

# Relatedness and competitive asymmetry – the growth and development of common frog tadpoles

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Individuals can compete either through direct interference or uptake of limiting resources. If competing individuals are able to recognize their relatives, relatedness of competitors may evoke kin selection, which favours relatively even resource share among relatives. Resource competition is often size-symmetric, i.e. proportional to an individual's biomass, while interference competition is asymmetric giving large individuals a disproportionate advantage over small individuals. Kin-selection is predicted to reduce the intensity of direct interference and competitive asymmetry, leading to increased mean and decreased variation in individual size. We tested these predictions by investigating the effects of relatedness on age and size at metamorphosis in the common frog *Rana temporaria* tadpoles in a laboratory experiment. We reared related (full- and half-sibs) and unrelated tadpoles of different sizes (small, large, small and large together) at two densities until metamorphosis. Relatedness had little effect on mean growth, but it reduced size variation, as measured with coefficient of variation. Furthermore, there was a significant interaction between relatedness and density in size at metamorphosis, so that relatives always grew better in lower density, but growth was less affected by density among unrelated individuals. This indicates that the effects of relatedness on tadpole performance may be context dependent. Initial size differences in the mixed size treatment evened out during the course of the experiment, and initially small tadpoles were able to compensate the early growth losses, although it took longer for them to reach metamorphosis. We conclude that although relatedness may have rather small effects on the growth and development of *R. temporaria* tadpoles, it increases the symmetry of resource share decreasing between-individual variation in size at metamorphosis.

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Competition takes place when limited resource availability does not allow maximal growth rate of all individuals in a population. When individuals interact only by depleting common resources, the interaction is indirect and commonly symmetric with respect to an individual's size (biomass; Weiner 1990, Schwinning and Weiner 1998). Competition may also take place in resource-unlimited conditions through direct interference (Steinwascher 1978), which may include the release of growth inhibitors (Steinwascher 1978) and aggressive

behaviour (Christian 1970). Direct interference is typically asymmetric, causing the large individuals of a population to perform disproportionately well in comparison to the small individuals (Weiner 1990, Schwinning and Weiner 1998). Hence, the competitive ability and the resource share of an individual are affected by its absolute biomass and its biomass in relation to the other individuals of the population (Lomnicki 1988).

The relatedness of the individuals in a population may lead to kin selection (Hamilton 1964), where the

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inclusive fitness of an individual is composed of its own reproduction as well as the relatedness-weighted additional reproductive success of its relatives caused by the actions of the focal individual (Grafen 1984). An individual may accept a reduction in its own fitness, if the costs are compensated with increased fitness of its relatives. Kin selection may therefore change the share of resources between individuals and lead to behavioural responses that lower the level of direct interference. Resource limitation will, however, unavoidably limit the growth of at least some individuals, and kin selection does not allow resource-limited individuals to escape competition. Genetic relatedness can therefore be expected to affect differently (1) the intensity of interference competition and (2) the share of resources in a population of relatives as compared to a population of unrelated individuals. If individuals are able to recognize their relatives and kin selection operates, they should show different behaviours towards kin and non-kin. For instance, relatedness may enhance the growth of individuals living in kin groups through decreased time and energy expenditure devoted to aggressive interactions (Hokit et al. 1996), relieving more time for feeding and hence, increasing resources available for growth. Under limited resources, individuals should direct intraspecific competition away from their relatives (Hamilton 1964), and consequently, the effects of relatedness should be different at high density than at low density.

Kin recognition, which is a prerequisite for preferential treatment of relatives over unrelated individuals, is widespread among animals (Fletcher and Michener 1987, Waldman 1988, 1991, Hepper 1991), and larvae of many anuran amphibians have been reported to discriminate between kin and non-kin (Blaustein and Waldman 1992). Kin recognition may be based on different types of cues, such as recognition of similar alleles, phenotypic matching based on traits of familiar conspecifics, associative learning through familiarity, or spatially based recognition (Holmes and Sherman 1983). In amphibians, chemical signals, which may be of environmental, genetic or maternal origin, are important in kin recognition (Blaustein and O'Hara 1982a), although some form of learning is obviously involved in many cases (Blaustein and Waldman 1992). The recognition ability may also be directed towards cues learned during early ontogeny (Pfennig 1990). Kin recognition may be context-dependent, so that it takes place only under certain conditions (Blaustein and Waldman 1992), or developmental stages (Blaustein et al. 1993), although some studies have shown that kin recognition ability may be present even among adult animals serving an incest avoidance function (Waldman et al. 1992).

