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Original article

Density dependent growth in adult brown frogs *Rana arvalis* and *Rana temporaria* – A field experiment

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ABSTRACT

In species with complex life cycles, density regulation can operate on any of the stages. In frogs there are almost no studies of density effects on the performance of adult frogs in the terrestrial habitat. We therefore studied the effect of summer density on the growth rate of adult frogs during four years. Four 30 by 30 m plots in a moist meadow were used. In early summer, when settled after post-breeding migration, frogs (*Rana arvalis* and *Rana temporaria* that have a very similar ecology and potentially compete) were enclosed by erecting a fence around the plots. Frogs were captured, measured, marked and partly relocated to create two high density and two low density plots. In early autumn the frogs were again captured and their individual summer growth determined. Growth effects were evaluated in relation to two density measures: density by design (high/low manipulation), and actual (numerical) density. *R. arvalis* in plots with low density by design grew faster than those in high density plots. No such effect was found for *R. temporaria*. For none of the species was growth related to actual summer density, determined by the Lincoln index and including the density manipulation. The result suggests that *R. arvalis* initially settled according to an ideal free distribution and that density had a regulatory effect (mediated through growth). The fact that there were no density effects on *R. temporaria* (and a significant difference in its response to that of *R. arvalis*) suggests it is a superior competitor to *R. arvalis* during the terrestrial phase. There were no density effects on frog condition index, suggesting that the growth rate modifications may actually be an adaptive trait of *R. arvalis*. The study demonstrates that density regulation may be dependent on resources in frogs' summer habitat.

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1. Introduction

The fact that many vertebrate populations rarely exhibit outbreaks in numbers has long been considered an indication of the importance of regulating factors such as competition and predation (Lack, 1954). Many studies have been conducted to identify these factors for populations of different taxa, including anurans (Berven, 1990; Altwegg, 2003; Harper and Semlitsch, 2007).

Most anurans have a complex life cycle with an aquatic and a terrestrial stage. Therefore, if a population is regulated this may involve either of the stages only, or both in combination (Wilbur, 1980). To fully understand the population dynamics of such populations, both stages should be studied.

Most of the research on amphibian population dynamics has so far focused on the tadpole stage. Competition in the adult stage has attracted far less attention and there are very few experimental studies relevant to population regulation during the terrestrial,

post-metamorphic phase (Pearson, 1955; Pechmann, 1994, 1995; Altwegg, 2003; Harper and Semlitsch, 2007).

To confirm the existence of regulation effects in natural populations, it is necessary to experimentally *manipulate natural* densities in the *field* (Bury, 2006; McCallum and McCallum, 2006). If one only *compares* performance in naturally high and low density sites, it may be that these sites also differ in resources, but not resources per individual. Density effects in studies involving *unnaturally* high densities may have no relevance to what actually happens in real populations. Also, densities measured under (more or less) *artificial* conditions may not be relevant to the relation between density and critical resources that is actually encountered in nature.

The theory of "ideal free distribution" (IFD) (Fretwell, 1972) predicts that local variation in density directly reflects among site variation in resources. If so, no variation in performance is expected in an observational study. Experimental manipulations, however, account for such effects. By conducting a field experiment involving several sub-sites, studying them for several years and by analysing both direct effects of manipulations and effects of actual density, this study attempts to approach the problem both with and without regard to the possibility of IFD.

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The present study is concerned with possible density regulation operating on adult *Rana arvalis* and *Rana temporaria* in the field. The reason that both these two species are included is that they are both common in the study area (Loman, 1984) and they are likely to compete as they have very similar habitat choice (Loman, 1978), food habits (Loman, 1979), and diurnal rhythm (Loman, 1980). Density effects on the tadpole stage of these two species have previously been studied in this area (Loman, 2001, 2004).

The basic strategy is to allow frogs to settle undisturbed in their summer habitat. Under an ideal free distribution, this would mean that the number of animals per unit of resource is similar across sub-sites at the start of the experiment. We then study effects of manipulated deviations from this ideal free distribution and effects of the absolute density. In the present study we monitor growth, rather than survival or reproduction. This is because growth is a variable that can be measured with more precision than survival and is likely to vary as a direct response to variations in resources during the summer feeding phase.

2. Method

2.1. Field site and procedures

The study site was a moist meadow in Skåne, southern Sweden (55°40′N, 13°30′E). There were breeding sites for both *R. arvalis* and *R. temporaria* in the vicinity of the study site.

The complete study site was 60 m × 60 m, divided into four 30 m × 30 m sections. A 60 cm high perimeter fence and inner subdivision fences were constructed from metal sheets (Fig. 1). The vegetation next to the fence at the perimeter and the subdivisions was regularly cleared to prevent frogs from crossing on overhanging vegetation. Also, sheets were dug into the ground to a depth of 20 cm in order to prevent frogs from escaping through shallow vole tunnels.

