

Intraspecific variation in calling, time allocation and energy reserves in breeding male common frogs *Rana temporaria*

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Time allocation during breeding was studied in unmated male common frogs *Rana temporaria* Linnaeus in three populations along a gradient of altitude, climate and length of feeding season. The length of the breeding period decreased with increased altitude. All three populations had low activity levels (0–33% of the time during peak chorusing). Peak chorusing in the lowland population was due to more males participating in the chorus, and not to increased individual calling activity. An increase in mating effort at this time was nevertheless indicated by the males' using more time for moving in the pond. At both montane localities, males called more sparsely, and not at all at night. During peak chorusing, calling and moving males became significantly rarer with increased altitude. Aggressive males were significantly rarer in the alpine population. Between-locality variation was evident in fat reserves after hibernation and during breeding; the relative fat body mass was significantly higher in lowland males than in mid-altitude and alpine males. We discuss male mating activity (here: calling, mate searching and aggression) in ultimate terms as a trade-off between mate acquisition and survival.

1. Introduction

Survival and reproductive success depend on how efficiently time is allocated to various activities. In this respect, seasonal environments produce strong selective forces acting upon individual behavior (e.g. Schoener 1971, Lundberg 1985). At high altitudes and latitudes, the seasonal variation in resource availability (e.g. food) is particu-

larly pronounced, which causes an annual activity such as breeding to be rather restricted in time. In this type of environment anurans breed during a relatively short period in spring.

The geographic range of some anuran species is wide, covering a multitude of environmental conditions. When regional differences exist in light regime, length of breeding and feeding seasons, and in food availability and predation pres-

sure, we may expect intraspecific differences in breeding behavior to occur. *Rana temporaria* is a suitable species in which to look for such effects, since it occurs from northern Spain to subarctic Scandinavia, breeding from January to June within this range.

Previous studies of other anuran species show that males which call more actively may enjoy greater mating success (e.g. Whitney & Krebs 1975, Gatz 1981, Sullivan 1982, 1987, Forester & Czarnowsky 1985, Klump & Gerhardt 1987). Thus, calling and other activities (e.g. moving) facilitating contact with potential mates might be positively correlated with reproductive success, at least in the current year. However, more active males may have an increased risk of mortality, due to depletion of the body energy reserves acquired during the previous summer and autumn. Moreover, depleted reserves may be difficult to replenish in environments with little food or a short feeding season, which in turn may lower the chances of survival during the following hibernation. Hence, at the ultimate level, there is a trade-off between costs and benefits associated with male mating activities.

We studied the patterns of time use during breeding in male *Rana temporaria* at three sites in north-central Sweden, comprising a gradient with respect to altitude, climate and length of feeding season. We predicted that males at the alpine locality would emerge from hibernation with lower energy reserves, and that they would use less time for mating activities than males at the lowland locality, where the feeding season is longer.

Wells (1977) classified *Rana temporaria* as an "explosive breeder", its breeding season generally lasting 12–24 days (e.g. Curry-Lindahl 1946, Günther 1969, van Gelder & Hoedemaekers 1971, Arak 1982, Elmberg 1990). A peak chorusing period lasting roughly a week is preceded and followed by periods of low to moderate chorusing activity (Curry-Lindahl 1946, van Gelder & Hoedemaekers 1971, Elmberg 1990). Spawning generally occurs during peak chorusing (Geisselmann et al. 1971, van Gelder & Hoedemaekers 1971, Elmberg 1990, but cf. Haapanen 1982).

Elmberg (1990) showed that the peak chorusing period of *Rana temporaria* also coincided with the peak number of males present in the breeding pond. A second purpose of the present study was

to find out if the peak in chorusing is correlated with increased individual calling activity (and thus not only the result of more males in the chorus).

2. Material and methods

Males of *Rana temporaria* were studied at three permanent breeding sites in northern Sweden:

- 1) Tvärån (lowland, 1988). A 300 m² stagnant pond rich in vegetation, located in a deciduous woodlot in an urban residential area (see Elmberg 1986 for a more detailed description).
- 2) Järnforsen (mid-altitude, 1988 and 1989). A 50 m² roadside ditch with sparse vegetation and some debris, adjacent to hilly coniferous woods and a meadow.
- 3) Kraipe (alpine, 1988 and 1989). A 200 m² pond partly rich in vegetation, located in a stream system on a montane heath above timberline. This is the most elevated breeding site of the species known in the area.

