Are the effects of kinship modified by environmental conditions in *Rana temporaria* tadpoles?

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Kin selection theory predicts that organisms should behave favourably toward their relatives, if the benefits of such behaviour, devaluated by relatedness, are larger than its costs. Under good environmental conditions, the costs of kin-biased behaviour are likely to be low, and kin-biased behaviour may lead to better average performance of related than non-related individuals. However, under poor environmental conditions, individuals should maximise their own fitness, and costly altruistic behaviour should be disfavoured. Consequently, certain environmental conditions could select for kin-biased behaviour. We tested these predictions in a laboratory experiment with common frog (*Rana temporaria*) tadpoles. We reared full-sib, half-sib and non-kin tadpoles in good and poor environments (constant and decreasing water levels crossed across low and high densities) and recorded time to and size at metamorphosis, both important fitness components in amphibians. Tadpoles metamorphosed earlier and at smaller size at high density. The effects of relatedness on size at metamorphosis interacted with density: positive effects of relatedness were detected at low density, whereas at high density relatedness did not affect metamorph size. Water level treatment did not affect development time, but at low density tadpoles metamorphosed at smaller size in the decreasing water level treatment. There was no interaction between relatedness and water level treatments in any of the traits. Our results indicate that the effects of kinship on fitness-related traits are modified by environmental conditions. Moreover, in the case of *R. temporaria* tadpoles, interactions with relatedness and density seem to be stronger than interactions with desiccation risk.

Introduction

Kin selection theory (Hamilton 1964) predicts that organisms should modify their behaviour in favour of relatives, if the relatedness-weighed benefits of such behaviour exceed its costs. Con-

sequently, kinship composition of a social group could influence fitness-related traits, such as growth, development rate, and disease resistance (Waldman 1988). Environmental variation, however, often challenges the development of organisms, and their survival and fitness are affected

by the ability to respond to this variation. In such situations, phenotypic plasticity may allow adaptive responses to varying environmental conditions (Stearns 1989, Newman 1992, Gotthard & Nylin 1995).

The relative costs and benefits of altruistic behaviour depend on environmental conditions, which also determine how large costs of altruistic behaviour the organisms may accept (Weigel 1981). Furthermore, fitness conditions of both the actor and the recipient influence the magnitude of benefits (McNamara *et al*. 1994). Under favourable conditions, where the survival prospects of all individuals are high, individuals may accept larger costs and behave altruistically towards their relatives leading to better performance of relatives as compared to non-related individuals. However, when the conditions deteriorate, individuals should above all maximise their own fitness, and consequently, kin-biased behaviour may become too costly. Thus the performance of relatives and non-relatives should not differ from each other under unfavourable environmental conditions.

Many amphibians recognize kin (Blaustein & Waldman 1992), and they appear a suitable group for studies investigating interactive effects of relatedness and environmental quality, particularly because larvae of many species live in ponds with varying, and often unpredictable, environmental conditions. In species showing trophic polymorphism there is evidence that kin structure of the population affects the occurrence of predatory (cannibalistic) morph (Pfennig & Colllins 1993, Pfennig *et al*. 1993, Pfennig & Frankino 1997, Michimae & Wakahara 2001). Otherwise, studies on kinship and environmental variation in amphibians have mainly focused on the interplay between relatedness and density (e.g., Smith 1990, Hokit & Blaustein 1994, Girish & Saidapur 1999, Michimae & Wakahara 2001, Saidapur & Girish 2001). While pond desiccation is a major source of environmental unpredictability facing amphibian larvae (Newman 1992, Loman 2002), it is not known whether kinship affects growth and development rates in drying ponds. Rapid growth and development are often favoured in temporary ponds and plasticity in timing of metamorphosis in response to pond drying is adaptive when it

allows the tadpoles to successfully complete their development and metamorphose before pond drying (Newman 1992, Gotthard & Nylin 1995). Several species have been shown to be able to adaptively respond to decreasing water volume by accelerating their development, however, the cost of accelerated development is smaller size at metamorphosis (Newman 1988, 1992, Gotthard & Nylin 1995, Denver *et al*. 1998, Laurila & Kujasalo 1999).