The study was conducted during four years, 1993–1996. In each of the four study years the sheets were put up 1 day before the start of captures. The end of June was chosen as the time to start the experiment because post-breeding migrations had been completed by then (Tramontano, 1998). This means that the initial densities found in the four sections were those "chosen" by undisturbed frogs, possibly representing an ideal free distribution. After the last capture bout in autumn, the sheets were removed to allow for the autumn migration and next year's post-breeding migration.

In all years, time for metamorphosis had only barely begun when the fence was put up, resulting in few metamorphs (young of the year) having entered the study site during the time of the experiment. These were disregarded and frogs studied were thus in their second summer or older.

In each year there were two capture periods; summer and autumn (Table 1). During each capture period, 17–26 capture bouts were conducted. The capture periods lasted for 17–27 days (summer) and 12–27 days (autumn). The capture bouts were on separate days or early morning and late afternoon/evening on the same day. A capture bout was conducted by slowly walking up and down the study site covering the whole area in about 2 h. All frogs spotted (Table 2) were captured by hand (if possible) and individually marked by toe clipping. The snout–urostyle (SUL) length was measured with calipers to the nearest 0.1 mm and the frog weighed to the nearest 0.1 g. Frogs were handled at the study site and released within 1 h. The purpose of the captures was threefold: (1) to relocate part of the frogs from designated low density to high density sections (summer only), (2) to provide an estimate of the natural (absolute) density of frogs in the four sections, and (3) to measure individual growth rate, within and between capture periods.

2.2. Density manipulations and measurements

When devising the size of an experimental manipulation in the field, a balance must be sought between too large a manipulation and too small a manipulation (Hairston, 1989). The former may result in densities (in the source areas) that are too low to yield meaningful samples and too high (in the recipient areas) to be considered natural. The latter decreases the power of the experiment because the sections that are contrasted are too similar in density. With this in mind, the following procedure was used.
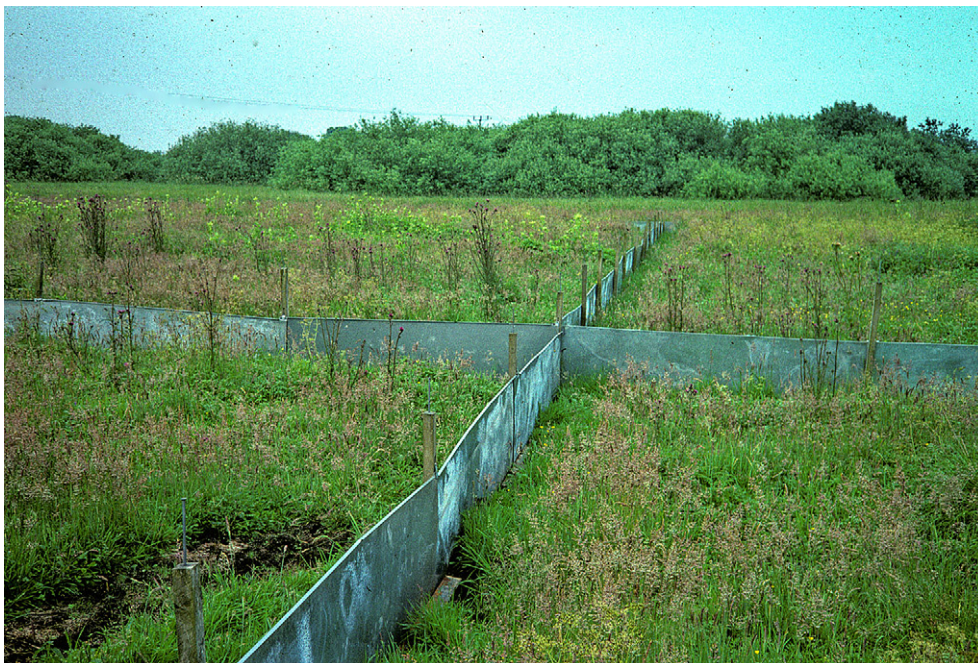

Fig. 1. The study site with metal sheet fences.

Table 1
Capture periods and number of captures (including recaptures within period) in the study plot. RA: *Rana arvalis*, RT: *Rana temporaria*.

