

Temporal variability of spawning site selection in the frog *Rana dalmatina*: consequences for habitat management

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Abstract

Temporal variability of spawning site selection in the frog Rana dalmatina: consequences for habitat management.— We evaluated whether *R. dalmatina* females laid their eggs randomly within a pond or preferred particular microhabitats. The same measures were performed in the same area in two consecutive years to determine whether the pattern remained constant over time. In 2003, we observed a significant selection for areas with more submerged deadwood and vegetation, presence of emergent ground and low water depth. However, these results were not confirmed in the subsequent year when none of the microhabitat features measured had a significant effect. Although microhabitat features can strongly influence tadpoles, the temporal variability of habitat at this spatial scale suggests that habitat management could be more effective if focused on a wider spatial scale.

Key words: Amphibians, Habitat management, Microhabitat, *Rana dalmatina*, Reproductive site, Spatial scale.

Resumen

Variabilidad temporal en la elección de los lugares de freza de la rana ágil Rana dalmantina: consecuencias para la gestión del hábitat.— Evaluamos si las hembras de *R. dalmantina* ponían sus huevos al azar en una charca o preferían microhábitats particulares. Durante dos años consecutivos se realizaron las mismas mediciones en la misma área, para determinar si el patrón era constante a través del tiempo. En el año 2003 observamos una selección significativa de áreas con mayor cantidad de ramas muertas y otra vegetación sumergidas, con zonas del fondo emergentes y aguas más someras. Sin embargo, estos resultados no fueron confirmados al año siguiente, en el cual ninguna de las características del microhábitat medidas tuvo un efecto significativo. A pesar de que las características del microhábitat pueden tener gran influencia sobre los renacuajos, la variabilidad temporal del hábitat a esta escala espacial sugiere que la gestión del hábitat podría ser más efectiva si fuera proyectada según una escala espacial mayor.

Palabras clave: Anfibios, Gestión del hábitat, Microhábitat, *Rana dalmantina*, Lugar de reproducción, Escala espacial.

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Introduction

Oviposition habitat selection is a key determinant of reproductive success for many oviparous animals since it can affect important traits such as survival, development and growth rate of the offspring (Mousseau & Fox, 1998). In pond-breeding amphibians, oviposition habitat selection is a process that can occur at several spatial scales (Resetaris, 2005). At the largest spatial scale, females select the ponds that are in the most favourable landscape, not only because the features of terrestrial habitat are critical for the survival of post-metamorphic stages but also because landscape features can influence the characteristics of ponds (Skelly et al., 1999; Halverson, 2003; Semlitsch & Bodie, 2003; Porej et al., 2004; Marsh et al., 2005). At a smaller spatial scale, within a suitable landscape, frogs do not usually select breeding waterbodies randomly. Both field observations and experimental studies have shown that females attempt to lay eggs in ponds with fewer predators, with greater food availability, with lower desiccation risk or with optimal thermal and chemical features, thus increasing survival or growth rate of tadpoles (e.g., Petranka et al., 1994; Viertel, 1999; Binkley & Resetaris, 2003; Ficetola & De Bernardi, 2004; Resetaris, 2005; Rudolf & Rödel, 2005). However, ponds are not homogeneous environments. Within each wetland, many microhabitats can be recognised, with differences in important features such as water temperature and depth, distribution of animals and plants, and sun exposure. These differences may affect survival and/or growth not only of embryos before hatching but also of tadpoles after hatching. Data on the movements of tadpoles in nature are scarce. However, in a given wetland, tadpoles that hatch close to the more suitable microhabitats could be advantaged when compared with tadpoles that hatched far from suitable areas. This suggests a third spatial scale at which the selection of laying site can occur, that is the microhabitat within a given pond (Tarano, 1998). Knowledge of a selection pattern for a given microhabitat within wetlands could have important consequences for the management of amphibian populations. However, only a limited number of studies have studied whether amphibians lay their eggs randomly within a pond and evaluated the possible consequences of site selection (Jacob et al., 1998; Tarano, 1998).

