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RESEARCH PAPERS

Communal Spawning in the Common Frog *Rana temporaria* – Egg Temperature and Predation Consequences

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Abstract

Females of the common frog, *Rana temporaria*, spawn synchronously at communal breeding sites, forming a communal egg mass of individual spawn clumps. A total of four spawning sites were studied. In the centre of the communal egg mass, daily maximum temperature was higher and minimum temperature lower than further out. Spawn clumps in the centre of the communal egg mass developed faster than single spawn clumps. In the centre of the egg masses, some spawn clumps suffered almost total egg mortality. This was probably the consequence of a cold spell with sub-zero temperatures in combination with a tendency for low minimum temperatures in the centre. In a laboratory study, worm leeches, *Erpobdella* spp., fed readily on eggs of common frog, while horse leeches, *Haemopis sanguisuga*, hardly ate any eggs. At the spawning sites, most worm leeches were found in single spawn clumps, far from the communal egg mass. Females which spawned late, when most of the spawning was over, preferred to spawn in the centre of the communal egg mass. This suggests that there is a net advantage for eggs in spawn clumps laid in the centre.

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Introduction

Frog species in temperate regions that breed early in spring often do so explosively and the females deposit their individual spawn clumps in communal egg masses (Wells 1977; Arak 1983). The reason for this temporal and spatial aggregation could be related to mate choice. If females passively choose males, they can do this by moving to the strongest source of conspecific cues (Parker 1983), e.g. calling males. There they are likely to mate with the competitively strongest males. This means that they will aggregate in space and time (Madsen 1987). However, the adaptive reason for aggregated female breeding may be related to something different from mate choice, as there could also be advantages for the offspring if eggs were deposited in a communal mass. A large egg mass

may confer advantages like better thermoregulation (Waldman 1982) and predator defence, either mechanically or through predator swamping (black headed gull *Larus ridibundus*: Kruuk 1964; *Hyla regilla*: DeVito et al. 1999).

This study deals with the common frog, *Rana temporaria*, which is an explosively breeding species. The males arrive first at the spawning site and the females later (Ryser 1989). The spawn clumps, one per female (Griffiths & Raper 1994), each containing about 1000–2500 eggs (Loman 2001), are usually deposited in a communal egg mass. Most of the spawn is deposited within 2 or 3 d, although some new spawn clumps can be found several days later (Elmberg 1990). Rarely, females also lay their spawn clumps singly.

This study investigates the effects of egg performance related to clump position in a communal egg mass. If such differences exist, this may be one ultimate explanation for the existence of communal egg masses. We studied the effects of egg survival and development, comparing differences in conditions for and performance of central, peripheral and single spawn clumps of the common frog *R. temporaria*. We studied the maximum and minimum temperatures, development time, leech predation and embryonic survival.

We also studied female spawn site choice, within breeding site. This could provide evidence of a mechanism, different from mate choice, that contributes to the large egg masses observed in this species.

Methods

Study Ponds

During the spring of 1992, we studied spawning sites at three small ponds 10–20 km to the east of Lund in southern Sweden (55°40′N, 13°30′E). There was one spawning site in each of two ponds and one pond where there were two (3:1 and 3:2). Spawning in the study ponds began between 3 and 11 April (Table 1). The total number of spawn clumps deposited at the studied spawning sites varied between 44 and 229.

Air Temperature

The daily maximum and minimum air temperatures for April 1992 were taken in Lund by the official meteorological station (SMHI 1992). The daily

Table 1: First and last spawning date and number of spawn clumps in the study ponds

Pond	Site	Day of first-laid spawn clumps	Day of last-laid spawn clumps	Number of spawn clumps
1	1	3 April	14 April	229
2	2	7 April	15 April	112
3	3:1	11 April	14 April	80
3	3:2	11 April	13 April	44

maximum temperature varied between +8°C and +16°C and the minimum night temperature varied between −3°C and +9°C. Only on the nights of 17, 18 and 21 April (after the last spawning and also hatching of the first laid eggs) did temperatures drop below zero.

