

Kin discrimination during egg-cannibalism in smooth newts: does competition matter?

Z. Tóth¹, H. Hoi² & A. Hettyey^{2,3}

¹ Department of Limnology, University of Pannonia, Veszprém, Hungary

² Konrad Lorenz Institute for Ethology, Vienna, Austria

³ Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, Budapest, Hungary

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Correspondence

Zoltán Tóth, Department of Limnology, University of Pannonia, Egyetem u. 10, 8201 Veszprém, Hungary.

Email: tothzoltan81@yahoo.com

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Abstract

Kin discrimination has often been investigated in the context of cannibalism, where differential treatment of kin may entail inclusive fitness benefits if closely related conspecifics are spared during foraging. Competition between related individuals can greatly modify the fitness benefits of such behaviour, but its effect has rarely been tested. In this study, we investigated how two competition-related parameters, that is, the actor's relatedness to the competitors of the recipient individual (r_{xe}) and the general decrease in fitness among these competitors originating from the altruistic act (d) influence egg-cannibalism in smooth newts, a facultatively cannibalistic species. We found that only 29% of the observed 31 females performed cannibalistic attempts after fasting, when kin and non-kin eggs were offered for consumption. These individuals attacked their own eggs less frequently than other conspecific eggs when kin ratio among the offered eggs (parameter r_{xe}) was low, but showed no discrimination when the ratio of kin was high. On the other hand, the total number of eggs (as a proxy for parameter d) did not affect the females' kin discriminative behaviour significantly. These results provide the first evidence for kin discrimination during egg-cannibalism in the smooth newt, and support the significance of kin competition for the evolution of altruism.

Introduction

Kin selection is one important theory involved to explain the evolution of cannibalism (Polis, 1981; Pfennig, 1997; Agarwala & Dixon, 1993; Anthony, 2003). Individuals, by not eating their kin, may provide direct benefits to their kin and as a result increase their own inclusive fitness, but in contrast they pay the cost of reduced growth rate or lower probability of survival when passing a meal (Crump, 1992; Pfennig, 1997). According to Hamilton's rule, such altruistic behaviour can be expected to evolve when the benefit of the actor (b), devaluated by the relatedness between actor and recipient (r_{xy}), exceeds the cost of performing it (c ; $r_{xy} \times b - c > 0$, Hamilton, 1964). In line with this, several studies on cannibalistic amphibians found that individuals indeed avoided eating their kin like carnivorous morphs of spadefoot toad tadpoles, *Spea bombifrons* (Pfennig, Reeve & Sherman, 1993), tiger salamander larvae, *Ambystoma tigrinum* (Pfennig, Sherman & Collins, 1994; Pfennig, Collins & Ziemba, 1999), or female red-spotted newts, *Notophthalmus viridescens* (Gabor, 1996). Similarly, cannibalistic marbled salamanders, *Ambystoma opacum* showed reduced aggression towards siblings (Walls & Roudebush, 1991), where sibs benefit from avoiding the consequences of frequent attacks such as higher risk of pathogenic infection

or lower probability of successful metamorphosis (Walls & Jaeger, 1987; Smith, 1990). Kin discrimination has also been found to be context dependent by several studies (e.g. Pfennig *et al.*, 1993; Hokit, Walls & Blaustein, 1996; Gibbons *et al.*, 2003), suggesting that the pay-offs of kin discriminative behaviour can vary according to social and ecological conditions (Waldman, 1988; Reeve, 1989; Hokit *et al.*, 1996).

Theoretical and empirical works pointed out that social aggregations of kin favour the evolution of altruistic behaviour towards relatives, but in contrast may increase competition, reducing or even completely removing the net advantage of altruism (Hamilton 1964; West, Pen & Griffin, 2002; Griffin, West & Buckling 2004). Limited dispersal (often due to physical constraints of the habitat) is typical at early life-history stages in many amphibians and often leads to high densities of conspecific individuals in particular close relatives. During that period competition can be high – especially among individuals of similar size – negatively affecting larval development, growth rate and survival (Van Buskirk & Smith, 1991; Van Buskirk, 2007). Under such circumstances kin discriminative behaviour may be affected by competition. Competition between relatives can be incorporated into Hamilton's rule in several ways (Frank, 1998; West *et al.*, 2002). For instance, West *et al.*

