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Larval Development and Recruitment of Juveniles in a Natural Population of *Rana lessonae* and *Rana esculenta*

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In most parts of central Europe the hybridogenetic water frog *Rana esculenta* lives (and mates) in mixed populations with its parental species *Rana lessonae*. Ratios of parental and hybrid animals vary from 1:9 to 9:1 among ponds, depending on various biotic and abiotic factors. These factors may directly cause the ratio differences through species-specific effects on larval performance, but previous experimental studies under laboratory and seminatural conditions produced conflicting results as to how parental and hybrid tadpoles respond to these factors. We investigated larval development and relative recruitment of juveniles in a natural population at three sites that differed ecologically. Species ratios at the different stages (eggs, tadpoles, metamorphs) and body size of tadpoles and metamorphs were compared. Differences in timing of reproduction and larval development were more pronounced within species between ponds than between species within ponds. During the egg and tadpole stages, hybrids outnumbered parental larvae by 60:40, but this ratio reversed during metamorphosis. Higher mortality rates of hybrid froglets during metamorphosis as well as lower dispersal rates after metamorphosis may explain our findings.

A major reason for the predominance of sexual over asexual reproduction is seen in the higher genetic variance in sexuals, which can serve as a tool for adapting to changes in environmental conditions (e.g., Stearns, 1987; Michod and Levin, 1988). In some cases, however, asexuals—including parthenogenetic, gynogenetic, and hybridogenetic species—are remarkably successful in terms of their geographical distribution and persistence over time (Lynch, 1984; Vrijenhoek, 1989; Quattro et al., 1992). The success of an asexual will depend on its competitive ability relative to that of sexuals; this, in turn, is likely to vary with ecological conditions. Hence, knowing the relative performance of sexuals and asexuals in different environments is crucial for understanding the structure and dynamics of their mixed populations.

Here we investigate the role of species and environment specific larval performance for the composition of mixed waterfrog populations consisting of two species, *Rana lessonae* and *Rana esculenta*. The Edible Frog *R. esculenta* (genotype LR) is originally a hybrid between the Pool Frog *R. lessonae* (LL) and the Lake Frog *Rana ridibunda* (RR; Berger, 1977). Its reproduction is hybridogenetic, that is, one parental genome (L) is premeiotically excluded from the germ line (Schultz, 1969; Tunner and Heppich-Tunner, 1991). Eggs and sperm contain only the other parental genome (R), which is normally transmitted clonally. Mating with *R. lessonae* restores hybridity. This so-called L-E-system is typical for central Europe, including our Swiss study sites; but other systems (e.g., mixed *R. ridibunda*/*R. esculenta* populations or pure hybrid populations composed of diploid and triploid individuals) occur in other areas.

In the L-E system, the relative frequencies of parental and hybrid animals vary among ponds with different ecological conditions, ranging from less than 10% *R. esculenta* in forest ponds or natural marshes to over 90% in gravel pits (Blankenhorn et al., 1973; Berger, 1983); but within ponds, species compositions remain stable over years (Berger, 1983; Holenweg Peter et al., 2002). For two reasons, this temporal stability is counter-intuitive. First, among the four possible mating combinations, only one (L × L; first letter = female, second letter = male) results in *R. lessonae* offspring, but two (L × E and E × L) result in *R. esculenta* offspring and one (E × E) leads to inviable *R. ridibunda* tadpoles (for details see Graf and Müller, 1979; Uzzell et al., 1980; Semlitsch and Reyer, 1992). Second, *R. esculenta* females, whose viable offspring are exclusively hybrids, have larger clutch sizes than *R. lessonae* females who, depending on the male type they mate with, produce either L or E offspring (Berger and Uzzell, 1980; Rastogi et al., 1983). All other things being equal, these two factors result in a primary fitness advantage for the hybrid, which first should lead to a continuous increase in *R. esculenta* numbers at the expense of *R. lessonae* numbers but, finally, to a collapse of both species because the hybrid, as