	Summer				Autumn			
	Dates	Bouts	Captures		Dates	Bouts	Captures	
			RA	RT			RA	RT
1993	June 26–July 23	26	195	223	Sept 5–Oct 2	24	97	73
1994	June 26–July 19	25	110	137	Sept 8–Sept 29	17	47	63
1995	June 21–July 7	25	200	687	Sept 5–Sept 21	21	83	259
1996	June 27–July 11	23	102	56	Sept 9–Sept 21	18	24	19

In the first study year, 1993, the SW and NE sections were designated low density sections. In each of these two sections, every third frog captured was moved to the SE section, every third was moved to the NW section, and every third was left in its own low density section. This scheme was followed separately for the two *Rana* species. The same scheme was followed in 1995. In 1994 and 1996 the high and low density sections were reversed.

Within sections, the number of frogs was computed using the Lincoln index (Table 2) (Caughley, 1975). The summer catch (including additions and excluding removals) provided the number of marked individuals. The autumn catch provided information on the proportion marked in the population. Assuming the same mortality rate for marked and unmarked individuals, this index is an estimate of the summer population. To estimate background variation (before manipulations) in frog numbers among years and sections the Lincoln index estimates were corrected by the number of frogs removed or added.

The growth rates were compared to two aspects of section density. A section's "Density by design" was either of two categories; sections that in that year was used as recipient (high density) or source (low density) for transferred frogs, respectively. "Absolute density" was the actual summer density (after translocations) estimated by the Lincoln index. We studied the effect of each species' density separately ("species density" in Table 5) and also the effect of the combined density. The latter measure is motivated by the fact that the two species have very similar summer ecology.

2.3. Growth rates and condition index

The dependent variable analysed in this study is growth rate. This is measured as body length (SUL) growth from the summer to the autumn period. Since frogs grew within capture periods (summer and autumn respectively), the calculated between period growth rate would vary with the dates (within the capture period) a frog was captured, adding unwanted noise to the analysis. Also, growth rates were found to be higher for small than for large frogs (Fig. 3, Table 3) and in summer than in autumn (Table 3). However, there was no effect of year on growth rate (Table 3). To correct for confounding effects, the following procedure was adopted.

As a first step, all lengths measured, in either of the two capture periods, were adjusted to correspond to the expected value on July 1st and September 15th, respectively. To do this we calculated the individual growth rate (mm/day) for all frogs captured at least twice and at least 6 days apart within a capture period from a regression of its measured sizes against date. These growth rates were then regressed on the respective frog's size to obtain size adjusted correction equations. For the summer period this gave the following equations:

$$S' = S - D*(0.392 - 0.0049*S)(R.\ arvalis)$$

$$S' = S - D*(0.460 - 0.0036*S)(R.\ temporaria)$$

S' is expected size (mm) on July 1st, S is measured size (mm) and D is date of measurement (number of days after July 1st). These equations were then applied to all measures in the summer

Table 2
Captures, between period recaptures, and estimated summer population densities in the sections. Type is H for high density sections that received relocated frogs and L for low density sections, from which frogs were removed. "Catch" is number of different individuals caught. Translocated frogs are scored in their new section. Population estimates are given both excluding ("before") and including ("after") effects of the translocations. The standard error estimate is the same for both estimates. "Recapt." is the number of frogs captured in autumn that were also captured in summer.

		Type	*R. arvalis*						*R. temporaria*					
			Summer				Autumn		Summer				Autumn	
			Catch	Population estimate			Catch	Recapt.	Catch	Population estimate			Catch	Recapt.
				Before	After	S.E.				Before	After	S.E.		
1993	NW	H	35	40.3	51.3	7.2	21	14	40	46.9	62.9	9.8	21	13
	NE	L	6	15.0	8.0	2.0	3	2	6	16.0	8.0	2.0	3	2
	SW	L	10	47.5	32.5	12.1	12	3	11	83.5	60.5	31.6	10	1
	SE	H	48	51.1	62.1	7.0	21	16	45	57.1	73.1	15.1	12	7
1994	NW	L	7	41.0	35.0	18.1	9	1	7	77.0	70.0	47.0	9	0
	NE	H	29	38.4	46.4	11.6	7	4	19	18.5	28.5	6.2	8	5
	SW	H	28	41.8	49.8	10.4	15	8	37	143.2	154.2	50.8	24	5
	SE	L	8	34.0	24.0	8.4	7	2	9	62.5	49.5	25.9	10	1
1995	NW	H	34	64.3	79.3	19.0	20	8	133	171.7	221.7	23.0	59	35
	NE	L	9	35.0	24.0	9.5	7	2	13	45.9	27.9	7.2	14	6
	SW	L	19	69.3	44.3	16.8	6	2	56	306.3	220.3	47.6	58	14
	SE	H	58	105.5	126.5	26.9	23	10	183	295.9	351.9	46.9	49	25
1996	NW	L	7	27.3	16.3	6.2	6	2	2	9.0	8.0	4.9	3	0
	NE	H	23	22.7	30.7	5.8	7	5	7	4.0	7.0	0.0	3	3
	SW	H	24	27.0	36.0	12.0	2	1	14	31.0	35.0	15.7	4	1
	SE	L	3	16.5	10.5	5.1	6	1	4	22.0	16.0	9.8	3	0

Table 3
ANCOVA test of factors affecting within period growth rate (mm/day) for individual frogs. Only frogs measured at least twice and at least 6 days apart within one period are included. An effect of period type means that growth rate differed between summer and autumn.