(2002) suggested that as the actor becomes more related to the competitors of the recipient individual (r_{xe}) and the altruistic behaviour causes greater decrease in fitness among these competitors (d), the indirect fitness benefit originating from being altruistic diminishes ($r_{xy} \times b - c - r_{xe} \times d > 0$). In other words, it may not be beneficial to help a relative if helping puts similarly related individuals at a disadvantage. However, if either the altruist is not related to the recipient's competitors or the altruistic act does not affect the competitors' fitness, the original rule will hold (i.e. the term $r_{xe} \times d$ is zero). This extension does not contradict to Hamilton's idea of inclusive fitness, because the fitness consequence of an altruistic act does not confine solely to the altruist and a related recipient, but concerns all individuals that possess the same genes and have been affected by the altruistic behaviour (Danchin, Cézilly & Giraldeau, 2008).

In this study, we tested how the two competition-related parameters, namely the actor's relatedness to the beneficiary's competitors (r_{xe}) and the decrease in fitness among competitors due to the altruistic act (d), affected kin discrimination in smooth newts *Lissotriton vulgaris* during cannibalistic foraging on eggs. Smooth newts are the most widespread newt species in Europe and breed in still and slowly moving shallow waters, small ponds and temporary pools (Steward, 1970). Breeding starts in early spring and lasts for up to 3 months; during that period females deposit their eggs continuously, up to 400 in total, wrapping leaves or other plant material around them (Nöllert & Nöllert, 1992). After oviposition, no parental care occurs in the species. Eggs, larvae and adults share the same habitats for several weeks, during which cannibalism of eggs and larvae by adult newts may take place (Bell & Lawton, 1975; Gabor, 1996). Kin recognition (avoidance of genetically similar mating partners; Jehle *et al.*, 2007) and the negative effect of competition on larval fitness (in interspecific context at least; Van Buskirk, 2007) have also been demonstrated in this species. Although in a previous study, Gabor (1996) did not find any indication for that female smooth newts would discriminate their own eggs from non-kin during cannibalistic foraging, this lack of kin discrimination may be due to the applied test conditions and does not exclude the possibility of kin discrimination under another set of circumstances (also see Gabor, 1996).

In order to test whether competition between relatives may influence kin discrimination in smooth newts, we observed female newts under different test conditions where kin and non-kin eggs were offered as prey items. Specifically, we investigated whether changes (1) in the relatedness between females and the kin's competitors (r_{xe}); and/or (2) in the fitness consequence of the altruistic act for these competitors (d) affect kin discriminative behaviour in adult females. According to the refined version of Hamilton's rule, we predicted that an increase in either parameter (r_{xe} or d) will decrease the probability of kin avoidance during cannibalistic foraging.

Materials and methods

Study subjects

We captured 35 male and female smooth newts, respectively, using underwater traps from five ponds in the Pilis Mountains, Hungary (three ponds at 47°42'N, 19°02'E and two at 47°43'N, 19°00'E) during 13–21 March 2009, at the beginning of the breeding season. At the site of capture, we measured snout-to-vent length of each individual with a plastic ruler (± 1 mm) and assigned each female to a male. Two females had to be assigned to males from a different site as we caught different numbers of males and females at the breeding sites. As we only used males to provide sperm for fertilization, this should not affect the interpretation of the results on these two females. Afterwards, the newts were transported to and held in captivity in the animal ecology laboratory of the Department of Systematic Zoology and Ecology, Eötvös Loránd University, Budapest, Hungary.

We housed each female–male pair separately in transparent plastic aquaria measuring 50 × 30 × 40 cm, filled with c. 18 L of aerated reconstituted soft water (RSW; American Public Health Association, 1985). Individuals were kept under a 12:12 photoperiod with ambient temperature varying between 20 and 25 °C, and were fed *ad libitum* with live *Tubifex* spp. Each container consisted of a sponge filter, a horizontally placed clay flowerpot to provide shelter and unmerged resting surface, and live *Elodea* threads (purchased commercially) attached to the pot as an egg-laying substrate. We changed water in aquaria weekly. Pairs started mating, and, thus, presumably became accustomed to the housing conditions within a few days after capture. On 1 April, we removed males from the housing containers and released them at the site of capture. Females remained in captivity until the end of experiment, and were released at their pond of origin on 25 April.