Marking and Relocation of Spawn Clumps

We visited the ponds daily from 3 April until all spawning had ceased (Table 1). On each day we marked and relocated a sample of 12 new spawn clumps at each site, or, if there were fewer new ones, all new. This was done by placing each spawn clump inside an elastic hair net. Mesh size of the net while extended in use was about 5 mm. The nets were tied around the masses, but loose enough to allow them to swell. Nets were made of thin thread and hence clumps were in complete contact with each other. The spawn clumps treated this way appeared to develop naturally. The hairnets around the new spawn clumps were closed with coloured elastic bands. The colour combination used were unique for each day. Three of the newly marked spawn clumps were then placed in the centre of the communal clump, three at the periphery, and three were placed singly, close to the communal clump (Fig. 1). These single spawn clumps were placed < 2 m from the communal spawning site. These three positions were used to compare temperature, survival and development time. Finally, three more clumps, if available, were placed singly and further away (> 4 m) from the communal mass. These clumps were termed single, distant spawn clumps and

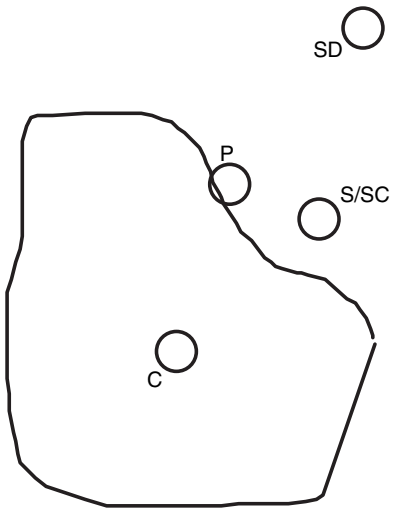

Fig. 1: Positions of relocated clumps. C: central (at or close to the geometric centre of the communal egg mass), P: peripheral (outside but touching the communal egg mass), S/SC: (< 2 m from communal mass) single or single, close, SD: (> 4 m from communal mass) single, distant (only used for predator recording)

were only used to compare the leech predation rates with that for clumps in the other three positions. Relocated spawn clumps were placed, and remained, close to the water surface. This mimicked the position of most spawn in their original place.

Spawn Clump Temperature

The maximum and minimum temperatures for each 24-h period were measured for a duration of 6 d at spawning site 1, 5 d at spawning site 2, and 3 d at spawning site 3:1. At each site, two thermometers were placed in central, two in peripheral and two in single spawn clumps close to the communal mass. For each site and position, the mean reading of the two thermometers was used. The temperature was measured in the middle of each spawn clump. The water depth at the measuring points varied among the ponds, from 15 to 24 cm, but not among positions within ponds. We also analysed the average of the maximum and the minimum temperature, assuming it to be an approximate index of daily average temperature.

Embryonic Survival

We studied embryonic survival in the relocated clumps in all ponds. In some spawn clumps none, or very few eggs ($< 5\%$), hatched. In all other clumps $> 90\%$ of the eggs hatched. The proportion of such low survival spawn clumps was compared among marked spawn clumps in the centre, periphery and single clumps close to the communal egg mass.

Development Time

We noted the time for hatching of the eggs in relocated spawn clumps. A spawn clump was considered to have hatched when approximately half of the eggs in it had done so as it took 1 or 2 d for all the eggs in an spawn clump to hatch. The development time was compared among the three positions: central, peripheral and single clumps close to the communal egg mass.

Leech Predation

Leeches were found only in ponds 2 and 3. In pond 2 there were only worm leeches, *Erpobdella* spp., while in pond 3 only horse leeches, *Haemopis sanguisuga* were found.

We counted the number of leeches in relocated spawn clumps at four positions: central, peripheral, single (close to the communal mass) and single (distant) for a duration of 4 d (13–16 April) in pond 2 and 6 d (13–16, 21 and 24 April) in pond 3. The average number of leeches per spawn clump was taken and compared among the four positions.