We studied the effects of relatedness on fitness-related traits – age and size at metamorphosis – in a factorial laboratory experiment with the common frog

*Rana temporaria* tadpoles. In amphibians, size at metamorphosis is an important fitness-related trait being positively correlated with size at maturity (Smith 1987), survival probability (Kaplan 1992), and fecundity (Smith 1987, Semlitsch et al. 1988). Seasonal factors (Berven et al. 1979, Berven and Gill 1983, Merilä et al. 2000a) or pond desiccation (Newman 1992, Denver et al. 1998, Laurila and Kujasalo 1999) limit the duration of favourable period for amphibian development, and consequently, fast development may be adaptive. Variation in time and size at metamorphosis may also affect population dynamics through changes in individual fitness. Frogs are feasible study organisms for studies of relatedness, as they have external fertilisation, and it is possible to perform artificial crossings and produce different types of relatives. Tadpoles can easily be reared in the laboratory, and a large number of offspring per female allows large-scale factorial experiments.

We have theoretically shown that relatedness leads to decreased variability in individual sizes, and may in the long run be reflected in population dynamics (Aikio and Pakkasmaa 2002). In the following, we investigate the effects of relatedness on growth and development of tadpoles empirically. We hypothesise that increased relatedness would lead to enhanced growth and decreased variation in size. We also manipulated the size of the tadpoles to include an aspect of competitive asymmetry in our experiment. An additional aim of the size-manipulations was to investigate whether tadpoles would compensate initial growth losses later on during their development, that is, whether they are able to exhibit compensatory growth. As the effects of relatedness have been suggested to be greater at high density (Hokit and Blaustein 1994), we performed the experiment in two different densities. Resource competition was assumed to increase with tadpole density, and thus we expected high density to have detrimental effects on growth and development rate.

## Materials and methods

### Parental individuals and crossings

The common frog is the most common amphibian species in northern Europe (Gasc et al. 1997). Its breeding sites vary from small temporary ponds to more permanent watercourses, and in Scandinavia the breeding takes place shortly after snow melt (Gislén and Kauri 1956, Gasc et al. 1997). We captured six amplexus pairs of common frogs from Häggedalen (59°51' N, 17°14' E), near Uppsala, central Sweden, 22 April 2001. The size of this frog population is estimated as several hundreds of breeding animals (J. Merilä et al., unpubl.), and by using a large population we wanted to

minimize the possibility of parental individuals being close relatives.

Artificial crossings were performed on the day following the capture using the procedure described in Berger et al. (1994) and Merilä et al. (2000). We used a breeding design where matrices of four full- and half-sib families were created by crossing two males with two females. Altogether, we had three independent matrices. The eggs from each crossing were divided in two batches, one for producing small tadpoles and the other for producing large tadpoles, transferred to 3 l plastic buckets filled with 2.5 l reconstituted soft water (RSW; APHA 1985), and moved to a climate room (15°C).

### Experimental set-up

We manipulated relatedness, initial tadpole size and tadpole density. Relatedness levels were full-sibs (expected relatedness level  $r = 0.5$ ), maternal and paternal half-sibs and non-related individuals ( $r = 0$ ). Half-sibs originated from two different full-sib families (sharing either mother or father; see below), and thus the relatedness among the individuals in an experimental unit was not symmetric, but on average  $r = 0.33$ . These relatedness levels are, however, theoretical expectations based on the assumption that parental individuals were not related. We used both full-sibs and half-sibs, as some studies have indicated a difference in association behaviour among full- and half-sibs (Blaustein and O'Hara 1982b), and even suggested the presence of a maternal component in kin recognition ability (Blaustein et al. 1990).