We collected deposited eggs together with the *Elodea* leaves they had been attached to by females daily during 25–31 March (mean \pm SE = 11.8 \pm 1.0 day⁻¹ individual⁻¹) and 9–11 April (13.5 \pm 1.7 day⁻¹ individual⁻¹). Outside these two periods, eggs were removed every third or fourth day. Eggs were stored separately for each female in aerated RSW (barely covering the eggs) at 10 °C to slow down their development. This temperature can be considered as the lower boundary of a range at which *Lissotriton* embryos normally develop in the wild (Horner & MacGregor, 1985). Fertile eggs (in which embryos were notably alive and developing), unwrapped but still attached to the leaf, were later used in the experiment. We obtained a sufficient number of eggs from 31 out of 35 females (mean \pm SE; 132.7 \pm 10.2 eggs individual⁻¹) at the start of the kin discrimination experiment. To create pairs of females that were not related to each other, we associated each female to another one originating from different ponds; within these pairs, one individual's own eggs were considered as 'kin', whereas the other individual's eggs as 'non-kin', and vice

versa. We did not investigate genetic relatedness *per se* between the assigned females, but we argue that using this method we could create relevant differences in females' relatedness to kin and non-kin eggs in the experiment (though this difference could be unequal between females). Adult smooth newts display strong pond fidelity, annual mortality is generally high (50%; Bell, 1977), and dispersed juveniles reproduce for the first time after 2 or 3 years [Halliday & Verrell, 1988; although most breeding adults were estimated to be 5–9 years old in a detailed study (Bell, 1977)], so the probability that females would have been similarly related to their own eggs and to eggs of another female from a different pond is likely to be low. Because of that, we used the terms 'kin' and 'non-kin' instead of 'own' and 'foreign', respectively. Eight females producing many eggs were assigned as 'non-kin' to more than one other female.

Experimental design

In the experiments, we manipulated the two competition-related parameters, that is, females' average relatedness to the competitors of their own egg (r_{xe}) and the general decrease in fitness of those eggs due to the females' foraging (d), at two levels to assess their effect on kin discriminative behaviour. We altered the parameter r_{xe} by changing the ratio of kin among the offered eggs: in the 'low kin ratio' group 1/4 of the eggs, while in the 'high kin ratio' group 3/4 of the eggs were the observed female's own eggs. In that way, we created two groups between which a female's average relatedness to its own egg's competitors varied considerably. The parameter d was manipulated by modifying the total number of eggs offered for consumption: in the 'few eggs' group the total number of eggs was four, whereas in the 'many eggs' group we used 12 eggs in total. We hypothesized that the *per capita* fitness consequence of the females' foraging behaviour on the kin eggs' competitors would differ between the applied two levels of d (as the relative fitness loss originating from the consumption of a competitor would be different), and feeding females would lower future intraspecific competition in these groups to a different extent. Using these two treatments, we had four possible combinations. Before the experiment, we randomly assigned each female to one of these four set-ups.

We also used two arbitrary levels of food deprivation (24 and 48 h) to enhance egg-cannibalism during foraging. Egg-cannibalism has been previously reported in smooth newts, but with unknown or low frequency: for example, Gabor (1996) found that only eight out of 35 females ate conspecific eggs when kin and non-kin eggs were offered for consumption. By applying food deprivation in our study, we aimed to increase the probability of egg-cannibalism, although it may also increase the cost of being altruistic towards kin (Pfennig *et al.*, 1993). To control for the effect of fasting in our analyses, we included food deprivation into the models as a possible confounding variable.

Collecting behavioural data

We performed experiments between 13 and 25 April, 24 or 48 h before the start of observations, we moved test animals to plastic boxes (10 × 15 × 12 cm) filled with 0.1 L of water taken from their original housing aquaria. After fasting, females were transferred to the testing containers (50 × 30 × 40 cm, filled with *c.* 12 L of aerated RSW), where kin and non-kin eggs were offered as prey items. Testing containers consisted of 12 homogeneously distributed, numbered plastic dishes (diameter 3 cm with a 2 mm high edge) fixed to the bottom. Into each dish we vertically thrust a pin, on which a 3 cm long green plastic tube was impaled. On each tube there was a 1 cm long cut at its lower end, into which an *Elodea* leaf with an attached egg could be fixed. In this way, kin and non-kin eggs could be placed in the centre of the dishes in a semi-natural position and we could ensure that currents caused by rapid movements of test animals would not sweep the highly buoyant leaves (with the eggs) away. For each female, kin and non-kin eggs were randomly distributed among the dishes according to the given experimental set-up. We recorded the behaviour of each female for 1 h (between 09:00 and 15:00 h) with a video recorder (Sony DCR-HC 35E, Sony Corporation, Tokyo, Japan) attached *c.* 1 m above the test container. We followed this procedure and observed females in random order at two fasting levels (24 and 48 h), with at least 48 h between the two trials.