In this study, we investigated whether, within a pond, the Agile Frog *Rana dalmatina* lays eggs in microhabitats with selected features. *Rana dalmatina* could be an excellent species to study within-pond spawning selection since their egg masses are easily identifiable and are usually fixed to the substrate, thus minimizing the risk of movements after the laying. Moreover, as *R. dalmatina* is an explosive breeder, temporal differences between laying dates of females are minimal, reducing the risk that differences in selection are caused by

temporal variation. Finally, *R. dalmatina* is a species that is rigorously protected in the European Union (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and wild fauna and flora) and wetland management is often performed to improve the survival of populations.

Methods

Rana dalmatina is a brown frog that is widely distributed in Central and Southern Europe. It inhabits deciduous forests from sea level to an altitude of about 800m (Grossenbacher, 1997). *Rana dalmatina* breeds in late winter-early spring in wetlands with stagnant water; each female lays a single egg mass that is usually fixed to the substrate (Nollert & Nollert, 1992). We studied a single *R. dalmatina* population breeding in a pond (diameter: about 50 m) within the "Ca'del Re" moor (Parco Regionale delle Groane, Lombardy, Northern Italy). The pond is generally permanent but can exceptionally be dry. A potential issue in studies analysing the relationship between species and habitat is their temporal stability. For the applicability of management studies, data need to be validated during subsequent intervals (Vaughan & Ormerod, 2005). We therefore collected the data in two subsequent breeding seasons (2003 and 2004) to evaluate whether the results obtained during one season can be generalized.

The number of *R. dalmatina* females breeding in this pond, estimated on the basis of egg masses, was 63 in 2003 and 72 in 2004. To improve its suitability for *R. dalmatina* and the Smooth Newt *Triturus vulgaris*, in 1998–2001 this wetland was subjected to habitat management (eradication of alloctonous plants; increase of wetland surface and depth) (Ferri et al., 2004). Two other species of amphibians are also present in this area, the Italian Tree Frog *Hyla intermedia* and the Pool Frogs belonging to the *Rana esculenta* complex.

In early spring 2003, we haphazardly selected 36 *R. dalmatina* clutches laid within this pond. To reduce spatial autocorrelation we allowed a minimum distance of 1 m between two selected clutches. We also randomly selected 29 further points. The minimum distance allowed between two random points or between a random point and a clutch was 1 m. Random points were selected along the pond banks, since all egg masses were laid close to banks. For each egg mass and for each random point, we measured eight environmental variables (table 1). A square frame (1 m²) divided by a 0.1 x 0.1 m grid was overlapped to each clutch and to each random point to improve measurement of environmental features. The same protocol was repeated in spring 2004 and we measured the microhabitat features of 20 clutches and 18 random points.

Table 1. Environmental features measured (average \pm SE).*Tabla 1. Características ambientales medidas (media \pm EE).*

Environmental features	Clutches		Random points	
	2003 (n = 36)	2004 (n = 20)	2003 (n = 29)	2004 (n = 18)
Slope of the nearest bank (0: < 30°; 1: < 45°; 2: > 45°)	0.69 \pm 0.12	0.11 \pm 0.11	0.52 \pm 0.14	0.20 \pm 0.12
Water depth (cm)	37.7 \pm 2.29	35.4 \pm 3.00	43.2 \pm 2.65	32.15 \pm 2.51
Distance from the woodland (m)	14.6 \pm 1.87	15.8 \pm 3.05	14.0 \pm 2.07	13.6 \pm 1.07
Number of submerged deadwoods (within the frame)	0.25 \pm 0.11	0	0	0
Submerged vegetation % (within the frame)	62.6 \pm 5.60	38.0 \pm 8.48	50.7 \pm 7.13	53.9 \pm 10.9
Emergent vegetation % (within the frame)	12.9 \pm 2.88	48.0 \pm 8.10	26.2 \pm 6.44	34.4 \pm 10.4
Emergent ground % (within the frame)	1.53 \pm 0.82	0	0	0
Submerged debris % (within the frame)	12.92 \pm 3.57	8.8 \pm 3.10	11.3 \pm 4.08	5.56 \pm 3.81

Data analysis

We used logistic regression to analyse clutch distribution, using likelihood ratio (i.e., the change in deviance if a variable is added to the model) to calculate the significance (Menard, 1995). We built all possible models including only significant variables, then ranked the models according to their AIC values (Burnham & Anderson, 2002). The model with the lowest AIC value accounted for the greater deviance on the basis of the smallest number of parameters. AIC was thus used to rank the models according to their performance (Rushton et al., 2004). Models differing less than 2 AIC units from the best model are usually considered good candidates (Burnham & Anderson, 2002). However, as all models differed > 3.6 AIC units from the best model, only the best model was considered and shown in the results. The logistic regression model was built using the data collected in 2003 and was validated using data collected in 2004. It was not possible to perform the inverse procedure since no significant models were built using data collected in 2004.

