Year: 2001

Dispersal rates and distances in adult water frogs, Rana lessonae, R. ridibunda and their hybridogenetic associate R. esculenta

Holenweg Peter, A K

Dispersal rates and distances in adult water frogs, Rana lessonae, R. ridibunda and their hybridogenetic associate R. esculenta

Abstract

Abstract: I investigated dispersal of adult water frogs between local ponds containing Rana lessonae, R. ridibunda and their hybridogenetic associate R. esculenta. Recent models indicate a strong influence of species specific dispersal on the dynamics of such mixed populations. However, empirical data on dispersal are still rare and populations are often defined through individuals which reproduce at the same site. In my study area near Zurich, Switzerland, 12.2% of the animals changed ponds in 1995 and 1996. Dispersal occurred throughout the whole year and was not restricted to specific periods. The dispersal rate decreased with increasing pond-to-pond distance and degree of isolation. In addition, I found differences in dispersal rate and distance related

DISPERSAL RATES AND DISTANCES IN ADULT WATER FROGS, *RANA LESSONAE, R. RIDIBUNDA* AND THEIR HYBRIDOGENETIC ASSOCIATE *R. ESCULENTA*

Anna-Katherina Holenweg Peter

Institute of Zoology, University of Zürich, CH-8057, Switzerland

Abstract: I investigated dispersal of adult water frogs between local ponds containing *Rana lessonae*, *R. ridibunda* and their hybridogenetic associate *R. esculenta*. Recent models indicate a strong influence of species specific dispersal on the dynamics of such mixed populations. However, empirical data on dispersal are still rare and populations are often defined through individuals which reproduce at the same site. In my study area near Zurich, Switzerland, 12.2% of the animals changed ponds in 1995 and 1996. Dispersal occurred throughout the whole year and was not restricted to specific periods. The dispersal rate decreased with increasing pond-to-pond distance and degree of isolation. In addition, I found differences in dispersal rate and distance related

to size, sex and genotype of the animals. Females moved relatively more often when smaller or younger and changed ponds more often during than beyond the breeding season. Males, in contrast, dispersed more often when larger or older and primarily outside the breeding season. In terms of genotypes, dispersal rates decreased and distances increased from *R. lessonae* through *R. esculenta* to *R. ridibunda*. Although only based on observed movements, these results suggest that there is geneflow among different ponds, because 96% of the migrating animals remained at the new pond for at least one breeding season and 92% did not move back at all. Hence, with the exception of one isolated pond, all water frogs from the investigated ponds seem to belong to one breeding population rather than to different populations.

Key words: *Rana lessonae*; *R. ridibunda*; *R. esculenta*; Dispersal; Breeding ponds; Hybridogenesis; Population; Distance

Introduction

Most landscapes consist of a mosaic of habitat patches, separated by areas which are not or less suitable for the species under consideration. Until not too long ago, studies of population dynamics focussed on birth and death rates within local populations, assuming that emigration and immigration sum up to zero (e.g. Odum, 1971). Over the last two decades, however, biologists have increasingly realized the importance of dispersal, i.e. movement among

patches, for all levels of complexity. On the level of genes, dispersal has implications for the degree of inbreeding and the maintenance of genetic diversity (Ehrlich and Raven, 1969; Slatkin, 1985, 1987; Barton, 1992; Dobson, 1994; Barton and Whitlock, 1997). On the level of individuals, behavioral ecologists have addressed the fitness costs and benefits of dispersal versus philopatry in relation to sex, age, dominance status, relatedness, density, available resources and several other internal and external factors affecting reproduction and survival (e.g. Donth, 1979; Greenwood and Harvey, 1982; Dobson, 1982; Fleischer et al., 1984; Johnson and Gaines, 1990; Pärt, 1994; Bélichon et al., 1996; Dingle, 1996). For the population level several models have indicated that movement between patches has a stabilizing effect on the population dynamics of both single and coupled species, such as predator-prey, parasite-host and interspecific competitors (e.g. Hastings, 1993; Gyllenberg et al., 1993; Molofsky, 1994; Doebeli, 1995; for reviews see Kareiva, 1990; Gilpin and Hanski, 1991).

These dispersal studies are not only interesting from an academic point of view. They are also highly relevant for many issues in conservation biology, including minimum viable populations (MVP), extinction and recolonization within metapopulations, source and sink habitats, habitat fragmentation, the importance of corridors connecting habitat islands, or the SLOSS debate. Which means the question whether survival chances and species diversity are better enhanced by a single large (SL) or several small (SS) reserves that add to the same total area (for reviews see e.g. Nunney and Campbell, 1993; Caughley, 1994; Rhodes et al., 1996).

Despite its importance for all these levels, empirical data on dispersal are still rare. A major reason is that they are difficult to obtain especially when animals (and plant gametes) move over large distances and/or live in habitats with poorly defined boundaries. In these cases it is hard to tell which organisms belong to the same population and where a new population begins. These problems seem to be less pronounced in anurans. Since they are confined to bodies of water for reproduction and have restricted movements of usually less than 5 km, prediction of potential dispersal sites seem to be fairly easy. Yet, even in this taxon, following marked individuals on land is difficult and, hence, populations are usually defined through groups of individuals of the same species which reproduce simultaneously at the same site (e.g. Blankenhorn, 1977; Berger, 1983; Blab, 1986; Ryser, 1989*). Where movement was studied, it traditionally dealt with annual migrations to specific sites for reproduction, nutrition and hibernation (e.g. Griffiths et al., 1986; Glant, 1986; Sinsch, 1988; Tunner, 1992; Denton and Beebee, 1993). Recent molecular investigations, however, have shown some – landscape dependent – gene flow between ponds (Reh and Seitz, 1990; Sjögren, 1991; Hitchings and Beebee, 1996); and long-term field studies have demonstrated the importance of dispersal within a metapopulation for preventing extinction of local populations (Sjögren, 1991; Sjögren Gulve, 1994).