We analysed foraging behaviour of each female on the video recordings using a blind approach, where the observer was unaware of whether the given behaviour was directed against kin or non-kin eggs. We counted the number of events when an individual crossed the border of a dish and measured the time it spent in the dish (± 0.1 s). We also defined 'egg investigation' as an event when the animal directly approached an egg (within 0.5 cm) with its head orientated towards it and spent some time in close vicinity of the egg. We noted both the number and duration of this behaviour as well. From these measures we calculated three variables, that is, number of investigations, duration of investigations, proportion of visited dishes with an egg, to describe an individual's exploratory behaviour. Using these variables, we were able to examine whether females encountered and/or inspected kin and non-kin eggs with equal frequency and duration. We also counted the number of attacks, that is, attempt to bite off an egg from the leaf, an individual performed against eggs and used this behaviour to investigate discriminative behaviour in females. We used attacks instead of egg consumption, because females often ceased attacking an egg after several unsuccessful efforts to detach it from the leaf and only few attacks ended with the ingestion of the egg (seven out of 33). It is possible that the observed fierce attacks on eggs only serve to inflict damage to the developing embryo rather than providing an important source of food to females. Whatever the ultimate evolutionary cause, we consider using the frequency of attacks as an adequate method to analyse kin discrimination in smooth newts (for similar argumentation and approach see e.g. Walls & Roudebush, 1991; Hokit *et al.*, 1996).

Table 1 Final LMM model of attacks against kin and non-kin eggs, with individual identity (id) as random factor

Model parameters	Estimates [CI]	d.f.	<i>F</i>	η^2 [CI]	<i>P</i>
Fixed effects					
Fasting	2.180 [−0.142 to 4.503]	1,24	3.76	0.14 [0–0.38]	0.065
Kinship	−8.382 [−13.098 to 3.665]	1,24	4.81	0.17 [0–0.41]	0.038
Kin ratio	−4.834 [−15.417 to 5.749]	1,7	0.36	0.05 [0–0.41]	0.569
Kinship × kin ratio	14.192 [4.340–24.044]	1,24	8.84	0.27 [0.02–0.50]	0.007
Random effects					
Between-individual sd	2.078 [0.854–5.057]				
Within-individual sd	3.375 [2.544–4.479]				

CI, confidence interval; LMM, linear mixed-effect model.

Data processing and statistical analyses

According to the video records, out of 31 females, seven investigated the eggs offered for consumption in only one trial and 17 investigated the eggs in both trials [number of investigations (mean \pm SE) = 11.1 \pm 2.7; duration of investigations = 70.9 s \pm 17.8]. However, only nine out of these 17 individuals attacked eggs at least once in either fasting level (number of attacks = 1.8 \pm 0.7, number of investigated eggs before the first attack = 3.53 \pm 1.2). We analysed the behaviour of these latter nine females to investigate how kin discrimination varied in the different experimental set-ups. We calculated *per egg* average values for each behavioural variable (i.e. number of attacks, number of investigation, duration of investigation and proportion of visited dishes with an egg) and used them as dependent variables in the models. We did so by dividing the variable's value for each individual in each kinship category and in each fasting level by the number of eggs that were present in given kinship group. In that way, our dependent variables became comparable across different experimental set-ups. We also applied Box–Cox transformation to the number of attacks per egg ($\lambda_1 = -0.42$, $\lambda_2 = 0.02$; Box & Cox, 1964), and square-root transformation to the number of investigation and duration of investigation to improve their fit to normal distribution.

