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Macro- and Microhabitat Distribution in *Rana arvalis* and *R. temporaria* (Amphibia, Anura, Ranidae) during Summer

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ABSTRACT—Subadult *Rana arvalis* and *R. temporaria* did not segregate in forest and meadow habitats. Adult frogs did segregate, *R. temporaria* being comparatively more often found in forest habitats. In meadow habitat, females of *R. arvalis* were found higher up in the vegetation than males. No such dimorphism was conclusively demonstrated for *R. temporaria.* It is suggested that the fact that the forest was structurally less complex (the herb stratum was more sparse there than in the meadows) was responsible for the near-exclusion of adult *R. arvalis* from this habitat.

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INTRODUCTION

Rana arvalis Nilsson and *R. temporaria* L. occur sympatrically over much of northern Eurasia. After metamorphosis they usually live in terrestrial habitats on or close to the ground. This study was carried out in order to investigate if they segregate in terms of macro- or microhabitat. No previous study has suggested any testable patterns with respect to habitat segregation and as this study was done on a local scale, no general patterns can be safely predicted from it. The patterns that are found in a local study may however well serve as hypotheses to be tested at other localities. Also, locally demonstrated patterns can strengthen or contradict nonspecific ecological hypotheses.

STUDY AREA AND METHODS

The work was conducted in the Revinge area (55° 40′ N, 13° 30′ E) in south Sweden. Two different habitats were studied; moist deciduous forests and meadows, both on peat soil. The vegetation in the herb stratum of the forests was sparse. The most common trees were *Betula pubescens* and *Alnus glutinosa.* The meadows have a dense growth of herbs and grasses. This habitat division was chosen because of its distinctiveness and because I felt that if any segregation in macrohabitat occurred, it would be revealed by this division into two habitat categories that differ in several respects, most notably insolation and protection against predation offered by the herb stratum.

In all, 10 plots in forests (60 captured frogs) and 12 in meadows (182 frogs) were sampled. The two most distant plots were 6 km apart. The distance from a forest plot to the closest meadow plot was never more than 500 m, usually less. The forest plots were situated in groves that were less than 10 ha. These facts should make sure that any differences found were not caused by differences in breeding habitat. This could have been the case if one of the species preferred breeding in forest ponds and, due to too long distances, could not reach a meadow plot in the summer. As some frogs were captured more than 200 m from possible breeding sites, this could not have been the case.

Each plot had an area of 1-2 ha and was sampled twice. The first sampling was made in July 1974 and the second in August 1974. At each sampling of a plot as many frogs as possible were captured by hand during a time of 30 minutes. Practically all frogs that were caught had

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been flushed (i.e. started to move at the approach of the collector) and 80% of those flushed were caught. The captured frogs were measured (snout to urostyle). In the following, *R. arvalis* at least 40 mm long and *R. temporaria* at least 50 mm long are classified as adults. Smaller frogs are classified as subadults. Frogs that had metamorphosed during the summer of the study (recognised by their size) were ignored. Their highly aggregated distribution probably reflected the distribution of breeding ponds.

The microhabitat parameters considered were the height of the herb stratum at the capture site (or what it had been, were the frog not sitting there) and perching height of the frogs before flushing. The use of the term "perch" does not imply that these frogs climb in the vegetation like Hylids or birds. The thick herb stratum merely supports the frogs sitting more or less in their normal position. When the frogs were not observed before they started to move, their perching height was estimated, as I consider the bias introduced if only easily visible frogs were recorded to be more severe than faults caused by some misjudgements of actual heights. Differences measured in this way should mirror real differences. These microhabitat data were collected at one meadow site in August 1973 and August 1975 (175 frogs), at two other meadow sites in August 1975 (42 frogs) and at two forest sites in August 1975 (31 frogs). Only adult frogs were considered in the microhabitat measurements.

RESULTS

Macrohabitat.—Among the subadult frogs a higher proportion of *R. arvalis* (42%) than of *R. temporaria* (31%) were caught in forest plots. This difference is not significant (χ^2 = 1.31, two-tailed test, $P > 0.20$). Among adult frogs a significantly higher proportion of *R. temporaria* (25%) than of *R. arvalis* (2%) were caught in forest plots (χ^2 = 50.4, two-tailed test, $P < 0.001$) (Table 1).