An excellent possibility to study the effects of dispersal on the population dynamics of interacting, rather than single species is offered by water frogs of the *Rana lessonae* / *R. ridibunda* / *R. esculenta* complex, which form a sexual

parasite-host system. *R. esculenta (E)* is originally an interspecific hybrid between *R. lessonae (L)* and *R. ridibunda (R)* (Berger, 1968; Blankenhorn et al., 1971; Günther, 1973); but in most areas hybrid populations are maintained by backcrossing with only one of the parental species. This is due to a reproductive mode known as 'hybridogenesis' (Schultz, 1969; Tunner, 1973, 1974). In diploid *R. esculenta* populations, hybrid males and females exclude one parental genome premeiotically (in Eastern Europe the R, in Central Europe the L) and produce only gametes containing the other genome. Since this remaining genome is transmitted clonally (Berger, 1977, 1983; Graf and Polls-Pelaz, 1989; Günther, 1990), the offspring from hybrid x hybrid matings are homozygous at all loci, including those with deleterious alleles. Hence, the tadpoles do not survive (Semlitsch and Reyer, 1992). As a result, *R. esculenta* can only persist by living as a sexual parasite; male and female hybrids have to mate with *R. ridibunda* (Eastern Europe) and *R. lessonae* (Central Europe), respectively, to regain the lost genome in each generation.

In this system the dynamics in the parental population are likely to influence the dynamics of the hybrid 'population' and vice versa. Several investigators have modeled these influences for mixed populations consisting of either E/R (Plötner and Grunwald, 1991) or E/L (Graf, 1986; Guex et al., 1993; Som et al., subm.) and have tried to identify the relevant factors for stability. The fact that all these models did not include dispersal among ponds probably reflects the scarcity of empirical data. However, a recent model by Hellriegel and Reyer (subm.) for the L/E-system shows that species and habitat specific dispersal can substantially influence the population dynamics of this system.

For evaluating how well the various models and their parameter spaces reflect reality, empirical data are badly needed.

The aim of this study was to provide such data on dispersal rates of *R. lessonae*, *R. esculenta* and R. *ridibunda* between neighboring ponds. Although the typical mixed water frog population in Central Europe consists of the first two species only, introduced *R. ridibunda* now occur sympatrically with them in many areas of Switzerland (Grossenbacher, 1988), including my study area. Since the effect of dispersal can vary with the identity of the disperser, I looked for differences not only among the three genotypes, but also between the sexes and age classes. I further separated dispersal rates from various time periods to distinguish real dispersal related to breeding from occasional back- and forth-movements with no considerable impact on population dynamics.

Methods

Study Area and Monitoring

I studied pond-to-pond movements of water frogs in a system of nine ponds (Fig. 1), all located within 2 km^2 of one another on a military training ground, near Zurich airport, Switzerland. The ponds differed in maximum depth (range 37 - 265 cm), surface area (30 - 1282 m^2), vegetation (none to dense), mean water temperature (14.7 - 19° C) and distance to the nearest other pond (77.5 - 670 m). Details of the area and the ponds are described in Holenweg (1999).

Fig. 1

In 1995 and 1996, frogs were caught at regular intervals at ponds no. 1 - 6. Pond no. 1 was surrounded by a fence made of aluminum flashing (1m high, dug 15 - 20cm into the ground) and equipped with paired pitfall traps (10l buckets) on both sides of the fence (Gibbon and Semlitsch, 1982). In each of the two years, the traps along this fence were checked daily between March 15th and November 25th and every 2-7 days depending on the air temperature during the rest of the year. If air temperatures were constantly below 2° C no frogs were moving and I checked the fence only once a week. At ponds no. 2 to 6 I caught as many frogs as possible every second week between April and September. In addition, frogs were caught once in 1996 (between June 12th and July 15th) at three additional ponds (A, B, C) and once in 1997 (between June 6th and 25th) at ponds 2 to 6.

All caught water frogs were weighed to the nearest 0.5g and their snout-vent-lengths (SVL) were measured to the nearest 0.5mm. Animals $\geq$ 40mm SVL were sexed by the presence or absence of vocal sac openings and determined to species, in cases of doubt via allozyme electrophoresis (Tunner, 1973; Vogel, 1973). I marked them individually by introducing a PIT-tag (Trovan ID 100, Pameda AG, CH-4142 Münchenstein) into their lateral lymphatic sac below the skin (Sinsch, 1992). These tags could be identified afterwards by a hand reader (Trovan LID 500). Sex and genotype of animals smaller than 40 mm SVL is more difficult to determine in the field; therefore they were only marked according to their pond of origin, either by cutting or injecting fluorescence color into one of their swim webs (fluorescent

elastomer, NMT International LTD, Washington 98286, USA). These swim web markings lasted for about one year, but hardly longer (above all the cutting). After handling, I released all frogs, either on the opposite side of the fence (pond no. 1) or back into their pond of origin (ponds no. 2 to 6).

Data and Statistical Analysis

The capture/recapture program outlined above yields data on pond-to-pond movement by adult frogs ($\geq$40mm) of different genotypes, sexes and body sizes and by cohorts of juveniles (< 40mm) from different ponds. In this paper, I will call these movements "dispersal". Dispersal rates are expressed as the ratio between the number of animals that moved over the total number of animals recaught (at either the same or another pond), rather than over the total number marked. The latter would have underestimated dispersal rate, because it includes all those frogs that were caught just once and, hence, could have moved undetected.

