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# Feeding behaviour, food consumption, and growth efficiency of hemiclonal and parental tadpoles of the *Rana esculenta* complex

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**Summary**

**1.** Clonally reproducing species are often assumed to lack sufficient genetic variability to evolve specific local adaptations to cope with environmental perturbation and competition from sexual species. Yet, many asexuals are extremely successful judged by abundance and wide range, suggesting high competitive abilities in resource exploitation.

**2.** In this study, food use and its effects on larval growth in a water frog system consisting of the two parental sexual species, *Rana lessonae* (Camerano 1882) and *Rana ridibunda* (Pallas 1771), and three different coexisting hemiclones of their hybrid, *Rana esculenta* (Linnaeus 1758) were investigated.

**3.** *R. esculenta* tadpoles spent 18·6% more time feeding than did tadpoles of either parental species, but feeding time was not affected by interspecific mixture.

**4.** *R. esculenta* tadpoles consumed 50·8% more food over the whole test period than did tadpoles of the two parental species.

**5.** *R. esculenta* tadpoles exhibited higher growth rates than did tadpoles of either parental species.

**6.** *R. lessonae* tadpoles had the highest and *R. ridibunda* tadpoles the lowest growth efficiencies with the *R. esculenta* tadpoles ranging between the two parentals.

**7.** The results obtained indicate that hemiclonal hybridogenetic *R. esculenta* tadpoles display significant phenotypic variation among coexisting hemiclones as well as outperform tadpoles of the parental sexual species *R. lessonae* and *R. ridibunda.* The primary mechanism for success of the hybrid tadpoles is probably behavioural, through increased feeding time and food consumption, and not physiological via growth efficiency.

*Key-words:* Development, feeding time, growth, *Rana,* resource competition

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## Introduction

Clonally reproducing species are often considered less variable owing to the lack of meiotic recombination, and are therefore assumed to be more sensitive to environmental perturbations. Nevertheless, they occupy remarkably broad geographic ranges and extreme habitats, and can be very abundant locally (Lynch 1984; Vrijenhoek 1989). It is hypothesized that clonals are more broadly adapted to the physical conditions found in extreme habitats than sexuals and may possess a 'general purpose' genotype (Baker 1965; Lynch 1984). It is proposed that this generality is maintained at the costs of competitive ability, and that asexuals will be out-competed by locally adapted sexual species over evolutionary time (Ghiselin 1974; Glesener & Tilman 1978; Bell 1982). A study of parthenogenetic brine shrimp (*Artemia parthenogenetica)* competing with a distantly related sexual species (*Artemia franciscana*) found that the clone was eliminated in 91% of the trials but when it competed with a closely related species (*Artemia tunisiana*) the sexual was eliminated in 98% of the trials (Browne 1992). When traits of sexual and parthenogenetic strains of the brine shrimp *Artemia salina* were compared, parthenogens were clearly superior for the two characteristics length of reproductive span and the number of immature adults per female, whereas the sexual strain was clearly superior for the age at first reproduction (Browne 1980). It has also been shown that many clonal organisms can achieve old evolutionary ages such as the ferns *Trichomanes* and *Vittaria* which completely eliminated the sporophyte stage ten million years ago.

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Despite this long period of evolutionary history, genetic diversity in the gametophytes remains comparable to that of sexual ferns (Farrar 1990). The relative advantages of sexual and clonal reproduction may vary with environmental conditions as illustrated by cases where animals change from sexual to clonal reproduction (or vice versa) depending on ecological conditions (e.g. *Ostracoda*; Havel, Hebert & Delorme 1990).

Clonal reproduction has also been observed in a number of vertebrate species; however, in all cases of clonality it is combined with hybridity (Dawley & Bogart 1989). Yet, these lineages have also achieved considerable evolutionary age (Hedges, Bogart & Maxson 1992; Quattro, Avise & Vrijenhoek 1992; Spolsky, Phillips & Uzzell 1992). Coexistence of sexual and clonal species has been explained in terms of the 'Frozen Niche-Variation' model which assumes that coexisting clones have distinct genotypes, 'frozen' in evolutionary space after clone formation and that they show reduced ecological overlap with one another and with the sexual progenitors. Differences among clones are considered to be frozen from genetic variability that existed in the sexual ancestors (Vrijenhoek, Angus & Schultz 1978; Weeks *et al.* 1992). Mechanisms of niche partitioning such as the use of food and spatial resources have recently been observed in coexisting sexual and clonal forms of the fish *Poeciliopsis* (Weeks *et al.* 1992). Thus, to offer a global explanation for the success of clonal species, clonality must be uncoupled from hybridity and we must identify specific ecological mechanisms of success.