Some characteristics of the localities and the populations are given in Table 1.

The lowland (Tvärån) pond, where breeding *Rana temporaria* have been studied since 1977, was visited around midnight at approximately three-day intervals throughout the breeding season. Here, in contrast to the other study sites, the frogs call only during the night. Only here did we study behavior throughout the breeding period. In the mid-altitude and alpine populations, however, our aim was to sample behavior in their respective peak chorusing periods only. The peak chorusing period is the part of the breeding period during which the number of calling males reaches a maximum. This period usually lasts for 3–7 days and often coincides with the peak in spawning activity (cf. Table 5 and Elmberg 1990: appendix 1). At our mid-altitude and alpine localities it is light all night at this time of the year. Therefore, the frogs were monitored around the clock, and behavior was studied at the time of the day when the frogs were most active.

To avoid disturbance, male behavior was studied from a distance; in daylight with binoculars. On each occasion, 10 males, or as many as possible if fewer, were selected consecutively and

randomly, and their behavior was studied during one or several four-minute periods. Males in amplexus were not included in the study. In all, at the three sites, males were studied for a total of 11 h 48 min. The number of seconds used for each of the following behaviors was noted:

Rest: no calls emitted, no aggression and no locomotion.

Calling: emission of advertisement calls (of type B and/or C in van Gelder et al. 1978; but cf. Walkowiak & Brzoska 1982), regardless of posture. Short, regular interruptions, regarded as breathing, were included in the time score.

Movement: swimming or diving without calling or aggression.

Aggression: movements directed towards another frog and resulting in physical contact. Included is openly aggressive behavior, such as butting, kicking, climbing, and clasping (to check the sex of frogs encountered).

Table 1. Characteristics of the three sites where the breeding behavior of *Rana temporaria* was studied. The feeding season is 1–1.5 months shorter than the annual period of activity. The breeding period is defined as the number of days from the first to the last day with a chorus (i.e. at least three calling males).

	Tvärån (lowland)	Jämforsen (mid-alt.)	Kraipe (alpine)
Location	63°50' N 20°15' E	65°54' N 16°20' E	65°51' N 16°22' E
Altitude (m)	10	400	800
Annual period of activity (months)	5	4	3
Breeding period	late April to mid-May	late May to early June	mid-June
Breeding period in 1988 (days)	23	10	8
Hours / night with sun below horizon during breeding	6	4	1
Appr. number of breeding males in population	100	25	15

Data on body energy reserves were drawn from a larger sampling program running in 1987–1989. We included adult males (body length >59 mm) collected within six weeks of emergence (i.e. before 16 June at Tvärån, before 1 July at Jämforsen and before 27 July at Kraipe). The males were stored for at least one day in water in a dark room at 5°C, and their bladders were emptied before they were weighed and sacrificed. At autopsy, both fat bodies and the liver (excluding the gall bladder) were excised, weighed and later related to total body mass (all wet weights; sample sizes in Table 6). As they are proportions, all relative weights were arcsin-transformed in the statistical analyses.

3. Results

In the lowland (Tvärån) population, a chorus comprising 10 males began on 2 May in 1988. Peak chorus (more than 50 males) lasted from 9 to 13 May. On 23 May, five calling males still remained in the pond. As in earlier seasons, there was a chorus only at night, lasting four to five hours each night. Throughout the study period, males remained resting for most of the time (Table 2). However, there was a significant decrease in resting during the peak chorus period, and an accompanying increase in individual time used for the “active” behaviors combined ($P < 0.05$, Kruskal-Wallis test; 5 nights with 10 studied males each ($n = 50$)). This was due to a significant rise in the time used for moving, taking place the day before and during peak spawning, and not to the time used for calling ($P < 0.05$ and $P > 0.05$, respectively; Kruskal-Wallis test, $n = 50$).

Mid-altitude males generally used less time for calling, moving and aggression than did lowland males (Table 3). However, in 1988 the proportion of time spent resting decreased (activity increased) significantly during the study period (until spawning onset on 4 June) ($P < 0.05$, $r_s = -0.94$, $n = 6$).

Alpine males were even less active than mid-altitude and lowland males (Table 4). Calling was very uncommon; for example it was noted only once during more than two hours of observation in 1988. The frogs were very sluggish, moving only in short bursts. Aggression was not recorded at all.

