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APPARENT LACK OF TERRITORIALITY DURING THE BREEDING SEASON IN A BOREAL POPULATION OF COMMON FROGS *RANA TEMPORARIA L.*

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ABSTRACT

The movements within a population of individually marked male Common Frogs *Rana temporaria* were studied during the breeding season. No signs of territoriality were found. The population was characterised by a high degree of disorder and internal movements. Site fidelity within the pond occurred, but was rare. Some other features of the reproductive biology of the species are also described.

INTRODUCTION

Anurans show a great interspecific variation in their behaviour at the breeding site. In most species, males seem to take the most active part in the activities in the breeding ponds. The ability of the females to actively choose a mate is somewhat difficult to prove, but has been discussed by Licht (1976) and Halliday (1983).

A survey of anuran reproductive and mating strategies is given in Wells (1977). As far as the temporal pattern is concerned, there seem to be two broad categories: *prolonged* and *explosive* breeders. Among the former we find species such as the Green Frog *Rana clamitans* and the Bullfrog *Rana catesbeiana*, which maintain well-developed social structures in their breeding ponds, and where male territoriality is an important aspect of the mating strategy (Emlen 1968, Emlen 1976, Howard 1978, Martof 1953 and Wells 1978).

The typical explosive breeders, on the other hand, have a short annual breeding period of one or a few weeks (Wells 1977). There seem to be no species within the group possessing territorial breeding pond behaviour.

The Common Frog, occurring widely in the cooler parts of the Palearctic, is considered a typical explosive breeder by Wells (1977). Its reproductive biology has been studied in Britain (Savage 1961, Ashby 1969), the Netherlands (van Gelder and Hoedemakers 1971, van Gelder, Evers and Maagnus 1978), Poland (Kozlowska 1971), Finland (Koskela and Pasanen 1975) and Sweden (Ericsson and Elmberg 1979, Elmberg and Ericsson 1980). The mating behaviour of its Nearctic relative the Wood Frog *Rana sylvatica* is described by Howard (1980).

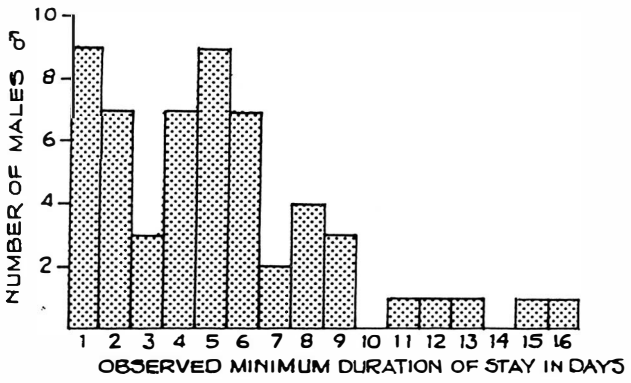

Fig. 6. Observed minimum duration of the stay in the breeding pond.

Even though this study focused on the males, all frogs were caught regardless of sex. In all, 13 females were caught, thus constituting only 14 per cent of the individuals (observed sex ratio 6.2 males to one female).

The average of R was 0.91 (SD ± 0.16) in the 22 frogs caught three times or more. The corresponding d value was 5.71 metres (SD ± 2.88). The relationships between R and d for the individual frogs are shown in Fig. 7. In theory, territorial or site tenacious frogs will show low values of both R and d.

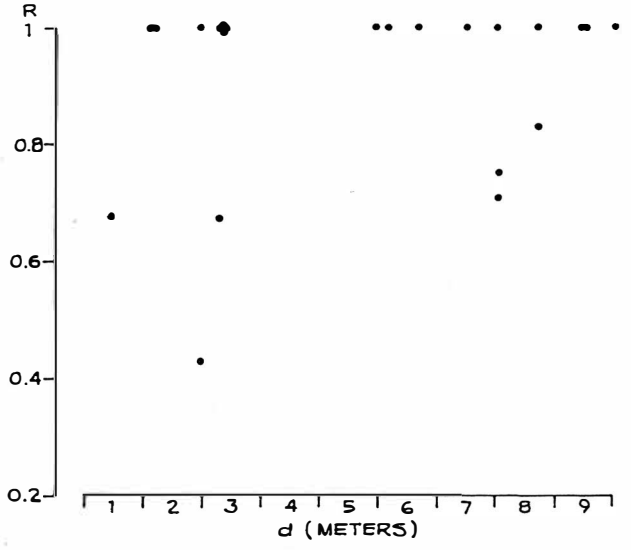

Fig. 7. Individual males plotted according to their R and d values (n = 22). Stationary males will hypothetically appear in the low left corner, and the mobile in the upper right.

No aggressive encounters between the males were observed. Spawning began 30th April and culminated 5-6th May.