The hemiclonal hybridogenetic water frog system (*Rana esculenta* complex) is an excellent experimental model for questions related to the maintenance of sexual and clonal reproduction. *R. esculenta* (genotype RL; Linnaeus 1758) is a natural hybrid between the parental species *Rana ridibunda* (RR; Pallas 1771) and *Rana lessonae* (LL; Camerano 1882). During gametogenesis, the hybrid *R. esculenta* excludes the *R. lessonae* genome (L) premeiotically and produces eggs and sperm containing only the *R. ridibunda* genome (R). Therefore recombination is normally prevented and the *R. ridibunda* genome is transmitted clonally (see review by Graf & Polls Pelaz 1989). *R. esculenta* × *R. esculenta* matings normally produce inviable RR offspring. In parts of central Europe (including Switzerland), where *R. ridibunda* does not occur natively, *R. esculenta* survives through sexual parasitism of *R. lessonae* to regain the lost L-genome each generation. Thus, the hybrid must coexist with *R. lessonae* in mixed populations.

The hemiclonal hybrid *R. esculenta* is common in many aquatic habitats, but its proportion to the genetic sexual host species *R. lessonae* can vary from 7% to 98% (Blankenhorn, Heusser & Notter 1973; Berger 1983, 1990). Semlitsch & Reyer (1992) found that the proportion of *R. lessonae* and *R. esculenta* successfully metamorphosing from ponds was determined by the interaction of tadpole species and environmental conditions. The hybrid *R. esculenta* produced more metamorphs under more severe environmental conditions of pond drying, high larval density, and interspecific competition that limits food availability, while the parental species *R. lessonae* did better in favourable growth environments with high food availabilty. They suggested that *R. lessonae* was more 'sensitive' to environmental conditions, and conversely, that the hybrid was more 'tolerant'. Semlitsch (1993a) also has shown that the success of *R. esculenta* is likely because of its ability to metamorphose earlier than *R. lessonae* under resource-limited conditions. A shorter time to metamorphosis in *R. esculenta* tadpoles relative to either parental species is regularly observed under a variety of natural conditions in central Poland as well (Berger & Berger 1992). It also has been shown that significant variation in time to and size at metamorphosis exists among coexisting hemiclones of *R. esculenta* (Semlitsch *et al.* 1996).

The purpose of this study was to test whether the differential success among tadpoles of coexisting hemiclones of the hybridogenetic species and the two parental species can be explained in terms of different exploitative abilities of shared resources in the aquatic habitat. A laboratory approach was used to compare feeding time, food consumption, and growth efficiency of even-aged cohorts of tadpoles under constant environmental conditions. Therefore any differences in the response variables were probably the result of genetic differences in the behaviour or physiology of the hemiclones and parental species, and were not because of differences in age, developmental stage, or feeding histories in natural aquatic habitats. The confounding effects of gross morphological differences also can be ignored because tadpoles in this complex are near identical, especially among hemiclones. The ultimate goal is to understand the mechanisms of ecological coexistence between larval populations of the hybridogenetic species and its genetic sexual host, the maintenance of hemiclonal diversity, and to explain the broad geographic success of *R. esculenta*. In addition, the study seeks to elucidate the relative role that behavioural and physiological mechanisms play in the evolution of growth patterns in anurans.

## Materials and methods

### BREEDING DESIGN

Artificial fertilizations were used to produce offspring of the two parental species *R. lessonae* (LL) and *R. ridibunda* (RR) and of three different coexisting *R. esculenta* hemiclones (GUT1, GUT2, & GUT3; Semlitsch *et al.* 1996). Adult *R. lessonae* and *R. esculenta* used for the crosses were collected on 12 and 15 May 1993 from a pond near Gütighausen, Kanton Zürich, Switzerland. Adult *R. ridibunda* were obtained from native populations near Poznań, Poland. All frogs were held in outdoor enclosures until used. During the

1993 breeding season, the frog population at Gütighausen contained 57% of the host species *R. lessonae* and 43% of hybridogenetic *R. esculenta*. The *R. esculenta* subpopulation consisted of four different hemiclones, distinguished by *R. ridibunda* alleles at the enzyme loci GPI, MPI, and LDH-B: hemiclone GUT1 (GPI *a* – MPI *c* – LDH-B *c*) 68%; GUT2 (*a-a-c*) 23%; GUT3 (*d-c-c*) 7%; and GUT4 (*a-c-a*) 2% (Hotz, Guex & Semlitsch, unpublished data). The taxon and hemiclone of each adult was determined, before crosses were made, by protein electrophoresis using the discriminating enzymes GPI, MPI, and LDH-B (Hotz 1983). Because of limited availability of GUT4, only the three most common hemiclones (GUT1-GUT3) were used in this study.

