumulation of lethal alleles (d and c in case of outbreeding).

In the above examples (a-d), both sexes benefit more or less equally from the right combination of genotypes. Thus, males and females should exhibit similar preferences and, at least in cases (a) and (b), the preference should lead to species or ecotype assortative mating. In the L/E system, however, there is a conflict of interest between the potential mates (cf. Parker 1983): the sex belonging to the hybrid form should seek to mate with the parental species, but the sex belonging to the paren-

tal species should resist mating with the hybrid. In the potential combination L female/E male this conflict is apparently won by the parental form, because this combination usually does not occur, even when the E male is smaller than the L female. In the reverse combination, however, the conflict seems to be won by the hybrid, because matings between E females and L males are frequent.

This raises the question of why L males “agree” to engage in – for them senseless – matings with E partners but L females do not. We suggest that this results from an asymmetry in the cost/benefit ratio for males and females (Trivers 1972). Males stay at a pond for several weeks and show continuous or repeated sexual activity while females of most north-temperate ranids usually lay all their eggs in a single clutch and then leave the pond. Consequently, the cost of mating with the wrong partner is smaller for males (which only lose some time) than for females (which lose the reproductive potential of a whole season). In addition, the genetically expected preference for L mates in both sexes is differentially modified by sex-specific size preferences. Within certain limits of the female/male size ratios that guarantee optimal fertilization success for mechanical reasons (Davies and Halliday 1977; Ryan 1985; Robertson 1990), males should prefer bigger, i.e. more fecund, females, while females should prefer smaller or at most equal-sized partners, because this will ease swimming and spawning (Licht 1976; Robertson 1986).

Thus, for females both size and genetic reasons predict a preference for the smaller or equal-sized L males. But for males the genetically expected preference for L females is opposed by a preference for bigger females, which in this case are E females. Size-related preference alone cannot fully explain the observed mating patterns, because (a) male size did not affect choice in our experiments and (b) sexual activity between small E males and large females of L and E, respectively, is low, even though within *R. esculenta* it is the small males who are sexually the most active (Blankenhorn 1974, 1977).

Relevance of laboratory results for non-random mating in the field

The preference of E females for L males found in this study *could* explain why in mixed populations $E \times L$ matings occur more and $E \times E$ -matings less frequently than expected if mating were random (Blankenhorn 1974, 1977; Polls Pelaz and Graf 1989). But at present we do not know whether this preference *is really* an important reason for the non-randomness, because in nature female choice is usually confounded by several factors. These include the spatial arrangement of potential mates, male-male competition (for review see Arak 1983; Haliday 1983a, b, 1987) and, in the L/E case, also the lower sexual activity of hybrid males as compared to males of the parental species (Blankenhorn 1974, 1977).

Nevertheless, we believe that female choice could, and probably does, occur in natural populations. Waterfrogs in Switzerland are of the “prolonged breeder” type (Wells 1977). Both L and E males congregate at the same ponds for 6–8 weeks (Blankenhorn 1974; Abt 1992) and try to attract the arriving females to their territories or positions in an arena by calling in mixed choruses. Where males are thus spatially separated, females can move from territory to territory, sample various males and then approach the preferred one to initiate amplexus (Emlen 1976). Females can also avoid contact with “undesired” males. More than once, we observed females fleeing from approaching males, adopting an almost vertical position in the water which makes initiation of amplexus difficult (termed “low” position by Emlen 1976) and rapidly carrying an amplectant male through the pond, thus eliciting the approach of other males. Similar observations have been reported by Blankenhorn (1974, 1977). Thus, the spatial arrangement of males and females seems to be important in this mating system. This conclusion is further supported by the results of nearest-neighbour analysis of field data (Abt 1992): females stay close to males more often than expected during some parts of the season, but less often during others.

Choice by non-genetic parental and/or resource quality, which has been demonstrated for a few anurans (Howard 1978; Summers 1989) can be ignored, because parental care is lacking and spawning often occurs away from the sites where the sexes first meet (Radwan and Schneider 1988; Günther 1990; Abt 1992). Thus, choice is likely to be based on heritable differences in male phenotypes, but it remains an open question which cues the females use. In our experiments, where males did not call, visual and/or chemical cues remain as the most likely candidates. Under natural conditions, calls probably aid in recognition, but they may be less important for mate choice than in several other anurans (Arak 1983; Sullivan 1983; Ryan 1985; Robertson 1986; Gerhardt 1991). In our pilot study, females responded better to non-calling males than to taped calls (Abt 1992), and Brzoska (1980), who measured thresholds of the electrodermal response to playback, found no evidence that the frogs distinguish between the mating calls of *R. lessonae* and *R. esculenta*. As the study continues we hope to answer some of these questions in the near future.

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