TABLE 1. AVERAGE WATER TEMPERATURES (1 C) WITH 1 STANDARD ERROR (SE) IN PARENTHESES FOR MAY AND JUNE, INCREASE IN AVERAGE TEMPERATURES FROM MAY TO JUNE, DATES OF FIRST CLUTCHES AND DURATION OF BREEDING FOR THE THREE PONDS (1–3) THAT WERE INVESTIGATED IN THIS STUDY. Pond numbers in parentheses refer to the same ponds in the study of Holenweg Peter et al. (2002) where further details about the ecological characteristics can be found in Table 2. Average monthly water temperatures are least-square means from an ANOVA testing for the effects of site, month, and site × month interaction while controlling for time of the day (covariate) when readings were taken.

Pond no.	Pond type	Mean water May	Temperature June	Δ temperature June–May	Date of first clutch	Duration of breeding season (days)
1 (2)	Vehicle ruts	16.8 (0.8)	26.2 (0.7)	+9.4	May 21	38
2 (4)	Vehicle ruts	17.6 (0.8)	24.9 (0.7)	+7.3	May 6	54
3 (1)	Peat bog	15.4 (0.8)	21.9 (0.7)	+6.5	June 2	11

a sexual parasite, cannot persist once the sexual host has declined to zero.

Potential factors precluding collapse of both species and enhancing stability of the system are nonrandom mating (Som et al., 2000; Reyer et al., 1999; Engeler and Reyer, 2001), reduced fertilization ability of E-males (Reyer et al., 2003), less regular breeding of E-females (Reyer et al., 2004), and environment related differences between L- and E-tadpoles in survival, growth, and time to metamorphosis (Hellriegel and Reyer, 2000). According to experiments, *Rana lessonae* tadpoles generally perform better under favorable conditions, such as low competition and predation coupled with high food abundance (Semlitsch and Reyer, 1992; Semlitsch, 1993a,b), whereas the hybrids are more tolerant of unfavorable environments such as limited food availability and more extreme physicochemical conditions (Fioramonti et al., 1997; Plenet et al., 2000). Discrepancies in details among experimental studies, however, lead to conflicting predictions about the composition and dynamics in mixed populations and do not suffice to explain what is happening in natural populations. To better understand stable L/E-ratios in nature, we sampled eggs, tadpoles, and metamorphs of the two species at three ecologically different sites. Specifically, we asked the following questions: Does the ratio between *R. lessonae* and *R. esculenta* change from eggs through tadpoles to metamorphs, which would signal differences in survival? Are there differences between the two species in body mass of tadpoles and metamorphs? This is relevant for the L/E-ratios among adults because larval growth and size at metamorphosis are positively related to postmetamorphic fitness (Altwegg and Reyer, 2003). Do species differences in survival and body mass vary among ponds with different ecological conditions?

MATERIALS AND METHODS

Study sites.—The study was carried out in 1996 at three sites, located within 100–250 m of one another close to the airport of Zurich, Switzerland. Site 1 consisted of four adjacent sun-exposed shallow pools, which tended to merge into a single pond after heavy rainfalls, whereas during hot periods in July and August they partly dried out. Site 2 was a narrow but long, permanent pond, with rich vegetation at the edges. The water was deeper than at site 1 and the pond received some shade from nearby trees. Site 3, also partly shaded by trees, was the pond with greatest water depth and the richest vegetation. For further pond details see Holenweg Peter et al. (2002). Because of these differences in sun exposure, water depth, pond size, and amount of vegetation, water temperatures and their seasonal changes differed among the three sites. Temperatures were measured every second or third day during the mating period between 1030 and 1500 h at typical oviposition sites at a depth of about 10 cm. The resulting monthly averages for May and June, and temperature increases during the season, are shown in Table 1, together with the times of first clutches and the duration of the breeding season.