To analyze during which time period most movements take place, I distinguish dispersal rates between years (1995 to 1996) from those within years (1995 and 1996) and further divide the latter into dispersal during and beyond the breeding season. Criteria for assigning a dispersal event to one of these periods were the following:

- 'during breeding season' - an animal was caught at one pond after the 1st of May (the date of the earliest egg masses) and recaptured at another

pond before the 10th of July (latest egg masses).

- 'beyond breeding season' - one or both catches were before the 1st of May and/or after the 10th of July, but not earlier than April 1st and not later than September 10th. These last date restrictions were imposed to make sampling data from the fenced pond (sampled all year-round) comparable to those from the other ponds.

- 'within one year' - an animal was caught at different ponds in the same year (April 1st-September 10th).

- 'between two years' - an animal was caught in the following year at another pond than the year before.

According to these criteria, a frog which changes ponds "during breeding season" or "within one year", but is recaught only after those periods, would falsely be classified as a "beyond breeding season" or "between two years" disperser. However, as long as these events are relatively rare and dispersal differences between periods are pronounced, this mistake is unlikely to profoundly change the results.

To approximate normal distribution, all proportions were arcsinsquareroot transformed. Statistics were calculated with Systat 6.0 for Windows (SPSS Inc. 1996) for Analyses of Variance (ANOVA) and with SPSS for Windows Release 6.1.3 (Norusis, 1995) for Logistic Regression. Where several comparisons were made with the same data set, I adjusted the conventional significance level (P=0.05) by the Bonferroni adjustment ($\alpha = 1 - 0.95^{1/n}$, where

n = number of different tests). Nonparametric statistics was used where requirements for parametric tests were not fulfilled.

Results

Dispersal Within and Between Years

I individually marked a total of 2730 frogs $\geq$ 40mm SVL in 1995 and 1996. 58% were caught only once, while 1144 were recaptured, 139 of them (12.2%) at a pond other than the one of the first capture. Of these 139 animals, one moved to a third pond after the first migration and 11 moved back to their home pond, 6 of them after having been at the new pond for one breeding season. This gives a total of 151 migrations between January 1995 and December 1996. Average dispersal rates within the two years (10.6%) did not significantly differ from the dispersal rate between years (14.5%), but there

Tab. 1 was a significant sex*genotype effect on dispersal rates (Table 1): dispersal did not differ in males, but decreased from *Rana lessonae* through *R.*

Fig. 2 *esculenta* to *R. ridibunda* in females (Fig. 2). As a result, there was also a significant overall genotype effect on dispersal (Table 1). Pairwise comparisons (Tukey test) revealed higher dispersal rate in *R. lessonae* than in *R. ridibunda* (P=0.046), but no differences in the other two genotype pairs (both P>0.13).

Out of the 1048 animals with a SVL < 40mm, which were only marked pond specifically, I recaptured 384. Out of those, 9.2% and 8.3% changed ponds

within 1995 and 1996, respectively. These ratios are not different from the ones observed in animals larger than 40mm (χ^2=1.1, df=1, P>0.25). A comparison between years was not possible, because the pond-specific markings (above all the cutting) was hardly visible for longer than one year.

Seasonal Variation in Dispersal Within Years

Tab. 2

Table 2 lists the dispersal rates for movements during and beyond the breeding season. Of the 96 animals dispersing within years, 4 were recaptured in both during 'breeding season' and 'beyond breeding season'. Of the 808 animals that were recaptured at the same pond, there were also 144 recaptured twice, during 'breeding season' and 'beyond breeding season'. These animals were randomly assigned to one of the two groups to avoid dependent data in the statistical analysis. An analysis of variance was performed with dispersal rate as the dependent variable, genotype, sex and season as independent variables and year as a block variable (Table 2). Dispersal rate was significantly effected by genotype, with no difference between *R. lessonae* and *R. esculenta* (P=0.123), but both moving more often than *R. ridibunda* (both P<0.026; Tukey test for pairwise comparisons). There was no overall effect of season on dispersal rate. Frogs moved equally often during and beyond the breeding season, but there was a significant interaction season*sex (Table 2): females moved more than males during and less than

Fig. 3 males beyond the breeding season (Fig. 3). There was also a tendency for a season*genotype effect, with dispersal decreasing from *R. lessonae* to *R. ridibunda* more steeply during than beyond breeding (Fig. 3). Animals with a

SVL < 40mm were only marked according to their pond of origin and could therefore not be assigned to recaptures during or beyond breeding season.

Differences Between Dispersing and Non-Dispersing Frogs

The calculations of dispersal rates per group (i.e. per genotype, sex, year and season) inevitably led to small sample sizes and, hence, to low power of the above statistical tests. I, therefore, performed an additional test, based on the much larger sample of individual frogs (n=904). For this test, I used all animals that were recaught within either 1995 or 1996, because the previous analysis had shown no seasonal effect on dispersal rates. However, I excluded animals that were recaught between two years to avoid dependence in data from individuals that were recaught during a year as well as between two years. Using a backward stepwise logistic regression, I related the binary dependent variable "non-disperser" (recaptured at the same pond) versus "disperser" (recaptured at a different pond) to the independent variables genotype, sex, year, mean SVL and all their interactions. The resulting model is shown in Table 3. It more or less confirms the results found before. There was a significant genotype effect, with dispersal decreasing from *Rana lessonae* through *R. esculenta* to *R. ridibunda*. Dispersal rates were slightly higher for males than for females (P=0.067). More frogs changed ponds in 1995 than the following year. The animals that moved did not differ in size compared to the ones that remained at the same pond, but there is a size effect between sexes, females tended to move when smaller, and males when larger (Table 4).

