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## OVERWINTER SURVIVAL OF *RANA LESSONAE* AND ITS HEMICLONAL ASSOCIATE *RANA ESCULENTA*

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**Abstract.** In central Europe, the hybridogenetic water frog *Rana esculenta* is a sexual parasite that only persists in the presence of the parental species, *R. lessonae*, with which it must mate in order to reproduce. *R. esculenta* is a superior larval competitor, and adult females are about three times more fecund than *R. lessonae*. This suggests that, in the absence of some balancing advantage to *R. lessonae*, *R. esculenta* should drive the parental species locally extinct, closely followed by itself. We measured annual survival rates over six years at two widely separated ponds using modern capture–mark–recapture methods to test whether differences in adult survival might contribute to the persistence of the water frog system. We marked 856 adult frogs and recovered 182 at least once. The data did not deviate significantly from the assumptions of the Cormack-Jolly-Seber model at either pond. There were no detectable differences in recapture probabilities between taxa, but females were, overall, less likely to be recaptured. Survival was higher for *R. esculenta* in all but one year. Therefore, some mechanism other than adult survival must be invoked to explain the persistence of this unusual breeding system. There was considerable year-to-year variation in survival, ranging from 6% over the winter of 1996–1997, to 98% over the winter of 1995–1996. Although the two ponds are separated by 35 km, pond identity did not contribute to the minimum models. A composite measure of winter severity constructed from a principal components analysis of weather data during the course of the study had a very close relationship with survival (*R. lessonae*,  $r = 0.905$ ; *R. esculenta*,  $r = 0.889$ ). Survival was lowest in winters with low minimum temperatures coupled with high and variable maximum temperatures.

**Key words:** adult survival rate; Anura; coexistence; Cormack-Jolly-Seber model; hybridogenesis; mark–recapture; *Rana esculenta*; *Rana esculenta complex*; *Rana lessonae*; winter severity; winter temperature.

### INTRODUCTION

A problematic and unresolved example of species coexistence is that of the hybridogenetic water frog *Rana esculenta* and its sexual parental species *Rana lessonae*. The common water frog of Europe, *R. esculenta*, is a hybrid between *R. lessonae* and *R. ridibunda* (Berger 1967, 1973, 1990). In many parts of *R. esculenta*'s range the parental species *R. ridibunda* is absent (Blankenhorn et al. 1971, Blankenhorn 1973). Under these conditions, hybrid offspring are formed when a hybrid mates with the remaining parental species, *R. lessonae*. All of the offspring of such a mating will be hybrids because *R. esculenta* produces only *R. ridibunda* gametes during a gametogenesis that excludes the *R. lessonae* genome (Schultz 1969, Uzzell and Berger 1975, Uzzell et al. 1980, Tunner and Heppich 1981, Tunner and Heppich-Tunner 1991). Moreover, the *R. ridibunda* gametes are identical to the parental genome because their chromosomes are unrecombined sister chromatid derivatives, and the off-

spring are therefore hemiclonally produced. The fitness of a *R. lessonae* that mates with a *R. esculenta* is zero because the resulting *R. esculenta* offspring produce exclusively *R. ridibunda* gametes. Matings between two *R. esculenta* produce fertilized eggs, but the larvae very rarely reach metamorphosis (Berger 1967, 1976, Blankenhorn et al. 1971, Graf and Müller 1979, Uzzell et al. 1980, Hotz et al. 1992). Populations of *R. esculenta* can only persist in the presence of *R. lessonae* because the *R. lessonae* genome is required to produce *R. esculenta* anew each generation. Such mixed populations constitute the widespread “L-E system” (Uzzell and Berger 1975).