Initial tadpole size was either small (S), large (L), or a combination of these (S + L). Tadpole density was either 4 individuals (low) or 10 individuals (high) per vial. With four relatedness treatments (full-sibs, maternal and paternal half-sibs, non-related individuals), three size treatments (S, L, S + L), and two densities (4 or 10), and six replicates (each representing a different family) of each treatment combination, the total number of experimental units was 144, and the number of tadpoles 1008.

### Tadpole rearing

Initial size differences were created by manipulating individual density and feeding regime during the early larval period. The density of small hatchlings during the early larval period was 130 individuals per vial, and that of large hatchlings 65 individuals per vial, and the food ration per vial for small individuals was half of that of large individuals. After 24 days of initial rearing, we started the experiment by randomly selecting tadpoles for the experiment. All tadpoles

were weighed before the onset of the experiment in order to know the initial size distribution in each experimental unit. Large tadpoles were nearly three times heavier at the onset of the experiment than small tadpoles (mean  $\pm$  S.D.  $0.128 \pm 0.023$  g vs  $0.044 \pm 0.011$  g for large and small tadpoles, respectively).

In pure small and pure large size treatments, the tadpoles were picked from one vial (full-sibs) or from two different vials (maternal and paternal half-sibs). In the mixed size treatment, full-sibs originated from two different vials (S and L) of the same family. Half-sibs of the mixed size treatment were selected so as that both families were represented in both size groups in equal numbers, and thus the tadpoles originated from four different vials. Non-related individuals always originated from different vials at the low density, and at the high density, a maximum number of two tadpoles were picked from the same vial.

Tadpoles were reared in plastic 3 l buckets in 2.5 l RSW in a climate room (15°C). Photoperiod was adjusted to 17L:7D. Due to temperature variation in different parts of the room, the rearing shelf was divided in six blocks, each with 24 buckets, each block with an equal number of experimental units from each treatment combination. Temperature was monitored daily from two selected buckets in each block. Water in the buckets was changed every 4th day, and simultaneously the tadpoles were fed with boiled spinach. Feeding was increased with tadpole growth, and the tadpoles in each experimental unit got the same amount of food at each feeding. Mortality during the first week of the experiment was compensated by replacing dead tadpoles with new individuals, which were randomly picked from the pre-rearing vials following the same system as at the onset of the experiment.

When the tadpoles started to approach metamorphosis, defined as the emergence of the first fore limb (stage 42, Gosner 1960), we started to check the buckets daily for metamorphosing individuals. Metamorphs were removed with a net and the remaining individuals were reared normally until all tadpoles had metamorphosed. Development time from the beginning of the experiment was recorded. Metamorphs were anaesthetized, and their body length and body mass were measured and the individuals were conserved thereafter. Growth rate was estimated as mass at metamorphosis divided by development time. Some mortality occurred during the experiment after the replacements, and altogether 954 tadpoles metamorphosed. If less than half of the tadpoles in the vial metamorphosed, that experimental unit was removed from the statistical analyses, as the density treatment was then considered to deviate too much from the intended. Consequently, the total number of experimental units in the statistical analyses was 139.

## Statistical analyses

We counted first vial means and coefficient of variation (CV) for the response variables – time to metamorphosis, body length, body mass and growth rate – and used these in the statistical analyses. The response variables were analysed with three-way analysis of variance with randomised block design where relatedness, density, and size treatment and all two-way interactions were included (three-way interactions were significant only for development time, and they were excluded from the other models). All factors were treated as fixed factors.

To test whether maternal and paternal half-sibs differed from each other, we first made an analysis for them separately. As there was no statistically significant difference in any of the response variables (one-way ANOVA, all  $p$ -values  $> 0.1$ ), and they represented the same level of relatedness, we pooled half-sibs together, and used three levels of relatedness (full-sib, half-sib and non-related) in the analyses.