TABLE 1. Number of frogs caught in different macrohabitats.

	R. arvalis		*R. temporaria*		*R. arvalis*	*R. temporaria*
	Adults	Subadults	Adults	Subadults	All	All
Forests	1	14	19	26	15	45
Meadows	48	19	57	58	67	115

TABLE 2. Number of frogs caught in the different meadow habitat plots.

R. arvalis	9	11	4	7	7	8	16	0	0	3	2	2
R. temporaria	5	14	12	12	17	7	0	18	11	3	10	7

χ^2 = 55.8, d.f. = 11 $P < 0.001$

In the meadow habitat, the proportion of the two species differed significantly between different plots (χ^2 = 55.8, two-tailed test, $P < 0.001$) (Table 2). This could be due to some habitat heterogenity within the set of meadow plots or to characteristics of breeding ponds close to different meadow plots. No correlation was found between the proportion of *R. arvalis* in the total catch from different meadow plots and their mean vegetation height (Spearman rank corr. test, $r_s = -0.05$, $P > 0.1$).

There was no significant difference in average size of *R. temporaria* caught in forest compared to meadow plots (47 and 49 mm respectively, t = 1.46, two tailed test, $P > 0.1$). Due to the dominance of subadults, *R. arvalis* from forests were considerably smaller than those from meadows, (34 and 41 mm respectively, t = 4.70, two-tailed test, $P < 0.001$). For *R. temporaria* there was a positive correlation between the mean size of frogs caught in different meadow plots and their mean vegetation height (Spearman rank corr. test, $r_s = 0.72$, $P < 0.05$). Such a correlation was not found for *R. arvalis* (Fig. 1).

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Microhabitat.—With respect to the height of the vegetation at the capture site no difference between the sexes or between the species was found (Table 3).

In both species females perched higher than males in the meadow vegetation (Table 4). The difference was greatest in *R. arvalis* and also significant only in this species. The high mean for female *R. arvalis* caused the mean for this species to be higher than the mean for *R. temporaria.* Male *R. arvalis* did not perch higher than *R. temporaria* of both sexes combined.

No correlation between the size of individual frogs and their perching height could be demonstrated (Pearson's corr. test, $P > 0.1$). As to interspecific differences, *R. temporaria,* the low-perching species, is the larger of the two, weighing nearly twice as much as *R. arvalis.*

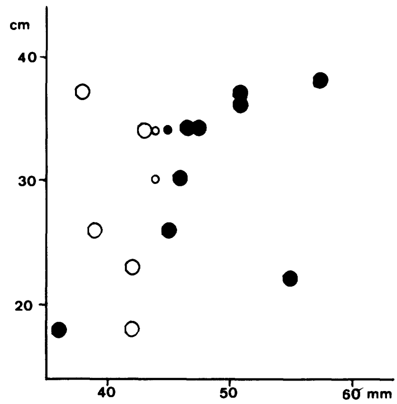

FIGURE 1. The relation between the mean size of frogs caught in meadow plots and the mean vegetation height of the plots. Open circles: *R. arvalis,* Filled circles: *R. temporaria,* Small circles: sample size less than five animals, Large circles: sample size at least five animals.

DISCUSSION

It is not self evident that metamorphosed frogs of these two species segregate during the summer, the limiting or regulating factors of the populations could operate during the breeding season or on the larvae. If the metamorphosed frogs are regulated by food during the summer, evolution can be predicted to have segregated the two species in some respect. If they are predator regulated there should not have been selection for a segregation pattern, though one could emerge if there is different suspectibility for the two species in different habitats. If they are segregated, of course, one cannot tell whether they are competing at present or not.

Within the meadow habitat, segregation was demonstrated as the proportion of the two species differed between different plots. The factor determining what species should dominate in a given plot was however not identified.

Between the two habitat types segregation also occurred. However, this segregation in macrohabitats was only manifest in adults and at least three mechanisms that explain this

TABLE 3. Distribution of vegetation heights at the capture sites of frogs.

