Alytes, 1984, 3 (4): 125-134.

DENSITY AND SURVIVAL OF *RANA ARVALIS* AND *RANA TEMPORARIA*

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ABSTRACT. - *The density of adult moor frogs and common frogs in a patch of luxuriant meadow in southern Sweden was determined by means of capture-recapture during five years. The frogs were classified as first-year adults or older on basis of their size and the successive densities were used to calculate their yearly survival. The density of catchable moor frogs decreased in September, probably due to the start of hibernation. There was no such decrease for common frogs before the study period ended in October. During the five study years, the density of moor frogs fluctuated between 140 and 680 adult individuals per hectare and that of common frogs between 50 and 530 adult individuals per hectare. It is suggested that factors influencing the survival of eggs and larvae are the most important ones determining the density of adults in the study plot. The average yearly survival was estimated to 60 % for moor frogs and 40 % for common frogs. Comparison with information on vertebrate frog predation in the surrounding area suggests that predation is the most important mortality factor for adult frogs.*

INTRODUCTION

Two of the least studied aspects of anuran ecology are density and survival. Because of the low catchability of most species, good estimates of these variables are difficult to obtain. Most previous population studies have referred to populations surrounding a breeding pond and densities have not been calculated (or even meaningful). This approach is however of limited utility for species such as moor frogs (*Rana arvalis*) and common frogs (*Rana temporaria*), which are not restricted to the vicinity of the breeding pond during the non-breeding season.

The main objective of the present study is to present data on the density and survival of the populations of moor frogs and common frogs in a study plot. The results will also be used for a comparison with the estimated predation on frogs by vertebrate predators in the surroundings of the study plot. This gives the relative importance of predation as a mortality factor.

STUDY AREA AND METHODS

The study was conducted in Southern Sweden (55°40'N, 13°30' E). The study plot (50 x 50 m) was situated in a moist meadow habitat having a herb stratum that was 20 to 80 cm high. There was less than 200 m to breeding sites of both species. The only other anuran present in the study plot was the common toad (*Bufo bufo*) but the density of this species was much less than that of the two *Rana* species. The study plot was searched 8 to 17 times (capture bouts) during each of one, two or three summer months from 1972 to 1976 (Table I). At each capture bout I searched the whole plot in a regular fashion for about one hour. All frogs found had been flushed and each adult was captured, measured (snout to end of urostyle), sexed, marked (by toe-clipping) and released at the capture site. Frogs were considered adults if they were at least 36 mm (moor frogs) or 46 mm long (common frogs). Frogs at or above this length may breed in the following spring (LOMAN, 1978 b). The size of the catchable population was determined, separately for each month, with the method of SCHUMACHER & ESCHMEYER (*in* SEBER, 1973: 139). To obtain a density value I divided the computed population sizes with the area of the study plot, increased with a border zone that had the width of the mean home-range radius. This was 8 m for moor frogs and 11 m for common frogs (pers. obs.). Data on the movements of these frogs indicate that most individuals have a restricted home-range (pers. obs.) and density values determined with this method should, at most, give a slight over-estimate.

The proportion of first-year adults was calculated for August each year by determining the proportion of all captured frogs that were between 36 and 46 mm (moor frogs) or 46 and 58 mm long (common frogs). The latter sizes are those that a frog of 36 or 46 mm respectively, can be expected to reach in one year (LOMAN, 1978 b).

Table I. - Catching success (density index) and calculated density of frogs during different periods.