## Results

### Development time

The size treatment significantly affected the development time (Table 1). The initially large individuals metamorphosed on average ten days earlier than the initially small individuals (mean  $\pm$  SE:  $38.9 \pm 0.36$  days vs  $49.5 \pm 0.23$  days). Density as such did not affect the average development time of tadpoles (Table 1). Relatedness had a small effect on development time (Table 1, Fig. 1): non-related individuals developed slightly faster (mean  $\pm$  SE:  $43.5 \pm 0.38$  days) than half-sibs (mean  $\pm$  SE:  $44.4 \pm 0.27$ ) or full-sibs (mean  $\pm$  SE:  $44.5 \pm 0.41$ ). Also the interactions were significant (Table 1). The interaction between relatedness and density was a consequence of non-related individuals and half-sibs developing faster in the higher density, whereas full-sibs developed faster in the lower density. The rearing block significantly affected development time due to small horizontal and vertical temperature variation in the climate room.

Variation (CV) in development time was affected by all main factors (Table 1), and it was larger among non-relatives than among half-sibs or full-sibs (Fig. 1), in the higher density, and in the mixed size treatment.

### Metamorph size

Both body length and mass at metamorphosis were significantly affected by the main factors of relatedness, density and size treatment (Table 1). Furthermore, the interaction effects of relatedness  $\times$  density and density  $\times$  size treatment were significant (Table 1). The

relatedness by density interaction was due to the fact that related individuals (both half- and full-sibs) became larger in the lower density, whereas rearing density had smaller effects on non-relatives, and the difference in average size between the two densities was relatively small among them. Half-sibs and full-sibs were on average larger than non-related individuals (Fig. 1). Growth rate was influenced by relatedness, density and size treatment as well as interactive effects between density and size treatment and relatedness and density (Table 1).

In addition to the main effect of size treatment, variation (CV) in body length was significantly affected by the interaction between density and size treatment (Table 1); in the lower density, variation was smallest among large tadpoles, whereas in the higher density, variation was smaller in mixed-size and small tadpoles. The effects of relatedness on variation in mass at metamorphosis were significant, and mass was least variable among relatives, whereas non-relatives were more variable in size (Fig. 1). Interactive effects of density were observed also here, and in the higher density, small and mixed-size treatment froglets were least variable in size, whereas in the lower density, large froglets were least variable. Furthermore, relatives were least variable in size in the lower density, whereas non-relatives were less variable in the higher density. Initial variation in body mass among individuals in each vial did not affect variation at metamorphosis, indicated by non-significant ( $p = 0.970$ ) covariate in the analysis of covariance on mass at metamorphosis.

Interesting findings appear, if we look at the growth of small and large individuals separately (Fig. 2). Both small and large individuals performed better in a mixed size group than in a pure group. At the low density, initially small tadpoles were smaller also at metamorphosis, but at the high density, initially small individuals became as large (body length) or even larger (mass) in the mixed size treatment than large individuals alone.

## Discussion

Our main question was whether relatedness affects fitness-related traits in common frog tadpoles in different experimental conditions. We predicted that related individuals (1) have higher mean growth due to less intense interference competition and (2) smaller size variation due to more equal resource share in populations of relatives as compared to unrelated individuals. The first prediction was supported weakly: relatedness was apparently beneficial to the growth of tadpoles, but the effects were rather small. The second prediction was better supported by the consistently smaller variability in size and development time in populations of relatives than among unrelated individuals. The results suggest

Table 1. ANOVAs on means (A) and CVs (B) of metamorphic traits in *R. temporaria*. Size refers to the applied size treatment. Dash (–) indicates that the effect was not included in the statistical model.