All females were injected with fish hormone LH-RH (H-7525, Bachem Inc., Bubendorf, Switzerland) to induce ovulation. After all of the females initiated ovulation (≈ 24 h) sperm suspensions were prepared by crushing both testes of a male in pond water in a Petri dish. Eggs from a female were stripped into the sperm suspension. After 5 min, the sperm suspension was rinsed into a new Petri dish if used again or discarded, and fresh pond water was added to cover the fertilized eggs. Eggs of the next female were then fertilized with the same sperm suspension or a newly prepared suspension. Replicate females and males of each parental species were crossed to create multiple full-sib families. For *R. esculenta*, one female of each hemiclone was crossed using the sperm of the same *R. lessonae* male ($n = 3$ in total). Three replicate females of each hemiclone ($n = 9$ in total) were used to account for individual female maternal effects. The three types of offspring resulting from this procedure were pooled into groups called *R. esculenta* (GUT1), *R. esculenta* (GUT2), and *R. esculenta* (GUT3), respectively. All crosses were made within 12 h on 20 May and the tadpoles hatched on 25–26 May 1993. After hatching all tadpoles were transferred to larger containers with 1·0 l of pond water.

### GENERAL EXPERIMENTAL PROCEDURES

Tadpoles were reared in plastic dishpans (31 cm × 21 cm × 11 cm) containing 3·5 l of aged tapwater. Tadpoles from each artificial cross were pooled within each parental species or hemiclone, counted into replicate groups of 40 individuals, and randomly assigned to multiple dishpans. Each group was fed a standardized amount of food (finely ground dry cat food) every 3 days. Water also was changed in each container every 3 days. Water temperature averaged 19·5 °C and the light period was 12 h from 0700 to 1900 h CET.

### FEEDING TIME

The purpose of this experiment was to test for differences in feeding time when each parental species or hemiclone of tadpole was observed alone and in mixed groups. Two food types were created (clumped and evenly distributed) to test whether the food distribution might mediate feeding time. However, each day only three observation trials of five treatments each could be made, one in the morning 0900–1100 h, one at midday 1300–1500 h and one in the afternoon 1500–1700 h CET (15 treatments per day). During each trial one species or hemiclone was observed without (one unmixed group) and together with each of the conspecifics (four mixed groups). The target species or hemiclone were used alternately, so that all possible orders of species or hemiclones were tested in all sessions. For each day, 15 treatments were randomly assigned to 15 clear plastic aquaria containing 4·5 l of aged tapwater. Test tadpoles were placed in aquaria 24 h before the observations were started and remained unfed until the beginning of the experiment. The density was always six tadpoles per aquarium. In mixed species groups it was necessary to stain one species with neutral red (Guttmann & Creasey 1973; Kaehli 1992) in order to differentiate tadpoles. The day before testing, a group of tadpoles were placed in a 8 mg $l^{-1}$ concentration of neutral red for 1–2 h, after which they were removed and placed in fresh water until the trial began. During this time the tadpoles remained unfed. This procedure caused no mortality and the tadpoles kept their colour for several days. Staining of the target species and hemiclones was alternated, respectively, between replicate trials to eliminate any possibility of systematic bias due to the procedure.

To start the experiment a surplus amount (275 mg) of standard unground dry chunk cat food was placed in the middle of the aquarium (clumped food) or evenly distributed over the whole aquarium but now finely ground (unclumped food). After 2 min measurements were taken for the next 20 min. One tadpole in each aquarium in the unmixed group and one tadpole of each species or hemiclone in the mixed group was chosen haphazardly and subsequently observed. The aquaria were placed on a table so that all sides could be observed. The cumulative time spent feeding was recorded with a stopwatch and the percentage of time spent feeding was calculated from the total observation time. In the mixed groups, tadpoles of both competitors were observed simultaneously because the feeding activity was greatest shortly after the addition of food and non-simultaneous observations would have led to systematic biases. Feeding was defined by visible mouth movements directed at the food sources (see Horat & Semlitsch 1994).