To avoid multicollinearity, we calculated pairwise correlation between variables in the two years, considering that the risk of multicollinearity arises if pairwise correlation among variables is > 0.7 (Berry & Feldman, 1985). For environmental data collected in 2003, the model was not biased by multicollinearity as all $|r|$ were $d \leq 0.6$. In 2004, we observed a strong, negative correla-

tion between the percentage of submerged vegetation and percentage of emergent vegetation ($r = -0.788$). However, as none of the variables were significant, multicollinearity could not be a source of bias.

We also used a *t*-test to determine whether pond features changed between 2003 and 2004. Only the features of random points were considered for this analysis. Approximated degrees of freedom were used if variances were not homogeneous between groups.

To meet the assumptions of parametric tests, if necessary data were transformed using arcsine-square root (percentage data) or natural logarithms (distance from the nearest woodland, density of submerged deadwood).

Results

We counted 63 egg masses in 2003 and 72 egg masses in 2004. In 2003, 35% of egg masses were isolated (no other egg masses at a distance < 1 m), while 65% of egg masses were aggregated in groups of 2–6 clutches. A similar pattern of aggregation was observed for a subset of 36 egg masses, for which we recorded the location in 2004 (table 2). The frequency distribution of aggregations was almost identical between the two years (Kolmogorov–Smirnov test, $Z = -0.120$, $P > 0.99$).

Our best model shows that, in 2003, clutch presence was positively associated to number of sub-

Table 2. Frequency distributions of aggregations of egg masses during 2003 and 2004: Ne. Number of egg masses per aggregation.

Tabla 2. Distribuciones de frecuencia de los agregados de masas de huevos durante los años 2003 y 2004: Ne. Número de masas de huevos por agregación.

Ne	Frequency	
	2003	2004
1	0.35	0.31
2	0.29	0.28
3	0.14	0.25
4	0.13	
5		
6	0.10	0.17
N measured	63	36

Table 3. Logistic regression model explaining *R. dalmatina* distribution: B. Logistic regression coefficients; Nsdw. Number of submerged deadwoods; Wd. Water depth; Sv. Submerged vegetation; Eg. Emergent ground; C. Constant.

Tabla 3. Modelo de regresión logística que explica la distribución de *R. dalmatina*: B. Coeficientes de regresión logística; Nsdw. Número de ramas muertas sumergidas; Wd. Profundidad del agua; Sv. Vegetación sumergida; Eg. Suelo emergente; C. Constante.

Variable	B	χ^2	d.f.	P
Nsdw	12.816	9.860	1	0.002
Wd	-0.062	6.318	1	0.012
Sv %	2.131	11.043	1	0.001
Eg %	24.503	5.695	1	0.017
C	0.348			

merged deadwoods within the frame, submerged vegetation % and emergent ground %, and negatively associated to water depth (table 3). The model explained 28.1% of null deviance and strongly suggested that *R. dalmatina* females do not lay eggs randomly ($\chi^2 = 25.153$, d.f. = 4, $P < 0.0001$).

In 2004, we did not detect the presence of deadwoods or emergent ground in the proximity of egg masses or in the random points (table 1); since these features were not variables we could not include them in the analysis. The model built in 2003 was not significant in 2004 ($\chi^2 = 2.516$, d.f. = 2, $P = 0.284$) and explained only 5% of the null deviance. Moreover, we failed to find any significant relationship between the distribution of egg masses in 2004 and the environmental features. The percentage of submerged vegetation was the variable showing the strongest relationship with distribution of egg masses, but this relationship was far from significance ($\chi^2 = 1.793$, d.f. = 1, $P = 0.240$).