Table 2. Time use by breeding lowland (Tvärån, Umeå) males of *Rana temporaria* in 1988. Only the data from 9 and 12 May are from the peak chorusing period, i.e. comparable to the data in Tables 3 and 4. Spawning began on 10 May and peaked on 12–14 May. – = data missing.

Date	Time	Background data			Behavior (in % of total time per occasion)			
		Water temp. (°C)	Males studied	Observation time (min.)	Resting	Calling	Moving	Aggression
5 May	01.00	4	9	36	95.4	3.0	1.5	0.1
9 May	01.00	5	10	40	82.3	10.0	7.6	0.2
12 May	01.00	11	10	40	79.5	11.1	8.5	0.8
15 May	01.00	–	10	40	85.2	10.5	4.1	0.3
17 May	23.30	–	10	40	91.4	5.2	3.1	0.3

Table 3. Time use by mid-altitude (Järnforsen, Lapland) males of *Rana temporaria* during peak chorusing in 1988 and 1989.

Date	Time	Background data			Behavior (in % of total time per occasion)			
		Water temp. (°C)	Males studied	Observation time (min.)	Resting	Calling	Moving	Aggression
1988								
31 May	23.00	1	4	16	100.0	0.0	0.0	0.0
1 June	16.00	3	5	20	95.0	5.0	0.0	0.0
1 June	20.00	4	1	4	100.0	0.0	0.0	0.0
2 June	17.00	9	9	36	90.3	5.8	3.9	0.0
2 June	18.00	9	4	16	85.4	5.2	9.4	0.0
3 June	13.00	11	8	32	66.9	7.8	20.3	4.9
1989								
27 May	19.00	4	6	24	89.7	0.7	7.2	2.4
28 May	10.00	5	9	36	97.7	0.0	1.7	0.6
28 May	15.30	6	10	40	98.0	0.0	2.0	0.0
29 May	11.00	9	20	80	86.2	2.4	8.2	3.2

Further general differences were: a) the calls of the montane frogs (Järnforsen and Kraipe) were brief, weak and rasping — unlike the longer, louder and more gentle/softer croaks of the lowland frogs, and b) the length of the breeding period decreased with increased altitude (Table 1).

The data presented so far are difficult to use for formal between-locality comparisons. Note, however, that no males were calling in 7 of the 18 sampling periods in the montane populations, even during the “peak chorusing” part of the breeding period. This is an important difference from the lowland and more southerly populations.

To make more formal comparisons, we used data from the peak chorusing period sampled at all three sites. Due to the different sample sizes and time intervals, we took the proportion of individuals at each locality showing a certain behavior (Table 5). Calling and moving males became significantly rarer with increased altitude. Males engaged in aggressive behavior were significantly rarer in the alpine population than in the mid-altitude and lowland populations. Take-over attempts, i.e. males trying to displace a male already in amplexus, were observed only twice (in the lowland population).

Table 4. Time use by alpine (Kraipe, Lapland) males of *Rana temporaria* during peak chorusing in 1988 and 1989.

Date	Time	Background data			Behavior (in % of total time per occasion)			
		Water temp. (°C)	Males studied	Observation time (min.)	Resting	Calling	Moving	Aggression
1988								
20 June	16.00	10	1	12	100.0	0.0	0.0	0.0
21 June	11.30	12	6	72	97.6	0.2	2.2	0.0
22 June	11.00	15	2	20	99.8	0.0	0.2	0.0
1989								
15 June	15.00	18	2	24	89.4	5.3	5.3	0.0
16 June	11.00	19	4	28	98.9	0.9	0.2	0.0
16 June	14.00	21	2	16	97.2	1.6	1.2	0.0
17 June	14.00	17	2	24	87.6	11.1	1.3	0.0
17 June	15.00	17	1	12	100.0	0.0	0.0	0.0

Table 5. Proportion of breeding males of *Rana temporaria* showing a certain behavior (e.g. 18 of 20 males sampled equals 90%). Data from the peak chorusing period only. Males in amplexus were excluded. Calling and moving males became significantly rarer with increased altitude. Significance of Tukey-type multiple testing among three proportions (Zar 1984:401–403); original data arcsin-transformed: *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, NS = $P > 0.05$.