	R. arvalis			R. temporaria		
	d.f.	F	P	d.f.	F	P
Year	3:163	0.85	0.47	3:314	0.36	0.78
Period type	1:163	21.6	<0.001	1:314	56.0	<0.001
Size	1:163	16.4	<0.001	1:314	77.5	<0.001

period. In autumn *R. arvalis* average growth was small (-0.005 mm/day) and not significantly different from zero ($t = 1.09$, d.f. $= 30$, $P = 0.28$). We therefore decided not to make any corrections of the autumn measurements for this species. In autumn *R. temporaria* average daily growth rate (0.11 mm/day) was significantly larger than zero ($t = 4.28$, d.f. $= 43$, $P < 0.001$) but there was no significant or apparent effect of size. The following equation was therefore used:

$$S' = S - 0.11 * D$$

where S' is now size on September 15th and D is measured in days after September 15th. These equations were applied to all *R. temporaria* measures in the autumn. In a second step, all frogs' within period sizes were calculated as the average of their date corrected size measures.

For frogs captured at least once in each of both periods of a year, within year growth (in mm increase from summer to autumn) could now be calculated. If a frog was translocated, it was scored for the new section.

Analysing between period growth we accounted for the fact that large frogs grew considerably slower than small ones (Fig. 3) using the approach recommended by García-Berthou (2001); we included the estimated summer size as a covariate in the linear mixed models. For the purpose of illustration, a different approach was used in order to make the graphs intuitive. Here growth rate was visualized as residuals from a regression of within year growth (mm) against frog summer size (mm) (Fig. 3).

Condition was estimated as the residual of a regression of autumn log weight on autumn log length. This means that the condition index was independent of length (Jakob et al., 1996). The residual was tested for effects of year and density treatment.

To account for the fact that measures from the same section were not independent, linear mixed models were used (SAS proc mixed, V 9.1). In these models, the four sections and the interaction between section and year (nested within density treatment) were used as random factors. Denominator degrees of freedom were estimated using the Satterthwaite approximation. In addition to density we tested for effects of year and the interaction between year and density, but excluded these factors unless $P < 0.1$. These tests were done for both growth rate and condition.

3. Results

3.1. Background density patterns

There were for both species large and significant differences in densities among years (Fig. 2, Linear mixed models (including section identity as a random effect) year effect: (*Ra*) $F = 4.74$, d.f. $= 3:12$, $P = 0.021$, (*Rt*) $F = 6.25$, d.f. $= 3:12$, $P = 0.009$). Apart from year effects, also section identity had a significant effect on *R. temporaria* (Fig. 2), but not on *R. arvalis* (Linear mixed model tests, ($X^2 = 16.34$, d.f. $= 1$, $P < 0.001$; $X^2 = 0.64$, d.f. $= 1$, $P > 0.1$,
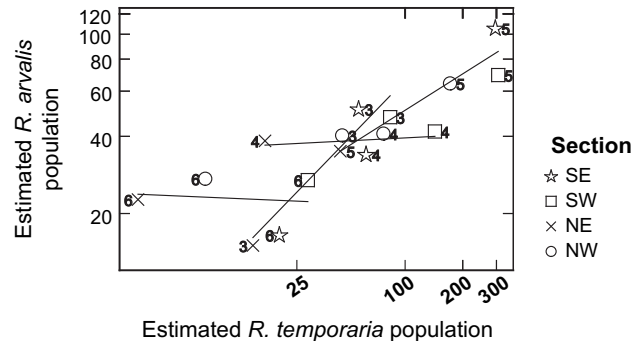

Fig. 2. Number of frogs in the different sections. Data symbols represent one year–section combination each. The population is the estimated number (by means of Lincoln index) per section at the start of the experiment and before any relocations. Data point labels refer to the respective year. The within year linear regressions (each based on four data points from different sections) are also shown.

respectively). Also, there was a correlation between the two species' densities in different sections, when correcting for the year effect (Fig. 2, Linear mixed model, $F = 109.4$, d.f. $= 1:1.86$, $P = 0.011$).

