Kin discrimination in cannibalistic tadpoles of the Green Poison Frog, *Dendrobates auratus* (Anura, Dendrobatidae)

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Abstract

Kin discrimination in cannibalistic tadpoles of the Green Poison Frog, *Dendrobates auratus* (Anura, Dendrobatidae). Cannibalizing a related individual can reduce the inclusive fitness of the cannibal. Hence, mechanisms that allow a tadpole to recognize and modify its behavior toward kin may reduce the inclusive fitness costs of cannibalism. Alternatively, ecological factors may cause preferential treatment of kin to be too costly to be favored by selection. We tested these two predictions in the Green Poison Frog, *Dendrobates auratus*. The effect of kinship on larval cannibalism was examined through a series of kin-discrimination trials. The behavior of large tadpoles was observed when presented with two small, tethered tadpoles, one a clutchmate and one an unrelated tadpole. In these simultaneous presentation tests, tadpoles displayed a significant preference for attacking kin. In a series of timed trials, pairs of unequally sized tadpoles were placed together in containers. The majority (70%) of large tadpoles took less than 24 hr to consume the small tadpole. Kinship did not affect the survival time of the small tadpole. Our results are consistent with observations that *D. auratus* is an indiscriminate predator. As conspecifics may be serious competitors, their swift elimination would be an advantage, particularly in the small, nutrient-poor pools used by this species.

Keywords: Anura, Dendrobatidae, cannibalism, kinship, larvae.

Resumo

Discriminação de relativos em girinos canibais de *Dendrobates auratus* (Anura, Dendrobatidae).
O consumo de indivíduos aparentados pode reduzir a aptidão inclusiva do canibal. Assim, mecanismos que permitam que um girino reconheça seus relativos e modifique seu comportamento pode reduzir os custos do canibalismo. Alternativamente, fatores ecológicos podem tornar o tratamento preferencial dos relativos custoso demais para que seja favorecido pela seleção natural. Testamos essas duas previsões no dendrobatídeo *Dendrobates auratus*. O efeito do parentesco sobre o canibalismo larval foi examinado por meio de uma série de tentativas de discriminação de parentes. Observamos o comportamento de girinos de grande porte diante de dois girinos menores imobilizados, um irmão e outro não-aparentado. Nesses testes de apresentação simultânea, os girinos mostraram uma preferência significativa por atacar irmãos. Em outra série de tentativas, pares de girinos de tamanhos diferentes foram colocados juntos em aquários. A maioria dos girinos de grande porte (70%) consumiu o girino menor em menos de 24 horas. O parentesco não afetou o tempo de sobrevivência do girino pequeno. Nossos resultados são consistentes com as observações de que *D. auratus* é um predador indiscriminado. Como os co-específicos podem ser fortes competidores, sua eliminação rápida poderia ser vantajosa, particularmente nas pequenas poças pobres em nutrientes utilizadas por essa espécie.

Palavras-chave: Anura, Dendrobatidae, canibalismo, parentesco, larvas.

Introduction

Hamilton's inclusive fitness theory provides a framework to understand the evolution of altruistic and aggressive behavior (Hamilton 1964). Hamilton's Rule predicts that altruism (or reduced aggression) will be favored when $rb - c > 0$, where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary and r is their genetic relatedness (Hamilton 1964). The rationale behind preferential treatment of related individuals is that it will aid the propagation of genes shared with kin.

To behave differently toward kin, related individuals must be recognized as such (Hamilton 1964). Kin recognition has been identified in a wide variety of organisms, including many amphibians (reviewed in Fletcher and Michener 1987, Sherman *et al.* 1997). Studies of kin recognition in amphibians have often examined it in the context of cannibalism (Walls and Roudebush 1991, Pfennig and Collins 1993, Pfennig *et al.* 1993, Pfennig 1997). Cannibalism, or the killing and ingestion of conspecifics, is widespread in nature (Polis 1981, Elgar and Crespi 1992) and is found in many groups of amphibians, with the most frequent type being that of larvae

consuming larvae (Crump 1992). The benefits derived from consuming conspecifics are primarily nutritional, allowing the cannibal enhanced growth or survival success (Crump 1992). There may be additional benefits of consuming conspecifics as they represent the proper proportion of nutrients required for the cannibal's growth (Nagai *et al.* 1971, Meffe and Crump 1987, Crump 1990, Wildy *et al.* 1998). Another benefit of cannibalism may be that it eliminates sources of competition (Polis 1981).

Despite the nutritional benefits of cannibalism, there are costs. These include the risk of injury to the attacking animal, greater exposure to species-specific disease and the risk of eating a relative (Polis 1981, Crump 1992). Cannibals tend to attack animals smaller than themselves or animals that are unable to defend themselves (Elgar and Crespi 1992), thereby reducing the risk of injury. More efficient spread of pathogens to conspecifics has been demonstrated in a variety of organisms (Polis 1981, Pfennig *et al.* 1991) and has been suggested as the main reason certain animals avoid cannibalism (Pfennig *et al.* 1998). The loss of inclusive fitness by eating a relative can have a direct selective impact (Hamilton 1964). A number of amphibian species reduce this

impact by avoiding cannibalizing kin (examples of anurans: *Bufo americanus* [Waldman 1985], *Spea bombifrons* and *S. multiplicata* [Pfennig and Frankino 1997], and salamanders: *Hynobius retardatus* [Wakahara 1997], *Ambystoma tigrinum nebulosum* [Pfennig and Collins 1993, Pfennig *et al.* 1999]). In contrast, some species do not seem to avoid cannibalizing kin (e.g., Walls and Blaustein 1995). The evolution of mechanisms of kin discrimination should depend on how larval ecology affects the costs and benefits of cannibalism.