Eggs.—The mating season lasts six to eight weeks during May and June. Eggs develop in approximately seven days (Vogel, 1977; pers. obs.). To estimate the L/E-ratio among the eggs produced in a pond, all three sites were checked for new clutches every second or third day from late April until mid-July. Clutch size was estimated by counting 10–40% of the eggs of the clutch and then extrapolating to total egg number by comparing the size of the counted egg mass with the size of the clutch mass. The reliability of this extrapolation method was test-

ed on 11 clutches by also counting the total egg number. On average, estimates were 4% too low, but the deviation was clutch size dependent in the sense that clutches below 2500 eggs were usually overestimated, whereas clutches larger than 2500 eggs were underestimated.

Clutches from all four mating combinations (L × L, L × E, E × L, E × E) look the same, but the parental mating combination can be detected by electrophoresis for lactate dehydrogenase (LDH; Vogel and Chen, 1976). Progeny do not produce their own LDH until they start moving (Vogel, 1977). Hence, analyzing the LDH of early embryos reveals the maternal genome, and analyzing LDH in tissues of free-swimming larvae identifies the species of the tadpole. Both analyses combined reveal the mating combination. Therefore, from each fertilized clutch some eggs were frozen and some tadpoles were raised in the lab. Then eggs and tadpole tissue were analyzed by electrophoresis (Vogel and Chen, 1976). The L/E-ratios produced at each site were calculated by multiplying the mean clutch size of either female type by the number of clutches of the respective species.

Females usually split their clutch into several packages and fix them to different waterplants. This complicates unambiguous identification of clutches from individual females, especially where several females spawn in close proximity. However, such lek spawning occurred only twice at the beginning of the season, in both cases during daytime when the number of ovipositing females could be counted by direct observation.

Tadpoles.—For comparing larval composition and development between sites, tadpoles were captured four times by netting and in wire-baskets placed into the pond for about two hours (four baskets at the large site 2; two each at the sites 1 and 3). The first sampling took place in the sixth week after the first oviposition peak; three subsequent samplings followed every third week. Each tadpole was weighed to the nearest 0.1 mg, staged according to Gosner (1960) and identified to species by electrophoresis (Vogel and Chen, 1976).

Metamorphs.—The metamorphs were sampled by hand and with small nets weekly from the time the first ones emerged until the end of September. Each metamorph was assigned to one of three stages of tail resorption: full tail, tail stump, no tail. Each froglet was weighed to the nearest 0.1 mg and marked by cutting a swim web and injecting fluorescence dye into another (VIE-system: Northwest Marine Technology, Inc., Washington). Species were identified by albumin electrophoresis (Tunner, 1973), based on lymph taken from the lymph chamber between the fourth and the fifth toe.

Data analysis.—Differences in development were analyzed with respect to species, site, and time of the season (= independent factors). We tested for differences in tadpole stage by using a nested ANOVA and for differences in tadpole and metamorph body mass by using nested ANCOVA with Gosner stage as the covariable (GLM, SYSTAT 7.0 for Windows). In metamorphs, this analysis was restricted to individuals with full tails and tail stumps (stages 42–45; Gosner, 1960) because age and origin of froglets without tails could not be identified unambiguously. Because of large differences between sites and species in the time first metamorphs emerged, time of metamorphosis was entered as a categorical factor with two levels: first and second two weeks of emergence. We further tested for differences in species composition among ponds in relation to five developmental stages: eggs, tadpoles and metamorphs with full tails, tail stumps, and no tails.

Results

Timing of reproduction and emergence of first metamorphs.—The beginning of reproduction, as well as the emergence of first metamorphs, differed among the three study sites. The date of first oviposition was inversely related to spring water temperatures (Table 1): at site 2, the warmest pond in May, it occurred on 6 May, followed by site 1 (21 May) and finally site 3 (2 June). Although breeding at the two warmer sites 1 and 2 lasted until the end of June (i.e., 38 and 54 days, respectively), oviposition at site 3 ended after only 11 days. At site 1, the pond with the largest increase in average temperature and the highest water temperature in June, *R. lessonae* began metamorphosis eight and *R. esculenta* 11 weeks after oviposition. At sites 2 and 3 with less warming and lower temperatures in June, the first metamorphs of both species were not found until 12 weeks after first oviposition peak.