	Catching bouts	Frogs captured per bout $\bar{x}$	S.D.	Estimated density (frogs per ha)	90% confidence interval
Moor frogs					
1972 July	12	5.1	3.4	1040	500 -
Sept.	12	2.4	2.7	310	150 -
1973 July	16	1.7	1.3	150	100 - 280
Aug.	14	2.1	1.8	140	80 - 440
Sept.	17	0.9	1.4	78	40 - 850
1974 Aug.	17	3.4	2.4	400	280 - 740
1975 Aug.	17	3.4	2.7	240	170 - 450
Sept.	8	2.6	1.8	200	60 -
1976 Aug.	13	10.6	2.3	510	430 - 610
Common frogs					
1972 July	12	1.3	1.2	25	15 -
Sept.	12	1.6	2.0	75	40 - 2300
1973 July	16	0.6	1.1	60	15 -
Aug.	14	2.6	1.6	115	75 - 210
Sept.	17	3.5	2.7	200	150 - 350
1974 Aug.	17	4.2	2.6	170	130 - 250
1975 Aug.	17	6.8	5.0	530	430 - 690
Sept.	8	8.1	2.8	750	300 -
1976 Aug.	13	5.5	2.4	130	110 - 160

I made an overall estimate of yearly adult survival using the following equation:

$$A = a_1x^2 + a_2x + a_3$$

where A is the mean number of adults (all age classes) in the years 1974, 1975 and 1976; a_1 is the mean number of first-year adults in 1972, 1973 and 1974; a_2 and a_3 corresponding values for 1973 to 1975 and 1974 to 1976 respectively. This value is a mean over years and age-classes.

Frog mortality was compared to information on frog predation in the 40 km^2 area surrounding the study plot (the Revinge area). This information was obtained from the analysis of scats and pellets and the application of experimentally determined correction factors. Information on the density of the predators was also available (ERLINGE et al., 1983). Frog predators covered by this study were pole cat (*Mustela putorius*), badger (*Meles meles*), buzzard (*Buteo buteo*), and tawny owl (*Strix aluco*). The only important frog predator not covered by this study was the heron (*Ardea cinerea*). The Revinge area contains 2.7 km^2 of the same habitat as the study area and another 1.6 km^2 where frogs were moderately common.

The mean weight of frogs that died in the Revinge area was computed thus. Weight was determined from the length-weight relation that was computed for a sample of frogs captured in August 1975 and 1977 close to the study plot. Information on mean growth per year (LOMAN, 1978 b) was used to calculate the expected length and weight distribution of all adult frogs after one year. I then assume that frogs dying in the next year had grown halfway to this size. This weight is multiplied by the proportion of frogs dying per year and the mean density for the five years to give the mean biomass of dying frogs per year. Multiplying this density with the total area of moist meadow habitat in the 40 km^2 Revinge area gives a minimum estimate of the biomass of frogs that die in the Revinge area per year.

RESULTS AND DISCUSSION

1. DENSITY VARIATION WITHIN THE SEASON

There was a tendency for the density of moor frogs to decrease in September and for that of common frogs to increase in August and September (Table I). Comparing the total number of captures in July and September (1972 and 1973) for both species shows a significant difference in the seasonal trend (1972: $X^2 = 4.29$, $P < 0.05$; 1973: $X^2 = 27.4$, $P < 0.001$).

I suggest that hibernation for some moor frogs starts already in September, removing them from the catchable population. The low density values scored for common frogs in July may partly be caused by using too large a size for delimiting adult frogs in July. Information gained during the course of this study shows that a frog that is 42 mm in the beginning of July may grow to mature size before the autumn. It is also possible that some

Table II. - Estimated success of reproduction in different years. The estimates are based on computed density of frogs and proportion of young adults (first-year adults) in different years.

	Estimated density (adult frogs per ha)	Proportion of adults that were first-year adults	Density of first-year adults	Year when first-year adults were eggs and larvae	Inferred success of reproduction this year
Moor frogs					
1972	680	63 %	430	1970	+
1973	140	29 %	40	1971	-
1974	400	66 %	260	1972	+
1975	240	34 %	80	1973	-
1976	510	54 %	280	1974	+
Common frogs					
1972	50	91 %	45	1971	-
1973	120	86 %	100	1972	
1974	170	70 %	120	1973	
1975	530	74 %	390	1974	+
1976	130	53 %	70	1975	-

individuals reduce their activity during the warmest and driest part of the summer. This, however, remains speculation.