The Neotropical anuran genus *Dendrobates* comprises many species with larval ecologies that make cannibalism advantageous. Most *Dendrobates* tadpoles have massive beaks with serrated teeth that would allow carnivory (Silverstone 1975, Caldwell and Myers 1990). Combined with this morphogical modification, the aggressive behavior of *Dendrobates* tadpoles renders them successful predators (Summers 1990, Caldwell and Araújo 1998, Summers 1999). The exceptions to this are the obligate egg-eating tadpoles of the *Oophaga histrionicus* Group that survive on unfertilized trophic eggs provided by the female parent (Weygoldt 1987), and therefore these tadpoles are excluded from further discussion.

Dendrobates deposit terrestrial eggs that develop into tadpoles, and then are transported by a parent to a pool of water to complete development. Females produce many small clutches of eggs year round so there is a steady supply of tadpoles to be deposited (Weygoldt 1987). All *Dendrobates* tadpoles are deposited in small pools of water (i.e., phytotelmata), which include water that collects in fruit husks, such as capsules of Brazil nuts (Caldwell 1993), calabash (Summers 1990) and cacao pods (H. M. Gray, pers. observ.), tree holes (Dunn 1941, Eaton 1941) and leaf axils of plants (Summers 1992, Brust 1993). Not only are these pools small and at risk of drying out, but often they are freshly formed the night before tadpole deposition, and thus are low in accumulated nutrients (H. M. Gray, pers. observ.).

For *Dendrobates auratus,* the benefits derived from consuming conspecifics are primarily nutritional, allowing the cannibal enhanced growth and survival (Crump 1992). *D. auratus* tadpoles are generally voracious predators and will consume any insect larvae, and heterospecific or conspecific tadpoles deposited in the same pool (Summers 1990, Caldwell and Araújo 1998). Conspecific tadpoles provide a relatively large prey item in a usually nutrient-poor environment. Increasing the food available to *D. auratus* tadpoles increases larval growth rate (Summers 1990). Although the consumption of conspecifics has not been shown to confer any additional advantage relative to other sources of calories and nutrients, cannibalism does eliminate the tadpoles' closest competitors, as well as their potential predators (i.e., other cannibals).

The costs of cannibalism in *Dendrobates auratus* include the risk of injury to the attacking animal, pathogen transmission, and the loss of inclusive fitness (Crump 1992, Polis 1981). The risk of injury to tadpoles attempting to cannibalize conspecifics is apparently high; in pools in which there are more than two *D. auratus,* individuals have damaged tails (Summers 1990). Tadpoles usually are able to complete metamorphosis despite tail damage (H. M. Gray, unpubl. data), although these injuries may impose a cost in terms of reduced growth and developmental rates as was found in *Rana catesbeiana* (Wilbur and Semlitsch 1990). Pathogen transmission via cannibalism in this species has not been explored. Also, it is unknown whether any mechanism exists to recognize kin and avoid a loss of inclusive fitness in *D. auratus.*

Field observations indicate that individual male *Dendrobates auratus* return to pools and deposit tadpoles from different clutches into the same pool, although they typically deposit tadpoles from a single clutch into different pools (Summers 1990). In most pools where tadpoles were deposited, more than one male was observed bringing tadpoles to the pool

(Summers 1990). Hence, pools typically contain a mixture of related and unrelated tadpoles. Because tadpoles are rarely deposited simultaneously, they typically vary in size. Even under experimental conditions when tadpoles are deposited at similar sizes, they rapidly diverge in size, owing to intraspecific competition (Summers 1990). Typically, the total number of tadpoles deposited is small; thus, cannibals do not have the option of choosing among a large number of relatives and non-relatives.

We examined tadpole choice by simultaneously presenting a large tadpole with a small related and a small unrelated conspecific. We also examined, in a series of paired timed trials, the time for a large tadpole to cannibalize a small tadpole, and whether kinship influences the outcome. The simplest prediction with regard to kin discrimination in *Dendrobates auratus* is that tadpoles will avoid eating relatives, thereby increasing their inclusive fitness. However, owing to the larval ecology of *D. auratus,* this prediction may be too simplistic. Selection may not favor kin discrimination if the small size and nutrient-poor status of the pools, and the associated high levels of competition and cannibalism, make kin discrimination prohibitively costly.