Species ratios from eggs to metamorphs.—One hundred fourteen clutches were found in total, 68 at site 2, the largest pond, and 23 each at sites 1 and 3. The mating combinations and the resulting tadpole types are known for 105 clutches. The remaining nine clutches suffered from fungus infestation, which prevented development of all eggs in the laboratory and of most

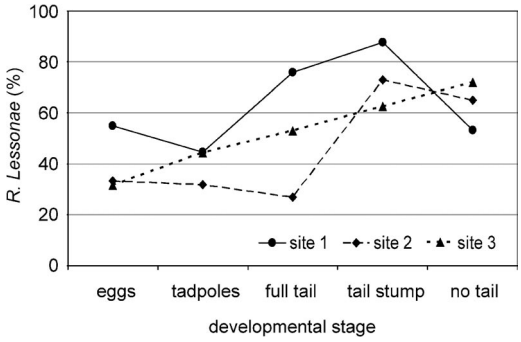

Fig. 1. Proportions of *Rana lessonae* at the three study sites during five developmental stages: eggs, tadpoles, and metamorphs with long tails, tail stumps and no tails. Proportions during the tadpole stage are based on only the first sampling (after six weeks), because some tadpoles at site 1 had already metamorphosed and left the pond before the second sampling (after nine weeks).

in the field. Thirty-four clutches resulted in *R. lessonae*, 46 in *R. esculenta*, and 25 in *R. ridibunda*. With a mean egg number of 1070 (± 750 SD), E-females tended to produce 37% larger clutches than L-females (780 ± 450 SD; ANOVA; df = 1, $F = 3.534$, $P = 0.064$). The total proportions of eggs leading to *R. lessonae* and *R. esculenta* tadpoles were 28% and 45%, respectively. The remaining 27% of eggs were potential *R. ridibunda* tadpoles, which can arise from matings within hybrids, within *R. ridibunda* (which occurred in low numbers at sites 1 and 2) and between hybrids and *R. ridibunda*. These tadpoles, however, usually die prior to metamorphosis, and they were rare in the samplings (between 0 and 8%). Therefore, we excluded *R. ridibunda* from all analyses.

Figure 1 shows the proportions of *R. lessonae* for five successive stages. At all three sites, L-proportions rose significantly from 32–55% during the egg stage to 63–88% during the stump stage (all $\chi^2_1 \geq 10.271$, all $P < 0.005$) but in different ways. At site 1, the major increase occurred between the tadpole and the first metamorph stage, at site 2, between the first and the second metamorph stage, and at site 3 it was continuous. Finally, there was a strong drop in L-proportions from the stump to the no tail stage at site 1 but not at sites 2 and 3.

Larval development.—Our analyses revealed no consistent difference between the two species in either developmental stage ($P = 0.442$) or body mass ($P = 0.411$; Table 2A). For stage, the major difference in development was over time ($P < 0.001$ for time [site]). At sites 1 and 2, stage development followed a sigmoid curve, with the steepest increase between samples 2 and 3 (Fig. 2A,B), whereas at site 3, stage increased rapidly from time 1 to time 2, less from 2 to 3, and reached a plateau between 3 and 4 (Fig. 2C).

Body mass also differed among sites, with additional influences of stage ($P < 0.001$) and time and species ($P < 0.004$ for species × time (site); Table 2B). After statistically correcting for differences in developmental stage, average masses at sites 1 and 2 decreased more or less pronounced through the larval period, with higher E- than L-values during almost all sam-

TABLE 2. SUMMARY OF TWO NESTED MULTIFACTORIAL ANALYSES TESTING FOR THE EFFECTS OF "SPECIES," "SITE," "TIME" (SAMPLINGS 1–4), AND THEIR INTERACTIONS ON (A) "DEVELOPMENTAL STAGE" AND (B) "BODY MASS" OF *Rana lessonae* AND *Rana esculenta* TADPOLES. In (B) developmental stage was entered as an additional covariable. (GLM procedure; time nested in site; $n = 712$).