After each trial all the aquaria were emptied, washed and refilled with aged tapwater. Tadpoles to be used the following day were randomly assigned to each aquarium. Ten replicate trials of each treatment were conducted and individual observations were

accumulated on more than 900 tadpoles. Each tadpole was used only once during the experiment.

### FOOD CONSUMPTION AND GROWTH

The purpose of this experiment was to measure the amount of food consumed by tadpoles under conditions of *ad libitum* food and the subsequent increase in body mass. On 14 June 1993, two tadpoles of each species or hemiclone were randomly assigned to each of 50 plastic dishpans (31 cm × 21 cm × 11 cm) containing 3·5 l of aged tapwater. Dishpans were arranged in a fully random design on a table in the same laboratory under the same conditions as described above.

Every 2 days a pre-weighed and pre-dried piece of food (range 200–300 mg, same catfood as above) was placed in each container. After 24 h the uneaten food was removed, dried again for 24 h at 50 °C, and weighed. The tadpoles received no food the following day. The difference in food mass was used to calculate the amount of food consumed by two tadpoles. To correct for the loss of food that was not related to consumption by tadpoles, such as loss due to handling, solubility, and redrying, a pilot study was conducted with 50 pieces of food (range 200–300 mg) to calculate a correction factor. Food was left in water without tadpoles for 24 h, removed, redried, and weighed as above. The resulting regression equation was used to correct all of the mass values of food removed from the containers ($Y = 0{\cdot}952x + 0{\cdot}005$, $r^2 = 0{\cdot}993$, $P < 0{\cdot}001$; Rist 1994).

The initial wet body mass of tadpoles was measured (to the nearest 0·5 mg) at the start of the experiment on 14 June (day 0). Tadpoles were again weighed on day 24. Wet body mass was converted to dry body mass using the equation (Feder 1981): dry mass = $0{\cdot}047^{1{\cdot}06}$ × wet mass. The gut contents were subtracted from the dry mass using the equation: gut mass = 0·24 × dry mass$^{0.766}$. The change in dry body mass between day 0 and day 24 was used to calculate the growth efficiency. The measure of growth efficiency was the quotient of total dry mass of food consumed during the 24-day period divided by the increase in dry body mass.

**Table 1.** Summary of the univariate analysis of variance of total feeding time (see Methods)

| Source of variation | df | Mean square | *F*-value | *P*-value |
|---|---|---|---|---|
| Genotype | 4 | 1·019 | 3·173 | 0·014 |
| Food distribution | 1 | 8·814 | 27·432 | <0·0001 |
| Mixture | 1 | 0·149 | 0·463 | 0·504 |
| Genotype × food | 4 | 0·453 | 1·410 | 0·321 |
| Genotype × mixture | 4 | 0·242 | 0·753 | 0·557 |
| Food × mixture | 1 | 0·049 | 0·153 | 0·701 |
| Genotype × food × mixture | 4 | 0·144 | 0·447 | 0·775 |
| Residual | 257 | 0·321 | | |

All data were transformed before analysis to increase the additivity of effects and the equality of variances (Snedecor & Cochran 1980). Time and mass were transformed logarithmically, growth efficiency by the arcsine square root. The outcome of the experiments was determined by analysis of variance and all pairwise comparisons were made with a Scheffe's test. For the purposes of analysis of variance, both parental species and the three hemiclones of the hybrid were considered as distinct genotypes. For purposes of explanation and when results of the Scheffe's tests permitted, the three hemiclones *R. esculenta* (GUT1, GUT2, and GUT3) were pooled to refer to them as 'hybrids', and pooled the two parental species (*R. ridibunda* and *R. lessonae*) to refer to them as 'parentals'.

