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Clutch size, egg survival and migration distance in the agile frog (*Rana dalmatina*) in a floodplain

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Abstract

In animals with complex life cycles, the cost of migration among habitats has to be balanced by optimization of growth and survival within each life-stage habitat. In this context, migration distance is expected to depend on local density and movement potential. In ectotherm species, because movement potential is related to body size, larger individuals are expected to cover longer distances than smaller individuals thus avoiding competition. This hypothesis was investigated in the agile frog (*Rana dalmatina*). For breeding, this species migrates from undergrowth towards ponds located in open environments. Most egg batches were found in sites located 50-100m from the forest edge. Batches from larger frogs were more numerous at greater distances, as far as 300m from the forest edge thus confirming the hypothesis. These results must be taken into account for the conservation of this endangered species.

Introduction

In animals with complex life cycles, migration from one life habitat to another represents a cost with respect to both energetics and survival. Evolution of complex life cycles supposes this cost to be balanced by optimum fit of each life stage with its particular habitat, a more specialized ecological niche providing better growth and better survival (Istock, 1967 ; Wassersug, 1974, 1975 ; Slade & Wassersug, 1975 ; Wilbur, 1980). As a consequence, variation in the cost of migration is expected to influence population viability and the evolution of complex cycles. Because the modification of connectivity by human activities can contribute to sudden increase of the cost of migration, this problem of evolutionary biology appears also to be relevant in conservation ecology.

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Most holartic anurans show a complex life cycle, with adults migrating from terrestrial towards aquatic habitats where they spawn and where larvae develop. While migrating, these animals have to cross environments which provide neither trophic resource nor high safety against predation. One can expect to be balanced by reproduction success in the site where breeding occurs.

In the holartic zone, such a complex life cycle with migration occurs in numerous species inhabiting forests. In the ponds located within forested areas, dead-leaf accumulation and shade induce hypoxia and low productivity (Williams, 1987). Conditions for tadpole development are then less favourable in these undergrowth aquatic sites than in sites in open environments. In fluvial forests that line the river, the presence of predatory fishes is more likely in undergrowth sites act as selective pressures which determine the species to breed in sites located outside the forested area.

Migration distance may be assumed to result in a trade-off between the cost of crossing non-habitats and the gain provided by the openness of the environment surrounding the breeding site. Because locomotory performances of an individual are generally related to its size (Peters, 1983), the largest individuals are expected to breed in sites that are most distant from the fluvial forest.

Because of the patchy distribution of habitat types, the floodplains of large rivers represent a suitable environment for such a study (Townsend, 1989, Petts & Amoros, 1996). The fluvial forest is inhabited by several anuran species (Joly, 1992). These species can breed either remaining within their terrestrial habitat and spawning in undergrowth ponds, or after migrating towards ponds located outside the forest in the open environment.

In this respect, *Rana dalmatina* is the most common brown frog inhabiting the alluvial forest of the Mid-Rhône floodplain (Joly & Morand, 1994 ; Morand & Joly, 1995 ; Morand, 1996). Its life cycle corresponds to the aim of this study, which is to test the hypothesis of a relationship between body size and distance of the breeding site from the forest (Wederkinch, 1988). This study took place in the Lavours Marsh which is one of the largest fluvial marshes remaining in Western Europe. In this marsh, the aquatic sites were sampled in order to account for variation in substratum (alluvium or peat) which may act as confounding factor.

Material and method

Study site

The Lavours Marsh is located 70 Km downstream from Geneva. It occupies a 1200 ha hallow between the Rivers Rhône and Seran just upstream from their confluence. The marsh originated in a post-glacial lake progressively filled with sediment. Water flow from the rivers to the marsh was checked by man-made embankments, mainly erected during the XIXth century. The marsh is now overflowed only in decennial floods. Whereas the floods have formed two side bars, mostly occupied by fluvial forest, the central zone of the marsh is filled with peat, where the water table is level with the peat surface. The fluvial forest is characterized by *Alnus glutinosa*, *Acer campestre* and *Fraxinus excelsior*. The peat-bog is occupied by *Schoenus nigricans*, *Carex elata*, *Molinia caerulea* and *Cladium marscus*. Detailed ecological descriptions of the Lavours Marsh are given in Ain & Pautou (1969), Bravard (1987) and Pautou et al. (1991).

