

Short Notes

Homing behavior of *Rana lessonae*, *R. ridibunda* and their hybridogenetic associate *R. esculenta* after experimental displacement

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Movements of animals between different breeding sites have implications for both the life history of individuals in terms of growth, survival and reproduction (Greenwood and Harvey, 1982; Kaitala et al., 1993; Dingle, 1996) and the structure and dynamics of populations with respect to density, sex ratio, age structure and genetic diversity (Slatkin, 1987; Kareiva, 1990; Hanski and Gilpin, 1997). Empirical data on such movements, however, are still rare for many species. For amphibians, most studies of migrations have shown high site fidelity to breeding ponds, especially between years (Glandt, 1986; Berven and Grudzien, 1990; Reh and Seitz, 1990; Denton and Beebee, 1993; Loman, 1994). Since populations are usually defined as groups of individuals which reproduce at the same site and time, such site fidelity might suggest that each pond holds its own isolated population. However, recent molecular investigations have revealed gene flow among different ponds (Reh and Seitz, 1990; Hitchings and Beebee, 1998) and long-term field studies have demonstrated the importance of movements within a metapopulation for preventing extinction of local populations (Sjögren Gulve, 1994).

Here, we investigate site fidelity and homing performance in the water frogs *Rana lessonae*, *R. ridibunda* and their hybridogenetic associate *R. esculenta*. In this species complex, the extent of site fidelity, respectively pond-to-pond movement, is also important for understanding the composition and stability of mixed populations with different ratios of hybrid and parental animals (Hellriegel and Reyer, 2000). A previous capture-mark-

recapture study had shown that many individuals change their breeding ponds within and between years (Holenweg Peter, 2001, in press). In this study, adult frogs from two ponds were experimentally displaced and rates of return were analyzed in relation to species, sex, size or age class and distance of displacement. To avoid seasonal effects on return rates (see Blab, 1986), the whole experiment was completed within the breeding period.

The experiment was performed on a military training ground near Zurich airport, Switzerland. We chose two ponds, 225 m apart from each other and separated from further breeding ponds by more than 400 m and a wide truck road. Pond I, with a water surface of roughly 750 m², was of circular shape and had a small island in its center. Pond II was larger (ca. 1200 m² water surface) and irregularly shaped, with several small side arms protruding from the main body of water. The area between the two ponds consisted of flat open grassland, with only a few scattered bushes and trees, most of them within 100 m of pond I. About half-way between the two ponds, a low ridge ran perpendicularly to the straight line connecting the two ponds, but due to its low height (<5 m) and its gentle slopes on both sides it represented no barrier to the frogs' movements.

On 12 June 1996 (i.e. during the breeding season, which lasted from 1 May till 10 July), frogs were collected at both ponds. Only animals larger than 40 mm snout-vent-length (SVL) were weighed and measured to the nearest 0.5 mm with the help of a slide gauge. They were sexed by the presence or absence of vocal sac openings and identified to species. In cases where morphological features were inconclusive, species identification was later accomplished with allozyme electrophoresis (Tunner, 1973; Vogel, 1973). We marked frogs individually with PIT-tags (Trovan ID 100[©], Pameda AG, CH-4142 Münchenstein) placed into their lateral lymphatic sac below the skin (Sinsch, 1992), which can be identified by a hand reader (Trovan LID 500[©]). Thereafter, we released equal numbers of animals (balanced for sexes and genotypes) at previously selected positions along the straight line connecting the ponds. These positions were determined by dividing the total distance between the ponds (225 m) into six equal sections of 37.5 m each. Together with the shortest distance (home pond, 0 m) and the largest distance (other pond, 225 m) this yielded seven release positions. Five, seven and fifteen days later (17, 19 and 27 June), both ponds were again sampled to determine if any of the tagged individuals had returned. These dates resulted from a combination of necessities which included repeated catching to obtain as many frogs as possible, avoidance of rainy nights and no catching on consecutive days to minimize disturbance.

We initially caught, marked and released a total of 134 frogs (98 from pond I and 36 from pond II) in the following numbers: 46 *R. lessonae* (13 females, 33 males), 13 *R. ridibunda* (11 females, 2 males) and 75 *R. esculenta* (34 females, 41 males). Sixty-nine frogs (51.5%) were never found again. Among the 65 frogs that were recaptured (47 on 17 June and 9 each on 19 and 27 June), the return rate to home pond I was 96% ($n = 48$) and that to home pond II 86.7% ($n = 13$). The remaining four animals were caught at the other pond than their home pond, two at pond I and two at pond II.