2. DENSITY VARIATION BETWEEN THE YEARS

There was considerable variation in density between the years. Comparing the values for August which, as demonstrated in the preceding paragraph, probably are the most representative, shows that the density of moor frogs fluctuated between 140 and 680 adult frogs per hectare (the latter value is the mean of the July and September estimates for 1972). The density of common frogs fluctuated between 50 and 530 adult frogs per hectare (the former value is the mean of the July and September estimates for 1972) (Table II). There was no correlation between the density of the two species in different years (fig. 1). The age structure of the two populations was unstable (Table II). The class of first-year adults dominated, especially in years with a high density. This class was born in the year be-

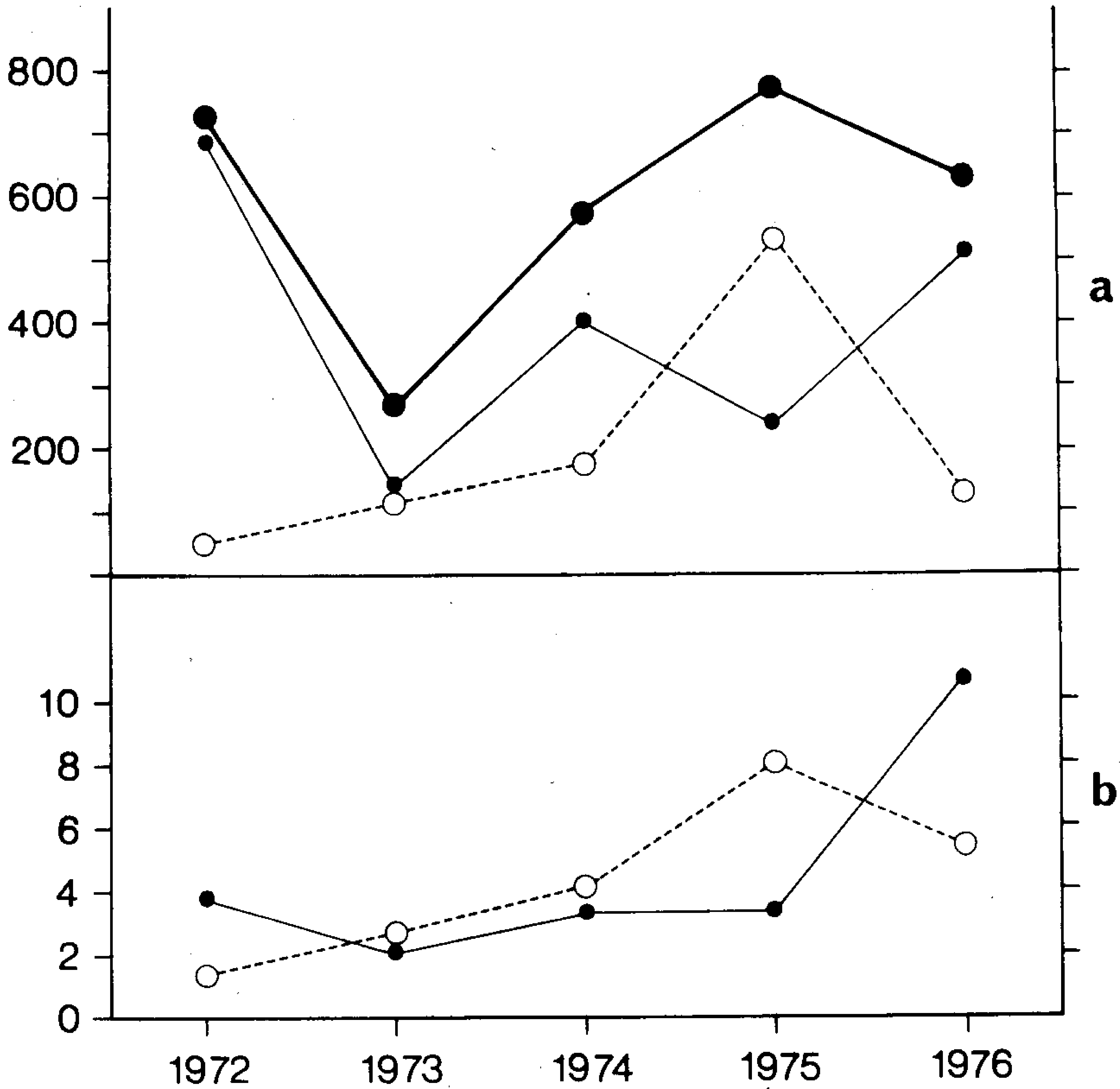

Fig. 1. - (a) Absolute density (individuals per hectare) and (b) catch per effort of moor frogs (solid lines) and common frogs (dashed lines). The combined density is represented by a thick line. The values for 1972 are the mean of the July and September results.

fore (common frogs) or two years before (moor frogs). These data suggest that 1974 was a successful year for the reproduction of both species. Correspondingly, 1971 probably was a year when reproduction failed for both species.

3. REPRESENTATIVITY OF THE STUDY PLOT

The study plot appeared representative of the surrounding 40 km², the Revinge area. Twelve meadow plots in the Revinge area were sampled by hand catching for one hour each in August 1974 and 1976. These sites were

Table III. - Comparison between the abundance of frogs in the study plot and in the 40 km² area surrounding this. All plots (the study plot and 13 control plots) were situated in moist meadow habitat. Only adult animals are included. The control plots were searched for one hour while the study plot was searched during the time required to complete the search according to the pattern described in the method section. Treating the frogs, measuring and marking, took only a short time, about one minute per frog. The total time required for a capture bout was usually about one hour. All captures were made in August.