A. Mean values

Source	Development time				Body length				Mass			Growth rate		
	df	MS	F	p	df	MS	F	p	MS	F	p	MS	F	p
Relatedness	2	<0.01	3.01	0.050	2	<0.01	6.38	0.002	0.05	5.07	0.008	0.03	2.67	0.074
Density	1	<0.01	0.02	0.899	1	0.09	139.25	<0.001	1.59	168.76	<0.001	1.62	133.53	<0.001
Size	2	0.12	48.03	<0.001	2	0.01	22.76	<0.001	0.18	18.78	<0.001	0.58	48.26	<0.001
Block	5	0.01	4.98	<0.001	–	–	–	–	–	–	–	–	–	–
Relatedness × size	4	<0.01	2.70	0.034	4	<0.01	0.58	0.677	<0.01	0.40	0.812	<0.01	0.43	0.784
Density × size	2	0.01	4.42	0.014	2	0.01	13.80	<0.001	0.15	15.92	<0.001	0.21	17.71	<0.001
Relatedness × density	2	0.01	4.60	0.012	2	<0.01	4.82	0.010	0.03	3.26	0.042	0.03	2.70	0.071
Rel × density × size	4	15.17	3.09	0.019	–	–	–	–	–	–	–	–	–	–
Error	116	<0.01	–	–	125	<0.01	–	–	<0.01	–	–	0.01	–	–

B. Coefficient of variation

Source	Development time				Body length			Mass			Growth rate		
	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Relatedness	2	0.38	2.45	0.090	0.28	1.50	0.227	0.48	3.15	0.046	1.05	6.37	0.002
Density	1	1.90	12.20	<0.001	0.02	0.10	0.758	<0.01	0.05	0.828	0.37	2.25	0.136
Size	2	5.43	34.88	<0.001	0.89	4.84	0.010	0.18	1.20	0.303	0.54	3.28	0.041
Relatedness × size	4	0.07	0.46	0.763	0.30	1.61	0.175	0.13	0.84	0.499	0.08	0.52	0.724
Density × size	2	0.53	3.38	0.037	1.06	5.74	0.004	0.38	2.51	0.086	0.11	0.65	0.522
Relatedness × density	2	0.15	0.93	0.396	0.11	0.59	0.556	0.28	1.86	0.159	0.64	3.88	0.023
Error	125	0.16	–	–	0.18	–	–	0.15	–	–	0.16	–	–