The ponds studied are located in the western part of the marsh near the Seran river ; this zone is managed as a natural reserve. Based on both substratum and openness of surroundings, the ponds studied belong to three types : alluvium and undergrowth (4 sites), peat and undergrowth (3 sites), peat and open surroundings (5 sites).

Egg number and survival

During the breeding periode of the first year (1994) of the study, 64 clutches were monitored in 12 ponds including representatives of the three habitat sites. Egg number was estimated by measuring the volume of each batch in a test tube. The relationship between egg number and batch volume was drawn from counting the egg in 30 batches. Eggs were counted by laying down the batch on the square-ruled bottom of a tank. The location of each batch in the pond was noted as one of three modalities : resting on the bottom, hangig under water from a support, or floating. Before hatching, egg survival in each batch was estimated by counting degenarative embryos.

Clutch size, female size and distance of site to the forest

During the second year (1995), 28 ponds were sampled according to their distance to the forest and were checked for clutches. Area, depth, substrate and distance to forest were measurd. In these sites, 107 egg batches were collected and their volme estimated as previously described. In this study, because egg number is closely related to female body size in ranids (Salthe & Duellman, 1973 ; Cummins, 1986 ; Joly, 1991), it is used as an indicator of female size.

Results

The volum (V) of 30 btchesvaried from 200 to 700ml (mean : 382 ± 26 ml). Egg numbers (N) varied from 526 to 2086 eggs. These data fit the linear model $N=2.35V+127.45$ ($r^2 = 0.81$, $p<0.0001$). This model is very close to that found by Waringer-Löschenkohl (1991) in the same species ($N=2.25V+134.97$; $n=10$). It will be used hereafter for estimating egg number.

Clutch size did not vary significantly among the three habitat types (table 1) (ANOVA on clutch volume : $p = 0.10$), nor did egg number of each clutch vary according to oviposition location (on the bottom : $n=1007 \pm 107$; hangig 929 ± 81 ; floating : 888 ± 75 ; ANOVA, $p=0.6$).

Habitat type	Number of clutches	Mean clutch size (ml)	Estimated egg number
Alluvium and undergrowth	21	315.7 ± 27.8	822.8 ± 59.1
Peat and undergrowth	15	322.0 ± 18.3	842.4 ± 57.8
Peat and open field	28	406.0 ± 38.8	1066 ± 97.2

Table 1. Mean clutch size according to habitat type

Egg survival varied significantly among habitat types ($\chi^2=5673$, $p<0.0001$) (table 2). Whereas it reached 100% in alluvium sites, egg survival varied from 66% to 100% in peat sites. In these sites, egg survival was significantly related to laying position with lower survival in batches resting on the bottom (67.7%) than in floating batches (86.1%) or hanging batches (88.1%) (χ^2 ; $p<0.0001$).

Habitat type	Batch location	N batches	Survival
Undergrowth, alluvium	On the bottom	0	-
	hanging	3	100
	floating	18	100
Undergrowth, peat	On the bottom	3	82.0± 1.3
	hanging	6	91.7± 3.8
	floating	6	100
Open surrounding, peat	On the bottom	16	65.6± 9.2
	hanging	7	85.7± 12.7
	floating	5	73.0± 13.9

Table 2. Relationship between survival and both habitat type and oviposition location.

The relationship between clutch size and adult migration distance was studied during the second year. Most of the batches (75%) were censused in open fields within 100m from the forest border. Batch density reached a maximum (1 batch per 4m²) in sites located from 50 to 80m from the forest and lowest values (1 batch per 20m²) for distances exceeding 100m (fig.1).