Most pond features changed little between the years (table 4). In 2004 the pond tended to be shallower, but the random points did not differ significantly for water depth between the years. Moreover, pond banks were significantly less steep in 2003 (table 4). The complete lack of submerged woods and of areas with emergent ground in 2004 (table 1) suggests that a substantial variations for these two features occurred.

However, the difference for the model between 2003 and 2004 was not entirely due to the lack of submerged deadwoods and of emerging ground in the pond during the 2004 breeding season. To show this, we built a logistic regression model for data collected in 2003, without including the variables

submerged deadwood and emergent ground. After the exclusion of these two variables, both water depth ($\chi^2 = 6.698$, d.f. = 1, $P = 0.010$) and % of submerged vegetation ($\chi^2 = 6.061$, d.f. = 1, $P = 0.014$) had a significant effect on the distribution of egg masses. The model including only these two variables still explained 11% of null deviance.

Discussion

Our study showed a different pattern in the two years. In 2003, a strong relationship was observed between microhabitat features and distribution of the egg masses of *R. dalmatina*. This relationship could suggest *R. dalmatina* selects the area where eggs are laid and allows speculation about the potential importance of this process for the offspring. However, in the same area the relationship was not confirmed during the successive year. The lack of validation with the dataset collected in 2004 makes it more complex to interpret the significant pattern observed in 2003 and to test its applicability in management.

The pattern of laying site selection observed in 2003 can be interpreted in light of the influence that environmental conditions can have on the development of embryos and tadpoles immediately after hatching (see below). Preference for areas with abundant submerged deadwoods is easily explainable since *R. dalmatina* and several other brown frogs frequently fix their eggs to submerged woods. Fixing eggs could reduce the risk of drifting, and at the same time, fixing eggs under the water surface could reduce the risk of freezing on cold nights and preda-

Table 4. Comparison of features of random points between 2003 and 2004: results of *t*-tests. Degrees of freedom are not always integer since in some cases they were corrected to account the non-homogeneity of variance: Wd. Water depth; Bs. Bank slope; Sv. Submerged vegetation; Ev. Emergent vegetation; Sd. Submerged debris; Dw. Distance from woodland.

Tabla 4. Comparación de las características de los puntos elegidos al azar entre 2003 y 2004: resultados de los tests *t* de Student. Los grados de libertad a veces presentan decimales, dado que en algunos casos fueron corregidos para tener en consideración la no homogeneidad de la varianza: Wd. Profundidad del agua; Bs. Pendiente de la orilla; Ev. Vegetación emergente; Sd. Restos sumergidos; Dw. Distancia desde el bosque.

	<i>t</i>	d.f.	<i>P</i>
Wd	1.911	45	0.062
Bs	2.302	44.931	0.026
Sv %	-0.227	29.531	0.822
Ev %	-0.750	45	0.457
Sd %	1.272	45	0.210
Dw	-0.322	45	0.749

tion by ducks (Pozzi, 1980). As deadwoods were absent from the study pond in 2004 it was not possible to validate this relationship.

The association with shallow water might be explained by the different thermal conditions of these areas. In areas with lower water depth, the temperature rises more quickly on sunny days: a warm temperature increases the growth and development rate of both embryos and tadpoles (Bachman, 1968; Skelly et al., 2002); in turn, fast growth and development are believed to be important measures for the performance of embryos and larvae and frequently correlate well with their survival (Semlitsch, 2002 and references therein). Thermal conditions of the water have previously proven a major force influencing breeding site selection at both landscape and pond scale (Skelly et al., 1999, 2002; Ficetola & De Bernardi, 2004, 2005a). Association with areas of the pond with emergent ground could be explained on a similar basis. Finally, in areas with more submerged vegetation, tadpoles could find more food and greater shelter from large predators, such as fish. The association of *R. dalmatina* clutches with abundant vegetation has also been shown by Kescés & Puky (1992). However, an association with areas with abundant veg-

etation is not always favourable, since invertebrate predators (such as Odonata) can be more abundant in such an environment (Gunzburger & Travis, 2004). It should be noted that we measured only the distribution of egg masses, and not the survival pattern or tadpole growth. For a complete picture of the effect of the egg mass distribution on fitness it would be necessary to measure survival of eggs and tadpoles, and even their growth rate.