To determine if the leeches actually feed on frog eggs, 16 leeches of each species were placed in glass containers with eggs of common frog. We used four containers, each containing four worm leeches, and seven containers, each containing two to three horse leeches. Twenty eggs were placed in each container. This meant they had free access to eggs but no alternative food. After 7–11 d we counted the number of remaining eggs and calculated how many eggs a leech of each species on average had eaten per day.

Individual Spawning Place within the Spawning Site

To determine the preferred location of the late-spawning females, we determined each day, at each spawning site, the position of all new and all old spawn clumps using a grid system. This was done by placing a wooden frame with a 1 dm wire grid over the spawning site. Each corner of the frame rested on a permanent support stick secured to the bottom of the pond. Between registrations, we removed the frame so as not to disturb the frogs. The supports made it possible to return the frame in the same position each day. New spawn clumps were easy to detect as they are not expanded to full size until the second day. Each day, or each period of 2–6 d (if there were none or very few new spawn clumps per day), the distance to the edge of the communal egg mass for the new spawn clumps was measured and compared with the corresponding distance for the old spawn clumps (Fig. 2). This activity did not interfere with normal breeding that mainly took place at night.

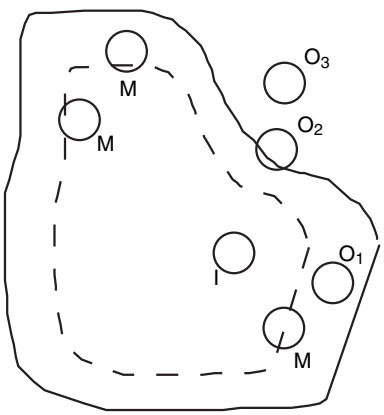

Fig. 2: Recording the position of naturally laid new clumps. The outline of the communal egg mass, as formed by all old clumps, is shown with the continuous line. The dashed line is drawn at the median clump distance from the periphery, based on all old clumps. Thus the number of old inner clumps is the same as the number of old outer clumps laid between the median line and the outline of the communal egg mass. I: Inner clump, a new clump laid in the inner part of the communal egg mass. M: New clumps laid as far inside the periphery as the median distance for old clumps. All clumps touching this line were so classified. O1–O3: outer clumps, new clumps laid outside the median line

The females that were considered 'late females' were those that spawned 1 d or later after spawning began at each site. As most of the spawn clumps were deposited already on the first day, these late females were the ones that most obviously had a choice of choosing a relative position in the communal egg mass for their spawn clumps.

Results

Spawn Clump Temperature

The maximum (day) temperature differed among the three positions [three-way ANOVA with the factors position, spawning site and date (nested under spawning site), $F = 30.8$, d.f. $= 2, 60$, $p < 0.001$]. It was significantly higher in the centre than in the periphery ($p < 0.001$) and single ($p < 0.001$) spawn clumps (Tukey's post hoc test). The difference between peripheral and single clumps was not significant ($p = 0.60$) (Table 2).

In addition, the minimum (night) temperature differed significantly among the three positions [three-way ANOVA with the factors position, spawning site and date (nested under spawning site), $F = 6.9$, d.f. $= 2, 60$, $p = 0.002$]. This temperature was significantly lower in the centre than in the peripheral ($p < 0.018$) and single ($p < 0.002$) spawn clumps (Tukey's post hoc test). The difference between peripheral and single clumps was not significant ($p = 0.64$) (Table 2).

The average temperature differed significantly among the three positions [three-way ANOVA with the factors position, spawning site and date (nested under

Table 2: Diel maximum and minimum temperatures (°C) and their average for spawn clumps in different positions at three spawning sites

Spawning site	Centre	Periphery	Single
1			
Max	15.1 (4.8)	13.7 (4.7)	13.2 (4.7)
Min	4.6 (2.0)	5.4 (2.0)	4.7 (2.1)
Avg	9.8 (3.3)	9.6 (3.3)	9.0 (3.2)
2			
Max	19.2 (2.8)	16.3 (2.2)	15.7 (1.7)
Min	1.7 (1.6)	1.9 (1.3)	2.9 (1.1)
Avg	10.4 (1.1)	9.1 (1.3)	9.3 (1.0)
3:1			
Max	14.6 (2.1)	13.3 (1.6)	13.1 (1.6)
Min	5.9 (1.7)	6.3 (1.3)	6.9 (0.9)
Avg	10.3 (1.7)	9.8 (1.3)	10.0 (1.2)