3.2. Effects resulting from the manipulation

R. arvalis living in sections that by design had a low density grew faster than those living in high density sections (Fig. 3, Table 4). For *R. temporaria*, there was no tendency for frogs living in low density sections to grow faster than those living in high density sections (Fig. 3, Table 4). The difference in effect of design density on the two species growth rates was real; testing the effects of design density on all frogs (both species) but including species identity as a factor showed a significant effect of the interaction species × density (d.f. $= 1:14.1$, $F = 4.80$, $P = 0.046$).

There was no effect of section density type on the condition of either species. (Table 4). However, there were significant year effects on condition.

3.3. Effects of variation in absolute density

For none of the species there were significant effects of absolute section density on growth rate (Fig. 4, Table 5). This was true both with regard to the combined density and that of the respective species (although there were hints that *R. arvalis* was affected by its own density ($P = 0.063$)). There were also no effects of absolute section density on condition (Fig. 5, Table 5).

4. Discussion

Using manipulations to study effects of density on performance (i.e. regulation) has two advantages over correlative studies. First, a correlative study cannot prove that poor performance at high frog densities is a causal effect. It may instead be a carry over effect from the tadpole phase if a successful recruitment of metamorphs results in many but small (due to competition at high tadpole density) froglets. A poor start may affect their growth pattern also later on, i.e., a reversed silver spoon effect. If this is the case we may infer density dependence during the terrestrial phase when there is none. A correlative study may also suffer from the opposite problem. Assuming patch quality is heterogeneous, higher densities of adult frogs may settle in high quality patches, growing as well as those few settling at low quality sites. This is the ideal free distribution (Fretwell, 1972). Focusing on the actual (natural) densities we may then erroneously dismiss the possibility of density dependent effects.
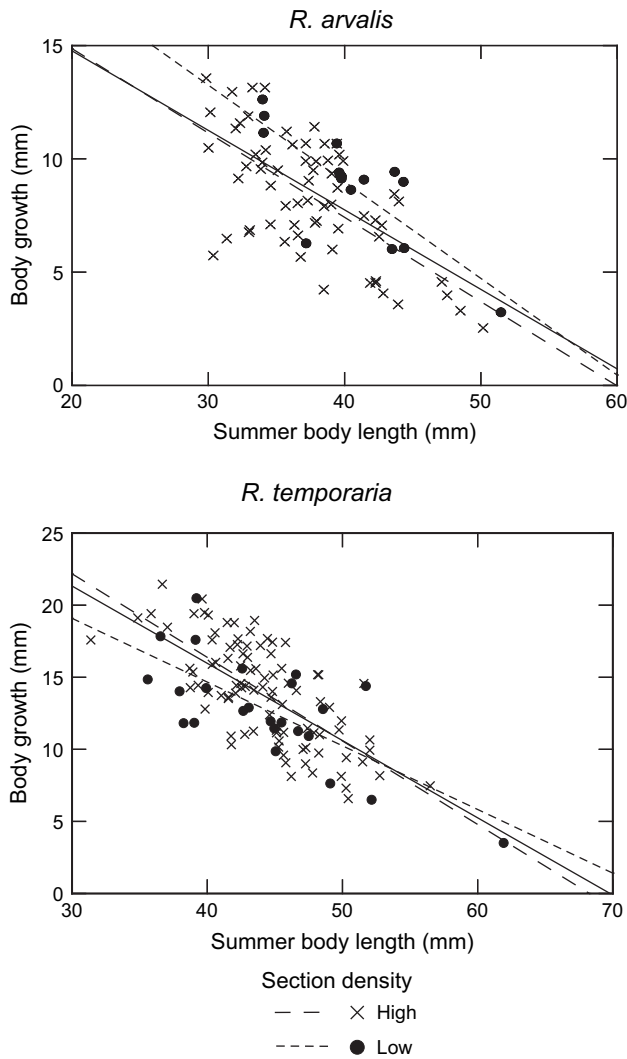
R. arvalis

R. temporaria

Section density

— — ✕ High

- - - ● Low

Fig. 3. Between period growth for frogs in high and low density section. Growth is the estimated growth from the summer period (standardized to July 1st) to the autumn period (standardized to September 15th). Overall mean slopes (continuous lines) and separate for frogs in high and low density sections (dashed lines) are shown.