Blaustein and Waldman (1992) hypothesised that limited resources could differentially influence kin and non-kin. Behaviourally mediated differences in resource share may lead to variable growth rates among groups of kin versus non-kin, which can have fitness consequences through different size at metamorphosis, and ultimately, differential survival. When resource levels go down the cost of helping a relative rises and individuals may be less willing to pay the cost of helping. However, at very harsh conditions helping may again be favoured if the benefit of helping in terms of inclusive fitness exceeds the expected individual fitness. At extreme level, an environmentally mediated response to kinship may remind facultative brood reduction in birds, where severe competition leads to killing of the smallest individuals by larger siblings (Drummond *et al*. 1986, Mock 1988, Blaustein & Waldman 1992). Studying the effects of relatedness under variable environmental conditions is a virtually unexplored area providing both theoretically and empirically interesting questions from the viewpoints of adaptive plasticity and kin selection theory. In spadefoot toads (*Spea bombifrons*) showing trophic polymorphism, hungry cannibalistic tadpoles are more likely to eat a sibling than satiated ones (Pfennig *et al*. 1993) indicating that the probability of cannibalism may be dependent on the resource level.

The common frog *Rana temporaria* breeds in a variety of freshwater habitats from small puddles to shore marshes of large lakes that show wide variation, among other things, in the amount of food resources and desiccation risk (Gislen & Kauri 1959, Laurila 1998, Laurila & Kujasalo 1999). Previous studies with *R. temporaria* have shown that tadpoles are able to respond to desiccation by metamorphosing faster (Laurila & Kujasalo 1999, Loman 1999, Merilä

et al. 2000, Laurila *et al.* 2002). Population sizes vary considerably among ponds, and tadpole population in a pond may be full-sibs, or a mixture of up to several hundred sibships (Laurila 1998). Hence, interactions between environmental conditions and relatedness appear relevant for the situation in nature (Smith 1990, Blaustein & Waldman 1992).

We studied the effects of relatedness in variable environments on developmental responses of *R. temporaria* larvae in a laboratory experiment. We reared full-sib, half-sib and non-kin tadpoles in good or poor environments determined by simultaneously manipulating water level and tadpole density. We recorded time to and size at metamorphosis, both important fitness components in amphibians influencing juvenile survival, size and age at maturity and reproductive success (Smith 1987, Berven 1990, Scott 1994, Reques & Tejedo 1997, Altwegg & Reyer 2003).

We predicted that under favourable environmental conditions tadpoles would behave altruistically towards their relatives, whereas in unfavourable environments they should maximise their own fitness and behave selfishly. Thus, in good environments (low density, constant water level) groups of relatives should perform better than groups of non-related individuals, whereas in poor conditions (high density, decreasing water level) positive effects of kinship were predicted to be unlikely. Furthermore, we predicted that tadpoles would respond adaptively to decreasing water level by accelerating their development, but shorter development time would imply fitness costs as decreased metamorph size. We expected to find the smallest size at metamorphosis in the poorest environments (high density and decreasing water volume).

Methods

Parental individuals and crossings

Rana temporaria is the most common amphibian species in northern Europe, and its distribution area ranges from northern Spain in the south to North Cap in the north (Gasc *et al.* 1997). In Scandinavia, breeding occurs shortly after ice melt. *R. temporaria* frequently spawns in temporary ponds, and desiccation is a major threat to the tadpoles (Laurila & Kujasalo 1999, Loman 2002).

The experiment was conducted in April–June 2001. We captured amplectant common frogs near Uppsala, central Sweden (Häggedal, 59°51´N, 17°14´E) on 22 April 2001. This population has several hundred breeding pairs and by using a large population we minimized the possibility that parental individuals were relatives. To obtain half-sib families we performed laboratory crosses according to the procedures of 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 four such matrices and 16 families. About 200 eggs from each family were transferred into individual 3-l plastic vials filled with 2.5 l reconstituted soft water (RSW, APHA 1985) and the eggs were reared until hatching in a 20 °C laboratory.

Experimental set-up

Our experimental design was a randomized block design with relatedness (four levels), density (two levels), water level (two levels) and block (four levels) as factors. The relatedness treatments were full-sibs, maternal half-sibs, paternal half-sibs and non-related individuals. Half-sibs originated from two different families having either common mother or father (*see* below). The density treatments were low (4 tadpoles) and high (10 tadpoles), and the water level treatments constant and decreasing (*see* below). With 8 replicates of each treatment combination, the total number of experimental units was 128.