The hybrid, *R. esculenta*, is a considerably larger frog and spawns up to three times more eggs than the parental species *R. lessonae* (Berger and Uzzell 1980). Moreover, larvae of *R. esculenta* are better competitors than *R. lessonae* under a variety of conditions (Semlitsch and Reyer 1992, Semlitsch 1993). Thus, all other things being equal, *R. esculenta* would rapidly displace the parental species and, lacking a viable sexual partner, would then go extinct (Graf 1986, Plötner and Grunwald 1991, Guex et al. 1993, Som et al. 2000). However, long-term observations indicate that the associ-

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ation between the two taxa is stable over decades (Blankenhorn 1974, 1977, Berger 1977). Some advantage to *R. lessonae* is necessary to explain the persistence of this system.

The preference of females from both taxa to mate with male *R. lessonae* (Reyer et al. 1999) likely contributes to the maintenance of this system, but is not sufficient to fully explain the persistence (Som et al. 2000, Hellriegel and Reyer 2000). One possibility beyond the larval aquatic stage is that *R. lessonae* has a survival advantage in the adult stage that overcomes the fecundity advantage of *R. esculenta* (Holenweg Peter 2001a). Alternatively, slight differences in habitat requirements or preferences between the taxa may lead to higher survival of *R. lessonae* in some sites (Negovetic et al. 2001, Pagano et al. 2001, Holenweg Peter et al. 2002) or in some years.

As part of an ongoing study of *R. ridibunda* haplotype (hemiclone) diversity in *R. esculenta*, frogs from two study sites were given unique identifying marks by toe-clipping. The toe clips were used to identify the hemiclone and genotype of the frogs at a set of allozyme loci using electrophoresis. This long-term data set provides a unique opportunity to measure the survival of parental and hybrid frogs over several years at two localities using modern mark-recapture methods (Lebreton et al. 1992, 1993, White and Burnham 1999). We use these methods to test whether *R. lessonae* and *R. esculenta* differ in their annual survival rates and whether there is significant variation in survival among sexes, locations, and years.

In general, very little is known of adult survival rates in amphibians. Although some long-term mark-recapture studies exist (e.g., Elmberg 1990, Kuhn 1994), they often confuse resighting rates with survival. That is, they don't take into account the probability of recapture independent of survival, which can seriously bias estimates of survival (Martin et al. 1995). Rigorous analyses of the data allow us to test competing hypotheses and can generate novel interpretations using robust estimates of demographic (survival) and methodological (recapture) parameters (Wood et al. 1998, Schmidt and Anholt 1999).

## METHODS

### *Study sites*

We captured adult frogs during the breeding season (early May to mid-July) by hand at night at two contrasting sites in Kanton Zürich, northern Switzerland. The first site, near Gütighausen (47°35' N, 8°43' E), is a man-made pond (8700 m<sup>2</sup>) surrounded by forest, where six hemiclones of *R. esculenta* comprise 61% of the water frog population. The second site, ~35 km south of Gütighausen near Hellberg (47°18' N, 8°49' E), is a natural bog pond (730 m<sup>2</sup>) surrounded by a band of trees and wet meadow (50–500 m) adjacent to agricultural fields. Only one hemiclone of *R. esculenta*

is present and comprises 30% of the water frog population (Semlitsch et al. 1996, 1997; H. Hotz and G.-D. Guex, *unpublished data*). These sites are free of introduced *R. ridibunda*, which are found in several locations in northern Switzerland (Grossenbacher 1988, Hotz et al. 1992, Holenweg Peter 2001b, Vorburger 2001).

We captured and marked animals from 1992–1998 at Gütighausen, and from 1992–1996 (omitting 1993) at Hellberg. The number of capture nights per pond varied from 3 to 8, and the capture team ranged from 2 to 6 people on any given night. We marked a total of 540 individuals at Gütighausen, of which 135 were recaptured at least once. At Hellberg, we marked a total of 316 individuals, of which 47 were recaptured at least once.

### *Identification and marking methods*

Captured frogs were returned to the laboratory and uniquely marked with toe clips using the coding system of Twitty (1966). The clipped tissue was stored at –80°C prior to electrophoresis. Frogs were held in ventilated boxes in a cold-room overnight (in some cases several days) while their taxon and genotype was being determined by protein electrophoresis (Uzzell and Berger 1975, Hotz 1983). A few individuals were retained for breeding tadpoles of defined genotypes, the remainder were returned to the natal pond. Any frogs that were sacrificed are noted in the mark-recapture data set. Because the time away from the pond was very short relative to the annual inter-capture interval, this should not introduce any extra-binomial variation that would affect the reliability of the estimates (White and Burnham 1999).

