

Spacing mechanisms in a population of the common frog *Rana temporaria* during the non-breeding period

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About 50% of the common frogs in a 50 × 50 m plot were removed. Comparison with a control plot showed that the experimental plot had been largely repopulated a little more than one month later. As the proportion of marked frogs decreased in the control plot during this month it is suggested that some of the invading frogs could be part of a transient segment of the population. To completely account for the observed repopulation it was also necessary to assume that some neighbouring resident frogs invaded the experimental plot.

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Около 50% обыкновенных лягушек было удалено с территории площадью 50 × 50 м. Сравнение с контрольным участком показало, что на опытной площадке популяция в основном восстанавливалась немного более, чем через месяц. Так как относительное количество меченых лягушек снижалось в контрольном участке в течение этого месяца, предполагается, что некоторые из вновь поселившихся лягушек могут относиться к кочующей части популяции. Для полной оценки наблюдаемого восстановления популяции необходимо также иметь в виду, что на экспериментальный участок переселяется часть резидентных лягушек с соседних территорий.

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Recent years have seen an increasing interest in the social structure of frog communities. So far, most studies have dealt with the situation during the breeding period (Davies and Halliday 1977, Wells 1977). For the common frog *Rana temporaria*, this is concentrated to about two weeks in the spring. During the rest of their active part of the year, they are dispersed over suitable feeding grounds up to several hundred meters from the breeding ponds. In this report, dealing with the non-breeding period, I demonstrate that the presence of other frogs can be a factor of importance for the "decision" whether or not a particular frog should settle down at a certain place. The strategy of the experiment was to remove frogs from an experimental plot in order to see whether and how it would be reinvaded.

The study was conducted in south Sweden (55°40'N, 13°30'E). The study plots were situated in a moist meadow with luxuriant vegetation of herbs and grasses about 60 cm high. The distance to the closest breeding sites was approximately 300 m. Two plots, 50 × 50 m and 50 m from each other were staked out. One was the experimental plot and the other the control plot. The size of the populations in the two plots were determined with a capture – recapture method. During eight capture bouts in the period 12–21 July 1977 as many frogs as possible were captured in both plots. Each bout consisted of a search in a regular pattern for about half an hour per plot. The captured frogs were measured, sexed, marked with toe-clipping (unless recaptured), and released (within one minute). The size of the populations were calculated according to the method of Eschmeyer and Schumacher (Seber 1973: 141). Thereafter as many frogs as possibly were permanently removed from the experimental plot. This was done during seven capture bouts in the period 21–27 July (the last of the eight previous bouts was identical to the first of the seven removal bouts). During the period 28 August to 9 September 1977, I repeated the capture – recapture procedure to determine the size of the populations in the two plots at this time. During the whole study all frogs in their second summer or older were considered. All but the smallest of these could be sexed on basis of the presence of nuptial pads.

During the removal bouts, 451 frogs were captured. This reduced the population in the experimental plot from an estimated number of 777 to 326 (Tab. 1). If there was no invasion and density changed in this plot at the same rate as it did in the control plot, one would expect 260 frogs to be present in September. If full density compensation took place one would, on the other hand, expect a number of 620. The obtained estimate for the experimental plot in September was between these two values and significantly above the lower one. I thus conclude that the experimental plot was partly invaded following the removal.

Two hypotheses that can explain the obtained results are considered. First, the result is due to transients passing through. Here I define transients as frogs that

Tab. 1. Size of the population of common frogs in the experimental and control plots. Values given are immediately before and one month after the removal of 451 frogs from the experimental plot. The estimates are followed by their 95% confidence interval.

	Before	After
Control plot	613 (418–1144)	489 (347–827)
Experimental plot	777 (487–1770)	551 (408–848)

Tab. 2. Sex ratio and age structure of the populations in the two plots before and after the removal and reinvansion. Sample sizes are given in parenthesis. Note that the smallest individuals of those that were in their second summer could not be sexed and are excluded. The size that parted frogs in their second summer from older ones could be determined from the size distributions that were clearly bimodal. Old frogs were 57 mm or longer (snout – urostyle) in July and 63 mm or longer in August–September.

	Before	After
Proportion females		
Control plot	47% (181)	40% (171)
Experimental plot	43% (201)	42% (141)
Proportion old frogs		
Control plot	30% (212)	15% (194)
Experimental plot	17% (223)	11% (167)

behave nomadically and if present in a plot in July certainly are not there in September. Residents, on the other hand, have a fixed home range and will not change the proportion of this home range that is contained in a study plot. In another study (unpubl.), I have shown that most common frogs are residents during summer and have a home range with a mean radius of about 11 m. Second, the result may be due to resident frogs with home ranges in the vicinity of the experimental plot that somehow perceive the reduced density and move in to set up a new home range.

If no transients are present, 212 [number of frogs marked in the control plot] / 613 [estimated July population in this plot] = 35% of all frogs captured in the control plot in September should be marked. This is 80, as 231 captures were made. However, significantly less, 50, were marked ($\chi^2 = 17.2$, $P < 0.001$). This suggests that about $30/80 = 37.5\%$ of all frogs present in July were transients. If this is true, one would expect the number present in the experimental plot in September to be $(62.5\% \times 260)$ [i.e. the number of residents remaining after the removal captures] + $(37.5\% \times 620)$ [i.e. the number of transients corresponding to the unmanipulated September density] = 395. As this number is below the 95% confidence interval of the September estimate for the experimental plot (Tab. 1), I conclude that the existence of transients that pass through is not a sufficient explanation for the observed repopulation of

the experimental plot. Thus it seems reasonable to assume that previously resident frogs in the vicinity of the plot invaded or that transients have settled as a result of the reduced density.

It was not possible to demonstrate any change in the sex or age composition of the population after the experiment (Tab. 2). All age classes and both sexes must thus have taken part in the repopulation.

The two mechanisms suggested in this report both tend to space the frog population evenly over homogeneous and suitable habitats.

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