The distance to the home pond had the strongest effect on the probability of homing by the water frogs (table 1). None of the 29 frogs that had been displaced over more than 150 m, i.e. either into the other pond or 37.5 m away from it, returned to their home pond (fig. 1A), but 10.3% of them were recaptured at the pond of release. At a displacement distance of 150 m, all frogs that were recaptured had returned to their home pond, even though the other pond was closer (fig. 1A). More water frogs returned to pond I compared to pond II (fig. 1B). This difference is most obvious and significant for the two shortest release distances ($P < 0.002$, $\chi^2 = 10.59$, $df = 1$): 30 of the 32 frogs released at 0 and 37.5 m from pond I were recaptured (93.8%) but only 8 of the 15 animals released at the same distances from pond II (53.3%). At longer distances the difference disappeared. This leads to the significant interaction between distance and home pond (fig. 1B). There was no significant effect of species, sex, body size or any of their interactions.

Table 1. Results from a stepwise logistic regression, with 'returning' (yes/no) as the dependent variable and the following factors as independent variables: homepond, species, sex, size, distance, species*sex, species*size, species*distance, sex*size, sex*distance, homepond*distance and species*sex*size. Starting with the full model, an independent variable or interaction was excluded if its *P*-value was larger than 0.05. Shown are estimates, standard errors ($s_{\bar{x}}$), *t*-ratios and *P*-values for only those independent variables that remained in the final model. Statistics were calculated with SPSS for Windows (Release 6.1.3; Norusis, 1995).

Effects	Estimate	$s_{\bar{x}}$	<i>t</i> -ratio	<i>P</i>
Distance	-1.701	0.310	-5.491	<0.001
Home pond	1.493	0.481	3.105	0.002
Distance*home pond	-0.667	0.310	-2.153	0.031
Constant	2.174	0.481	4.522	<0.001

Model: $\chi^2 = 71.6$, $df = 3$, $P < 0.001$, $R^2 = 0.387$

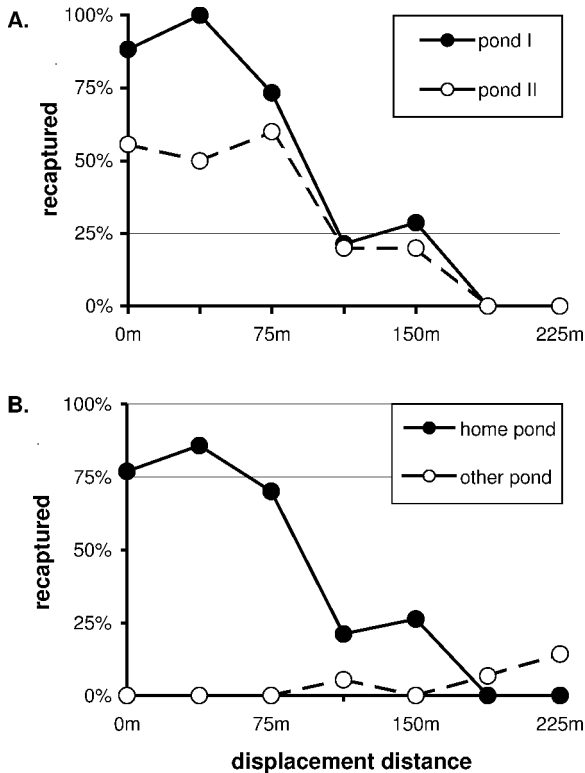


Figure 1. Percentage of water frogs that were recaptured in relation to the distance over which the animals had been displaced. Recaptures are broken down by pond locality (i.e. pond I or II) in figure A and by pond of origin (i.e. home or other pond) in figure B.

Recaptures at distance 0 reflect the capture probability or the probability of frogs to stay at a pond rather than a probability of returning. Therefore, we performed a second logistic

regression, based only on data from animals that were displaced ≥ 37.5 m from their home pond. Of the 108 frogs in this subsample, 41 (=38%) returned. The result of the analysis closely resembled the previous one, with significant effects of distance ($P < 0.001$), homepond ($P = 0.027$) and a tendency for the homepond*distance interaction ($P = 0.10$; model: $\chi^2 = 60.2$, $df = 3$, $P < 0.001$, $R^2 = 0.420$).