Locality	Tvärån	Järforsen	Kraipe
Altitude	10 m	400 m	800 m
Date	9, 12.5.88	2–3.6.88 28–29.5.89	20–22.6.88 16.6.89
Calling	90% 18/20	*** 33% 17/51	* 15% 2/13
Moving	95% 19/20	*** 67% 34/51	*** 31% 4/13
Aggression	20% 5/20	NS 39% 0/51	*** 0% 0/13

← *** →

Lowland males had significantly larger fat bodies after hibernation and during breeding than did mid-altitude and alpine males ($P < 0.05$, $F = 6.3$, one-way ANOVA of arcsin-transformed values of relative total fat body mass; Table 6). Energy may also be stored as glycogen in the liver, but there was no significant difference in relative

Table 6. Relative weights of fat bodies and liver (% of total body weight) in adult males of *Rana temporaria* caught within six weeks of the close of hibernation. Mean \pm SD.

	Tvärån (lowland) n=27	Järforsen (mid-alt.) n=23	Kraipe (alpine) n=16
Fat bodies	0.08 \pm 0.10	0.06 \pm 0.09	0.07 \pm 0.08
Liver	2.63 \pm 0.62	2.77 \pm 0.46	2.95 \pm 0.43

liver mass among the localities ($P > 0.05$, $F = 0.28$, one-way ANOVA of arcsin-transformed values of relative liver mass; Table 6). All frogs had empty guts.

4. Discussion

The overall proportion of time used for mating activities in the populations studied is very low compared with previous studies (cf. MacNally 1984, Forester & Czarowsky 1985, Robertson 1986). Compared with the congeneric and territorial *Rana clamitans* Yarrow (Wells 1978), our frogs used little time for aggressive behavior. In a British *Rana temporaria* population similar in size to the present lowland population, males frequently attacked other males and females, often

several times per minute (Arak 1982). We never observed more than one attack per minute in any frog. Unlike us, Arak (1982) observed frequent take-over attempts. Thus, there is striking intraspecific variation with respect to aggressiveness and frequency of take-over attempts between our Swedish and Arak's English populations. This may lead to corresponding intraspecific variation in the opportunity for sexual selection.

In the lowland population, moving was the only behavior that increased significantly during peak chorusing, indicating an increased individual mating effort during this part of the breeding period (cf. Whitney & Krebs 1975, Gatz 1981, Sullivan 1982, 1987, Forester & Czarnowsky 1985, Klump & Gerhardt 1987). Despite much higher water temperatures, alpine males spent less time calling and moving than did both mid-altitude and lowland males. Thus, our data show that water temperature may not be the only determinant of calling activity, and that the latter may be more successfully explained in ultimate than in proximate terms.

There are two probable explanations for the lower energy reserves of the montane males after hibernation (as compared with lowland males): a) their shorter previous feeding season, or b) their longer hibernation. Regardless of which is true, it may not pay off for them to invest as much in mating activities, because that could mean lower future energy reserves, which in turn could reduce survival during hibernation and also future reproductive success. To montane frogs the latter may be particularly relevant, because they live longer (Elmberg 1991a) and because survival more than mating activity seems to influence lifetime reproductive success (Elmberg 1990).

Both our original predictions were fulfilled, i.e. individual mating activity was higher in the population with a longer feeding season, and males in this population emerged from hibernation with larger energy reserves. Our observations that montane males had shorter breeding periods, gave weaker calls, were generally more sluggish, and used less time for mating activities are all in line with the idea of minimizing energy expenditure.

However, other hypotheses have been offered to explain intraspecific differences of the type

documented by us. Apart from temperature, mentioned above, the role played by population size and density has been discussed. The reports on their effect upon individual mating activity are not consistent (Höglund & Robertson 1988 versus Savage 1961, Walkowiak & Brzoska 1982, Arak 1982, Tejedo 1988, Woolbright et al. 1990), but strongly suggest that there is often a positive correlation. In other words, males in large or dense populations can be expected to be more active than those in small or less dense populations. Our data do not allow us to exclude the effect of population size, but population density was highest among the mid-altitude males, the behavior of which was most similar to that of the alpine males. Experiments with *Rana temporaria* show that density has to reach values much higher than those for the present lowland population before any effect on aggressiveness (measured as take-over attempts) is noted (Elmberg 1991b). Further, in 11 seasons of field work in lowland populations of sizes and densities comparable to those of the montane populations in this study, J.E. has never observed males with the behavioral characteristics described here for the latter. We argue that the intraspecific variations in breeding behavior revealed by the present study exceed those that could be produced by differences in population size and density.

To test our ideas further, we need more information about male energy expenditure during breeding (cf. Ryser 1989), about the influence of individual behavior on energy reserves, and about survival in relation to energy reserves.

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