Site tenacity, within and between summers, of *Rana arvalis* and *Rana temporaria*

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Adult moorfrogs *Rana arvalis* and common frogs *Rana temporaria* were marked, released and recaptured during five summers in a 50 × 50 m large moist meadow site. All capture sites were noted. The distribution of number of captures per frog and the distance between successive capture sites were analysed. It is concluded that most frogs that were captured at least twice in the area occupied a permanent home range there. However, there was probably some change of centre of activity over time. The size of these home ranges was about 150 m² for *R. arvalis* and 330 m² for *R. temporaria*. There was no difference between sexes, nor between large and small frogs. Some frogs captured only once, especially *R. arvalis*, were probably temporary visitors. Many frogs returned to the study area in successive years, usually to the same part of the study area where they had spent the previous year.

INTRODUCTION

In the old days, an animal ecologist marked animals. Hopefully the animal could be recaptured or observed and identified. A massive effort of this type yielded all sorts of basic autecological information: estimates of individual growth rate, population densities and individual movements. The prime example is the marking program of FITCH (1958) at the University of Kansas. No mammal, reptile or amphibian was allowed to remain unmarked. I carried out a similar program for Swedish brown frogs (*Rana arvalis* and *Rana temporaria*) on a small scale (50 × 50 m). I have previously published compilations of growth rate (LOMAN, 1978) and population dynamics (LOMAN, 1984) emerging from this work. The compilation of movements was not published at that time but follows here.

This study is an analysis of *R. temporaria* and *R. arvalis* marked and recaptured in a restricted area during part of five summers. The results are analysed to provide evidence for the nature of the frogs' summer movements. In contrast to what had been possible if radio transmitters were used, details in the movement patterns cannot be tracked. The study aims at determining whether a restricted home range is used, at least for part of the summer, and at yielding an estimate of the size of any home range used. I will also give information of the between-year home range use of the frogs.

Study area and methods

The study was conducted in a moist meadow habitat in southern Sweden (55°40'N, 13°30'E). The study site was a 50 × 50 m part of a meadow with a uniform vegetation consisting of a thick layer of grasses and herbs, about 40 to 80 cm high. Scattered *Salix* bushes also occurred. The site was about 200 m from the closest possible breeding sites for the study species.

The study site was thoroughly searched during each summer from 1972 to 1976. The study periods were July 11 to October 7 1972 (26 searches), July 2 to October 7 1973 (30), July 8 to September 9 1974 (17), August 4 to October 6 1975 (25), and August 6 to August 30 1976 (13). Each search lasted for about one hour. I walked back and forth on fixed paths in order not to disturb the habitat more than necessarily. These paths were about 2 m apart. All frogs seen were captured if they were considered possible adults (*R. arvalis* at least 36 mm long and *R. temporaria* at least 46 mm long). Frogs of this size may breed in the following spring (LOMAN, 1978). Only frogs actually measured to these sizes were considered further. Each frog was individually marked by toeclipping and the capture site noted to the closest 1 m coordinates. Wooden sticks were placed as a 10 m grid to facilitate positioning.

Distances and time intervals between captures were significantly non-normal for both species (Lilliefors test, WILKINSON, 1990: all cases $P < 0.001$). After log transformation, the distributions for the *R. temporaria* data were not significantly different from normal (Lilliefors test: times, $P = 0.141$; distances, $P = 0.401$). By this criterion, the moor frog data differed somewhat from normality (Lilliefors test: times, $P = 0.047$; distances, $P = 0.030$). Nonetheless, the transformed data were used for both species in the significance tests.