Values are in mean (SD).
Each value is based on the mean of two spawn clumps and the average for 3–6 d, depending on the site.

spawning site), $F = 13.5$, d.f. $= 2, 60$, $p < 0.001$]. Because differences among daytime temperatures were larger than those among nighttime temperatures, the average of the two was highest for central spawn clumps, being significantly higher than for both periperal ($p < 0.001$) and single ($p < 0.001$) spawn clumps (Tukey's post hoc test). The difference between these was not significant ($p = 0.95$).

Development Time

Central spawn clumps tended to develop faster than the peripheral ones, which in turn usually developed faster than those outside the communal egg mass [three-way ANCOVA with the factors position, spawning site and date (nested under spawning site), $F = 16.8$, d.f. $= 2, 86$, $p < 0.001$; Table 3]. A Tukey's post hoc test showed that the differences were significant between single and peripheral ($p = 0.001$), single and central ($p < 0.001$) but not between peripheral and central clumps ($p = 0.49$).

Embryonic Survival

The proportion of spawn clumps with few surviving eggs was higher in the centre than at the periphery and for single egg masses (Fig. 3). The effect of position was tested by a logistic regression model that also accounted for effects of pond and laying date. This showed that the effect of position was significant ($\chi^2 = 35.7$, d.f. $= 2$, $p < 0.001$). The proportion of low-survival spawn clumps in the centre changed during the spawning period. Only among spawn laid from 8 April and later were such clumps found (Fig. 4).

Leech Predation

In the laboratory, the worm leeches ate, on average, 0.125 eggs per leech per day (together the 16 worm leeches ate 16 eggs during the test period) while the horse leeches ate only 0.006 eggs per leech per day (together the 16 horse leeches ate one egg during the test period).

The number of worm leeches differed among spawn clumps in the four positions. There were more leeches in single, distant spawn clumps (>4 m outside

Table 3. Development time (days) for spawn clumps in different positions

Spawning site	Centre	Periphery	Single
1	10; 10.0 (1.1)	15; 11.1 (1.6)	16; 13.4 (1.5)
2	6; 11.8 (1.0)	8; 11.8 (1.5)	7; 12.7 (1.0)
3:1	9; 13.6 (0.5)	11; 14.5 (0.9)	12; 14.8 (0.6)
3:2	5; 14.6 (0.5)	5; 14.8 (0.5)	5; 14.6 (0.5)

Values are in n; mean (SD), respectively.
The values are the average of all marked spawn clumps in each spawning site.

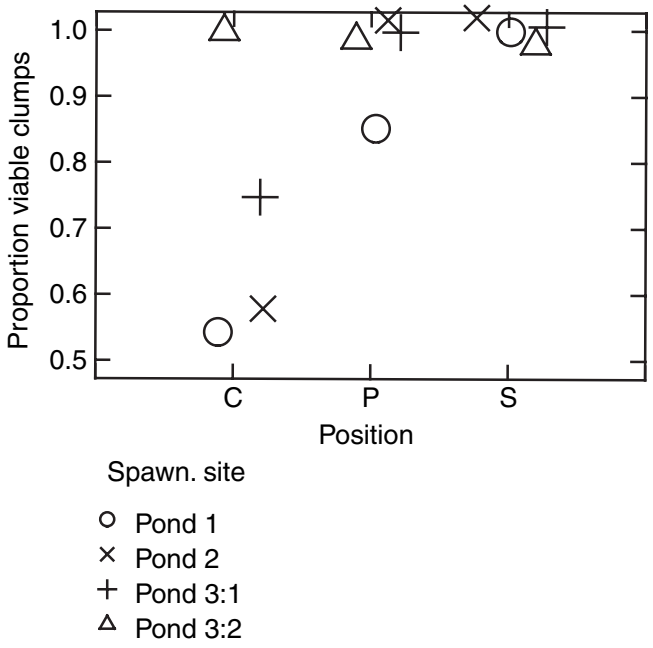

Fig. 3: Viability of spawn clumps in central, peripheral and single positions (Fig. 1). Viable clumps are those with >90% hatching eggs. All other had <5% hatching eggs. Symbols are slightly dislocated to avoid overlap