### *Analysis*

We tested the goodness of fit of the recapture histories to the time-dependent Cormack-Jolly-Seber (CJS) model using program RELEASE (Burnham et al. 1987) and the bootstrap goodness-of-fit procedure implemented in program MARK, version 1.9 (White and Burnham 1999). The bootstrap method calculates mark-recapture statistics on data simulated from the parameter estimates that meet all of the assumptions of the method. We compared the deviance of the observed data with that of the simulated data. We restrict ourselves to using Akaike's Information Criterion (AIC) for choosing among models and report estimates and their 95% profile likelihood confidence limits. AIC mediates a trade-off between the deviance explained by a model and the number of parameters required in the model. Simulations have shown that this method is more likely to recover the true underlying structure of the data than a reliance on likelihood ratio tests (Burnham et al. 1995).

We investigated whether a cohort model for recapture might better describe the data because amphibians sometimes have a tendency to breed in alternate years

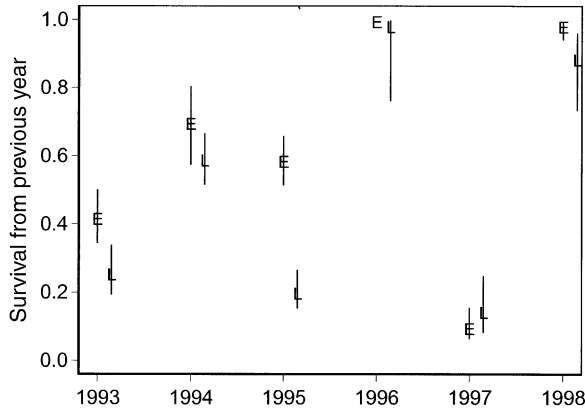


FIG. 1. Best estimates of survival ( $\pm 95\%$  CL) of *Rana esculenta* (E) and *R. lessonae* (L) based on the weighted average of the two best models (see Table 1).

(Bull and Shine 1979). We also examined cohort effects on survival because there might be lower survival after the first capture occasion due to the marking procedure, as has sometimes been seen in amphibians (Davis and Ovaska 2001, Parris and McCarthy 2001). Either of these conditions would contribute to a lack of fit in a standard time-dependent model. Prior to the definitive analyses, we also examined whether classifying *R. esculenta* by hemiclone or classifying both taxa by LDH-B genotype provided useful predictions of the probability of survival.

The definitive analyses examined whether there were differences in survival or recapture that could be attributed to location, taxon, sex, or year. We analyzed both locations simultaneously, and fixed the probability of recapture at zero for those years when there was no capture effort at Hellberg. We began the analysis with a list of candidate models and applied model selection methodology (Burnham and Anderson 1998) to choose the best model. All of the candidate models included the effects of time and location on recapture because of differences in effort among locations and years. These were combined with the effects of sex and taxon with and without their interaction terms. Survival pa-

rameters for time, location, sex, and taxon were included in the list of candidate models. Because of model selection uncertainty, we report parameter estimates and confidence limits that are weighted by the  $AIC_c$  weights of the models.

We acquired climate data from the nearest meteorological site maintained by the Swiss Meteorological Bureau at the Zürich Airport (*unpublished data*). From the winter months of each year, November to March, we extracted the lowest temperature recorded for each winter, the monthly mean of the daily minimum, maximum, and average temperature. For each winter, we also calculated the standard deviation for each of these three monthly averages. Because we have seven measures of winter severity that are all correlated with each other and only six observations of survival per species, we extracted the first principal component of the correlation matrix of the temperature data and regressed survival rates against the winter PC1 score.