Results

Distribution of captures per frog — estimating the population's size

Most frogs were only captured once (fig. 1) and were thus potential transients. To evaluate how common these were, I need an estimate of the total number of frogs at risk of capture in the study area, pooled over all study years. I estimated the size of this "population" (the sum of the five study years' population sizes) by fitting a negative binomial distribution to the data (CAUGHLEY, 1975: 154) and this yielded a surprisingly good fit for the moor frog (Table I). Extrapolating the fitted distribution to the zero class (frogs available for capture but never captured) yielded values for the total population at risk of capture. These were 1270 (3.5 times the total number captured) for *R. arvalis* and 598 (1.9 times the total number captured) for *R. temporaria*.
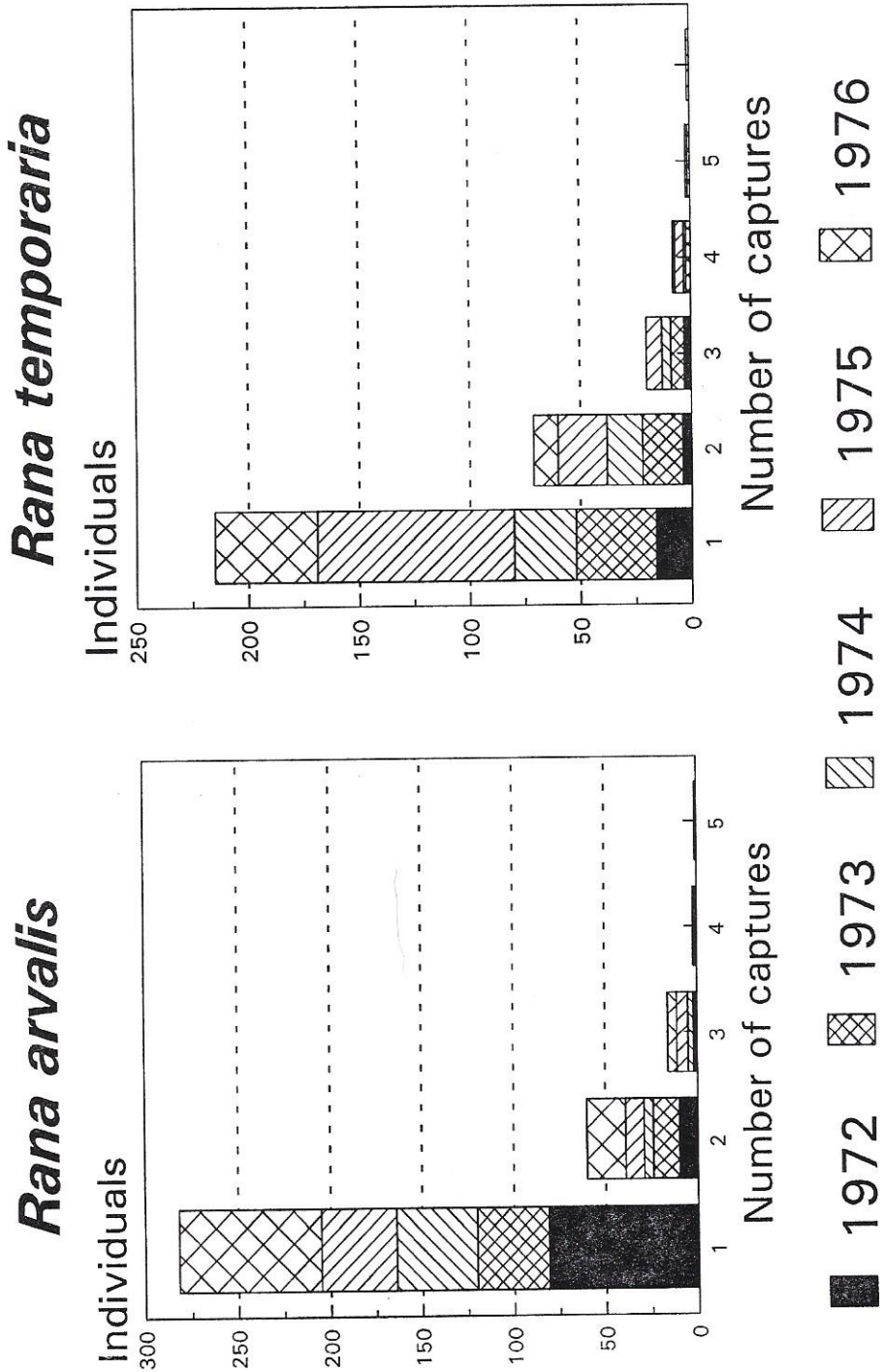
Rana arvalis

Rana temporaria

Fig. 1. — Distribution of number of captures per frog and year.

1972 1973 1974 1975 1976

Table I. - Frequency distribution found and expected from a fitted negative binomial distribution. The classes of animals captured 4 times or more are pooled for the $\bar{x}$-tests.