The experiment was started when the tadpoles had reached stage 25 (Gosner 1960; absorption of external gills and fully developed operculum). At this point, we randomly selected tadpoles for the experiment. Full-sibs within an experimental unit were all picked from the same family-specific vial, whereas half-sibs were picked from two different vials (sharing one parent) at equal proportions. The non-related individuals within an experimental unit were all picked from different family-specific vials.

Tadpoles were reared in RSW in 20 °C laboratory, and the plastic 3-l rearing vials were placed in a shelf system with four horizontal blocks, two vials from each treatment combination in each block. The blocking accounted for known temperature variation in the room and the position of experimental units within a block was randomised. Water was changed every fourth or fifth day, and simultaneously with water change, tadpoles were fed with boiled spinach. The amount of food was the same in all treatments within each feeding bout but was increased with tadpole growth. It was selected to be in excess at low density, but limiting at high density. Constant water volume treatment was 2.5 ls throughout the experiment, whereas decreasing water volume treatment implied a decrease of 20% with each water change. At the average time of metamorphosis (day 30), water volume had decreased to 524 ml. Light was provided by solar light and fluorescent lamps, and the photoperiod followed natural seasonal variation with increasing day length during the course of the experiment (17 L:7 D at the onset of the experiment).

When tadpoles approached metamorphosis, defined as the emergence of the first fore limb (stage 42; Gosner 1960), we checked the vials daily for metamorphosing individuals. Metamorphs were removed, weighed with an electronic balance (0.001 g), body length was measured with an electronic calliper (0.01 mm), and time to metamorphosis was recorded. The experiment was terminated when all the individuals had metamorphosed.

Response variables and statistical analyses

Mean values of age and size at metamorphosis in each experimental vial were used as response variables in statistical analyses. For survival the proportion of individuals surviving in each vial was used. Size and age at metamorphosis were log-transformed and survival arcsin-squareroot transformed before the analyses to assure normal distribution and homogeneity of variances. The data were analysed with factorial ANOVAs with type III mean squares. Relatedness, density, water level treatment and block were included as factors. Three-way interactions were never significant and were excluded from all the models. Preliminary analyses indicated that maternal and paternal half-sibs did not differ in any of the response variables (all $P > 0.1$). Consequently, they were pooled and three classes of relatedness (full-sib, half-sib, non-kin) were used in the analyses.

Results

Mortality during the experiment was very low, and altogether 861 out of 896 tadpoles metamorphosed. Relatedness did not affect mortality ($F_{2,120} = 1.70$, $P = 0.189$), and none of the other factors or their interactions significantly influenced survivorship (all $P > 0.2$).

Age at metamorphosis depended only on tadpole density (Table 1 and Fig. 1) being roughly one day shorter at high density. Neither water

Table 1. Factorial ANOVAs on the effects of relatedness, density and water level treatments on metamorphic traits in *Rana temporaria*.

Source	df	Development time		Body length		Mass	
		F	P	F	P	F	P
Relatedness	2	0.16	0.852	1.97	0.144	2.62	0.077
Density	1	3.88	0.051	86.33	< 0.001	106.05	< 0.001
Water level	1	0.98	0.325	26.56	< 0.001	27.12	< 0.001
Block	3	25.86	< 0.001	4.00	0.01	2.41	0.071
Rel. × Den.	2	0.04	0.965	3.86	0.024	4.56	0.012
Rel. × Water	2	0.10	0.903	0.88	0.418	0.56	0.572
Den. × Water	1	0.41	0.528	14.60	< 0.001	23.19	< 0.001
Error	115						

level, relatedness, nor any of the interactions affected age at metamorphosis. The significant block effect was due to the temperature variation within the laboratory room, and tadpoles developed fastest in the warmest block.