Tab. 3

Tab. 4

Differences Between Ponds

Considering all migrations between January 1995 and December 1996 (*n*=151), frogs moved between all ponds (including ponds A, B and C) except pond no. 6 east of the highway (Fig. 1). I observed no dispersal to or from this pond, even though I marked a large part of the population there (Holenweg, 1999). For three of the other five regularly sampled ponds (no. 1, 4 and 5), there were more immigrants than emigrants and in two ponds the reverse was true (no. 2 and 3). In pond no. 1 mainly *R. lessonae*, in no. 4 and 5 mainly *R. esculenta* immigrated, while mainly *R. lessonae* left pond no. 2 and *R. esculenta* pond no. 3 (Table 5).

Tab. 5

Dispersal Distances

The longest distance an animal moved was from pond No. 4 to C and back again (2 x 880 m, Fig. 1). The distances between ponds with regular sampling, where dispersal occurred, ranged from 77.5 m to 328.5 m. I tested if the animals moved over all of these rather short distances with the same probability. Because these ponds have different population densities and/or capture probabilities one would not expect to find the same number of animals moving within all distances, even if the frog movement were independent of the distance. Therefore, I calculated the expected number of dispersers between any two ponds by multiplying the number of all dispersers with the

ratio of recaught animals at these two ponds over twice the sum of all

recaught animals (i.e.: expected dispersal $_{pond1-2}$ = dispersal $_{all\ ponds}$ *

[recaptures $_{pond1,2}$ / 2 * recaptures $_{all\ ponds}$]). All animals recaptured within 1995

or 1996 (n=904) were taken for the reasons mentioned already before. The

ratio of observed to expected animals that moved between each combination

of two ponds decreased with increasing distance (Fig. 4). The relationship is

best described by a logistic function (F=17.499, df=1,8, P=0.003, R^2=0.686).

Fig. 4

But it is not distance alone that explains the lack of migration to and from

pond no. 6. This follows from an additional analysis based on all animals that

were marked at pond no. 1 before December 1995.I caught 28 of them at

ponds 2, 3, 4, 5, A, B and C in 1996 but none at pond no. 6. Figure 5 shows

Fig. 5

for each pond the ratio of these "dispersers" to the number of totally caught

frogs in 1996 in relation to the distance they moved. I performed a backward

regression with these ratios as dependent variable and the distance

(logarithmically transformed), category 'main road' and category 'highway' as

independent variables (Table 6). Categories 'main road' and 'highway'

Tab. 6

distinguish between the ponds that were separated or not from pond no. 1 by

the main road and highway, respectively (Fig. 1). Besides the distance, it

seems to be the highway that influences dispersal negatively (P=0.002) and

not the main road.

Considering only the migrations between the regularly sampled ponds, the

three genotypes exhibited different dispersal distances (Fig. 6, Kruskal Wallis

Fig. 6

test: χ^2=8.611, df=2, P=0.013). *R. ridibunda* moved over longer distances than

the other two genotypes (Mann Whitney U-test: between *R. ridibunda* and *R. lessonae* *P*=0.006, *R. ridibunda* and *R. esculenta* *P*=0.036, *R. esculenta* and *R. lessonae* *P*=0.11, without correction). The dispersal distances did not differ between females and males (Mann Whitney U-test: *P*=0.507).

Discussion

There was a considerable exchange of individual water frogs between 8 of the 9 neighboring breeding ponds. 10.6% of the population changed ponds within a year and 14.5% did so between two successive years. 96% of the migrating animals remained at the new pond for at least one breeding season and 92% were not observed to move back at all. Therefore, I assume that most of these dispersing animals reproduced at the new site, which means there is gene flow between these local sites (Krebs, 1985; Slatkin, 1987; Ebenhard, 1991; Gilpin, 1991; Waser and Elliott, 1991; Barton, 1992). Consequently, all animals of these breeding ponds belong to one population, rather than to different populations.

Ecological Effects on Dispersal

The extent of dispersal varied with environmental conditions both in time and space. In terms of time, dispersal was not restricted to specific periods, and even occurred during the breeding season, contrary to what Juszczyk

(1952), Van Gelder and Hoedemaekers (1971) found. In 1996 fewer animals changed ponds than the year before. This may have been related to water balance and thermoregulation, which constrain the migratory behavior of amphibians. In 1996 we had only an average of 2.4mm rainfall per day compared to 3.6mm in 1995. In terms of space, migration rate decreased with increasing distance between ponds already within some 100 m. Sjögren (1991; Sjögren Gulve, 1994) found a similar effect in a northern *Rana lessonae* metapopulation. He pointed out that population proximity i.e. distance from each pond to the closest other pond with water frogs is a key factor preventing extinction, respectively enhancing colonization. But my study shows that the distance between two ponds is not the only factor that determines whether there is dispersal or not. The highway west of pond no. 6 seems to isolate this pond from all the others. A similar effect has previously been shown in *Rana temporaria* (Reh and Seitz, 1990, 1993; Seitz et al., 1992). The main road in my study area apparently had no effect on dispersal rates. I do not know whether it is the lower traffic of this road, the smaller width of a single-track road, or the missing highway slope that cause this difference.

<center>*Differences Between Size Classes, Sexes and Genotypes*</center>

In addition to this overall pattern, I found effects on dispersal related to size, sex and genotype.

Size -- There was no overall size difference between dispersing and non-dispersing animals. It seems that individually marked females moved relatively

more often when smaller or younger and males when larger or older. However, I only individually marked animals ≥ 40mm, which mainly represent the adult stage. Whether the findings also hold for freshly metamorphosed animals and for juveniles has to be tested. Following movements of these younger animals over a longer time period than two years may also increase the dispersal rates over those reported here (cf. Sjögren, 1988; Berven and Grudzien, 1990). Nevertheless, my results show that dispersal is not a phenomenon restricted to a specific life stage in water frog populations (mainly the juvenile stage, as often postulated, iid.); it seems to occur throughout the whole life.