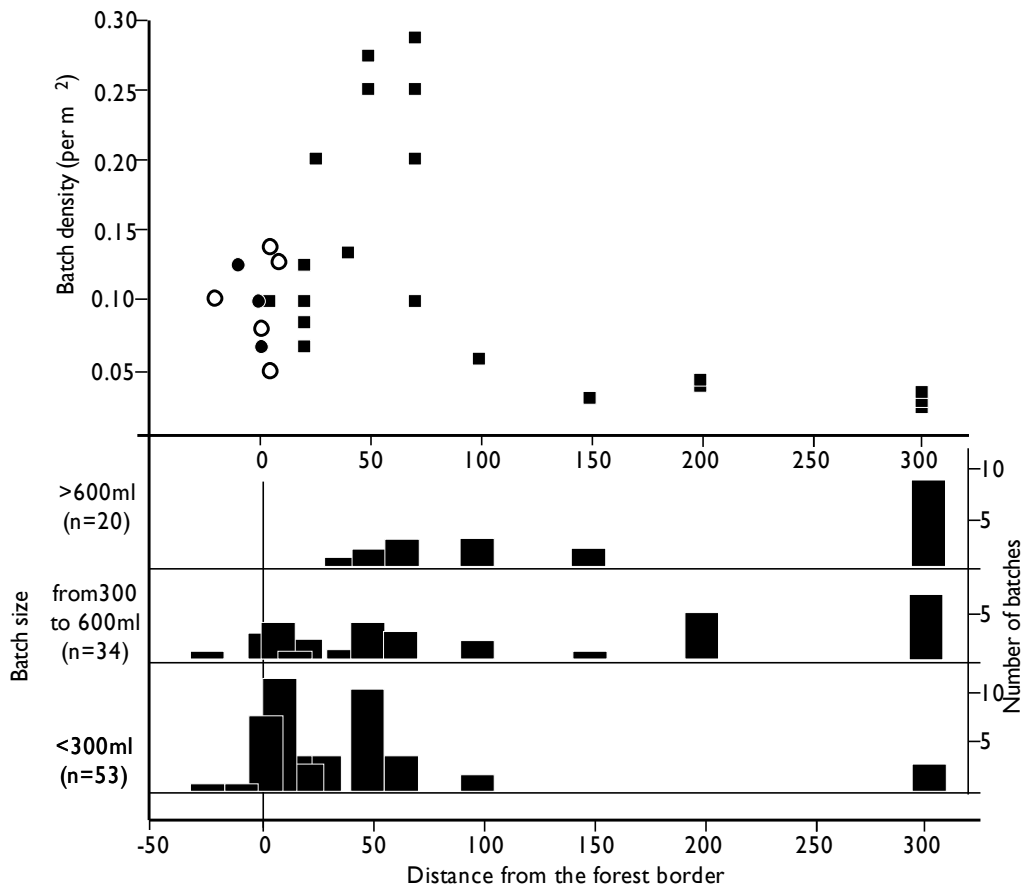


Fig. 1. Top : Relationship between batch density and distance to the forest. Black dots : fishless sites ; open dots : sites with fish. Circles : sites in alluvium ; squares : sites in peat. Bottom : distribution of batch numbers in relation with both batch size and distance to the forest.

Clutch size was related to distance from the forest. Whereas the smallest batches were mainly recorded in sites within 100m (72.7% of >600ml batches ; n=20). Batches with intermediate size distributed on both sides of a 100m distance from the forest (59.4% of batches between 300 and 600ml in sites within 100m distance ; n=34) (fig.1). This variation in batch distribution related to size was highly significant (χ^2 ; $p < 0.0001$). Because egg number is strongly related to female size in ranids (Salthe & Duellman, 1973 ; Cummins, 1986 ; Joly, 1991), migrations were longer in larger females than in smaller females (mean distance = 40.8 ± 9.6 m for batches <300ml) and led them to the most distant sites from the forest (mean distance 171 ± 26 m for batches > 600ml). Migration distances were intermediate for medium-size females (mean distance = 115.0 ± 19.8 m for batches from 300 to 600ml).

Discussion

As expected, most frogs spawned outside the undergrowth. This result confirms the former study of Wederkinch (1988), which showed that in an agricultural zone most egg-clutches were laid within a 200m distance from the forest. However, in the present study, the distance covered by the larger females was greater than covered by the smaller ones.