## Results

### FEEDING TIME

There was a significant difference in the percentage of time spent feeding among genotypes (Table 1). Differences occurred between hybrids and parental species (Scheffe's test, $P<0{\cdot}05$), but not among the three hemiclones (Scheffe's test, $P>0{\cdot}05$) or between the two parental species (Scheffe's test, $P>0{\cdot}05$; Fig. 1a). The hemiclonal *R. esculenta* hybrids spent 18·6% more time feeding ($x=38{\cdot}2\%$) than did the parental species *R. ridibunda* and *R. lessonae* ($x=32{\cdot}2\%$). There was no effect of the presence or absence of heterospecifics (Table 1). Tadpoles of all genotypes spent nearly the same percentage of time feeding in mixed ($x=36{\cdot}2\%$) and unmixed ($x=35{\cdot}4\%$) groups. The food distribution had a large influence on the feeding time. The time spent feeding was longer when food was clumped ($x=41{\cdot}5\%$) than when food was evenly distributed ($x=30{\cdot}1\%$). The two-way interactions genotype × food, mixture × food, genotype × mixture and the three-way interaction genotype × food × mixture were not significant (Table 1), indicating that genotype differences in feeding time were not mediated by the presence of heterospecifics or the distribution of food.

### FOOD CONSUMPTION

There was a significant difference among genotypes in the amount of food eaten over 24 days ($F = 14{\cdot}15$, df = 4, 45, $P < 0{\cdot}001$, Fig. 1b). Even between GUT1 and GUT3 the rate of food eaten was significantly different (Scheffe's test, $P < 0{\cdot}05$) but not between the two parental species (Scheffe's test, $P > 0{\cdot}05$). The three hemiclones (GUT1, GUT2, GUT3) consumed more cumulative food dry mass ($x_1 = 45 \pm 2$ mg, $x_2 = 39{\cdot}4 \pm 3{\cdot}7$ mg and $x_3 = 31{\cdot}2. \pm 1{\cdot}5$ mg, respectively) than did either *R. lessonae* or *R. ridibunda* ($x_1 = 24{\cdot}7 \pm 1{\cdot}6$ mg and $x_2 = 26{\cdot}4 \pm 1{\cdot}5$ mg; Scheffe's tests of all pairwise differences $P < 0{\cdot}05$). Only GUT3

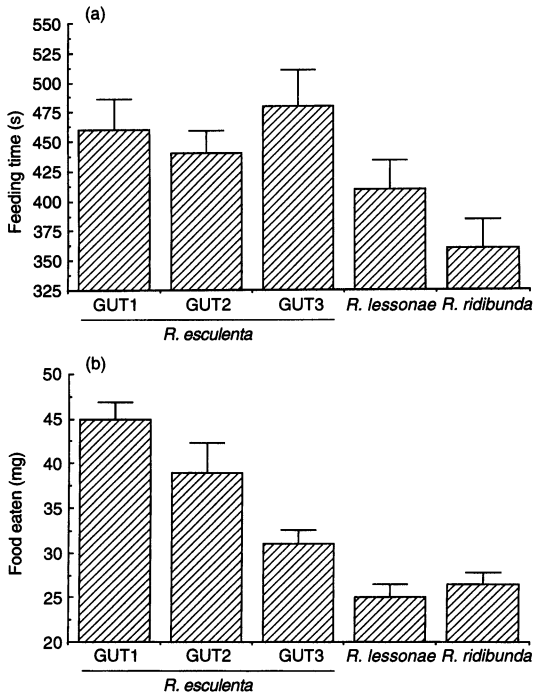


**Fig. 1.** Genotype differences in mean feeding time (a) out of a total observation time of 1200 s, and mean food consumption (b) of tadpoles during a 24-h period. Values plotted for feeding time were averaged over all treatments and represent means + one standard error ($n$ = 40 tadpoles). Values plotted for food consumption represent means + one standard error ($n$ = 10 tadpoles).

did not differ significantly from the parental species (Scheffe's test, $P > 0{\cdot}05$).

WEIGHT INCREASE

The dry body weight at the beginning of the experiments differed significantly between *R. ridibunda* and all the other genotypes (Scheffe's test, $P < 0{\cdot}05$). The *R. ridibunda* tadpoles were smaller and weighed only $3{\cdot}6 \pm 0{\cdot}6$ mg whereas the others averaged $30{\cdot}25 \pm 0{\cdot}8$ mg. There was a significant difference among genotypes in dry body weight over the growth period of 24 days ($F = 16{\cdot}95$, df = 4, 45, $P < 0{\cdot}001$) but not among the three hemiclones (Scheffe's test, $P > 0{\cdot}05$) nor between the two parental species (Scheffe's test, $P > 0{\cdot}05$; Fig. 2a). Accounting for initial differences in body weight, the hemiclones pooled together had a greater weight increase ($x$ = $74{\cdot}6 \pm 4{\cdot}9$ mg) than either parental species (LL = $56{\cdot}5 \pm 5{\cdot}0$ mg, RR = $40{\cdot}3 \pm 1{\cdot}2$ mg; both Scheffe's tests, $P < 0{\cdot}05$). GUT1 always grew most, followed by GUT2, GUT3, *R. lessonae*, and *R. ridibunda* which was always the species with the least weight increase. Because the genotypes remained in the same rank order of size over the whole growth period, it is argued that different weight increases reflect real genotype differences and were not caused by size or developmental stage differences at the beginning of the experiment.