RESULTS

Program RELEASE detected no deviation from multinomial expectations for the full data set, or either study site alone. However, recaptures were sufficiently sparse that few of the tests were deemed to have enough data for powerful tests. One thousand parametric bootstrap simulations of the full model also showed no significant deviations from the assumptions of the Cormack-Jolly-Seber model for either the Hellberg ( $P = 0.15$ ) or Gütighausen data ( $P = 0.07$ ). Although the Gütighausen data set was approaching significance, a cohort model was not better than a time-dependent (year of capture) model for predicting survival ( $\Delta AIC_c = +15.9$ ) or recapture probabilities ( $\Delta AIC_c = 3.0$ ). We therefore retained the standard Cormack-Jolly-Seber parameterization. Predictions of survival were not improved by classifying *R. lessonae* by LDH-B genotype ( $\Delta AIC_c = +18.1$ ), or *R. esculenta* by hemiclone ( $\Delta AIC_c = +34.9$ ) or LDH-B genotype ( $\Delta AIC_c = +58.2$ ). These factors were not examined further to simplify the analysis.

TABLE 1. The ten best models of survival and recapture of *Rana lessonae* and *R. esculenta* as determined  $AIC_c$ .

Model	$AIC_c$	Weight	No. parameters
1) $\phi$ (taxon $\times$ yr) $P$ (loc $\times$ sex $\times$ yr)	1282.20	0.7622	30
2) $\phi$ (taxon + yr) $P$ (loc $\times$ sex $\times$ yr)	1284.63	0.2258	25
3) $\phi$ (taxon $\times$ sex $\times$ yr) $P$ (loc $\times$ sex $\times$ yr)	1290.62	0.0113	42
4) $\phi$ (taxon $\times$ sex yr) $P$ (loc $\times$ yr)	1297.78	0.0003	21
5) $\phi$ (loc $\times$ taxon $\times$ yr) $P$ (loc $\times$ sex $\times$ yr)	1299.55	0.0001	42
6) $\phi$ (taxon + yr) $P$ (loc $\times$ yr)	1300.01	0.0001	17
7) $\phi$ (taxon) $P$ (loc $\times$ sex $\times$ yr)	1301.01	<0.0001	20
8) $\phi$ (taxon $\times$ yr) $P$ (loc + sex + yr)	1306.99	<0.0001	21
9) $\phi$ (taxon $\times$ yr) $P$ (loc $\times$ sex + yr)	1307.34	<0.0001	22
10) $\phi$ (yr) $P$ (loc $\times$ sex $\times$ yr)	1311.17	<0.0001	24

Note: Abbreviations:  $\phi$  = probability of survival, and  $P$  = probability of recapture.

TABLE 2. Loadings of temperature measures from the Zürich airport, Switzerland, on their first principal component and correlation of annual survival estimates from Gütighausen and Hellberg with temperature measures.

Species	Winter minimum temperature (0.401)		Low temperature			
	<i>r</i>	<i>P</i>	Average (0.382)		SD (0.209)	
			<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
<i>Rana esculenta</i>	0.788	0.062	0.657	0.156	0.092	0.862
<i>R. lessonae</i>	0.902	0.014	0.723	0.105	-0.094	0.859

Note: First principal component (PC1) loadings are given in parentheses following each temperature measure; *r* = correlation coefficient.

The best model included separate survival parameters for the two taxa for each year, but not among sites (Fig. 1, Table 1). This model was more than three times better supported than the next best model, which also included parameters for taxa, but the effect of year was additive. The combined AIC<sub>c</sub> weights of these two models was 0.987. Estimates of overwinter survival weighted by AIC<sub>c</sub> weights from the first two models varied from a low of 0.06 to a high of 0.99 (Fig. 1) and did not differ between sites or sexes (Table 1). In five of six years, overwinter survival was significantly higher for *R. esculenta* than *R. lessonae*. The average survival rate across all years for *R. esculenta* was 0.621 per year, while that of *R. lessonae* was 0.379 (Model 7 in Table 1). The probability of recapture varied among locations and years, reflecting the amount and timing of capture effort.