The effect of relatedness did not affect body length or mass at metamorphosis significantly (Table 1). However, there were significant interactions between density and relatedness in both traits (Table 1). The tadpoles in the kin treatments (both full and half-sibs) being roughly 15% heavier and 4% longer than non-kin tadpoles at low density, whereas there was no difference between kin and non-kin treatments at high density (Fig. 1). Tadpoles were significantly larger in low than high density and in constant than decreasing water level (Fig. 1). However, a significant interaction between density and water level in both size traits (Table 1) indicated that while tadpoles were much smaller in the decreasing water level than in the constant water level at low density, the water level treatments had no effect on tadpole size at high density (Fig. 1).

Discussion

Our main objective was to test the effects of genetic relatedness on fitness-related traits in common frog tadpoles in variable environmental conditions. We found that kinship effects interacted with tadpole density, so that at low density (implying favourable conditions) relatives grew larger, whereas at high density, the growth performance of kin and non-kin did not differ. Consequently, our hypothesis of better performance of kin under favourable environmental conditions was supported. Moreover, we found that density and water level treatments affected metamorph size. Metamorphs were smaller at high density, but the negative effects of decreasing water level were only visible at low density. However, only tadpole density affected development time.

The effect of relatedness on body size was modified by tadpole density. At low density, relatives grew larger than non-relatives, whereas at high density there was no difference in body size. It seems that density modifies intraspecific competition, and influences kin and non-kin differentially (Blaustein & Waldman 1992). These
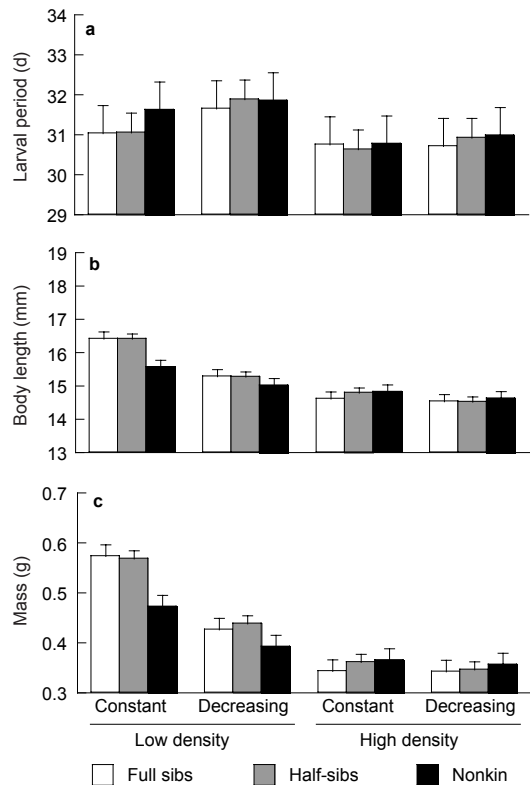

Fig. 1. Length of larval period (**a**), body length (**b**) and body mass (**c**) at metamorphosis (all presented as least-square means + SE) of full-sib, half-sib and non-kin *R. temporaria* tadpoles in the two water level and density treatments.

results are in line with the previous studies on amphibians (Smith 1990, Waldman 1991, Hokit & Blaustein 1994, 1997, Girish & Saidapur 1999, Saidapur & Girish 2001, Pakkasmaa & Aikio 2003, but *see* Hokit & Blaustein 1994). However, contrary to our expectations we found no evidence for interaction between relatedness and water level treatments. It seems possible that the decreasing water level treatment in the present experiment was relatively mild. This is supported by the fact that metamorph size was negatively affected by decreasing water level only at low density, and there were no effects at high density. An alternative, and simple, explanation is that the mechanism by which desiccation risk affects metamorphosis is independent of the corresponding mechanisms by relatedness. Under such a scenario, no interaction between relatedness and desiccation risk is expected.

The enhanced growth performance among siblings at low density may be mediated through different mechanisms. It has been suggested that kin aggregation of anuran tadpoles could lead to faster and more uniform growth (Jasienski 1988). Alternatively, enhanced growth could be a result of increased foraging activity: sibling groups of *R. cascadae* have been shown to be more active than solitary tadpoles or tadpoles in groups of mixed relatedness (Hokit & Blaustein 1995), and increased cooperation may allow more efficient foraging (Waldman 1991). For instance, in salmonid fishes decreased levels of aggression among siblings allowed more time for feeding and thus enhanced growth (Brown & Brown 1993).