All statistical analyses were performed in the R computing environment (R 2.9.2; R Development Core Team, 2009). We used linear mixed-effect models (LMM; 'lme' function of the 'nlme' R package; Pinheiro & Bates, 2000) to investigate the effect of kinship, kin ratio and total number of eggs on females' attacking and exploratory behaviour. In LMMs, parameter estimation is unaffected by our unbalanced design (as the number of females differed between the experimental set-ups; Pinheiro & Bates, 2000). We included individual identity (id) as random factor into these models to control for potential pseudoreplication, because this random factor design is equivalent to repeated measures models in R (Pinheiro & Bates, 2000; Faraway, 2006). We used restricted maximum likelihood method for model estimation and *F* values to define significance of the predictors ('anova.lme' function). We used backward removal procedure (Grafen & Hails, 2002), starting with fasting and the other predictors together with the interaction of kin ratio

and total number of eggs with kinship, then dropped the predictor with the highest *P*-value in each step, retaining only $P \leq 0.10$ effects (if there were any) in the final models. We estimated effect sizes for the predictors in the final models (Garamszegi, 2006) as the proportion of variance explained by each trait, that is, η^2 and provide 95% confidence intervals (CI) (Cohen, 1988). All tests were two-tailed and we set α to 0.05.

Results

We found a significant effect of kinship on the frequency of attacks as female newts initiated less attacks against kin eggs than against non-kin eggs (Table 1). This kinship effect was mainly due to the significant kinship \times kin ratio interaction: individuals attacked kin eggs less frequently when the ratio of kin eggs was low, but did not discriminate between kin and non-kin when the ratio of kin eggs was high (Table 1; Fig. 1). Fasting had a marginally non-significant effect on egg attacking: females tended to attack more eggs after 48 h of food deprivation, than after 24 h (Table 1). The total number of eggs had no effect on attacks either by itself ($F_{1,6} = 0.488$, $P = 0.511$), or in interaction with kinship ($F_{1,23} = 0.003$, $P = 0.960$).

All aspects of females' exploratory behaviour (i.e. number of investigations, duration of investigations and proportion of visited dishes with egg) differed significantly between the two fasting levels: females investigated eggs more frequently ($F_{1,26} = 16.28$, η^2 [CI] = 0.36 [0.10–0.58], $P = 0.0001$), investigated them for a longer period ($F_{1,26} = 7.74$, η^2 [CI] = 0.23 [0.01–0.46], $P = 0.010$) and visited a larger proportion of dishes with egg ($F_{1,26} = 6.24$, η^2 [CI] = 0.19 [0.004–0.43], $P = 0.019$) after 48 h of food deprivation, than after 24 h. However, all the variables were unaffected by the examined predictors and their interaction with kinship (all $P \geq 0.369$), suggesting that females encountered and inspected kin and non-kin eggs with similar frequency and duration.

Discussion

Despite the applied levels of fasting, we found that only 29% of the observed 31 females performed cannibalistic attempts during foraging, when kin and non-kin eggs were offered as

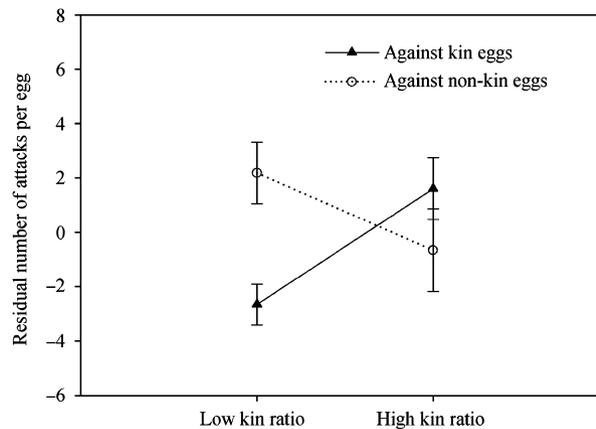


Figure 1 Residual number of attacks per egg against kin and non-kin eggs in different experimental set-ups. Means are shown \pm SE. Dependent variables are plotted as residuals from the final linear mixed-effect models without the examined interaction and its main effects. The two treatment groups differed in kin ratio among the offered eggs: in the 'low kin ratio' group ($n=12$ data points) 1/4 of the total eggs, while in the 'high kin ratio' group ($n=6$ data points) 3/4 of the total eggs were the females' own egg. Kin eggs were a female's own egg, whereas non-kin eggs were the eggs of a different individual caught in another pond and randomly assigned to given female.

prey items. These individuals attacked their own eggs at a lower frequency than non-kin eggs when the ratio of kin (parameter r_{xe}) was low, but showed no discrimination when the ratio of kin among the offered eggs was high. On the other hand, the total number of eggs (a proxy for parameter d) did not significantly affect female kin discriminative behaviour. These results are in accordance with the predictions of inclusive fitness theory and provide evidence for kin discrimination during egg-cannibalism in smooth newts.