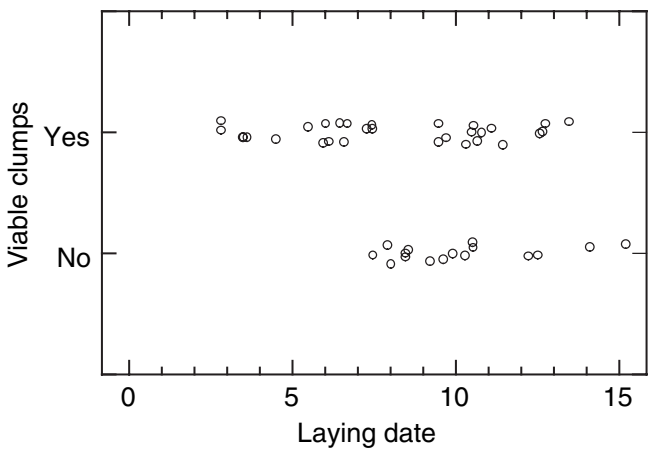

Fig. 4: Embryonic survival for spawn clumps in the centre of the communal egg mass during the spawning period (ponds 1–4). Symbols are slightly dislocated to avoid overlap. 'Viable' means that >90% of eggs hatched and 'no' that <5% did so. Symbols are slightly dislocated to avoid overlap

the communal egg mass) and successively fewer in single close spawn clumps (< 2 m from the communal egg mass), in peripheral and in central clumps (one-way ANOVA, $F = 36.9$, d.f. = 3, 33, $p < 0.001$; Fig. 5). A Tukey's post hoc test indicated that single, distant clumps had significantly more leeches than those at all other positions (single distant–single close, $p = 0.033$; single distant–peripheral, $p = 0.005$; single distant–central, $p = 0.001$). The other differences were not significant. The number of horse leeches did not differ among the four positions (one-way ANOVA with the factor position, $F = 0.85$, d.f. = 3, 55, $p = 0.47$; Fig. 5).