There are several, not mutually exclusive, explanations for this low proportion of recaptured frogs. (1) Not all marked frogs are recaptured, even when they are present in the pond. The average of 36 (=27%) marked frogs recaptured per night during this experiment is almost identical to the mean recapture probability of 26% (range: 12-45%) found in another study where water frogs were not displaced experimentally (Holenweg Peter, 2001). (2) Within a year, an average of more than 10% of the frogs leave their home ponds and move to others which can be more than 800 m away (ibid.). (3) Animals stay away from ponds for some time. Some water frogs, equipped with radio transmitters, used a terrestrial habitat for longer than one week (Holenweg, unpubl.; Heym, 1974).

Among those frogs that were recaptured, the likelihood of returning from short distances was higher for pond I than for pond II, whereas from larger distances it did not differ (fig. 1B). This probably has biological and methodological reasons, which both are related to the topography of the experimental area. In terms of biology, the larger number of bushes and trees within about 100 m of pond I may have improved the frogs' orientation and aided them in finding back, whereas the open grassland around pond II provided fewer cues. In terms of method, the larger size, more irregular shape and overhanging vegetation at pond II rendered spotting and catching of frogs more difficult than in the regular and open pond I. Hence, the recapture rate was lower for animals displaced over (and returning from) short distances, but did not differ for those displaced over larger distances from where the majority of them did not return anyway.

Homing was not significantly related to species, sex and body size (table 1), but this result has to be regarded with caution, because of the small sample size. With 134 marked water frogs, consisting of six species-sex-classes and distributed over seven releasing positions, the average sample size on which percentages are based is only three animals per category. Another study, based on a much larger sample of "voluntarily" moving water frogs, showed that dispersal rates decreased from *R. lessonae* through *R. esculenta* to *R. ridibunda* and were related to a sex*size interaction, with females moving when smaller, and males when larger (Holenweg Peter, in press). Together, this experimental and the previous comparative study reveal that water frogs do show homing behavior and pond fidelity within a season. This is probably advantageous in terms of breeding in a known locality, which initially may have been chosen for ecological conditions that enhance growth and survival of their offspring (Günther, 1974; Semlitsch and Reyer, 1992; Semlitsch, 1993a, b; Rist et al., 1997). However, the probability of homing is strongly related to the distance and the topography of the area.

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Epicoracoid overlap in fire-bellied toads, *Bombina bombina*, from parents of known morphology

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Recent studies (Borkhvardt and Ivashintsova, 1994; Borkhvardt and Malashichev, 1997; Greer and Mills, 1997) have supported evidence (Martin, 1972) that the ratio of animals with the left epicoracoid in the dorsal (i.e. the deep, not superficial, when viewed ventrally) position to those with the right epicoracoid in the dorsal position (L.top/R.top ratio, hereafter called also overlap index) is specific for a species or group of species. At the same time, the index in the fire-bellied toad, *Bombina bombina* can vary drastically in the progenies of different parents (Borkhvardt and Malashichev, 1997). In this study we tested the hypothesis that the pattern of the epicoracoid overlap may depend on the type of the pectoral girdle structure in parents. Earlier we proposed a simple and effective non-invasive technique for determining epicoracoid arrangement in living animals by moving the forelimbs of a toad and observing the medial edge of the superficial epicoracoid (Borkhvardt and Malashichev, 1997; see also Malashichev and Nikitina, 2001). Therefore, the question of the heritability of the epicoracoid position could be addressed. We also aimed to determine whether other factors such as mortality of tadpoles may influence the overlap index.

Twenty-four mature *B. bombina* (8 from the Tula region, 54°12'N, 37°36'E, and 16 from the Belgorod region, 50°36'N, 36°36'E of Russia) were caught in natural habitats in April-May, 1999, during the breeding season, and transported to St.-Petersburg. Animals from the Belgorod region were captured in the vicinities of the same artificial reservoir as those used in Borkhvardt and Malashichev (1997). We combined five pairs (No. 1-5), in which both parents had the left epicoracoid in the dorsal position (L.top pairs) and five pairs (No. 6-10), in