	1974		1976	
	Moor frogs	Common frogs	Moor frogs	Common frogs
Mean number of frogs caught in 12 control plots	4.8	5.6	3.3	7.2
Number of frogs caught in a plot immediately adjacent to the study plot	8	7	8	4
Number of frogs caught per capture bout in the study plot	3.4	4.2	10.6	5.5
Number of capture bouts	17	17	13	13

situated up to 5 km from the study plot. The mean density in these twelve plots was similar to that of the study plot (Table III). However, moor frogs dominated in the study plot more in 1976 than in 1974, while the opposite applied to the mean of the twelve meadow plots. Very local factors may thus be important for the yearly fluctuations of the two species.

From published data there is a tendency for the "richest" habitats (meadow, deciduous forest) to carry the highest densities (Table IV).

4. YEARLY SURVIVAL

Yearly survival was computed to 0.63 for moor frogs and 0.36 for common frogs. The higher survival of the moor frogs corresponds to the fact that this species seems to breed at the age of three years while common frogs usually breed at two in the study area (LOMAN, 1978 b). Also, common frogs lay larger clutches in the study area (pers. obs.). In all three res-

Table IV. - Published estimates of density of moor frogs and common frogs. Localities are given in order of herb layer productivity.

	Study area (ha)	Density (frogs/ha)	Habitat	Reference
Moor frogs	0.25	150 - 1000	Moist meadow	Hoc loco(1,2)
Common frogs	"	50 - 750	"	" (1,3)
Moor frogs	0.28	400(1)	Deciduous forest	GŁOWACINSKI &
Common frogs	"	125(1)	"	KOWSKI (1970)
Moor frogs	1.00(4)	50 - 100	Coniferous forest	INOZEMTSEV
Common frogs	"	25 - 50	"	(1972)

(1) Only adult frogs are considered. (2) Values from September are not considered. (3) Values from July are not considered. (4) Three different areas, one hectare each.

pects moor frogs have the traits of a more K-selected species (PIANKA, 1970).