In our study area, there were (before manipulations) consider-able differences in densities among the study sections. Actually, for both species, the SW section always had a naturally high density while the NE section had a low density. Accounting for year, this was

R. arvalis

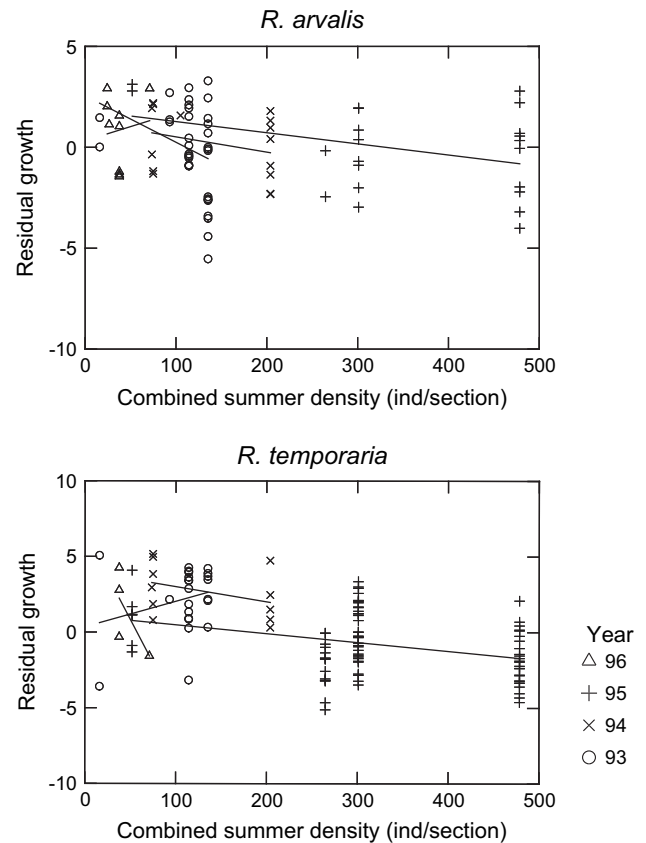## R. temporaria

Year
△ 96
+ 95
✕ 94
○ 93

Fig. 4. Residual between period growth in relation to section density. Growth is the estimated growth from the summer period (standardized to July 1st) to the autumn period (standardized to Sept. 15th). Residual means that this growth has been corrected for effects of starting size (at July 1st). Section density is the sum of the estimated summer density of the two species. The figure shows separate slopes for the four years.

indeed a significant effect for one of the species. Most herbs present were perennials and the nature of the vegetation cover similar over years. The size of the experimental units (30 × 30 m) is sufficient for a meaningful site specific choice of a frog's summer home range; the size of these species average summer home ranges in this habitat is about 15 m across (Loman, 1994). Although other interpretations

Table 4
Effects of density by design (high or low density section), year and section (NW, NE, SW, SE) on growth and condition of individual frogs, analysed with linear mixed models. Growth is the estimated length growth from the summer period (standardized to July 1st) to the autumn period (standardized to September 15th). Condition is estimated as the residual from a regression of weight on size in autumn. Non significant (at $\alpha > 0.1$) interactions and non significant random factors were removed before the final analysis shown here.

	Rana arvalis			Rana temporaria		
	d.f.	F	P	d.f.	F	P
Growth						
Density	1:13.4	5.73	0.032	1:9.7	0.003	0.87
Year				3:7.9	3.79	0.059
Length	1:75.6	65.4	<0.001	1:108	175.5	<0.001
Condition (weight)						
Density	1:9.83	3.14	0.11	1:3.81	0.58	0.49
Year	3:10.3	5.63	0.015	3:11.2	20.5	<0.001

Table 5
Effect of absolute density (combined or species d.) on growth and condition of individual frogs, analysed with mixed linear methods. Growth is the estimated length growth from the summer period (standardized to July 1st) to the autumn period (standardized to September 15th). Effect on growth is corrected for starting summer size (length), year and section. Combined density is the effect of the sum of the two species densities, each computed with the Lincoln index. Species density is the effect of *R. arvalis* density on *R. arvalis* performance and *R. temporaria* density on *R. temporaria* performance, respectively. Non significant interactions were removed before the final analysis, shown here.

	Rana arvalis			Rana temporaria		
	d.f.	F	P	d.f.	F	P
Growth						
Combined density	1:12.6	2.59	0.13	1:1.68	4.58	0.19
Length	1:75.3	67.0	<0.001	1:111	173.7	<0.001
Species density	1:15.8	38.989	0.063	1:2.35	3.43	0.19
Length	1:74.8	68.3	<0.001	1:111	174	<0.001
Condition						
Combined density	1:11.6	2.71	0.12	1:16.1	1.91	0.18
Year				3:7.45	6.31	0.019
Species density	1:14.5	1.29	0.27	1:44.8	2.65	0.11
Year				3:21.5	6.73	0.0023