Avoiding spawning in the undergrowth presents several advantages. Our results show that the presence of fish in pond is indeed more frequent within the fluvial forest where floods occur more often. Fish are among the most efficient predators of tadpoles (Semlitsch & Gibbons, 1988). The highest batch densities were recorded in a zone 50-100m from the forest border, just outside the one where fish occurred. On the other hand, despite the lack of measures of oxygen concentration and algal productivity, we can assume that the accumulation of organic mater (dead leaves, dead wood) together with the shading in undergrowth ponds are causes for less food and less oxygen in thses sites than in the open environment.

However, the relationship between migration distance and frog size cannot be explained only by the probability of fish occurrence and variation in productivity. If we reasonably accept that medium-sized frogs can travel the minimum distance for reaching the suitable sites closest to the forest border, an optimality model would predict that the largest-sized frogs should also spawn in these closest sites (fig.2A). Because this expectation was not validated, the model must be modified by incorporating a negative impact of tadpole density on habitat quality (fig.2B). The negative effect of density on tadpole growth has been demonstrated in numerous studies (Wilbur, 1977 ; Travis, 1984 ; Mahapatro & Dash, 1987 ; Tejedo & Reques, 1992) and we can expect that reproductive success of a female is inversely related to density of tadpoles in the spawning site. Tadpole density is expected to reach its highest level in the sites closest to the forest border. This second model shows how such a decrease of medium-sized and large-sized frogs. Tadpole density and migration distance are expected to interact in sharing the decrease in habitat quality as show in Fig.2C, thus separating the optimum migration distances for the three size classes.