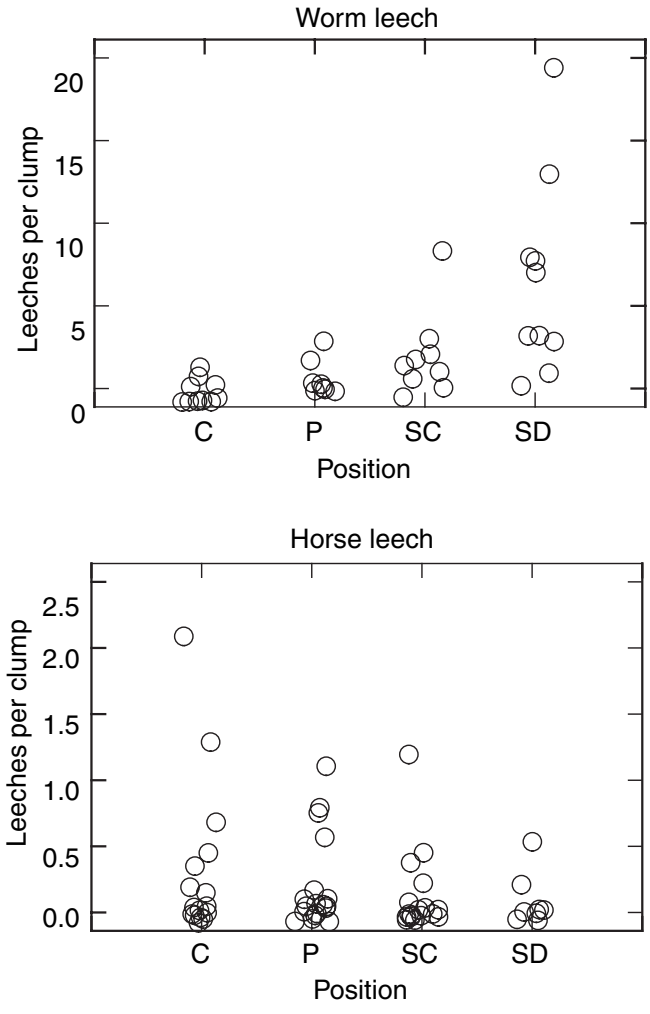

Fig. 5: Average number of leeches in spawn clumps in different positions (pond 2). C, central; P, peripheral; SC, single and close to egg mass; SD, single and distant. Symbols are slightly dislocated to avoid overlap

Individual Spawning Place within the Spawning Site

Late frogs tended to spawn on top of the already laid spawn. Of all 198 new clumps recorded, 95 were closer to the centre than the median value for all old clumps already present at the site (inner clumps), 61 were at the median distance and the remaining 42 were closer to the periphery (outer clumps). Of those 42 outer clumps recorded, only 10 were actually at (touching, Fig. 2, O2) the periphery and only four were recorded singly outside the communal egg masses. The remaining 28 were inside the communal egg mass, outside the median line (Fig. 2, O1). There was a variation among sites in this pattern ($\chi^2 = 16.2$, d.f. $= 4$, $p = 0.003$, the test excludes the site with the lowest number of new clumps recorded). The tendency was least pronounced at the largest spawning site (site 1) (Table 4). At all sites there were more 'inner' than 'outer' new clumps. Testing the three sites used for the chi-squared test separately, there was actually a significant tendency for new clumps to be closer to the centre than the median distance of those already present at two of the sites (Table 4).

Discussion

Spawn Clump Temperature

The maximum temperature was higher in clumps at the centre of the communal egg mass than it was in those further out. The difference was largest at the spawning sites in pond 1 and 2, which were the two with most spawn, but it was also present in the small spawning site 3:1. During the day, frog eggs receive conductive heat from the warm air, and they also act as black bodies, receiving heat from solar radiation (Seale 1982) and they produce metabolic heat [Savage 1961; Hassinger 1970 (in Howard 1980)]. These factors contribute to an increase in temperature. Restrictions of water movement around central spawn clumps can

Table 4. Location of new clumps relative to that of those already present at the site

Site	Inner	Median	Outer	p-value
1	45	22	32	0.167
2	22	14	8	0.016
3:1	26	19	2	0.001
3:2	2	6	0	

'Inner' means that the new clump is farther from the periphery and closer to the inner centre than the median distance for clumps already present; 'median' means that it is at the median distance and 'outer' that it was closer to the outer periphery (or outside the periphery) (Fig. 2).

p-values are for two-tailed binomial tests, computed according to Siegel & Castellan (1988) and based on 'inner' and 'outer' only, disregarding ties (median clumps). There are too little data for meaningful tests at site 3:2.

further enhance temperature elevations within them [Licht 1971; Howard 1980 (in Seale 1982)]. Actually, the combination of conductive and radiation heat did lead to jelly temperatures above that of the air (Table 2). Single spawn clumps, however, lose much of the incoming heat to the surrounding water and thus did not become much warmer than the water. Therefore a larger communal egg mass should have greater temperature differences among different positions than a small one. Indeed, in this study the small spawning site 3:1 had the smallest temperature differences.

The nighttime temperatures were lowest in the centre of the communal clump. At night, the air temperature is usually lower than the water temperature. The spawn clumps float very close to the water surface and they lose heat to the cold air by conduction and they also lose heat by radiation. If a spawn clump is close to the water surface, the part of it that is in contact with the air is probably equal to spawn clumps in different positions. Thus, the amount of heat loss by conduction to the air and radiation does not differ much between spawn clumps in different positions. Single and peripheral spawn clumps seem to be less insulated from the surrounding warmer water and therefore they did not become much colder than the water. Central spawn clumps were, however, apparently insulated from the surrounding water by the communal egg mass. Thus, they lost heat to the air without receiving heat from the surrounding warmer water, and therefore, they could cool below the water temperature.