Sex —Compared to 'beyond breeding season', more females than males changed ponds 'during breeding season' (Tables 2 and 3). It is probably more costly for the males to change ponds during breeding season, because of their mating behavior. Males can – at least theoretically - reproduce several times during breeding season. Hence, they remain in a pond for several weeks and often defend a territory (Tunner, 1976; Blankenhorn, 1974), which they would have to achieve again at a new pond. In contrast, the females' chances of reproducing are unlikely to increase with time spent at a pond. Females can lay their eggs within an hour or within a few days at most. Afterwards they have to develop new eggs, which takes them usually until the next breeding season (G. Abt and F. Balmelli, pers. communication). Thus, they do not lose if they move to another pond. It might even be advantageous for a female to check more than one pond before laying her eggs, because the survival of her tadpoles depends strongly on the habitat in which they grow up (e.g.

Semlitsch and Reyer, 1992; Semlitsch, 1993; Stauffer and Semlitsch, 1993).

Genotypes. —More *Rana lessonae* moved than *R. esculenta* and *R. ridibunda*, but the latter moved the longest distances. *R. esculenta* showed an intermediate behavior in both the dispersal rate and the dispersal distance. I see two possible explanations for this: reproductive and ecological reasons. In terms of reproduction, *R. esculenta* should follow its sexual host (in central Europe *R. lessonae*), whereas *R. lessonae* should move away from ponds with a high proportion of *R. esculenta* to avoid mixed matings which lead to the loss of the parental L-genome in the next generation (Berger, 1977, 1983; Graf and Polls-Pelaz, 1989; Günther, 1990). Contrary to this expectation, *R. esculenta* showed a tendency to move towards those ponds (e.g. 4 and 5) with already a high proportion of *R. esculenta* (Holenweg, 1999). This could indicate movement for ecological reasons. In its ecological requirements, *R. esculenta* is intermediate between *R. lessonae* and *R. ridibunda* from which it originated through interspecific hybridization. The two parental species prefer different habitat types (e.g. Berger, 1970; Günther, 1990; Holenweg, 1999), and when experimentally subjected to different conditions, relative growth and survival rates of parental and hybrid tadpoles vary with conditions (Semlitsch and Reyer, 1992; Semlitsch, 1993; Fioramonti et al., 1997; Negovetic, 1995). *R. lessonae* mainly inhabit small marsh ponds with a lot of vegetation, whereas *R. ridibunda* prefer large deep ponds or even lakes with little vegetation. Natural marsh areas usually contain several small ponds in close proximity while areas with large ponds or lakes often do not have other ponds nearby. Even though in my study area both genotypes were found in all

investigated ponds, they still exhibited these different preferences (Holenweg, 1999) which may have influenced their dispersal behavior through the spatial arrangement of these ponds. The small highly vegetated ponds (1, 2, 3, 4) – preferred by *R. lessonae* – lie close together while the two large ponds (5, B) – preferred by *R. ridibunda* – are further apart (Fig. 1). This spatial situation decreases the probability of pond change and increases the distance for those that do disperse in *R. ridibunda*, whereas in *R. lessonae* it increases the rate and decreases the distance. As a result, the hybrid *R. esculenta* can be expected to show the observed intermediate values for both rate and distance.

To fully understand the reasons for pond-to-pond movements within and beyond the breeding season, we need further investigations on the dispersal behavior of the three genotypes and should combine them with studies on survival and mating success at different ponds. This is particularly important since a recent model by Hellriegel and Reyer (subm.) indicates that the species specific dispersal (shown in this study) not only crucially influences the overall population dynamics; the precise effect also depends on whether adults move for ecological reasons (suitable habitat) or reproductive reasons (seeking and avoiding mixed matings, respectively).

Literature Cited

Barton, N. H. 1992. The genetic consequences of dispersal. Pp. 37-59. *In* N.
C. Stenseth and W. Z. Lidicker (Eds), Animal dispersal: small mammals
as a model. Chapman and Hall.

Barton, N. H. and M. C. Whitlock. 1997. The evolution of metapopulations. Pp.
183- 214. *In* I. A. Hanski and M. E. Gilpin (Eds.), Metapopulation
biology: ecology, genetics, and evolution. Academic press.

Bélichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness
components beteween philopatric and dispersing individuals. Acta
Oecologica 17(6):503-517.

Berger, L. 1968. Morphology of the F1 generation of various crosses within
Rana esculenta complex. Acta Zool. Crac. 13:301-324.

Berger, L. 1970. Some characteristics of the crosses within *Rana esculenta*

complex in postlarval development. Ann. Zool. (27):273-416.

Berger, L. 1977. Systematics and hybridization in the *Rana esculenta*

complex. Pp. 367-388. *In* D. H. Taylor and S. I. Guttmann (Eds), The

reproductive Biology of Amphibians.

Berger, L. 1983. Western palearctic water frogs (Amphibia, Ranidae):

Systematics, genetics and population compositions. Experimentia

39:127-130.

Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana

sylvatica*): Implications for genetic population structure. Evolution

44(8):2047-2056.

Blab, J. 1986. Biologie, Ökologie und Schutz von Amphibien. Schriftenreihe

für Landschaftspflege und Naturschutz, Heft 18, Bonn-Bad Godesberg.

Blankenhorn, H. J., H. Heusser, and P. Vogel. 1971. Drei Phänotypen von

Grünfröschen aus dem *Rana esculenta*-Komplex in der Schweiz*.* Rev.

Suisse Zool. 78:1242-1247.

Blankenhorn, H. J. 1974. Soziale Organisation einer Mischpopulation von

Rana lessonae Camerano und *Rana esculenta* Linnaeus. PhD thesis,

University of Zürich.

Blankenhorn, H. J. 1977. Reproduction and mating behaviour in *Rana

lessonae – Rana esculent*a mixed populations. Pp. 389-410. *In* D. H.

Taylor and S. I. Guttmann (Eds), The reproductive Biology of

Amphibians.