Source	Sum-of-Squares	df	Mean-Square	*F*-ratio	*P*
(A) developmental stage					
Species	7.237	1	7.237	0.593	0.442
Site	67.743	2	33.871	2.775	0.063
Time (site)	4847.849	9	538.650	44.137	<0.001
Species × site	48.543	2	24.272	1.989	0.138
Species × time (site)	183.639	9	20.404	1.672	0.092
(B) body mass					
Stage	60.642	1	60.642	1206.176	<0.001
Species	0.034	1	0.034	0.676	0.411
Site	11.508	2	5.754	114.448	<0.001
Time (site)	8.188	9	0.910	18.096	<0.001
Species × site	1.023	2	0.511	10.174	<0.001
Species × time (site)	1.238	9	0.138	2.735	0.004

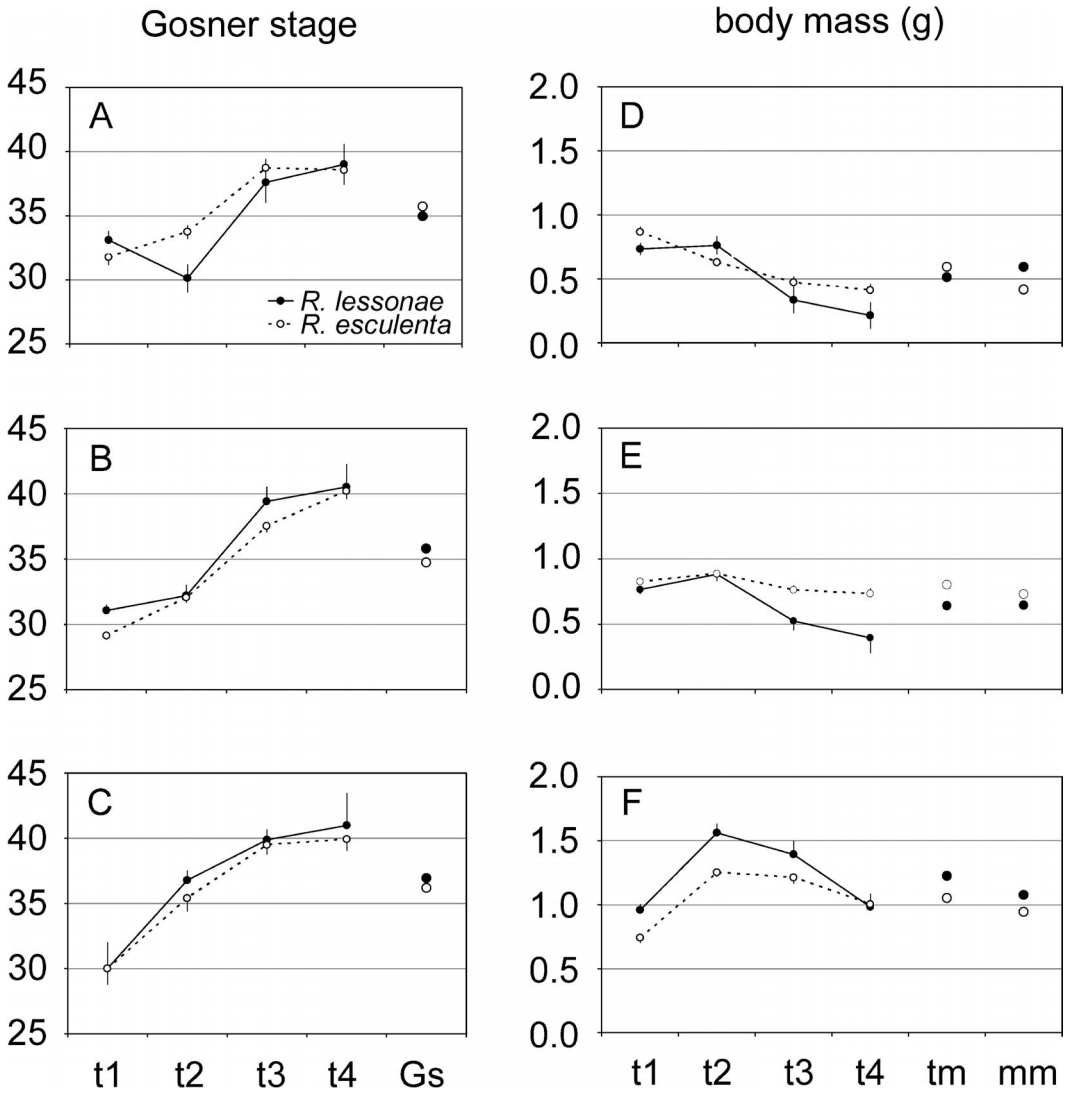

Fig. 2. Developmental (i.e., Gosner) stage (left) and body mass (right) of *Rana lessonae* (●) and *Rana esculenta* (○) tadpoles in relation to study site (A,D = site 1; B,E = site 2; C,F = site 3) during four sampling periods (t1–t4). Shown are least-square means and standard errors (SE) from the analyses of variance in Table 2. To improve clarity, SE are plotted only as plus or minus. Some SEs are so small that they disappear behind the symbols for the means. Also shown are the overall species-specific means for Gosner stage (Gs) and tadpole mass (tm), both averaged over t1–t4, and metamorph mass (mm), averaged over time and stage of tail resorption.

pling times (Fig. 2D,E). At site 3, in contrast, L-masses were higher than or equal to E-masses, and both species increased body mass markedly between sampling times 1 and 2 and subsequently decreased it from time 3 to 4 (Fig. 2F).

Metamorphs.—In metamorphs, body mass differences among sites ($P < 0.001$; Table 3) resembled those in tadpoles (Figs. 2D–F). Averaged over all times and tail categories within a site, metamorph mass increased from site 1 (0.50 g) through site 2 (0.69 g) to site 3 (0.97 g). The precise