The temperature differences in different locations may affect the development time of eggs and also have impact on adult frogs breeding there. A high temperature may increase mobility which is beneficial in the case of a predator attack. However, much of the breeding takes place at night which does not support this explanation for the preference for spawning in central positions. The direct measurements of development time in this study supports the first possibility, an effect on egg development. This is especially likely if development rate increases progressively with increasing temperature as found for *R. temporaria* by Beattie (1987). If so, the surplus daytime temperature in the centre of the egg mass will more than offset the nighttime deficit here.

Others have also found higher temperatures in the central spawn clumps in communal clumps of frog spawn (Guyétant 1966; Howard 1980; Waldman 1982; Waldman & Ryan 1983). After hatching, tadpoles of the common frog aggregate on top of the egg mass. This concentration of black tadpoles in a communal mass results in an elevated temperature (Malkmus 1982). Another evidence that communal breeding may have evolved to take advantage of this temperature effect comes from the behaviour of the southern leopard frog, *R. sphenocephala*. This species has two breeding seasons. In the warm breeding season in autumn, the spawn clumps are laid singly, while in the cold breeding season in spring, the spawn clumps are laid in a communal egg mass (Caldwell 1986). Sjögren et al. (1988) showed that pool frogs *R. lessonae* prefer breeding in the warmest part of a pond. Indeed, this part may change position over time within a season and the breeding site differs accordingly. Moreover, this finding stresses the importance of an optimum temperature for the eggs.

Development Time

The development time was shortest in the centre of and longest outside the communal egg mass. This is probably because of the fact that average temperature was highest in the centre as frog eggs develop faster at higher temperatures (to a limit) (Beattie 1987). If development rate increases progressively (Beattie 1987) with increase in temperature, it is evident of the contribution of the high maximum temperatures at the centre.

Embryonic Survival

The proportion of spawn clumps with low egg survival was highest in the centre and lowest among single spawn clumps. This may be due to the extreme temperatures in the centre; it is possible that the eggs could not survive too high and/or too low temperatures. In the present case, the low, sub-zero, temperatures in the middle of April may have been harmful. This is supported by the fact that only clumps laid after 8 April suffered catastrophic mortality. Most eggs laid before that date had already hatched by the time of the start of the cold spell, 17, 18 April. The temperature measurements showed that nighttime temperatures were lowest in the centre of the egg mass. This would especially affect late spawning female's egg mass that was placed more or less on top of older spawns, increasing exposure to air and low nighttime temperatures. This may explain why almost all catastrophic mortality affected central spawn clumps. If this is true, central positions may occasionally, in case of extreme cold spells, be disadvantageous. However, temperature need not be the only factor that influences hatching success. Licht (1971) (in Seale 1982), suggests that oxygen availability could become an important limiting factor in large egg aggregates. It is possible that spawn clumps in the centre are not only indirectly affected by heat, but also directly by oxygen shortage. When water temperature is high, the water may contain less oxygen. It is also possible that the centre contains less oxygen late in the season, not because of the heat, but because the developing embryos have used up most of the dissolved oxygen.

A result similar to ours was found by Kiesecker & Blaustein (1997). They found higher egg mortality in communal breeding species (*Bufo boreas* and *R. cascadae*) than in species that deposits egg clumps singly (*H. regilla*). Within the comunally breeding species, mortality was higher for egg in clumps at the communal mass than for those found adjacent or at a distance. They attributed the effect to infection by pathogenic fungi. There were no evidence for this in the present study. Guyétant (1966) found that eggs at the bottom of a communal mass (probably at the bottom of the pond) developed slower and speculated, as did we, that oxygen depletion might negatively affect the eggs. However, also in this case, temperature effects are a plausible explanation.