R. arvalis
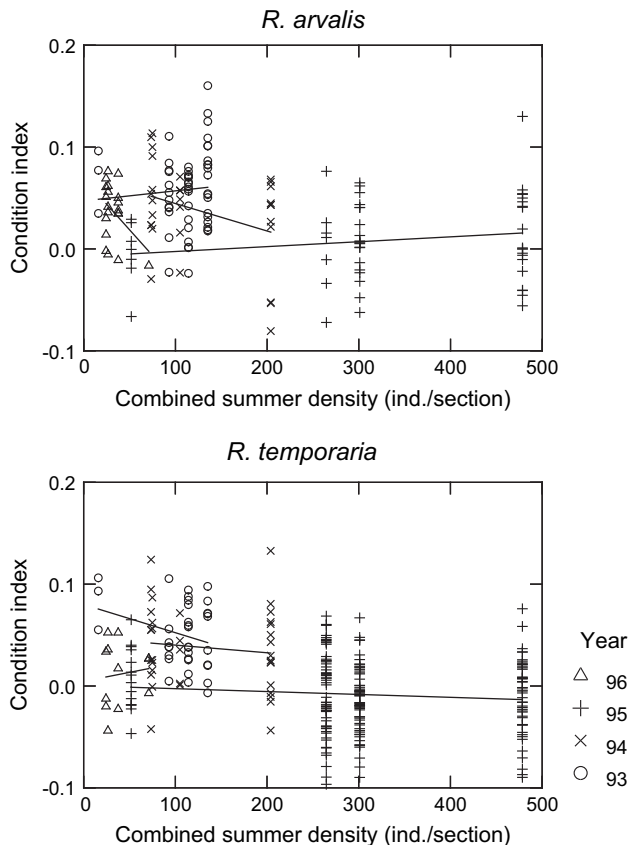

R. temporaria

Fig. 5. Condition in relation to section density. Condition is the residual of a regression of log weight against log length.

are possible, we find it likely that these initial density differences represent consistent differences in resource levels, perceived by the frogs. An alternative interpretation could be that the differences are related to distances from breeding sites. However, the size of the study sections, their placement and likely distances to local breeding sites makes this far fetched. Predation risk, mediated by vegetation density is a possibility. However, there is an indirect connection between high predation risk and poor resources as a frog perceiving a high risk of predation probably is less efficient in its food search (Skelly, 1992). In this situation it is meaningful to consider IFD as a possibility when interpreting the different density effects.

It should be noted that the design of the study makes it impossible to separate intra- and interspecific competition effects. One analysis is based on "species density" (Table 5) but because density variation in the two species is correlated, this is not a pure intraspecific effect. The design was motivated by the fact that the two species in our area usually occur in high densities together in this habitat. Because of their similar ecology, manipulating only one population had reduced the potential power of the manipulation considerably. An experimental design aimed at separating these two effects had required more replicates. However, we believe that the identification of any competitive effects in these populations is of some interest.

The study shows an effect from one of the two aspects of density on the growth of R. arvalis, but from none on the growth of R. temporaria. The most likely reason for the effect found is competition for resources, either through exploitation (prey depletion) or interference (behavioural interactions among the frogs). Indirect effects mediated by a high predator pressure in high frog density areas affecting frog activity and feeding rate are also possible. Only density by design, not absolute (=actual) density, seemed to affect growth

rate. Hence, a high frog density at one place may not mean the same to a frog as a high density at another place. This is what one expects if the initial density was the result of an IFD.

There was also variation in condition among years (for both species) but within a given year density affected only growth rate, not condition. By adjusting growth rate to available resources, the frogs seemed to be able to maintain their condition.

The fact that only growth of R. arvalis, but not clearly that of R. temporaria, was affected by the "density by design" could suggest that the latter species was not distributed according to a resource related IFD. Alternatively, it could be less sensitive to density effects (at the levels encountered in this study). This could mean that the R. arvalis population, but not that of R. temporaria, at this site is approaching its carrying capacity. If indeed this is so, this means that the latter species has the potential to outcompete the former in this type of landscape. Because of the among-section variation and, especially, the large among-year variation (partly influenced by tadpole processes) in density, the experimental manipulation has limited power to detect the full potential for competition. Only in a few years may the adult density be such that adult competition is detectable. It is therefore not possible to draw too far reaching conclusions from a negative result (as in the present case for R. temporaria).

To evaluate the result it is necessary to have an idea about the size of the manipulation. To estimate this, we need to know what proportion of frogs were actually captured, and thus subject to the relocations scheme. Based on the summer density estimates (Table 2), the relocation scheme on average reduced density in low density sections to 80% and 77% for R. arvalis and R. temporaria respectively. In high density sections, density was on average increased to 150% and 141% respectively. Assuming an average starting 1:1 per capita resource level in the two types of sections, this was thus changed to 0.53:1 and 0.55:1 respectively. This should be kept in mind when looking at the effect size of our density manipulations on frog growth (Fig. 3).