	Rana arvalis		Rana temporaria	
Captures	Observed	Expected	Observed	Expected
1	282	286.5	215	254.3
2	60	63.0	71	82.9
3	16	13.8	20	26.1
4	2	3.0	8	8.1
5	1	0.7	2	2.5
6	0	0.1	1	0.8
7	0	0.0	0	0.2
$\bar{x}$	0.75		9.22	
d.f.	1		1	
P	>0.10		<0.01	

DISTANCE BETWEEN SUCCESSIVE CAPTURES

The average distance between two captures of an individual within a year was 6.10 m for *R. arvalis* and 9.45 m for *R. temporaria* (Table II). These distances are significantly different (t = 2.89, d.f. = 171 [pooled variances], P < 0.001). They are also both significantly different from the average distance of 100 random distances, 26.50 m (*R. arvalis* vs. random: t = 14.2, d.f. = 176 [pooled variances], P < 0.001; *R. temporaria* vs. random: t = 10.7, d.f. = 193 [pooled variances], P < 0.001). These random distances were formed as the distance between 100 pairs of rectangular distributed (in the interval 0 to 50) random coordinates.

Sex and size effects

There was no difference in the average distance between two captures, between the sexes, in any of the species (Tables II and III). There was no effect of size, which presumably would reflect age (LOMAN, 1978) (Table III).

Successive captures of individual frogs

First to second versus first to third capture

If a frog was recaptured more than once, the second recapture tended to be about as far from the original site as the first recapture (Table IV).

Time between captures

There was a slight tendency for capture sites based on captures far apart in time to be further apart than those separated by only a short time (fig. 2). Based on all captures

Table II. - Distance between successive captures of one frog. For frogs captured more than twice, an individual mean value was used; a frog captured N times yielded N-1 values; distance between capture 1 and 2, between 2 and 3, etc. The table reports the average of these individual mean values.

	Mean	S.D.	N	Test for a sex difference	
				t	P
Rana arvalis					
Females	6.78	5.70	36	0.60	0.55
Males	5.74	4.14	39		
All	6.10	4.90	78		
Rana temporaria					
Females	9.80	9.89	33	0.73	0.47
Males	9.24	7.86	61		
All	9.45	8.53	95		
Random	26.50	13.15	100		

Table III. - Four way ANOVA, testing simultaneously for effects of year, sex, frog size, and time between capture and recapture on the distance between two captures.

Species	Source	d.f.	F	P
Rana arvalis	Year	4	0.27	0.89
	Sex	1	1.39	0.24
	Size	1	0.96	0.22
	Time int.	1	2.83	0.039
Rana temporaria	Year	4	0.92	0.46
	Sex	1	0.16	0.69
	Size	1	0.28	0.60
	Time int.	1	1.66	0.20

Table IV. - Distance between first and second versus distance between first and third
    capture of a frog. Values for frogs captured more than three times is based on a
    mean value for each frog. A frog captured N times yielded N-2 values. Only
    frogs captured at least three times are considered in this table. The test is a pair-
    wise t-test and the probabilities given are one-tailed.

		1st to 2nd site		1st to 3rd site		Test	
	N	Mean	S.D.	Mean	S.D.	t	P
Rana arvalis	17	7.63	5.23	7.13	6.85	0.15	0.44
Rana temporaria	29	8.30	5.89	9.83	7.31	1.46	0.075

(including several values for some frogs, recaptured more than once), this effect was
significant for both species. When correcting for other factors, this increase in distance was
only found to be significant for *R. arvalis* (Table III).

TIME SINCE MARKING FOR RECAPTURED FROGS

    If marked frogs tended to leave the study area after some time, those frogs that were
recaptured would be a biased sample of all frogs marked. They would mainly be those that
had been marked (for the first time in that year) during the time shortly preceding the time
of attempted recapture. The time they had been marked should be less than the
"population mark age", i.e. the average time all frogs marked that year had carried their
marks. Because successively more of those marked early would leave the study area, this
tendency should increase with time passed since marking started in that season. However,
there were no such tendencies (fig. 3).