Predation

As shown by the laboratory study, at least the worm leeches feed on eggs. The communal egg mass, however, seemed to give a rather good protection against such predation. Very few leeches of this species were found in the centre of the egg mass. However, this was also true for clumps at the periphery of or outside but close to the egg mass. Therefore, apart from physical protection, the difference in leech number per spawn clump may provide a predator swamping advantage (Kruuk 1964; Duncan & Vigne 1979). In particular, this holds for the difference between single, distant and single close spawn clumps. Isolated spawn clumps are more exposed to predators than are spawn clumps at the communal clump, which are protected both by predator swamping and, possibly, physically by surrounding masses (Jennings & Schaefer 1978; Henrikson 1990; Majecki & Majecka 1998).

The feeding habits of the horse leeches were less clear. It is possible that this species did not thrive in the laboratory conditions and therefore refused to eat. Actually, Kwet (1996) reports it as a predator on toad (*B. bufo*) eggs. It is also possible that this species does not normally feed on *Rana* eggs but was attracted to the spawning sites by the presence of adult frogs. In pond 3 where this species lived, we found an unusually high number of dead frogs, all with attached horse leeches. On some of the dead frogs, there were as many as 12 horse leeches feeding. We could not, however, determine whether the frogs had died from a leech attack or if the leeches fed only on already dead frogs. The communal egg mass is obviously not a very good protection against horse leeches. Horse leeches are considerably larger than worm leeches and may therefore find it less difficult to penetrate among the spawn clumps. It is, however, possible that leeches of this species are found at the centre, not because of the eggs, but to feed on adult frogs and therefore are not important in the point of view of egg survival.

Predation on anuran eggs has been described in other studies. Leeches of the species *Macrobdella decora* feed on eggs of wood frogs, *R. sylvatica* (Cory & Manion 1953) and bull frogs *R. catesbeiana* (Howard 1978). Majecki & Majecka (1998) report predation of caddis fly larvae on *Rana* eggs. Newts (*Triturus* sp.) have been reported to feed on frog's eggs (Kwet 1996; Zahn 1997). Larger tadpoles have also been found to feed on anuran eggs (Banks & Beebee 1987; Petranka & Thomas 1995). The latter authors also suggested that the synchronous breeding of *R. sylvatica* was an adaptation to reduce cannibalism. However, this does not also explain the spatial concentration of, e.g. *R. temporaria* breeding.

There are even more predators on tadpoles than on eggs (Lardner & Loman 1995). To the extent that the communal egg mass protects the eggs by predator dilution, as suggested above for worm leeches, this does also apply to the protection of tadpoles during their first days of life. During this time they stay on top of the communal egg mass (P. Håkansson & J. Loman, pers. obs.), as also reported for *R. sylvatica* by Thurow (1997).

Individual Spawning Place within the Spawning Site

The females seemed to prefer spawning at the centre of the communal egg mass. This supports the idea that there is some advantage associated with the centre for their eggs and tadpoles. The high maximum temperature and resulting short development time for the eggs may be one important factor favouring central spawn. If the eggs develops fast, they are available to predators for a shorter time and also run less risk of being stranded on the shore in case of warm and dry weather. This is not an uncommon source of egg mortality in the study area (Jon Loman pers. obs.). Another advantage for eggs placed in the centre is protection from predators (Jennings & Schaefer 1978; Henrikson 1990; Majecki & Majecka 1998). However, in the present study, hatching success was lower in the centre, but this may be compensated for by the other advantages. It is also possible that this low hatching success was not typical, but was an effect of the exceptional cold spell on 17 and 18 April.

It is noteworthy that Waldman (1982), like us, found the central positions most favourable for spawn of *R. sylvatica* but in that study late spawn was simply added to the periphery of the existing egg mass. In the present study, however, late-spawning females actually chose to spawn in the, apparently favourable, centre of the communal egg mass.

Communal Spawning: an Adaptation for Mate Choice or Offspring Care?

What is the ultimate force behind communal spawning? If the communal spawning of the common frog is related to mate choice, one may argue that late females spawn centrally because the males are already there or because a central position facilitates aggregation of more prospective mates, supporting passive mate choice (Madsen 1987). However, having attracted a suitable male, females have no reason to spawn at any particular position among the already laid spawn clumps. Even if they actually chose their mate centrally, they are free to move to any position while in amplexus. For this reason, we favour offspring care as an explanation for communal spawning in *R. temporaria*.

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