GROWTH EFFICIENCY

There was a significant difference in growth efficiency among genotypes over the 24-day period ($F = 6{\cdot}35$, df = 4, 45, $P < 0{\cdot}001$). A Scheffe's test indicated that the differences in growth efficiency were primarily between *R. ridibunda* and *R. lessonae* ($P < 0{\cdot}05$) and between *R. ridibunda* and GUT3 ($P < 0{\cdot}05$, Fig. 2b). The largest difference was between *R. ridibunda* which converted 14·5% of the food into body mass and *R. lessonae* with 19·8%. Interestingly, the two parental species had the same food intake (Fig. 1b) but produced different biomass (Fig. 2a). When the hemiclones and the parental species were pooled separately, growth efficiency was essentially the same (hemiclones $x = 17{\cdot}24\%$, parentals $x = 17{\cdot}15\%$). For all tadpoles combined, the increase in body mass was significantly correlated to the total dry mass of food consumed ($r = 0{\cdot}82$, $P < 0{\cdot}001$) while the overall efficiency was significantly correlated to the total weight increase ($r = 0{\cdot}37$, $P = 0{\cdot}008$) but not to total amount of food input ($r = -0{\cdot}21$, $P = 0{\cdot}144$).

## Discussion

Anurans display large amounts of phenotypic variation in larval growth rate and development time which is strongly affected by food availability (Wilbur & Collins 1973; Alford & Harris 1988). Phenotypic variation may be manifested in the timing of metamorphosis and the size at metamorphosis; larval traits

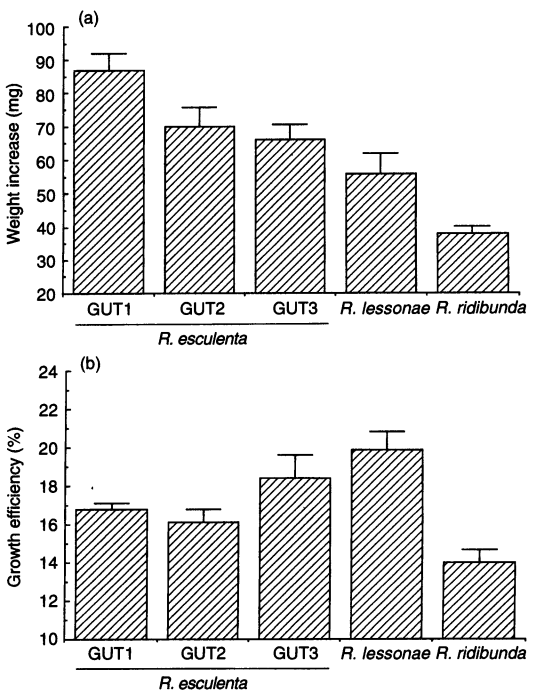


**Fig. 2.** Genotype differences in mean weight increase (a) and mean growth efficiency (b) of tadpoles for a 24-day period. For both weight increase and growth efficiency values plotted represent means + one standard error ($n$ = 10 tadpoles).

which can strongly influence fitness. For example, high growth rates enable tadpoles to metamorphose quickly at a small size to escape drying in ephemeral ponds (Smith 1983; Newman 1988a,b), or alternatively to maximize size at metamorphosis in more permanent ponds (Wilbur & Collins 1973). Larger size at metamorphosis can result in better physiological and locomotory performance in the terrestrial environment (Pough & Kamel 1984; Goater, Semlitsch & Bernasconi 1993), higher juvenile survival, earlier first reproduction, and larger size at first reproduction (Berven & Gill 1983; Smith 1987; Semlitsch, Scott & Pechmann 1988; Berven 1990).