BETWEEN-YEAR RECAPTURES

Return rate

    Quite a large number of marked frogs were recaptured in the following year.
Information of growth rate obtained during the present field work and previously
published (LOMAN, 1978) was used to classify frogs as "large" or "small" adults. As large
adults were, in each year, those classified that already in the previous year were adults (i.e.
at least 36 and 46 mm respectively) and thus subject to capture and marking (if found)
already in that year. Overall, 33 % (*R. arvalis*) and 47 % (*R. temporaria*) of all "large"
adults found in one year had actually been captured and marked also in the preceding year
(Table V). This is only moderately less than the proportion expected (42 % and 67 %
respectively) if all frogs that were marked in one year and survived to the next also
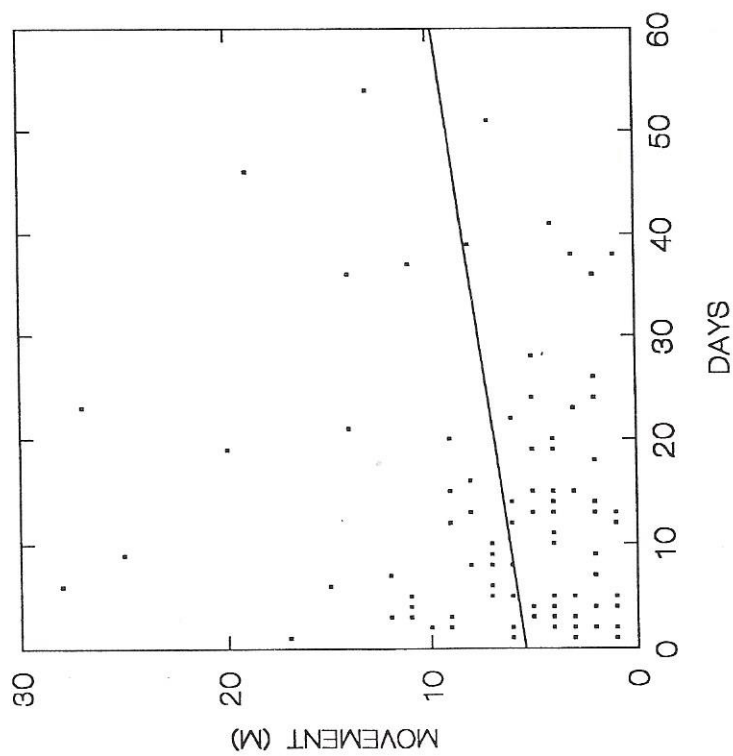returned to the study area.
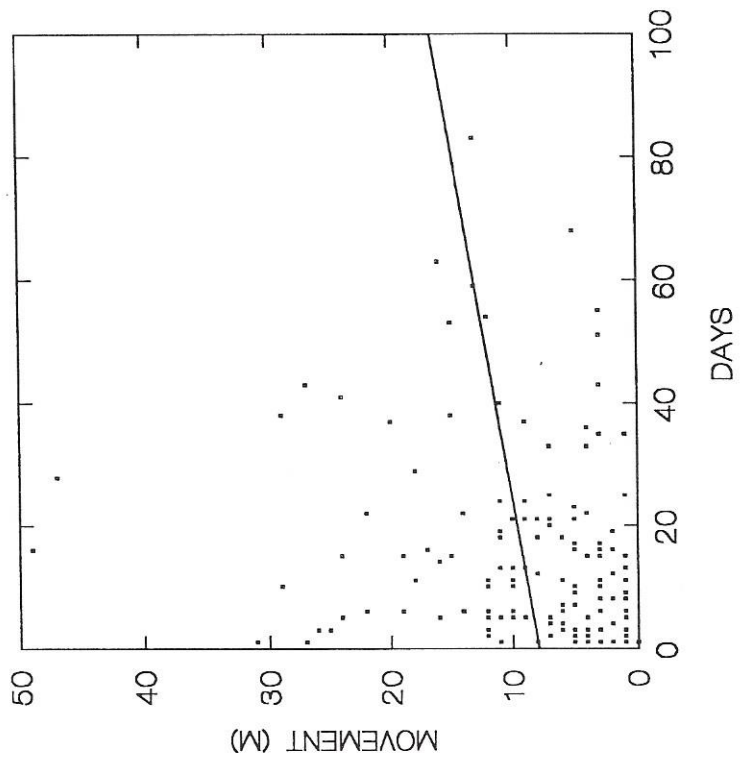