In amphibians, large metamorphic size increases juvenile survival and, as size differences at metamorphosis tend to persist through later life, probably also adult reproductive success (Smith 1987, Berven 1990, Scott 1994, Altwegg & Reyer 2003). Hence, our results suggest that tadpoles raised together with their kin at low density may have higher fitness. Kinship has been reported to positively influence growth in several animal and plant species (e.g., Waldman 1988, Tonsor 1989, Brown *et al.* 1996, Andalo *et al.* 2001). Effects on amphibians are somewhat controversial: some studies have found better growth performance among related individuals (Jasienski 1988, Smith 1990, Girish & Saidapur 1999, Pakkasmaa & Aikio 2003), but also inhibited or unchanged growth has been reported (Waldman 1991, Hokit & Blaustein 1994). Discrepancies among studies may be due to differences in environmental conditions, as also suggested by the relatedness–density interaction found in the present study, or species- or age-specific differences in kin recognition ability or aggregation tendency (Blaustein & Waldman 1992, Griffiths & Denton 1992, Blaustein *et al.* 1996, Nicieza 1999). Clearly, future behavioural and physiological studies would be valuable in increasing our understanding of the mechanisms behind kin-mediated growth enhancement.

The difference in metamorphic size between full-sibs and half-sibs was insignificant. A relatively small number of shared alleles may be enough for altruistic behaviour to be profitable (Hamilton 1964). As the half-sibs in a half-sib vial always originated from two different full-sib families (i.e. there were always several individuals from the same full-sib family, *see* Methods), the average relatedness of an individual within a vial was closer to full-sib relatedness ($r = 0.33$ and $r = 0.36$ low and high density treatments, respectively), and this may explain the small difference between full- and half-sibs. Previous studies have shown that tadpoles can discriminate between full-sibs and half-sibs (Cornell *et al.* 1989, Gamboa *et al.* 1991, Pfennig & Collins 1993), but we are not aware of any comparisons on fitness effects between these groups.

Tadpole density had a clear effect on metamorph size and timing of metamorphosis: at high density, metamorphic size was smaller and larval period shorter than at low density. This is in line with theoretical and empirical studies (e.g., Wilbur & Collins 1973, Scott 1990, Smith 1990, Hokit & Blaustein 1994, 1997, Reques & Tejedo 1997). Density effects are probably due to decreased environmental quality in terms of resource availability, which is expected to lead to lower growth rate and shorter development time (Wilbur & Collins 1973).

Contrary to our expectations, decreasing water level did not affect development rate, although such a response was found in previous studies (Newman 1988, 1992, Denver *et al.* 1998, Laurila & Kujasalo 1999). There are at least two possible reasons for the lack of response in development time. First, lack of adaptive response to desiccation risk may be due to population-specific selection pressures favouring other types of developmental responses, with the cost of reduced plasticity in development time (Laurila *et al.* 2002). For instance, in permanent ponds tadpoles often face a continuous predation risk by fish, and larval developmental rate may be maximised by the strong selection pressure to escape from the pond as soon as possible, leaving no room for plasticity (Leips *et al.* 2000). Second, acceleration of development is controlled by an endocrine hormonal mechanism (Denver 1997), and it is possible that the applied desiccation treatment was not strong enough to activate this mechanism. The smaller size at metamorphosis in decreasing water level treatment indicates that although there were no effects on development time, desiccation still induced stress for the developing tadpoles. These

results suggest that metamorph size may be a more sensitive trait to desiccation risk than age at metamorphosis.

We have demonstrated that in good environments, *R. temporaria* tadpoles benefit from the company of their genetic relatives by growing larger, but in poorer environments no such effect was observed. The applied environmental manipulations were relatively benign in the sense that they did not affect tadpole survival. The harsher the conditions, the higher the costs of altruism are expected to be, although these are ultimately dependent on the animal's state (McNamara *et al.* 1994). Kin-biased behaviour is one possible mechanism through which the observed benefits were mediated, and further studies are needed to unravel this in detail. Our results indicate that effects of relatedness on fitness-related traits are affected by environmental conditions and suggest that the role of environmental variability should be considered in future studies on kin selection.

Acknowledgements

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