pattern, however, depended on complicated combinations of site, species, tail stage and time of the season (see significant interactions in Table 3). With respect to the site × species interaction, metamorph mass did not differ between L and E at sites 2 and 3 (both $P \geq 0.221$, Scheffe's test), but L was heavier than E at site 1 ($P = 0.025$). Thus, mass relative to the other species reversed from L < E among tadpoles to L > E among metamorphs at site 1 but

TABLE 3. SUMMARY OF ANALYSIS OF VARIANCE WITH "BODYMASS" OF *Rana lessonae* AND *Rana esculenta* AT METAMORPHOSIS AS THE DEPENDENT VARIABLE AND "SPECIES," "SITE," "TIME," "TAIL LENGTH," AND THEIR INTERACTIONS AS FACTORS. (GLM procedure; time nested in site; $n = 323$.)

Source	Sum-of-Squares	df	Mean-Square	*F*-ratio	*P*
Species	0.312	1	0.312	10.671	0.001
Site	2.337	2	1.169	39.998	<0.001
Time (site)	0.762	3	0.254	8.691	<0.001
Tail	0.112	1	0.112	3.827	0.051
Species × site	0.689	2	0.334	11.786	<0.001
Species × time (site)	0.164	3	0.055	1.871	0.135
Species × tail	0.168	1	0.168	5.744	0.017
Tail × site	0.604	2	0.302	10.340	<0.001
Tail × time (site)	0.262	3	0.087	2.984	0.032
Species × tail × time (site)	0.237	3	0.079	2.706	0.046
Error	8.794	301	0.029		

remained unchanged at the other two ponds (cf. overall means in Fig. 2D–F). With respect to time, mean mass of metamorphs decreased as the season progressed ($P < 0.001$ for time [site]), with no significant difference between the two species ($P = 0.135$). With respect to stage, mass tended to decrease from the long tail (0.76 g) to the tail stump stage (0.68 g; $P = 0.051$). The precise development, however, varied with species, site and time, which is reflected by significant *P*-values for all four interactions involving tail (Table 3).