Fig. 2. — Relation of time between two captures and distance between the two sites. The correlation is significant for both species (*R. arvalis*: r = 0.23, d.f. = 101, P = 0.010; *R. temporaria*: r = 0.16, d.f. = 137, P = 0.024). If the degree of freedom-values are reduced to the number of different frogs involved, the values are still significant (*R. arvalis*: d.f. = 78, P < 0.025; *R. temporaria*: d.f. = 95, P < 0.05). All P-values are based on one-tailed tests.
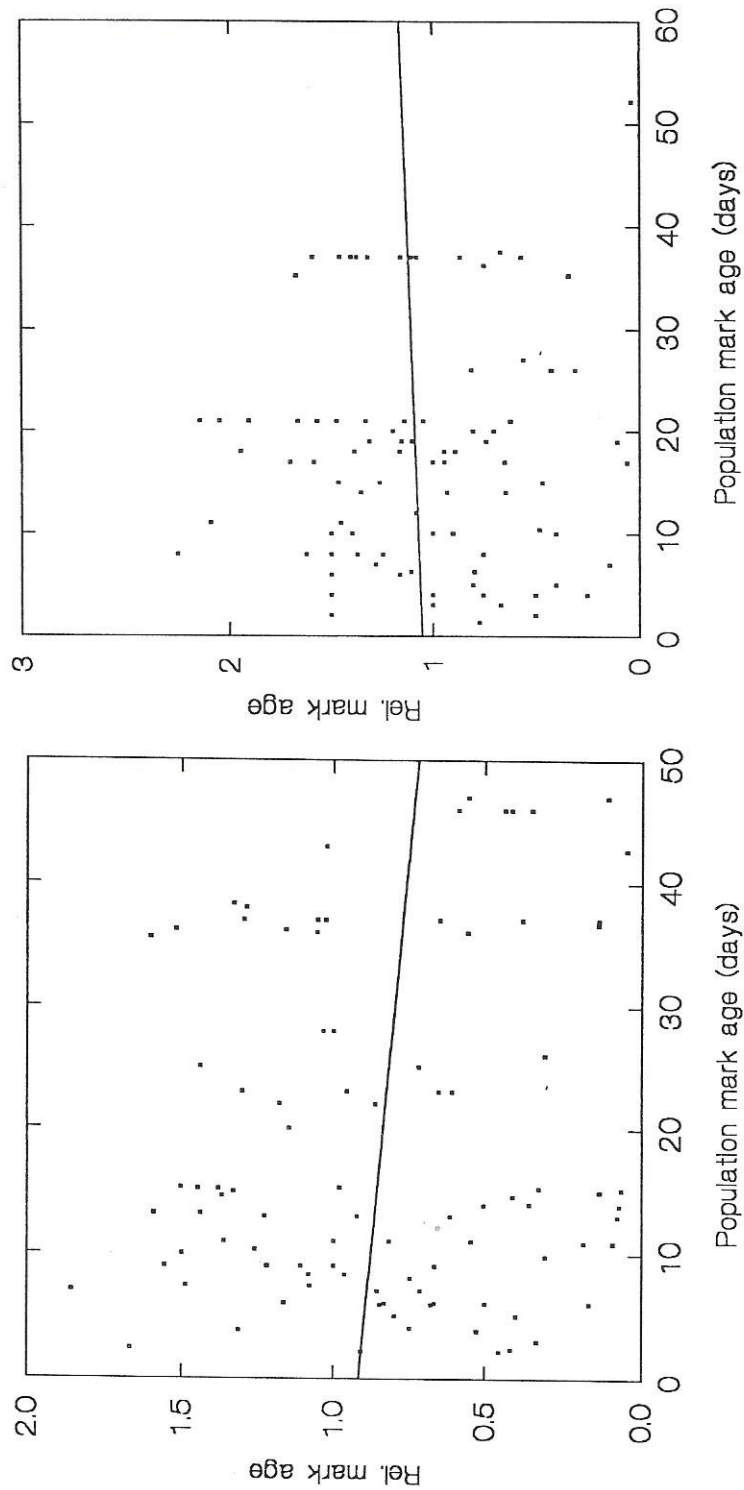
Fig. 3. – Relation between the "relative mark age" and the average time all frogs marked in that year had carried their marks ("population mark age"). "Relative mark age" is, for each capture, the time since the recaptured frog was first marked, divided by the "population mark age" on the day of that capture. There is a positive correlation for *R. temporaria* but it is far from significant ($r = 0.045$, d.f. $= 105$, $P = 0.65$). The slope for *R. arvalis* is negative, a direction that is excluded from being significant a priori (i.e. a one-tailed test).