Caughley, G. 1994. Directions in conservation ecology. J. Anim. Ecol. 63:215-

244.

Denton, J. S., and T. J. C. Beebee, T. J. C. 1993. Summer and winter refugia of natterjacks (*Bufo calamita*) and common toads (*Bufo bufo*) in Britain. Herpet. J. 3:90-94.

Donth, A. A. 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologoa 42:139-157.

Dingle, H. 1996. Migration, the biology of life on the move. Oxford University Press.

Dobson, F. S. 1994. Measures of gene flow in the Columbian ground squirrel. Oecologia 100(1-2):190-195.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30:1183-1192.

Doebeli, M. 1995. Dispersal and dynamics. Theor. Pop. Biol. 47(1):82-106.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. Biol. J. Linn. Soc. 42:105-121.

Ehrlich, P., and P. H. Raven. 1969. Differentiation of populations. Science 165:1228-1232.

Fioramonti, E., R. D. Semlitsch, H. –U. Reyer, and K. Fent. 1997. Effects of Triphenyltin and pH on the growth and development of *Rana lessonae* and *Rana eculenta* tadpoles. Environmental Toxicology and Chemistry 16(9):1940 – 1947.

Fleischer, R. C., P. E. Lowther, and R. F. Johnston. 1984. Natal dispersal in house sparrows: possible causes and consequences. Journal of Field

Ornithology 55(4):444-456.

Gibbons, J. W., and R. D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: an effective technique for qualitative sampling of animal population. Brimleyana 7:1-16.

Gilpin, M. 1991. The genetic effective size of a metapopulation. Biol. J. Linn. Soc. 42:165-175.

Gilpin, M., and I. Hanski. 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic Press, London.

Glant, D. 1986. Die saisonalen Wanderungen der mitteleuropäischen Amphibien. Bonn. zool. Beitr. 37(3):211-228.

Graf, J.-D. 1986. Population genetics of the Rana esculenta complex: a model. Pp. 175-180. *In* Z. Rocek (Ed.), Studies in Herpetology, Prague.

Graf, J.-D., and M. Polls Pelaz. 1989. Evolutionary genetics of the *Rana esculenta* complex. Albany: New York State Museum, Bulletin 466:289-301.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13:1-12.

Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. Journal of Animal Ecology 48:123-142.

Griffiths, R. A., and J. D. Harrison. 1982. The natal dispersal of birds. Annu. Rev. Ecol. Syst. 13:1-21.

Griffiths, R. A., J. D. Harrison, and S. P. Gittins. 1986. The breeding

migrations of amphibians at Llysdinam pond, Wales: 1981-1985. Pp.
543-546. *In* Z. Rocek, Z. (Ed), Studies in Herpetology.

Grossenbacher, K. 1988. Verbreitungsatlas der Amphibien in der Schweiz.
Schweizerischer Bund für Naturschutz, pp. 122-126.

Guex, G.-D., P. Beerli, A. D. Barbour, and H. Hotz. 1993. A dynamic model to
describe equilibrium conditions in mixed populations of a hemiclonal
hybrid and its sexual host in European water frogs. 4th Congr. Europ.
Soc. Evol. Biol.

Günther, R. 1973. Ueber die verwandtschaftlichen Beziehungen zwischen den
europäischen Grünfröschen und den Bastardcharakter von *Rana
esculenta* L. (Anura, Amphibia). Zool. Anz. 190:250-285.

Günther, R. 1990. Die Wasserfrösche Europas (Anuren-Froschlurche).
Wittenberg: Neue Brehm Bücherei.

Gyllenberg, M., G. Söderbacka, and S. Ericsson. 1993. Does migration
stabilize local population dynamics? Analysis of a discrete
metapopulatin model. Math. Biosci. 118:25-49.

Hastings, A. 1993. Complex interactions between dispersal and dynamics:
Lessons from coupled logistic equations. *Ecology* 74(5):1362-1372.

Hellriegel, B.; and H.-U. Reyer, (subm.): Factors influencing the composition
on mixed populations of a hemiclonal hybrid and its sexual host. Subm.
Oikos.

Hitchings, S. P., T. J. C. Beebee. 1996. Persistence of British natterjack toad
Bufo calamita Laurenti (Anura: Bufonidae) populations despite low

genetic diversity. Biol. J. Linn. Soc. 57:69-80.

Holenweg, A.-K. 1999. Dispersal and population dynamics in water frogs, *Rana lessonae*, *R. ridibunda* and their hybridogenetic associate *R. esculenta*. Unpubl. PhD thesis, University of Zürich, Switzerland.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21:449-480.

Jusczcyk, M. W. 1952. The migration of the aquatic frog *Rana esculenta* L. Bull. Ac. Sci. Cracov Ser.B: 369-541.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B 330:175-190.

Krebs, C. J. 1985. Ecology. Harper Collons Publishers.

Molofsky, J. 1994. Population dynamics and pattern formation in theoretical populations. Ecology 75(1):30-39.

Negovetic, S. 1995. Effects of food and temperature on development of hemiclonal hybrid Waterfrog tadpoles and their sexual host parental species. Diploma thesis, University of Zürich, Switzerland.

Norusis, M. J. 1995. User's guide: SPSS Advanced Statistics 6.1. SPSS Inc., Chicago, IL, USA.

Nunney, L., and K. A. Campbell. 1993. Assessing minimum viable populations size: demography meets population genetics. Trends Ecol. Evol. 8:234-239.

Odum, E. P. 1971. Fundamentals of ecology. Saunders, Philadelphia.

Pärt, T. 1994. Male philopatry confers a mating advantage in the migratory collared flycatcher, *Ficedula albicollis*. Animal Behaviour 48:401-409.