Comparative information is meagre. BRIGGS & STORM (1970) found a yearly survival of 0.59 for *Rana cascadae* and TURNER (1969) a survival of 0.61 for *Rana pretiosa*, both North American species. Both values are mean for all age classes. TURNER (1969) explicitly states that he could not find any difference between different age classes. LICHT (1974) found a yearly survival of 0.69 for adult *R. pretiosa* and 0.64 for adult *R. aurora*. In contrast to TURNER, he found considerably lower survival for juvenile *R. aurora* than for adults.

5. FROG MORTALITY AND PREDATION

The biomass of dead adult frogs was computed and compared to the amount of frogs consumed by vertebrate predators in the Revinge area. The mean fresh weight of adult moor frogs in late summer (the study period) was 12.7 g, their expected weight when dying 14.3 g, the mean density 390 adult individuals per hectare and thus the total weight of dying moor frogs per hectare and year 2.5 kg. The corresponding figures for common frogs were 17.4 g, 22.5 g, 200 adult individuals, and 2.8 kg per year and hectare. The total weight of dying frogs in the 270 hectares of moist meadows in the study area was thus (2.8 + 2.5) x 270 = 1430 kg. This is a minimum estimate for the whole study area as frogs were also fairly abundant in 160 hectares of moist deciduous forest in the study area. They were however not as abundant in this habitat as in the moist meadow habitat (LOMAN, 1978 a).

The average amount of frogs taken by pole cats in the study area was 1080 kg per year (ERLINGE, pers. comm.). The corresponding figures for the buzzard was 45 kg (SYLVÉN, pers. comm.), for badger 380 kg (GÖRANSSON, pers. comm.), and for tawny owl 150 kg (NILSSON, pers. comm.). These predators consumed mainly adult frogs and the total amount taken by predators was thus estimated to 1655 kg per year in the Revinge area. Although the heron is not accounted for I suggest that this is close to the total amount consumed by vertebrate predators in the area. Comparing this amount with that calculated for all dying frogs suggests that vertebrate predation is an important mortality factor for adult frogs.

ACKNOWLEDGEMENTS

I thank Sam ERLINGE, Görgen GÖRANSSON, Ingvar NILSSON, and Magnus SYLVÉN for permission to use unpublished data on frog predation in the Revinge area. Sam ERLINGE and Staffan ULFSTRAND gave helpful comments on the manuscript.

RESUME

Durant cinq années consécutives, les densités des Grenouilles des champs (*Rana arvalis*) et des Grenouilles rousses (*Rana temporaria*) adultes, vivant dans une parcelle de prairie humide luxuriante située dans le sud de la Suède, ont été évaluées par la méthode de capture - recapture. Les Grenouilles étaient réparties en deux catégories d'âge selon leur taille: les adultes de première année d'une part et les adultes plus âgés d'autre part. Le taux de survie annuel de ces espèces a été calculé à partir des densités successives observées. La densité apparente des Grenouilles des champs décroît en septembre, probablement à cause du début de l'entrée en hibernation, diminuant ainsi la proportion des individus capturables. Une pareille diminution de la densité n'a pas été observée pour les Grenouilles rousses jusqu'à la fin des observations en octobre.

Au cours des cinq années d'étude, la densité des Grenouilles des champs a fluctué entre 140 et 680 adultes par hectare et celle des Grenouilles rousses entre 50 et 530 adultes par hectare. L'auteur pense que les facteurs les plus importants déterminant la densité des adultes sur la parcelle étudiée sont les taux de survie des oeufs et des larves. Le taux moyen de survie estimé est de 60 % pour les Grenouilles des champs et de 40 % pour les Grenouilles rousses. Les informations disponibles sur la prédation des Grenouilles par les vertébrés (Mustélidés et rapaces) dans les zones avoisinantes, conduisent à penser que le facteur de mortalité le plus important pour les Grenouilles adultes est la prédation.

(Résumé rédigé par J.-J. MORERE)

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