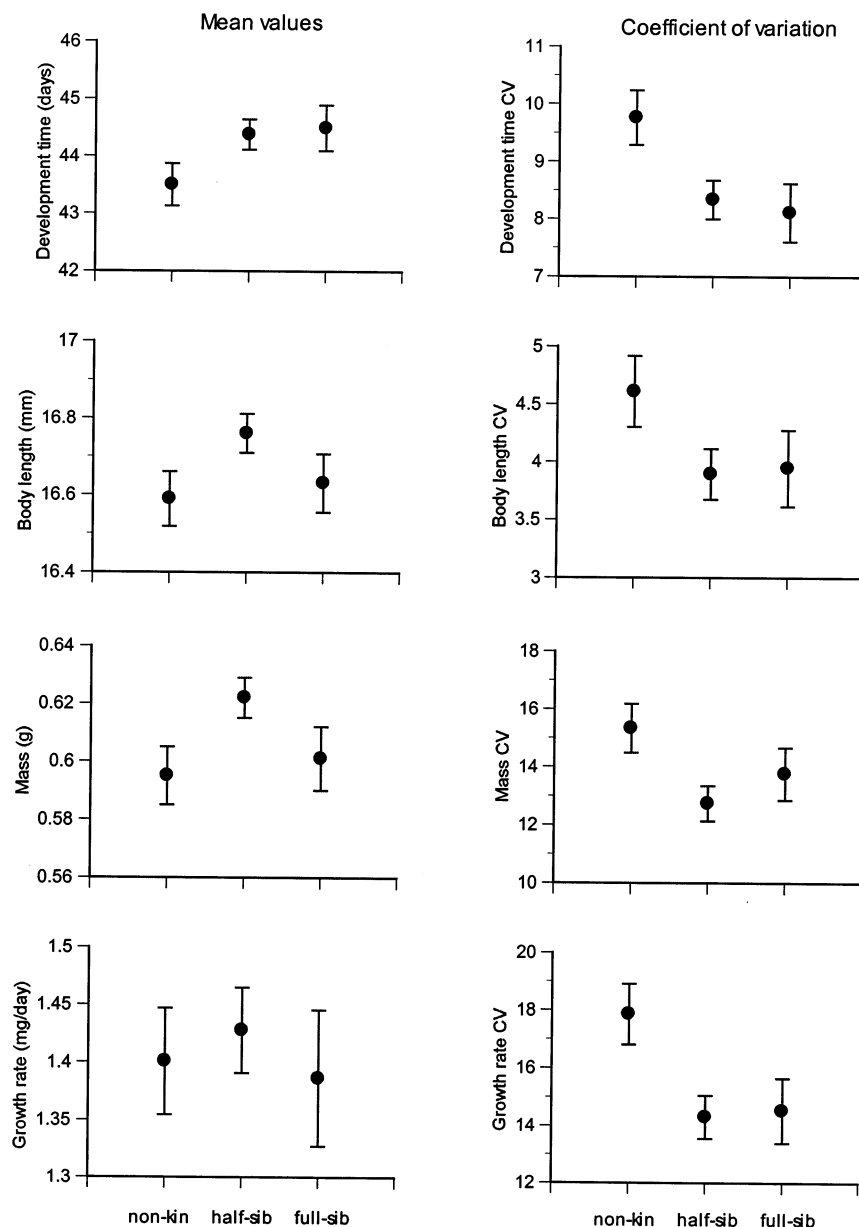


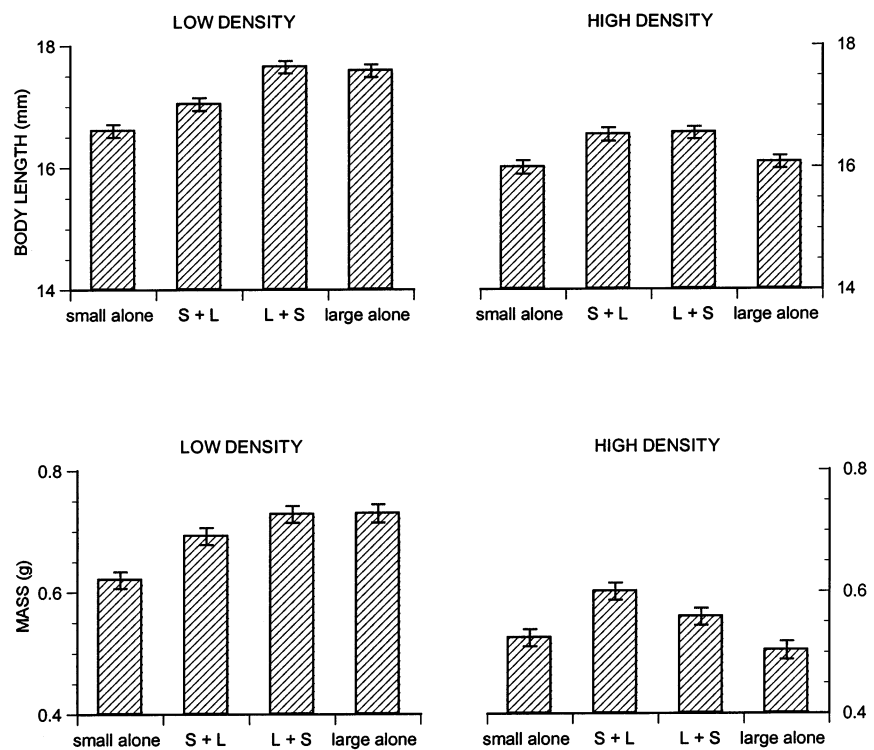
Fig. 1. Mean values ( $\pm$  SE) and coefficients of variation for development time, body length, mass at metamorphosis, and growth rate for full-sib, half-sib, and non-related *R. temporaria* metamorphs.

that common frog tadpoles have mainly indirect interactions when competing for food, and interference plays only a minor role. Relatedness therefore had little effect on the mean resource gain of individuals, but affected the division of resources between the individuals of a population.