In this study, feeding time and food consumption of tadpoles in the laboratory were higher for all hybrid hemiclones than for either of the parental species, and this was correlated with an increased weight gain. The physiological growth efficiencies that were measured varied in the opposite direction from the increased weight gain (i.e. hybrid tadpoles had lower growth efficiencies than *R. lessonae* tadpoles). Because food quality was constant and was provided in surplus in all experiments, the hybrids could achieve similar weight increases only through increases in food consumption. One possible reason for the lower growth efficiency of hybrid *R. esculenta* tadpoles was the greater energy use resulting from higher activity levels (metabolic costs of increased feeding and swimming). Thus, the hybrids were less efficient than *R. lessonae* tadpoles which have lower activity levels (Kaehli 1992; Horat & Semlitsch 1994). Although tadpoles were not tested under food-limited conditions, the results suggest that *R. esculenta* tadpoles might be at a disadvantage under such conditions unless higher quality food were selected or feeding efficiency were higher than for parental species. The data on feeding time and food eaten for *R. esculenta* indicate, however, that they spent 18·1% more time feeding but had a 50·8% higher food intake than the parental species thereby suggesting they are indeed more efficient feeders. Results from artificial pond experiments at high larval density (low food availability) indicate that *R. esculenta* performs better than *R. lessonae* and thus supports the suggestion of greater feeding efficiency in the hybrid hemiclones (Semlitsch 1993a,b).

The *R. ridibunda* tadpoles had both a low food intake and a low growth efficiency resulting in low weight gain, but they can achieve body sizes at metamorphosis comparable to the other species through longer larval periods (Semlitsch, unpublished data). Because *R. ridibunda* in central Europe typically inhabits large permanent bodies of water they can afford a longer larval development without risking desiccation. Predation in these habitats also may be avoided by temporal shifts in feeding activity (Gavasso 1992). Because body size at metamorphosis is generally the same for *R. esculenta* and *R. lessonae* under a wide range of environmental conditions (Semlitsch 1993a,b), and growth rate is faster for *R. esculenta* tadpoles, they clearly need less time to metamorphose. This is particularly advantageous in short-lived breeding ponds and may be one reason for the higher proportions of *R. esculenta* found in temporary or disturbed habitats such as gravel pits (Blankenhorn *et al.* 1973; Berger 1990). There is some evidence that the tadpole behaviours measured in the laboratory are relevant to behaviours in the field. Warketin (1992) found that tadpoles of *Rana clamitans* ate similar amounts under light and dark conditions, and that feeding rates in the laboratory were similar to those measured in open areas in natural ponds with the same water temperature. Thus, it is suggested that the success of *R. esculenta* in natural habitats may be achieved through behavioural mechanisms related to feeding activity and not to physiological mechanisms related to the conversion of food into tadpole biomass.

Our results indicate that such behavioural differences are genetically based, especially among hemiclones, because the comparisons were carefully controlled for environmental effects (both maternal and physical). Differences between *R. lessonae* and *R. ridibunda* in growth efficiency are probably the result of natural selection, perhaps based on the availability of food in temporary as opposed to permanent aquatic habitats. The cause of genetic differences between hybrids and parental species, and among hemiclones can be related to two mechanisms: (1) heterosis resulting from hybridity, and (2) interclonal selection. Although spontaneous heterosis is not universal among clonal hybrids (Wetherington, Kotora & Vrijenhoek 1987), it has recently been demonstrated in the larval performance of newly generated $F_1$ hybrids of *Rana esculenta* (Gutmann *et al.* 1994). Nevertheless, because this study was performed using natural lineages of hemiclones, subjected to many generations of selection, it is also likely that interclonal selection has acted upon the life history traits of individuals to yield a subset of best-adapted coexisting hemiclones in populations (Vrijenhoek *et al.* 1978; Semlitsch *et al.* 1996). In reality, both heterosis and interclonal selection probably act together, hybridity providing the unique combinations of genomes upon which interclonal selection can then act.

Few other studies have documented genetically based differences in behavioural mechanisms that affect important components of fitness (e.g. in fish Present & Conover 1992), yet models of evolutionary change require such a genetic basis. Thus, it is suggested that behavioural mechanisms related to feeding activity might serve an important role in the maintenance of phenotypic variation and the evolution of differential growth patterns in anurans as well as other organisms with larval stages devoted to rapid development. Further study of geographic and phylogenetic variation in growth patterns should help elucidate the generality of such important mechanisms.

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