Table V. - An analysis of the probability that a frog returns to the study area in successive years. "Captures T-1" is the number of frogs captured and marked in the study area in the year preceding T. "Population size T-1" is the estimated number of frogs in that year. Population size was estimated with the method of SCHUMACHER & ESCHMEYER (in SEBER, 1973: 139) (LOMAN, 1984). "Proportion marked in T-1" is the quotient between these. "Large adults T" is the number of frogs captured year T that were large enough to have been catchable in year T-1 (LOMAN, 1978). "Recaptures T" is the number of frogs captured in year T that were marked in the previous year. "Proportion recaptures T" is the quotient between the last two figures. There were too few captures of R. temporaria in 1973 and 1974 to warrant the computation of the last quotient.

Year T	Captures T-1	Population size T-1	Proportion marked T-1	Large adults T	Recaptures T	Proportion recaptured T
Rana arvalis						
1973	91	269	0.34	19	6	0.32
1974	48	54	0.89	13	6	0.46
1975	48	161	0.30	37	13	0.35
1976	56	96	0.58	38	10	0.26
Total	243	580	0.42	107	35	0.33
Rana temporaria						
1973	25	24	0.83	1	1	
1974	68	53	0.65	3	2	
1975	51	82	0.62	9	5	0.55
1976	129	249	0.52	14	6	0.43
Total	273	408	0.67	30	14	0.47

Between-year site tenacity

The frogs that returned to the study site and were recaptured in a second year were usually found close to the site where they had been found in the preceding year. The mean distance between the two sites was 6.5 m (S.D. = 6.37, N = 28) for *R. arvalis* and 12.8 m (S.D. = 9.64, N = 12) for *R. temporaria*. If there were several captures in one year of an individual, the arithmetic mean was used. These distances were not significantly different from the average distance between two capture sites in one year (Table II) (*R. arvalis*: t = 0.30, d.f. = 104, P > 0.10; *R. temporaria*: t = 0.51, d.f. = 105, P > 0.10).

DISCUSSION

NATURE OF HOME RANGES

What was the nature of the summer movements of the frogs? The site tenacity was striking. Distance between any two captures of a frog was significantly shorter than that between two random points in the study area. This distance was found by simulation. Therefore it is obvious that at least most frogs that were recaptured did have a home range, in the sense of a "restricted area, more or less regularly used". The most extreme model for a summer home range would be a definite, small area, traversed throughout almost daily. Such a model is supported by the fact that the distance between capture sites 1 and 3 was not larger than that between 1 and 2. Thus, sequences of distances between three captures of a frog did not indicate any sort of directional movement.

However, there was a significant (but numerically rather slight, see the linear regressions in fig. 2) tendency for captures far apart in time to also be far apart in space. This can be interpreted as representing a gradual shift in home range location, or at least in centre of activity within home range, over time.

If frogs tended to stay in a home range for some time, but then move much further and at least leave the study area all together, this would "dilute" the marked population. At the beginning of the study period each year, all marked (but see below) frogs would be available for capture. The average time a recaptured frog had been marked would be similar to the average time since marking for all marked frogs in the population. However, later in the season, some of the frogs marked early would have left the study area and a disproportionate fraction of those recaptured would have been frogs that settled (and were marked for the first time) recently. The average time a recaptured frog had been marked would at this time tend to be less than the average time since marking for all frogs in the population. However, such a pattern was not discernible (fig. 3). This suggests that frogs with a home range in the study area at the beginning of each study season (July-August) tended to stay there at least until the end of this (up to September). However, if some frogs moved very quickly through the study area, only being available for capture once, they would not affect this pattern. They would be equally unavailable for capture at the beginning as at the end of the capture season.

ON TRANSIENTS

Although the evidence is that most frogs captured at least twice were permanent residents in the study area, this cannot be shown for all those captured only once. These may have been unavailable for recapture because they were only temporarily present in the study area. The question can be somewhat elucidated by analysing the distribution of captures. It is appropriate to attempt fitting the distribution found to a negative binomial (see first section of *Results*) as this distribution results from situations with different capture probabilities for different individuals (CAUGHLEY, 1975). This was obviously the