Tadpoles grew slightly better in groups of related individuals than in groups of unrelated individuals, suggesting a benefit from growing in sibling groups. Possible mechanisms of kinship advantages have been discussed extensively. We reason that resource competition may not be released by kin selection, but interference competition may be less intense between related

than unrelated individuals, allowing more time for feeding and growth. In heterogeneous natural environments, resource competition may actually be more intense among relatives due to their similar resource use, which may lead to better performance in groups of mixed relatedness as compared to siblings (Griffiths and Armstrong 2001). The explanation about relaxed interference is supported by the finding of Hokit and Blaustein (1995), who observed that sibling groups of *R. cascadae* tadpoles were more active than solitary tadpoles and groups of mixed relatedness, suggesting enhanced feeding efficiency and greater interference. Furthermore, decreased levels of aggression among

Fig. 2. Metamorphic size (mean  $\pm$  SE) for small and large *R. temporaria* in low and high density. Relatedness effects are ignored in this figure. S + L and L + S refer to the mixed size treatment, and the two left-side columns in each panel represent small individuals, whereas the two right-side columns are large individuals.



siblings may allow more time for feeding and thus enhanced growth (Brown and Brown 1993).

Ecological factors may interact with kinship to influence interactions between individuals (Hokit and Blaustein 1997), and consequently, kinship effects may be context-dependent. Kinship has been reported to affect the growth of several animal species (summarized in Waldman 1988). For instance, Brown et al. (1996) found that juvenile Arctic charr grew better both in terms of length and weight in groups of full-sibs than in groups of mixed relatedness or non-kin. In amphibians, the evidence is somewhat controversial: both enhanced (Jasienski 1988, C. K. Smith 1990, Girish and Saidapur 1999), inhibited (Hokit and Blaustein 1994) and unchanged growth (Jasienski 1988, Waldman 1991) has been observed among siblings as compared to non-relatives. The responses may partially be species specific, but differences in experimental and/or environmental conditions may also explain some of the inconsistency in results. For instance, in salmonids the occurrence of kin-biased behaviour has been found to depend on environmental conditions (Griffiths and Armstrong 2000). Also our experiment suggests context dependency, as relatedness effects were influenced by tadpole density.

Relatedness is predicted to decrease size variation (Aikio and Pakkasmaa 2002), and this seems to hold in *R. temporaria* tadpoles, although variation was in many cases smallest among half-sibs. It thus seems that already a small number of shared alleles is enough for

relatedness effects to occur (Hamilton 1964). Even other experimental evidence demonstrates reduced size variation in populations of relatives (Jasienski 1988, Saidapur and Girish 2001). There is also evidence of the opposite effects of relatedness: size variability was greater in full-sibs groups of *Bufo americanus* tadpoles as compared to individuals reared in mixed sib groups (Waldman 1987). Our explanation for the decrease in size variation in the present study is based on kin selection: both small and large individuals may benefit from large individuals altruistically reducing their growth to the benefit of their smaller relatives (Aikio and Pakkasmaa 2002). Alternatively, it is also possible that the observed growth advantages among relatives were a consequence of kinship-based genotypic uniformity (Jasienski 1988) rather than a result of altruistic behaviour.

Density effects are likely to be mediated through intraspecific aggression as well as increased competition for limiting resources (Petranka 1989, Hokit and Blaustein 1997). However, density effects may affect related and non-related individuals differently (Waldman 1991). In fact, we found that relatives (both full-sibs and half-sibs) grew better in the lower density, whereas for non-related individuals, density was less important, and size differences between densities were smaller than for relatives. Interactive effects of density have been observed also in other studies. Hokit and Blaustein (1997) found interactive effects of density, access to substrate, and kinship on growth and survival of *Rana cascadae* tadpoles. Also in salamanders

(*Ambystoma opacum*) variation in genetic relatedness, or its interaction with initial density, affected larval performance, although kinship did not affect density-dependent larval performance in experimental ponds (Walls and Blaustein 1994). Density effects on competition and thus performance may also be modified through different types of competition: Tregenza et al. (1996) suggested that at low density, interference competition prevails, whereas higher density leads to competition for resources. On the other hand, Humphries et al. (2000) suggested that there is no general rule describing how relative competitive ability would change with group size. Nevertheless, group size has effects on, for instance, differences in growth rate, which have been observed to increase under competitive conditions (Rubenstein 1981). Density effects may be far-reaching: experimental evidence from salamanders (*A. opacum*) indicates that both density-dependent and density-independent factors affect recruitment to the adult population (Scott 1990), and consequently, may influence population dynamics.