The first principal component of the temperature data set accounted for 59.2% of the variation. PC1 had positive loadings from the lowest recorded temperature, the average low temperature, and its standard deviation (Table 2). The remaining measures, average high and average mean temperatures, and their standard deviations, had negative loadings on PC1. Low values of PC1 represent winters with consistently low minimum temperatures, but high and variable maximum temperatures among months. Overwinter survival rates of both taxa were well predicted by PC1 scores (*R. esculenta*,  $r = 0.889$ ,  $P = 0.018$ ; *R. lessonae*,  $r = 0.905$ ,  $P = 0.013$ ; Fig. 2).

#### DISCUSSION

We found that adult *R. lessonae* never had higher annual survival than *R. esculenta* in six years of study at two widely separated sites that differed in the number of hemiclones of *R. esculenta* present. Thus, coexistence of the two taxa is not likely to be enhanced at these sites by differences in survival in the terrestrial environment. Higher survival rates of *R. esculenta*, in addition to its higher fecundity, will tend to increase the probability of it establishing numerical dominance and eventually driving its sexual host extinct, closely followed by itself (Som et al. 2000).

Coexistence might still be possible on a broader scale because the two taxa appear to differ in their optimal habitat requirements. Estimates from another site in

Switzerland found that *R. lessonae* had higher survival rates in each of three years (Holenweg Peter 2001a). The present study differs in two major respects. First, the system studied by Holenweg Peter is in an area where *R. ridibunda* and related frogs from many regions of eastern Europe, the Balkans, Anatolia, and the Near East have been introduced multiple times by humans (Grossenbacher 1988; J. Plötner, *personal communication*, H. Hotz and G.-D. Guex, *unpublished data*). Such frogs, stemming from, and probably adapted to, a wide variety of climatic conditions, can mate with native *R. esculenta* as well as *R. lessonae*. This has resulted in ~5% of the *R. esculenta* carrying novel *R. ridibunda* genomes as primary hybrids (Vorburger 2001). Second, the ponds at Gütighausen and Hellberg are larger and deeper than those studied by Holenweg Peter. *R. lessonae* larvae have higher survival rates and faster growth rates at warmer temperatures compared to *R. esculenta* and preferentially choose warmer parts of ponds (Negovetic et al. 2001). The relative abundance of *R. esculenta* and *R. lessonae* adults is related in part to the depth and vegetation of the pond (Pagano et al. 2001, Holenweg Peter et al. 2002). The difference between the study done by Holenweg Peter (2001a) and this study may then be due to differences in habitat and taxon-specific adult survival. Dispersal among ponds would then be required to maintain the system (Hellriegel and Reyer 2000).

The survival estimates provided by mark-recapture are apparent survival estimates that treat emigration from the population as death. Dispersal among ponds can be up to 12.2% per year (Holenweg Peter 2001b). However, the nearest ponds to both the Gütighausen and Hellberg ponds are much further than the distance where no dispersal was detected by Holenweg Peter. Recapture efforts at the ponds nearest to Hellberg (1.3 and 1.7 km) as well as at those nearest to Gütighausen (1.3 and 2.3 km) encountered no marked animals (B. R. Anholt, G.-D. Guex, and H. Hotz, *unpublished data*). In addition, similar overwinter survival rates at two sites that are separated by 35 km, but vary in concert over six years, argues that these values are not the result of dispersal.

The similarity of survival rates at Hellberg and Gütighausen suggests that these rates are at least partly determined by regional weather. Strikingly, the pattern



TABLE 2. Extended.