Behavioural interactions can also have important consequences on the distribution of egg masses. For example, Vieites et al. (2004) showed that mating pairs of the frog *Rana temporaria* are often followed by clutch pirates which try to fertilize eggs in the deposited clutches after deposition. On one hand, females may spawn only when relatively undisturbed by pirates, while on the other, they may gain benefits from pirates as such behaviour may increase the rate of fertilization of the eggs. This trade-off of interests may well influence the distribution of egg deposition and it is also likely to occur in *Rana dalmatina* (see K. Grossenbacher, unpublished video recording, cited in Hettyey & Pearman, 2003). Furthermore, at the peak of the breeding season *Rana dalmatina* males can form aggregation and choruses which may increase the likelihood of attracting females and then scramble-compete over approaching females, but later in the breeding season fewer males may be present and they may be distributed more randomly over the ponds, forming territories (Picariello et al., 2006). The distribution of males across the pond is strongly affected by these intraspecific interactions and probably plays an important role in the distribution of egg masses. As *Rana dalmatina* is the only species of brown frog breeding in this pond, interspecific interactions (see discussions by Petranks et al., 1994; Hettyey & Pearman, 2003, 2006; Ficetola & De Bernardi, 2005b, 2006) are not possible.

Surprisingly, the relationship observed in 2003 was not confirmed in the subsequent year even though the same sampling protocol was applied, and it is rather difficult that it occurs since during 2004 as we did not observe variation for two main features. Microhabitat features can be difficult to study, and at this spatial scale changes from the expected patterns are often seen (but see also Rudolf & Rödel (2005) for an example of model transferable in time). For example, Halverson et al. (2006) studied the distribution of tadpoles of the Wood Frog *Rana sylvatica* in two ponds less than 50 m apart. From the outcome of laboratory studies, it would be expected that tadpoles were aggregated in kin groups (Blaustein & Waldman, 1992). However, Halverson et al. (2006) observed an aggregated distribution of kin groups in only one of the two ponds, and found an opposite pattern in the second pond, with kin tadpoles more distant than would be expected if they were randomly distributed. This suggested that the optimal distribution of tadpoles can be context dependent and strongly modified by microhabitat variations. In our study, the absence of relationships might be caused by

the change in pond features over the two years. In 2004 the pond was shallower and slightly smaller, and no deadwoods were present. Nevertheless, the number of egg masses laid did not decrease between the years, suggesting that these changes in microhabitat did not have a major effect on the reproductive output of *R. dalmatina*.

Differences between years in tadpole performance are possible but these were not investigated in the present study. The contradictory results between the two years suggest that a larger sample is needed (higher number of oviposition sites collected over more years), as pond microhabitat features show a wide variation. Moreover, sampling more ponds would be necessary to evaluate whether the results are consistent across space.

Non-random choice of egg deposition site within breeding ponds has been demonstrated for several amphibians, including the Newt *Triturus marmoratus* and the anurans *R. dalmatina*, *R. temporaria* and *Physalemus pustulosus* (Ancona & Capietti, 1996; Jacob et al., 1998; Tarano, 1998). However, interpretation of relationships at this spatial scale can be difficult as patterns are not always confirmed in successive periods. Small environmental variations can partially explain the difficulty in finding a general pattern. Lack of a clear pattern and fast variation of microhabitat features with time can hamper the use of this information for habitat management (Wittingham et al., 2003). Indeed, actions performed at a microhabitat level can be quickly neutralized by natural events such as changes in precipitation or in the growth of vegetation. We therefore suggest concentrating the management effort at the largest spatial scales (pond and landscape) as these suffer less temporal instability. Features at the largest spatial scale can influence those at the smaller scale; the presence of surrounding woodlands, for example, can influence the presence of deadwoods but also the chemical and physical features of the waterbodies (Kiffney et al., 2003; Ficetola et al., 2004). Analogously, the introduction of fish can modify other features such as turbidity and the distribution of vegetation (Sheffer et al., 1993). Acting at the largest spatial scales could therefore provide more effective results for the management of amphibian populations.

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