Field experiments with larval salamanders suggest that size differences among competing individuals do not reduce the negative effects of competition (C. K. Smith 1990). In nature, weather conditions are often variable during the reproductive period of common frogs, and cold spells may interrupt initiated breeding. Asynchronous breeding can lead to the presence of different-sized and aged tadpoles in the same breeding pond, and different-sized individuals may even be relatives, if the same male mates more than once (Laurila and Seppä 1998). In our study, individual length and biomass at metamorphosis responded in a predictable way to the density and size treatments. High density led to greater resource limitation than low density, with the consequence of a smaller mean size at high density than at low density. Several amphibian species respond to crowding with reduced growth, development rate and survival to metamorphosis (D. C. Smith 1990, Hokit and Blaustein 1994, 1997, Girish and Saidapur 1999).

Initially large tadpoles metamorphosed earlier than initially small ones. Competition may have been most intense among pure groups of initially large individuals. In mixed-size groups faster development of initially large individuals relaxed competitive pressure on initially small individuals, which were able to catch up the initial size advantage of large individuals. Thus, amphibian tadpoles are able to compensate growth, which has recently been discussed extensively in the literature (Arendt 1997, Metcalfe and Monaghan 2001). Although early environmental conditions may have profound effects on performance later on in life both in amphibians (Travis 1984, Audo et al. 1995, Kaplan 1998, Merilä et al. 2000b) and in other organisms (Rossiter 1996, Merilä and Svensson 1997, Lindström 1999), our results support the view that individuals may

be able to compensate initial growth losses later on (Semlitsch and Gibbons 1990, Niecieza and Metcalfe 1997, Maclean and Metcalfe 2001). Also Audo et al. (1995) found with *Hyla chrysoscelis* tadpoles that individuals starved early during ontogeny caught up to the size of constantly fed individuals by metamorphosis. This results from later changes in food levels having relatively greater effects on body size at metamorphosis (Leips and Travis 1994). This also contradicts the statement that the size rank of individuals would not change, i.e. the large individuals remain largest even if the size difference to smaller individuals decreases, as observed in some studies (Tregenza et al. 1996).

Fast development of tadpoles minimizes their exposure to predation and decreases the risk of unfinished growth if the pond dries out. Both are significant causes of mortality in natural populations of frogs (Newman 1992). As expected, initially large tadpoles developed faster than initially small ones. We found that relatives developed slightly slower than unrelated individuals, but the difference was small. Density did not have direct effects on development time, but it had significant interaction with the effects of other treatments, thus modifying (and its effects being modified by) the effect of relatedness and size treatment. Variation in development time was largest in the mixed size group, as development time followed a bimodal distribution with large individuals developing faster than small ones. It has been suggested that if living conditions deteriorate, tadpoles should metamorphose earlier and at a smaller size than in favourable conditions (Newman 1992). Therefore, larvae at the high density can be expected to develop faster than those in lower density. Differences in development times between the two densities were very small, but the average development time was slightly faster in the higher density. However, after the very first individuals had metamorphosed, the living conditions for the remaining individuals improved through released competition, and they could retard their development and invest more on growth. This should also lead to increased variation in development times and individual biomasses, and variation in development time was indeed slightly larger in the higher density, but there were no effects on metamorphic size.

To conclude, the effects of relatedness on the growth and development of *R. temporaria* tadpoles were rather small, but increased relatedness decreased variability among individuals. The decreased size variability in populations of relatives may be a consequence of kin selection and/or higher genotypic uniformity among relatives as compared to non-related individuals. There effects of relatedness depended on individual density, suggesting that the effects of relatedness on competition, and consequently, fitness-related traits in tadpoles, are highly context-dependent.



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