DISCUSSION

The results of this study allow two major conclusions: (1) Differences in timing of reproduction and larval development are more pronounced within species between ponds than between species within ponds; and (2) At all three ponds, the species ratio (L/E) changed from an excess of hybrids during the larval stages to an excess of parentals after metamorphosis.

Timing of reproduction and larval development.—In contrast to experiments under laboratory or seminatural conditions, this field study did not reveal any marked differences in larval development of *R. lessonae* and *R. esculenta*. In spite of several ecological differences among the study ponds (Holenweg Peter et al., 2002), tadpoles of the sexual parental species and the hemiclonal hybrid performed about equally well, at least during early tadpole stages. Differences were more pronounced between ponds than between species. Although based on data from only one year, this pattern is likely to be representative, at least for our study area, where ecological conditions differ more among ponds than among years (Holenweg Peter et al., 2002).

The crucial factor influencing timing of reproduction and larval development was water temperature (Table 1). Pond differences in the date of first oviposition can be explained by water temperatures in May (warmer = earlier). Differences in time to metamorphosis were related to the temperature in June and the increase in temperature from May to June (higher increase = shorter time). Warm water usually accelerates development at the expense of body weight (Bachmann, 1969; Smith-Gill and Berven, 1979; Berven, 1982), and this acceleration is relatively higher in *R. lessonae* than in *R. esculenta* (Negovetic et al., 2000). Thus, pond temperatures in June can explain why tadpoles metamorphosed earlier and lighter in the warmest pond (1) than in the coldest pond (3) and why in pond 1 tadpoles of *R. lessonae* were, on average, lighter than those of *R. esculenta*. Pond 2, which was intermediate in terms of June water temperature and temperature increase, was also intermediate in time to and mass at metamorphosis (cf. means in Fig. 2D–F).

However, these temperature-development relationships can neither explain why average tadpole body mass also increased with decreasing water temperatures from pond 1, through 2, to 3 (cf. means in Fig. 2D–F), nor why in pond 3 larvae of *R. lessonae* were, on average, heavier than those of *R. esculenta* (Fig. 2F). One possible explanation for these results is that other pond-specific environmental factors such as predation, food, and time constraints modified the developmental pattern. Their effects have been shown in several experiments (e.g., Semlitsch and Reyer, 1992; Altwegg, 2002), but we have no data to test for such effects in the field. A second possible explanation is that average tad-

pole masses were affected by a methodological artifact. At pond 3, breeding lasted for only 10 days; hence, tadpoles represented a fairly uniform age cohort showing a consistent temporal development for both species (Fig. 2C,F). In contrast, breeding at ponds 1 and 2 lasted for about one and a half months, resulting in a mix of different age cohorts at any one sampling time, which led to unexpected or even biologically unrealistic changes in stage and body mass. These include (A) constant or decreasing body mass over time (Fig. 2D,E), (B) a ''development'' from higher to lower stages (cf. t2 vs t1 for *R. lessonae* in Fig. 2A) because of early metamorphosis of *R. lessonae* at this site and, hence, the disappearance of advanced stages, and (C) more or less pronounced differences between the species (Fig. 2A,D,E). Yet, the mass differences between species, sites, samplings, and their interactions are real, since developmental stage was statistically controlled for (Table 2B).