	Number of caught frogs					
	R. arvalis		*R. temporaria*		*R. arvalis*	*R. temporaria*
Height (cm)	Females	Males	Females	Males	All	All
Meadow localities:						
0-20	19	7	9	22	26	31
21-40	24	29	11	48	53	59
41-80	18	17	16	27	35	43
mean (cm)	34	38	37	35	35	35
χ^2	5.20		4.16		0.09	
P (two-tailed test)	0.10-0.05		0.20-0.10		0.80-0.70	
Forest localities:						
0-20	6	1	5	8	7	13
21-40	2	1	3	1	3	4
41-80	1	2	0	1	3	1
mean (cm)	24	40	8	15	29	13

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TABLE 4. Perching height of captured frogs.

	Number of Frogs					
	R. arvalis		*R. temporaria*		*R. arvalis*	*R. temporaria*
Height (cm)	Females	Males	Females	Males	All	All
Meadow localities:						
0-10	33	41	27	79	74	106
11-20	11	11	5	12	22	17
21-40	15	1	2	5	16	7
41-80	2	0	2	1	2	3
mean (cm)	17	12	13	10	15	11
χ^2 (the two categories 21-40 and 41-80 have been pooled in this analysis	14.9		0.67		6.52	
P (two-tailed test)	0.001		0.50-0.30		0.05-0.02	
Forest localities:						
0-10	9	3	8	10	12	18
11-20	0	1	0	0	1	0
mean (cm)	1	8	0	2	4	1

pattern can be envisaged: 1) redistribution through migration as the frogs grow older, 2) different survival due to different feeding efficiancy in the two habitats, 3) different survival due to different suspectibility to predation in the two habitats. The first, if it were demonstrated, I think should support the hypothesis of past or present competition. This pattern would also suggest the hypothesis that competition is more keen among adults than among subadults, perhaps because of large prey, suitable for adult frogs, being less abundant than smaller prey.

One general hypothesis states (MacArthur, 1972:177) that a structurally more complex habitat will hold a more diverse fauna than a less complex one. In this study I consider the herb stratum of the meadows the more complex and that of the forests the less. This is however open to question as the sparse herb stratum of the forests with completely bare patches sometimes alternating with tussocks (that however were present in the meadows too) might be considered horizontally the more complex one. The meadows, however, clearly gave more opportunities for vertical segregation, opportunities that were used (Table 4). If diversity is measured as $-\sum^{a,t} p_i^2 \log p_i$ (where p_i is the proportion of all caught frogs belonging to each species, e.g. $p_{a(rvalis)} = 0.05$ and $p_{t(emporaria)} = 0.95$ (adult frogs in forest) according to Table 1), a value for the adult frog fauna in the forests of 0.11 and in the meadows of 0.25 is found. For all frogs the corresponding values are 0.24 and 0.28 in forests and meadows respectively. At least for adults this is consistent with the hypothesis. Another testable hypothesis states that the species with the broadest microhabitat niche in one habitat will also have the broadest macrohabitat niche. As one special case, Terborgh (1975) stated that tropical birds with broad vertical foraging height niches will be the ones most likely to penetrate secondary habitat. In this study the hypothesis is contradicted. The microhabitat niche breadth (with respect to perching height in meadows, categories as given in Table 4, measured as $1/\Sigma\, p_i^2$, where the p_i's give the proportion of adult frogs caught at different heights) is 2.1 for *R. arvalis* and 1.5 for *R. temporaria.* The species with the broadest perching height niche breadth (*R. arvalis*) however has the narrowest macrohabitat niche: 1.0 as opposed to 1.6 for *R. temporaria* (measured for adult frogs).

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The large size of *R. temporaria* in plots with a high herb stratum may be due to better protection against predation offered by the vegetation and a resulting higher mean age for the individuals living in these plots. Frogs of these species show a year to year site tenacity (Haapanen, 1972 and pers. obs.). It could however also be a bias, small frogs being comparatively more difficult to find in high vegetation. It is however difficult to see why this should not apply to the other species as well.

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