Plötner, J., and C. Grunwald. 1991. A mathematical model of the structure and the dynamics of *Rana ridibunda/esculenta*-males-populations (Anura, Ranidae). Z. zool. Syst. Evolut.-forsch. 29:201-207.

Reh, W., and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog (*Rana temporaria*). Biol. Cons. 54:239-249.

Reh, W., and A. Seitz. 1993. Populationsstudien beim Grasfrosch. Naturschutz und Landschaftsschutz 25(1):10-16.

Rhodes, O. E., R. K. Chesser, and M. H. Smith. 1996. Population dynamics in ecological space and time. The University of Chicago Press, Chicago.

Ryser, J. 1989. The breeding migration and mating system of a Swiss population of the common frog *Rana temporaria*. Amphibia-Reptilia 10:13-21.

Schultz, R. J. 1969. Hybridization, unisexuality and polyploidy in the teleost *Poeciliopsis* (Poecilidae) and other vertebrates. Amer. Natur. 103:605-619.

Seitz, A., U. Faller-Doeper, and W. Reh. 1992. Radio-tracking of the common frog (*Rana temporaria*). *In* I. G. Priede and S. M. Swift (Eds.). Wildlife Telemetry. Proceedings of the 4th European Conference on Wildlife Telemetry, Ellis Horwood, Chicester.

Semlitsch, R. D. 1993. Asymmetric competition in mixed populations of

tadpoles of the hybridogenetic *Rana esculenta* complex. Evolution
47(2):510-519.

Semlitsch, R. D., and H. U. Reyer. 1992. Performance of tadpoles from the
hybridogenetic *Rana esculenta* complex: interactions with pond drying
and interspecific competition. Evolution 46:665-676.

Sinsch, U. 1988. Themporal spacing of breeding activity in the natterjack toad,
Bufo calamita. Oecologia 76:399-407.

Sinsch, U. 1992. Zwei Markierungsmethoden zur individuellen Identifikation
von Amphibien in langfristigen Freilanduntersuchungen: Erste
Erfahrungen bei Kreuzkröten. Salamandra 28(2):116-128.

Sjögren, P. 1988. Metapopulation biology of *Rana lessonae camerano* on the
northern periphery of its range. Unpubl. PhD thesis, University Uppsala.
Sweden.

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the
case of the pool frog (*Rana lessonae*). Biol. J. Linn. Soc. 42:135-147.

Sjögren Gulve, P. 1994. Distribution and extinction patterns within a northern
metapopulation of the pool frog, *Rana lessonae*. Ecology 75(5):1357-
1367.

Slatkin, M. 1985. Gene flow in natural populations. Annu. Rev. Ecol. Syst.
16:393-430.

Slatkin, M. 1987. Gene flow and the geographic structure of natural
populations. Science 236:787-792.

Som, C., B. Anholt, and H.-U. Reyer, (subm.):The effect of assortative mating

on the coexistence of a hybridogenetic waterfrog and its sexual host.

SPSS Inc. 1996. Systat 6.0 for Windows: User's guide: Statistics. Chicago, IL, USA.

Stauffer, H. P., and R. D. Semlitsch. 1993. Effects of visual, chemical and tactile cues of fish on the behavioural responses of tadpoles. Anim. Behav. 46:355-364.

Taylor, L. R., R. A. J. Taylor, I. P. Woiwod, and J. N. Perry. 1983. Behavioural dynamics. Nature 303:801-804.

Tunner, H. G. 1973. Das Albumin und andere Bluteiweisse bei *Rana ridibunda* Pallas, *Rana lessonae* Camerano, *Rana esculenta* Linné und deren Hybriden. Z. Zool. Syst. Evolutionsforsch. 11:219-233.

Tunner, H. G. 1974. Die klonale Struktur einer Wasserfroschpopulation. Z. Zool. Syst. Evolutionsforsch 12:309-314.

Tunner, H. G. 1976. Aggressives Verhalten bei *Rana ridibunda*, *Rana lessonae* und der hybriden *Rana esculenta*. Zool. Anz. Jena 196(1/2):67-79.

Tunner, H. G. 1992. Locomotory behaviour in water frogs from Neusiedlersee (Austria, Hungary). 15 km migration of *Rana lessonae* and its hybridogenetic associate *Rana esculenta*. Pp. 449-452. *In* Z. Korsos, and I. Kiss (Eds.). Proc. Sixth Ord. Gen. Meet. S. E. H. Budapest 1991.

Van Gelder, J. J., and H. C. M. Hoedemaekers. 1971. Sound activity and migration during the breeding period of *Rana temporaria* L., *R. arvalis* Nilsson, *Pelobates fuscus* Laur. and *Rana esculenta* L. J. Anim. Ecol.

40:559-568.

Vogel, P. 1973. Elektrophoretische Untersuchungen der Serumproteine von Grünfröschen aus dem Rana esculenta-Komplex. Unpubl. Msc thesis, University of Switzerland.

Waser, P. M., and L. F. Elliott. 1991. Dispersal and genetic structure in Kangoroo rats. Evolution 45(4):935-943.

Table 1.—Dispersal rates within one year and between two years (top) and analysis of variance with dispersal rate of animals $\geq$ 40mm SVL as dependent factor and within or between years, genotype, sex as independent factors (bottom). Dispersal rates of animals < 40 mm SVL could only be detected within a year because they're marking method did not hold longer than one year. "n" denotes the absolute numbers of recaught animals at the same or at another pond, the numbers of migrating animals are written in parenthesis below the relative values.