The body mass differences after metamorphosis (Table 3) largely paralleled the pattern among tadpoles (Fig. 2D–F). Only at site 1 did the relative size switch from E > L among tadpoles to E < L among metamorphs. This switch may be related to the fact that this pond was very shallow and partly dried in mid-June. To escape the resulting high temperatures close to the water surface, tadpoles retreated into the mud where feeding activity probably was low. If that led to body mass reduction, the loss in weight is likely to have been higher in E-tadpoles than in L-tadpoles, which escaped earlier from the drying pond (see above) and, hence, probably lost less weight from the larval to the metamorph stage. The decrease in metamorph mass with progressing season is best explained by an increasing time constraint that forces late offspring to leave the pond even when still small (Altwegg and Reyer, 2003). Finally, the complicated interactions of site, species, and time with mass loss during tail resorption are probably caused by the sampling of mixed age cohorts that left the three ponds at different times and stages of tail resorption.

Changes in species ratios.—In addition to reasons originating from the mating system, the original excess of hybrids during the egg and larval stages (Fig. 1) can be attributed to differences in fecundity. With average egg numbers of 1070 and 780, respectively, clutches of *R. esculenta* were 1.4 times larger than those of *R. lessonae.* Both averages, as well as the differences between them, are low compared to the factor of 2–3 reported from other investigations (Berger, 1977; Rastogi et al., 1983; Reyer et al., 1999). However, because clutch size increases with female size in both species, direct fecundity comparisons between studies are meaningless, unless additional data on female size distributions in the particular areas and years are available. Nevertheless, our data confirm the previously reported higher fecundity of hybrid than parental females. The subsequent switch from an excess of hybrid to one of parental animals could be caused by the hybrid's higher mortality during metamorphosis, its earlier dispersal after metamorphosis, or a combination of these two factors.

Mortality during metamorphosis.—When raised under laboratory or seminatural conditions, *R. esculenta* and *R. lessonae* normally do not show marked differences in mortality during metamorphosis (R. Semlitsch, pers. comm.), but things may be different under less benign conditions. Metamorphosis is a physiologically stressful event (Smith, 1987; Pough and Kamel, 1984; Berven, 1990) and hybrids, which suffer from several defects (Günther, 1990), may have increasing problems in coping with this stress, as environmental conditions get harsher. Metamorphosis can also increase vulnerability to predation (Wassersug and Sperry, 1977), but whether such risk is higher for hybrid than parental metamorphs has not been investigated in the field yet. After successful metamorphosis, juvenile survival does not differ between the two species (27% vs 25%; Altwegg, 2002; Altwegg and Reyer, 2003); and among adults, survival also seems to be similar: two studies found slightly higher E- than L-survival (Anholt et al., 2003; Reyer et al., 2004) and one found the reverse (Holenweg Peter, 2001a).

Dispersal after metamorphosis.—As for many other anuran species, there is a lack of field data on dispersal of juvenile water frogs and, hence, on potential differences in dispersal times and rates between *R. lessonae* and *R. esculenta.* However, given that the two species apparently do not differ in juvenile survival, the drop in L-proportions from metamorphs with stumps to those with no tail (Fig. 1) is likely caused by higher emigration of L versus E. Consistent with this hypothesis is that recapture rates of marked metamorphs at sites 1 and 2 were lower in *R. lessonae* than in *R. esculenta* (site 1: 2.9 vs 4.8; site 2: 5.4 vs 6.8) and that among adults, dispersal rates are also higher in *R. lessonae* than in *R. esculenta* (Holenweg Peter, 2001b).

Even if differences in survival are only partly responsible for the observed switch from an excess of *R. esculenta* prior to metamorphosis to an

excess of *R. lessonae* after metamorphosis, this will help to compensate for the hybrid's primary fitness advantage and stabilize mixed populations of sexual and asexual (in this case hemiclonal) species (Som et al., 2000; Hellriegel and Reyer, 2000). However, the fact that adult L/E ratios vary from 90:10 to 10:90 among populations (Blankenhorn et al., 1973; Berger, 1983; Holenweg Peter et al., 2002) shows that we will not understand the long-term stability of mixed sexual/hemiclonal L-E populations without further empirical field data on mating frequencies, age-specific fecundity and survival and dispersal from metamorphosis to sexual maturity.

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