case because the effort differed between different years. The fit was very good for *R. arvalis*, so some confidence can be put in the expected number of individuals not captured at all in this species, more than three times the total number captured. This capture efficiency was surprisingly low. The individuals never captured are both those that remained resident in the study area without being captured and those that only briefly entered it (some of these latter could also contribute to the high number of frogs captured only once). It seems however improbable that all these should have remained for long in the study area without being captured. I judge a substantial number of those *R. arvalis* only captured once to be transients. The evidence is less conclusive for *R. temporaria* because the fit was poorer and because the estimated class of zero captures was smaller. Still, I would suggest also that some *R. temporaria* were transients to the study area. Apart from possible true nomads, these are frogs changing home range (though I have shown above that this is not a very common behaviour), or frogs that make temporary excursions from home ranges outside the study area. I have previously (LOMAN, 1981) shown that the presence of transient frogs is necessary to explain the pattern of recolonisation of an area where *R. temporaria* were removed. DOLE (1965a) has shown that leopard frogs (*Rana pipiens*) make long excursions, outside their regular home ranges, during rainy nights. Such a phenomenon may explain the pattern found here.

An alternative explanation to the presence of transients would be high mortality. However, yearly mortality in the study population was previously calculated to 61 % (*R. arvalis*) and 36 % (*R. temporaria*) which appears to be normal for terrestrial ranids (LOMAN, 1984). Also, I would expect most mortality to take place during the spring and autumn migration.

SIZE OF HOME RANGES

For both species, the data suggest that males and females as well as small and large individuals, had home ranges of similar size. What was the actual size of the home ranges? The small number of recaptures makes it impossible both to infer the shape of the home ranges and the individual variation. However, a rough impression can be gained from the following calculation. By means of simulations, the home range size that would give the same average distance between two random points (in the simulated home range) as the observed distance (Table II) between two capture sites can be calculated. These calculations were based on two alternative models for the nature of the home range. With a rectangular distribution model I calculated the diameter of the home range periphery. This was 13.3 m for *R. arvalis* and 20.5 m for *R. temporaria* respectively. With a normal distribution model, I calculated the diameter of a circle encompassing 95 % of the activity. This was 15.5 m for *R. arvalis* and 24.0 m for *R. temporaria* respectively. Because we do not know the actual distribution of activity in the home range and there are several forms of sampling errors, the values calculated can only be considered a rough estimate of the magnitude of the home ranges. One conclusion is that, at least for the *R. temporaria* which had the largest home ranges, most frogs had home ranges that overlapped the border of the study site. This should further tend to underestimate home range sizes. Also, it is

obvious from the information of density in the study area (see first section of *Results* and LOMAN, 1984) that the home ranges of the studied frogs overlapped widely, both intra- and interspecifically.

BETWEEN-YEAR MOVEMENTS

Surprisingly many frogs returned to the study area in successive years. The proportion of all "large" adults that were already marked when captured for the first time in a year was almost as large as the proportion of all frogs estimated to have been marked in the study area in the previous year (see second section of *Results* and Table V). This calculation suggests that 79 % (0.33/0.42) of all *R. arvalis* and 70 % (0.47/0.67) of all *R. temporaria* returned to the study site. These figures rely heavily on the estimations of population sizes. Because of biases and sampling errors in these estimates as well as sampling errors in the other figures, it is only possible to state that a substantial proportion, possibly almost all frogs alive, returned to the study site. Because of the arbitrary nature of "return" (here defined as return to a 50 × 50 m square), a more precise answer, even if it were possible to give, would only be of limited use. However, the tendency for many frogs to return precisely to the same summer home range is clear; those that returned did actually do so to the part of the study area where they spent the previous summer.

COMPARISON WITH OTHER STUDIES

It is striking that few studies of this subject seem to have been published recently. The original list of references, compiled in 1981, contained quite a few comparable studies (Table VI). One of the few recent studies of amphibian summer home ranges is that by SINSCH (1988a). He employed a more sophisticated technique, trailing toads (*Bufo bufo*) with special devices, leaving a thin thread after the animal. That technique has previously also been used by DOLE (1965a), working with leopard frogs (*Rana pipiens*). However, it seems that everyone now expects studies of animal movements to employ radio transmitters. Though this certainly is justified, it emerges that little work, based on radio transmitters, has been published on frog movements. Studies that do are work by VAN GELDER and BUGTER (1987) on (one) *R. arvalis*, a report by FALLER-DOEPNER et al. (1991) on the post-breeding migration of *R. temporaria*, a study of summer home ranges of *Bufo americanus* (WERNER, 1991) and another study by SINSCH (1988b) on breeding behaviour of *Bufo calamita*. It seems that the promise of radio transmitters has discouraged work employing conventional capture-recapture studies. Actually, it is probably only recently that transmitters small and long lived enough for useful work with frogs (but for the largest species) have been available. Future work with radio transmitters will yield more realistic descriptions of frog movements and home range use than is possible with capture-recapture methods, the results of which must be analysed to provide indirect evidence for the nature of the movements.