High temperature				Mean temperature			
Average (-0.286)		SD (-0.428)		Average (-0.483)		SD (-0.439)	
<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
0.441	0.382	-0.147	0.781	-0.012	0.982	-0.109	0.837
0.439	0.383	-0.162	0.760	-0.120	0.821	-0.177	0.737

of survival is similar to that observed for Pond 4 in Hohenweg Peter (2001a: Fig. 3). Survival was highest over the winter of 1995–1996, lowest over the winter of 1997–1998, and intermediate for 1995–1996. Our composite measure of winter severity, PC1, was negatively associated with low temperature and with variable temperatures during the five months of winter. Survival in both taxa declined in winters with extremely low temperatures and when there was wide variation in temperature over the course of the winter. Although many frogs can tolerate freezing temperatures (Schmid 1982, Storey and Storey 1986), there is a lower limit to the effectiveness of any cryoprotectant. The winter of highest mortality, 1996–1997, experienced a minimum low temperature of  $-12.9^{\circ}\text{C}$ , the lowest temperature recorded during the study. Less intuitive is the negative effect of warm and variable winter temperatures. *R. lessonae* and *R. esculenta* do not hibernate for the entire winter. Some frogs move in November and December, even when the air temperature is near freezing (Holenweg and Reyer 2000). Increased metabolic rate at warmer temperatures may risk exhaustion of energy reserves before the frogs can begin feeding again in spring. Thus, winters with periods of warmer weather may not lead to higher survival. Lower survival during winters with variable temperatures may

be associated with increased activity during times of high temperature, leading to the animals being trapped when the temperature drops again. This could be due to an inability to find an adequate hibernation site after moving or a loss of cryoprotection associated with leaving hibernation and beginning feeding (Storey and Storey 1987).

We were unable to detect differences in survival between hemiclones or LDH-B genotypes. However, our sample sizes restricted detection of differences in survival of  $\sim 0.1/\text{yr}$  (Fig. 1) for the whole data set. Our power will be correspondingly less when we subdivide each taxon into smaller classes. Clearly, much larger data sets will be required for this level of resolution. We can conclude, however, that if there are differences among hemiclones or LDH-B genotypes, they are likely to be within the confidence limit for each taxon.

The marking of amphibians by toe-clipping has sometimes been shown to reduce survival (Davis and Ovaska 2001, Parris and McCarthy 2001). We would expect this to be reflected in a lower probability of survival in the year immediately following marking. Sublethal effects of marking might be reflected in a lower rate of recapture in the year immediately following marking. However, incorporating the effect of marking cohort into the analysis dramatically reduced the model fit. Therefore, in this system, marking has no discernible effect on the frogs. A lack of a marking cohort effect on recapture rates also argues that the probability of breeding is not contingent on whether that individual bred the previous year (but see Schmidt et al. 2002).

Any predictions about the viability of a population requires reliable demographic estimates including annual survival rates. Modern mark–recapture methods provide these estimates along with a measure of their uncertainty. Our estimates have also provided us with some insight into the causes of the annual variation in mortality rates of the *Rana esculenta* hybridogenetic complex of central Europe. Analyses of other long-term data sets using these methods and their descendants will tell us whether these relationships are general or not.

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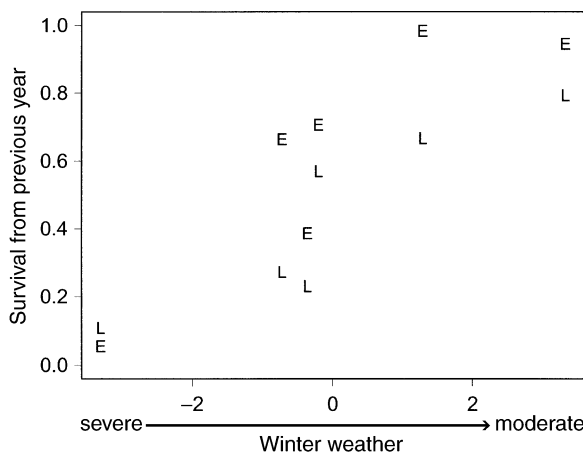


FIG. 2. Relationship between measures of winter severity (PC1) and the probability of survival for *R. esculenta* (E) and *R. lessonae* (L) adults. Negative PC1 values are associated with winters with low minimum temperatures, high average and maximum temperatures, and increased temperature variation among months.

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