	Within one year (%)		Between years (%)
	1995	1996	1995 - 1996
Animals < 40 mm	*n*=251	*n*=133	
Total (total numbers)	9.2 (23)	8.3 (11)	
Animals ≥ 40 mm	*n*=503	*n*=401	*n*=297
R. lessonae females	14	11.6	23.9
R. lessonae males	19.5	10	8.3
R. esculenta females	10.5	7.5	13.1
R. esculenta males	11.2	7.9	16.5
R. ridibunda females	4.1	3.2	0
R. ridibunda males	10	11.1	16.7
Total (total numbers)	12.1 (61)	8.7 (35)	14.5 (43)

Source (animals ≥40mm)	Sum-of-squares	df	Mean-square	F-ratio	*P*
(within or between)					
Years	0.002	1	0.002	0.210	0.659
Genotype	0.068	2	0.034	4.609	0.047
Sex	0.020	1	0.020	2.680	0.140
Sex * genotype	0.067	2	0.034	4.543	0.048
Year * genotype	0.013	2	0.006	0.844	0.465
Year * sex	0.001	1	0.001	0.092	0.770
Residual	0.059	8	0.007		

$R^2 = 0.734$

Table 2.—Dispersal rates during and beyond breeding season (top) and
analysis of variance with dispersal rate as dependent variable and season,
genotype, sex as independent factors and 'year' as a block variable (bottom).
Abbreviations see Table 1.

	During breeding season (%) (May 1st – July 10th)		Beyond breeding season (%) (before May 1st or after July 10th)	
Animals $\geq$ 40mm	1995	1996	1995	1996
	n=218	n=121	n=285	n=280
R. lessonae females	21.9	25	9.3	6.5
R. lessonae males	23.1	5.6	17.1	13.6
R. esculenta females	12.5	6.3	9.5	7.8
R. esculenta males	10	3.8	12.2	9.5
R. ridibunda females	3.7	5.9	4.5	0
R. ridibunda males	0	0	11.1	14.3
Total (total numbers)	14.2 (31)	9.1 (11)	10.5 (30)	8.6 (24)

Source (animals $\geq$ 40mm)	**Sum-of-squares**	**df**	**Mean-square**	**F-ratio**	*P*
Season	0.003	1	0.003	0.391	0.543
Genotype	0.191	2	0.095	13.301	0.007
Sex	0.000	1	0.000	0.003	0.958
Genotype * sex	0.001	2	0.000	0.059	0.943
Season * genotype	0.049	2	0.025	3.414	0.064
Season * sex	0.111	1	0.111	15.453	0.002
Year	0.023	1	0.023	3.269	0.094
Residual	0.093	13	0.007		

R^2 = 0.802

Table 3.—Stepwise logistic regression with dispersal or non-dispersal as dependent variable. We started the model with genotype, sex, mean SVL, year and all their interactions as independent factors. A factor was excluded if its p-value was larger than 0.05. Wald statistics means (estimated coefficient / standard errors)^2, which has a chi-square distribution (Norusis 1995).

Variable	Estimated coefficient	Standard errors	Wald	df	*P*
Genotype			10.413	2	0.006
genotype (1)	0.734	0.464	2.499	1	0.114
genotype (2)	1.380	0.496	7.752	1	0.005
Sex	2.514	1.372	3.359	1	0.067
Mean SVL	0.023	0.013	2.854	1	0.091
Year	-0.471	0.227	4.308	1	0.038
Mean SVL*sex	-0.049	0.024	4.065	1	0.044
Constant	-4.903	1.3725	12.760	1	0.000

Table 4.—Size differences between "dispersing" and "non-dispersing" females and males.

	Females			Males		
	Number	Std. error	Mean SVL (mm)	Number	Std. error	Mean SVL (mm)
Non disperser	479	0.517	56.52	329	0.454	54.71
Disperser	51	1.284	55.37	45	1.454	55.76

Table 5.—Differences between the ponds that were regularly sampled considering their immigrating and emigrating frogs ('les' = *R. lessonae*, 'esc' = *R. esculenta*, 'rid' = *R. ridibunda*). Data were pooled over 1995 and 1996.

Pond	Immigration			Emigration			Total
	les	esc	rid	les	esc	rid	
1	33	22	3	21	29	1	+ 7
2	3	8	0	14	13	2	- 18
3	7	4	0	7	8	1	- 5
4	19	27	2	23	18	2	+ 5
5	5	15	3	2	8	2	+ 11
6	0	0	0	0	0	0	0

Table 6.—Backward regression with dispersal rate as dependent variable and distance (logarithmic transformed), category 'main road' and category 'highway' as independent factors.

Effect	Coefficient	Std error	df	F-ratio	*P*
In					
Distance (log trans.)	-0.018	0.007	1	6.355	0.053
category 'highway'	0.058	0.01	1	31.970	0.002
Out	Part. corr.				
Category 'main road'	0.165		1	0.112	0.755

$R^2 = 0.923$

Figures

Fig. 1.—Map of the study area. A drift fence surrounds pond no. 1, ponds no. 2 to 6 were sampled at regularly intervals, at pond A to C we caught just once.

Fig. 2.—Dispersal rates of *R. lessonae*, *R. esculenta* and *R. ridibunda* females and males. Data are presented as the average percentage ($\pm$ standard errors) of genotype-sex classes moving within 1995, 1996 and between both years.

Fig. 3.—Dispersal rates during and beyond breeding season (1995 and 1996) divided up into the sexes (top) and genotypes (bottom) respectively. Data are presented as average percentage ($\pm$ standard errors) of sexes or genotypes.

Fig. 4.—Ratio of the observed to the expected number of dispersing frogs in relation to the distance covered. The dashed line shows a logistic function with y=7.702-1.308*log(x).

Fig. 5.—Dispersal rates of pond no. 1 to all other ponds (see numbers or letters in the graph) in relation to the distance to pond no. 1.

Fig. 6.—The average distance moved by *R. esculenta*, *R. lessonae* and *R. ridibunda* respectively. Movements between the regularly sampled ponds are taken into consideration. Data are presented as mean distances ($\pm$ standard errors).