DISCUSSION

The total catch could have been increased by adding some sampling nights. However, this would also have increased the disturbance, and was ruled out considering the short breeding period. The following discussion concentrates on the 22 individuals caught three times or more.

The number of males caught for the first time remained at a relatively constant high level during the first part of the main calling period (Fig. 3b). This is because the migration from the wintering site (river Tvärån) to the pond takes some time to complete for the population as a whole. Obviously, the continuous movement of frogs arriving and departing over a large part of the breeding season is likely to hinder the establishment and defence of territories.

The time that each individual spends in the pond is of great importance for the possibility of establishing territories within the population. As the observed minimum average duration of the stay is only 5.1 days, it is concluded that many males spend only part of the main calling period in the pond. Consequently, it may be a poor investment of energy to establish and defend a territory under these circumstances.

The spatial distribution of the catches shows a marked concentration to certain parts of the pond. Also among the squares in which catching activities were prevented by high water levels, there was an obvious concentration of the chorus to the ones bordering the other favoured, accessible squares. This clustering of the calling males may hinder the establishment of territories. In the territorial *Rana clamitans*, a regular spacing between the calling males was noted by Martof (1953). Emlen (1968) estimated the minimum territory radius of *R. catesbeiana* to be approximately three metres. The spatial distribution and the density of the Umeå population are clearly not compatible with a territorial structure like that of either *R. clamitans* or *R. catesbiana*. Rather, they are in good agreement with the general characteristics of explosive breeders as described by Wells (1977).

The movements of the individual frogs are harder to interpret. Out of the 22 caught three times or more, 16 were found at least once in the square where they were first caught, or in a neighbouring square. Only one of the 22 was caught in all three major calling areas of the pond (the southern , northwestern and northeastern parts — Figs. 1 and 5). Nine individuals were caught in two of the major calling areas, while the remaining 12 were caught in one only. These observations indicate that the movements within the pond are limited in most males, and that certain areas are preferred.

Of the three males caught the most times, two fit well into the pattern of limited movement described above. The third, on the other hand, was caught all seven times in a minor clump of sedge in squares 41, 51 and 61. It is worth pointing out that this male not less than seven times moved from outside the grid in the northern end of the pond to this very spot! This could hardly be termed as anything else than a remarkable site fidelity. Surprisingly enough, this male was caught twice the preceeding year — in the same area as in 1980!

The R values show that most of the frogs have been caught in a good number of squares, that is, a new one on almost every occasion. In absolute terms (average of d), though, the movements seem less extensive. No comparisons can be made at this point, however, and

future studies may show whether this population of Common Frogs had a high or low degree of internal movement.

In conclusion, there is an impression of disorder, but individual movements are usually restricted to a certain part of the pond, and a few males exhibit a high degree of site fidelity. If we assume that the males establish territories smaller than the squares of the grid of this study, the expected spatial distribution of the calling males would be quite different from the one found. The small and irregular distances among the calling males and observations of their behaviour show that territoriality *sensu stricta* was not in effect in this population. Also, as no territorial pattern was established, the frogs remained mobile.

According to Wells (1977), the mate-locating behaviour among explosive breeders varies with the density of the population; at high densities males move widely or adopt a strategy of 'limited area searching', and at low densities they become more or less stationary. The population here studied seem to be dominated by 'limited area searching' males. Assuming that the density of the population studied (80-100 males in $300m^2$) could be termed as high, my data would support the general pattern in Wells (1977).

It should be noted, though, that there is always a risk of over-simplifying when trying to describe anuran reproductive behaviour. The great variation among the males in this study stresses this important point. Mating strategies are individual, and great caution must be taken when applying the term to populations or species.

What was then the breeding success of the males? Out of the 11 found amplexed with females, only three belonged to the category caught three times or more. The percentage of successful matings in this category was equal (14 per cent) to that of the frogs caught one or two times only. Although the sample in this study is small, there seems to be no reason to believe that males calling actively and for a long time have markedly higher breeding success than those who do not.

The observed sex ratio of 6.2 males to one female seems somewhat high compared with the 2:1 ratio of a nearby population censused during migration (Elmberg and Ericsson 1980). This discrepancy may be within the normal variation between years or populations, or random, but may also result from the fact that the males are so much easier to catch in the breeding pond than females (due to more exposed habits and longer stay). Nevertheless, the number of males greatly exceeds the number of females in the breeding pond at any given moment. If not territorial, the Common Frog must have another means of assuring that mating is not a random process.

There is a need for further studies establishing the actual mating strategy generally adopted by the Common Frog. Attention must be paid to characters such as size and sound of the males, and the effects of the latter on males as well as on females in the breeding pond (see Howard 1978). Comparisons of mating strategies in populations in different parts of the range of a species would be of wide interest to the understanding of the reproductive biology and evolution of anurans.

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