Nonetheless, most previous studies, like this one, have reported that frogs during the nonbreeding season tend to occupy restricted areas, home ranges. Examples include: *Rana*

Table VI. - Published information on summer home range areas in frogs. Age categories are adult and subadult. If only mean distance between capture is given, this is found in the table, together with an estimate of home range area (made with the "rectangular model" above). DOLE (1965b) and KRAMER (1974) give direct estimates of home range area, computed with the minimum polygon method. Sizes of adult frogs are from CONANT (1958), STEBBINS (1966) and own data. ad: adult; sad: subadult. MD: Mean distance between captures (m).

	Age	Size (mm)	MD	Area (m²)	N	Reference
Rana pretiosa	ad, sad	50-100	12	(534)	23	CARPENTER, 1954
Bufo boreas	ad, sad	60-125	13	(627)	19	CARPENTER, 1954
Gastrophryne olivacea	ad	20-35	33	(4040)	52	FITCH, 1958
Acris crepitans	-	15-35	36	4810)	34	PYBURN, 1958
Bufo terrestris	-	40-75	13	(627)	27	BELLIS, 1959
Rana sylvatica	ad, sad	35-65	12	(534)	298	BELLIS, 1965
Rana arvalis	sad		12	(534)	16	HAAPANEN, 1970
Rana arvalis	ad	35-55	5	(93)	35	HAAPANEN, 1970
Rana temporaria	sad		8	(237)	96	HAAPANEN, 1970
Rana temporaria	ad	45-70	8	(237)	23	HAAPANEN, 1970
Bufo americanus	ad	28-50		21	5	WERNER, 1991
Bufo bufo	ad	50-70	4	(59)	29	HAAPANEN, 1974
Bufo bufo	sad		5	(93)	22	HAAPANEN, 1974
Pseudacris triseriata	ad	20-35		490	9	KRAMER, 1974
Rana pipiens, site I	ad	50-85		370	28	DOLE, 1965b
Rana pipiens, site I	sad			280	17	DOLE, 1965b
Rana pipiens, site II	ad	50-85		90	18	DOLE, 1965b
Rana pipiens, site I	sad			80	4	DOLE, 1965b
Rana arvalis	ad	36-55	6	(133)	78	This study
Rana temporaria	ad	46-70	9.5	(330)	95	This study

clamitans (MARTOF, 1953), *R. pretiosa* (CARPENTER, 1954; TURNER, 1960), *R. sylvatica* (BELLIS, 1965), *R. pipiens* (DOLE, 1965a-b), *R. arvalis* and *R. temporaria* (HAAPANEN, 1970); *Bufo boreas* (CARPENTER, 1954), *B. terrestris* (BELLIS, 1959), *B. bufo* (HEUSSER, 1968; HAAPANEN, 1974; SINSCH, 1988), and *B. americanus* (WERNER, 1991); *Acris crepitans* (PYBURN, 1958); *Pseudacris triseriata* (KRAMER, 1974); and several tropical species (INGER, 1969). The home range areas reported are similar in size to those found by me (Table VI).

According to some authors, the home range may change during the course of one season: see BRECKENRIDGE & TESTER (1961) for *Bufo hemiophrys*, TURNER (1960) for *Rana pretiosa*, and WERNER (1991) for *Bufo americanus*. I could not detect evidence of this. This may mean that it was really of unusual occurrence in my populations. It could also be because my study only lasted for part of the summer seasons. Also, it may be a matter of how to interpret a pattern. Based on telemetry, VAN GELDER & BUGTER (1987) published

Study area and methods

The study was conducted in a moist meadow habitat in southern Sweden (55°40'N, 13°30'E). The study site was a 50 × 50 m part of a meadow with a uniform vegetation consisting of a thick layer of grasses and herbs, about 40 to 80 cm high. Scattered *Salix* bushes also occurred. The site was about 200 m from the closest possible breeding sites for the study species.

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