To put the results into perspective, one should also compare the densities measured in this study (on average 760 adult ind. per ha for R. arvalis and 970 for R. temporaria) to what is typical for the two species. One study in a similar meadow habitat close to the present study site (Loman, 1984) had a similar density of R. arvalis but much lower of R. temporaria than that recorded here. Other published densities are from forest habitats and give much lower densities, less than 100 adult frogs (of either species) per ha (Inozemtsev, 1969; Glowacinski and Witkowski, 1970; Pasanen et al., 1993). Only Zimka (1971) records a higher density, about 1000 frogs per ha. However, it is not clear if juveniles (young of the year) are included in this figure. This does however not mean that other populations, with comparatively low densities, cannot show competition effects on growth rates. This may well be the case if they were studied in habitats with lower resource availability.

Density effects does not necessarily require that density is directly affecting the population size. It only requires an ultimate effect of density on survival or reproduction. The present study does not directly analyse these effects. There were too few recaptures within the autumn periods for reliable density estimates during this period, permitting an analysis of survival. Also, because the manipulation only produced quantitatively small effects on size and none on condition, we do not expect substantial effects on survival. However, it has indeed been shown that small frogs have lower winter survival (Lyapkov, 1997). It has also repeatedly been shown that large frogs produce larger clutches than smaller ones (Hönig, 1966; Gibbons and McCarthy, 1986; Joly, 1991; Ryser, 1996, Lardner and Loman, 2003). A direct effect of feeding rate on egg production has been shown (Girish and Saidapur, 2000; Lardner and Loman, 2003). Therefore we believe the present result do suggest density is actually regulating the populations, at least that of R. arvalis.

There are few previous studies of the importance of adult amphibian densities for population regulation. The earliest was done by Pearson (1955) who conducted an experiment very similar in setup to ours. He found that growth rate of *Scaphiopus holbrooki* (spadefoot toads) in 72 m^2 field pens doubled as the density of frogs decreased by a factor of four. This early work is actually the only field study of direct effects from adult density on adult performance that we have found. Berven (1990) found, in a field study of two ponds, that *Rana sylvatica* (woodfrog) clutch volume was negatively correlated with adult population size. There were also effects of adult density (number of clutches deposited) on tadpole performance (survival, size at and time for metamorphosis) that contributed to density dependent regulation of the population. In another study Berven (1995) actually demonstrated, by key-factor analysis, that larval mortality (which in some populations was density dependent) explained adult *R. sylvatica* population variation. Pechmann (1995) however found no effect of density of adult salamanders (*Ambystoma opacum*) on their survival in large field enclosures where their density varied by a factor of two. Observational (Lyapkov et al., 2007 (*R. arvalis*)) and experimental studies (Altwegg, 2003 (*Rana lessonae*), Harper and Semlitsch, 2007 (*Bufo americanus* and *R. sylvatica*)) show density effects on growth rates of frogs during their first year after metamorphosis, thus up to the age when the present experiment started. One of the studies (Harper and Semlitsch, 2007) even found effects on survival.

Although numerous studies have documented density effects on growth and survival of larval amphibians (Cummins, 1989), there is also here little information from the field. Smith (1983), Berven (1990), and Van Buskirk and Smith (1991) have however all documented density effects on survival of tadpoles. This was also found for *R. temporaria* (Loman, 2004) at a study site close to the present one. However, a study of *R. arvalis* in the same area (Loman, 2001) failed to find effects on survival although effects of density on tadpole growth rate were found. Analysing long time-series, Meyer et al. (1998) found evidence of population regulation in two (but not in a third) populations of *R. temporaria*. Thus, the actual evidence for population regulation in amphibians is scarce. The evidence for regulatory effects of adult density is even less. However, the main reason for this is probably a lack of studies.

The little evidence that there is suggests that density regulation could operate on either stage in amphibians. Given the diversity of landscape types used this is not surprising. If population regulation is density dependent, a population should increase in a landscape until the critical resources become limiting – be it resources in ponds (for the tadpole stage) or terrestrial resources. There is no *a priori* reason to expect either habitat to always be the limiting, even within a given species.

Summarizing, this study shows that there are direct effects of population density on adult frog *R. arvalis* performance during the summer and that ideal free distribution may be important for the terrestrial distribution of frogs. This in turn implies that their growth is indeed limited by the availability of summer food resources. Also, the results suggest that *R. temporaria* is potentially a superior competitor to *R. arvalis* as adult.

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