Similar to another study (Gabor, 1996), we found that egg-cannibalism occurred only at low frequency in spite of the applied food deprivation treatment. In fact, our fasting had only a very slight effect on the number of cannibal females (nine out of 31) compared with Gabor's (1996) study (eight out of 35), suggesting that egg-cannibalism is not a common foraging strategy even under unfavourable conditions (i.e. after fasting), and most individuals avoid consuming conspecific eggs during the reproductive period. Although egg-cannibalism has been reported by previous studies (e.g. Bell & Lawton, 1975; Griffiths, 1986; Miaud, 1994), suggesting that such behaviour may be beneficial for some individuals or under some circumstances, future investigations are needed to identify what ecological factors elicit egg-cannibalism in smooth newts. Although the small number of cannibalistic females may be the reason why the fitness consequence of the altruistic act on the beneficiary's competitors (parameter d) did not influence the foraging decisions of females in our study, and also prevented us to test the potential impact of multiple interactions between all investigated parameters, we were able to successfully manip-

ulate at least one competition-related parameter (namely parameter r_{xe}) to induce kin discrimination in the examined individuals.

We found that female smooth newts discriminated their own eggs from unrelated conspecific eggs during cannibalistic foraging in a context-dependent manner. This result contradicts earlier findings, where females ate kin and non-kin eggs with a similar frequency (Gabor, 1996). However, as Hokit *et al.* (1996) pointed out, kin discrimination may be condition dependent as the cost/benefit ratio of such behaviour may vary with different environmental, temporal and social factors (Hokit *et al.*, 1996; Gibbons *et al.*, 2003; Harris *et al.*, 2003; Pakkasmaa & Laurila, 2004). For instance, not cannibalizing kin may be costly for an individual in poor condition, but not in other circumstances, as found in cannibalistic spadefoot toad, *S. bombifrons*, tadpoles (Pfennig *et al.*, 1993). Similarly, adult female red-backed salamanders, *Plethodon cinereus* (Gibbons *et al.*, 2003) and marbled salamander, *A. opacum* larvae (Hokit *et al.*, 1996) avoided eating their kin only in particular contexts. Several theoretical models provide possible explanations for such context dependence, pinpointing different ecological factors that may modify the fitness consequences of kin discrimination (see in Reeve, 1989; Hokit *et al.*, 1996). If such behaviour occurs in aggregations of closely related individuals, competition among kin may be one of these factors as any kind of kin discrimination will affect not only the recipient kin, but also other, similarly related individuals in these circumstances. Density dependence and the effect of competition on kin discrimination during cannibalism has been found in several species (e.g. marbled salamanders, *A. opacum*: Hokit *et al.*, 1996; sharptooth catfish, *Clarias gariepinus*: Hecht & Appelbaum, 1988; acorn woodpeckers, *Melanerpes formicivorus*: Stanback & Koenig, 1992), but, to our knowledge, this is the first study which specifically aimed to test the effect of competition-related parameters in a cannibalistic context.

The ability of kin discrimination has been documented in several caudate species, but its proximate mechanism is less known. In tiger salamanders, Pfennig *et al.* (1994) found that kin discrimination is mediated by olfaction; chemical cues may be similarly important in our model species. Larval and adult smooth newts often use olfactory cues in detection of predators (Mathis, 2003; Orizaola & Braña, 2003) or conspecific individuals including mating partners (Aragón, López & Martín, 2000; Secondi, Haerty & Lodé, 2005), so that chemical cues may also be of significance for kin recognition. In some anuran species, maternal labels in the egg jelly have been found to play an important role in the recognition of kin eggs (Waldman, 1991); similar chemical cues may act as a basis for kin discrimination in newts as well.

In conclusion, we found that smooth newts perform egg-cannibalism at a very low frequency even after 48 h of food deprivation. However, our results suggest that – in contradiction with a previous study (Gabor, 1996) – female smooth newts that practice egg-cannibalism can discriminate between their own eggs and between those of other

females, but that this behaviour is condition dependent. Females took kin ratio among eggs into account when they attacked conspecific eggs, which support the importance of kin competition for the evolution of altruistic behaviour.

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