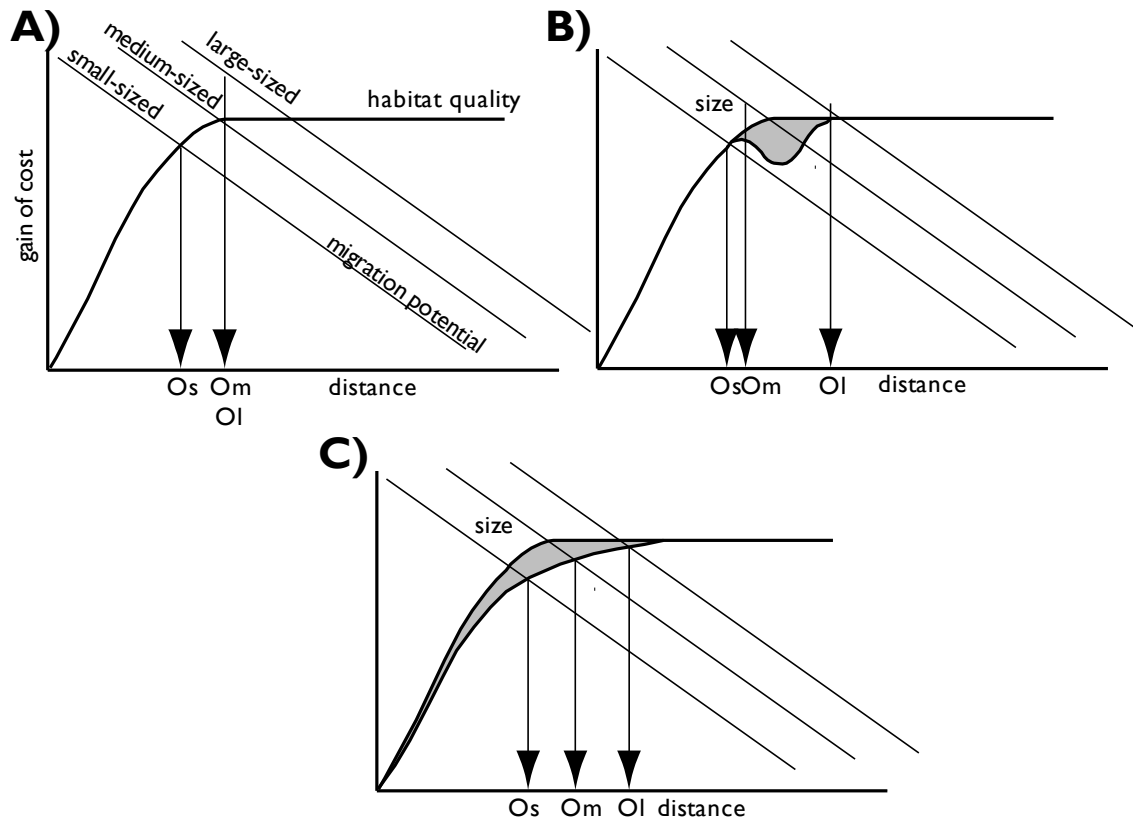


Fig. 2. Graphical optimization models explaining the relationship between migration distance and body size (expressed by clutch size). The model considers that habitat quality, and consequently expected fitness gain, increase with the distance to forest border until a limit beyond which habitat quality remains constant. Before reaching this limit, habitat quality is altered by accumulation of dead leaves, forest shade, and predation by fish. Migration potential represents the energetic investment in movement and mortality risk associated with movement. It is assumed to decrease linearly with the distance covered. The potential is higher in large-sized frogs because of higher movement capacity in large-sized animals. The optimum migration distance is the shortest migration distance maximizing the trade of between migration cost and gain in reproduction. In A, the optimum distance is similar in medium-size (O_m) and large-sized (O_l) frogs. In B, habitat quality is assumed to be altered by high tadpole density at the optimum distance estimated in A. As a consequence, optimum migration distances of medium-sized and large-sized frogs diverge. In C, interactions of tadpole density and migration constraints share the impact of density on the habitat quality curve (shaded area), defining new migration distance optima for each size class (O_s : optimum for the small-size frogs).

If such graphical models are useful in identifying testable hypotheses, models using evolutionary stable strategy (ESS) would predict more formally the fitness equilibrium under both constraints of tadpole density and migration distance.

If we expect a better survival and better growth rate of tadpoles in ponds far away from the forest border, a problem remains in the higher cost of the migration of the juveniles towards the forest than in closer sites. No data are available to evaluate such a cost, and we can assume that the benefits from growing in low density sites, such as reaching a greater body size than in high density sites, compensate for migration cost.

In contrast with these expectations, egg survival was lowest in the ponds furthest from the forest. We hypothesize that the peat substratum of these sites explains such mortality, because mortality was highest when the eggs were in contact with the peat. In single batches, only the lower eggs which were in direct contact with peat died. In this context, the spawning behaviour of the agile frogs that hung up their batches on midwater supports (stems, branches) proved to be adaptive. However, within the peat-bog of the Lavours Marsh, the ponds were not sufficiently deep to avoid contact of the batches hung up with the bottom. As a consequence, egg mortality was relatively high in these shallow sites (the mean depth where batches were laid was 25cm in the study of Kecskes & Puky, 1992). This result does not agree with the former conclusion according to which the frogs would benefit from spawning outside the fluvial forest. However, a conclusion to the advantage of migration would require a measure of tadpole growth and survival in the ponds where the frogs spawn. On the other hand, the presence of a large peat marsh in the vicinity of a fluvial forest is not very common in alluvial floodplains. More often ponds are the remnants of former channels and their bottom is made of alluvium rather than of peat.

Another difficulty results in disagreement between the hypothesis of optimization of migration distance and the hypotheses of philopatry or of site fidelity which are commonly accepted. However, philopatry still remains a matter of debate, because this concept has never been validated unequivocally in amphibians. Site fidelity has been experimentally evidenced only in few species (Joly & Miaud, 1989 ; Sinsch, 1992) and nomadic behaviour has also been demonstrated in other species (Fog, 1993). Site fidelity is expected to occur in iteroparous species in which migration mechanisms can use information gathered from previous reproductive events. In species where most individuals breed only once, such as *Rana dalmatina* (Guarino et al., 1995), other criteria than previous experience may prevail in migration guidance. On the other hand, despite an indeterminate growth, a positive relationship between age and body size has never been evidenced in frogs of the genus *Rana* (Gibbons & McCarthy, 1986 ; Augert, 1992). As a consequence, a larger body size does not suggest a previous experience of breeding migration.

The agile frog has been listed as an endangered species in Appendix II of the Bern Convention. This study contributes to the conservation ecology of this species in demonstrating the necessity of preserving together the fluvial forest and the ponds located within several hundred metres from the forest. Moreover, migration success needs high connectivity between ponds and forest. When ponds are lacking, they can be restored by dredging provided a sufficient connectivity with the forest is established.

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