Materials and Methods

Tadpole collection and maintenance

Experiments were conducted during May–July 1998 and May–August 1999 in the Republic of Panama. Sibling *Dendrobates auratus* tadpoles were obtained from two sources. Tadpoles were collected from the backs of males transporting more than one tadpole. Males usually transport a single tadpole, but occasionally transport more. During a 2-mo period, the number of tadpoles being transported by males was counted at the two field sites (Cerro Ancon, 8°56'N,

79°34'W and Isla Taboga, 8°47'N, 79°34'W). Of 46 males observed transporting tadpoles, 42 (91.3%) were transporting a single tadpole, 3 (6.52%) were carrying two, and 1 individual (2.17%) was carrying three tadpoles. Males were assumed to be the father of the tadpoles that they carried. Cuckoldry of one male by another has not been observed in field studies of the mating system of *D. auratus,* and the aggressive territoriality of males in this species makes cuckoldry unlikely (Summers 1989). Because multiple tadpoles on a given male's back were always of the same size, they were assumed to be of the same clutch.

The second source of tadpoles was a group of captive *Dendrobates auratus.* Breeding pairs of adults were captured in the field and were maintained in 10-gal (37.85-L) terraria at the Tupper Center of the Smithsonian Tropical Institute in Panama City. Terraria were kept at ambient temperature and were furnished with leaf litter, a hollowed branch, a bowl of dechlorinated water, and a dish containing pieces of ripe fruit. Animals were fed lab-reared, wingless *Drosophila* dusted with vitamin powder. They were also able to eat the insects that were attracted to the rotting fruit in the terraria. Tadpoles were collected from the water bowls placed in the terraria with a single pair of frogs. The date tadpoles were collected was noted in order to keep track of which tadpoles were from the same clutch. All related tadpoles used were full siblings. In total, 29 sibships were used in the experiments. Nineteen different sibships were examined for the kin discrimination trials, and 10 different sibships were used in the timed trials. Experiments were conducted with tadpoles that were 7–14 days old.

Tadpoles to be used as the unrelated individuals were collected from the field in areas known to have large breeding populations of *Dendrobates auratus.* Small plastic cups, filled with dechlorinated water, were placed in areas not overlapping with the source areas for

the related tadpoles. The next day, all tadpoles deposited in these cups were collected. Tadpoles from all sources were maintained individually in plastic cups containing 75 ml of dechlorinated water and were fed commercial goldfish food every few days.

Experiment 1: Kin discrimination trials

Each kin discrimination trial involved three tadpoles—i.e., a pair of siblings and one unrelated individual. One of the siblings was designated the test tadpole. This animal was fed fish food and mosquito larvae ad libitum for the week prior to trials. The other tadpoles were fed limited fish food only. The trials were conducted with unequal-sized individuals because this allowed the experiment to progress more rapidly. In the field, when individuals of the same size share a small pool, one will outcompete the others and will increase in size much more rapidly than the others (Summers 1990).

The day before the trial, tadpoles were weighed (Salter AND electronic balance FX-200) and their body length from the snout to the junction of the posterior body wall with the tail, or snout-vent length (SVL), measured with dial calipers. In 1998, only the small tadpoles were measured, whereas in 1999, the test tadpoles also were measured. Each small kin tadpole was carefully matched for size with an unrelated tadpole. All three tadpoles were placed into separate containers with clean water and left without food for 24 hr to ensure that the animals were all at the same hunger level during trials.

The experimental arena (Figure 1) was a clear plastic rectangular tank (18.5 × 13.25 cm). A black line was drawn on the bottom of the tank dividing it into halves. The tank was filled with water to a depth of 2.5 cm. We placed an open-ended net cylinder in the middle of the tank, straddling the centerline. The cylinder was a tube of fine open-meshed material (tulle) with wire rings (5-cm diameter) at either end to give the tube rigidity. The test tadpole was placed in
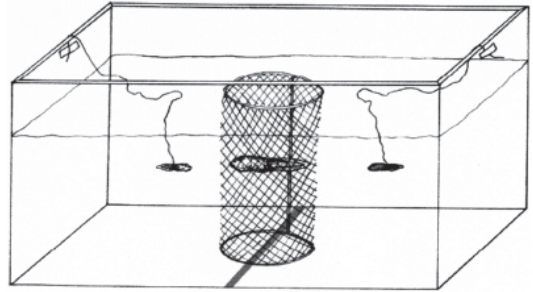

Figure 1 - Experimental arena during acclimation period. After 20-min of acclimation, the net cylinder was removed and the interactions between the test tadpole and its clutch mate and an unrelated tadpole (shaded grey on the right side of the tank) were filmed. Tethering ensured that the small tadpoles remained on opposite sides of the tank.

this cylinder during acclimation to the arena. A short piece of black thread was tied around the base of the tail of each of the small tadpoles. The end of the thread of each tethered tadpole was then taped to opposite sides of the test arena. In this way, the small tadpoles were able to swim freely around in their half of the test arena but were unable to cross the center line. The side of the tank occupied by the related or unrelated tadpole was switched for each trial. After a 20-min acclimation period, the cylinder was removed and the test tadpole was able to swim freely about the entire arena. Interactions between the test tadpole and its smaller sibling and the smaller unrelated tadpole were filmed for 1 hr with a video camera (Sony Hi-8 video CCD-TR100 NTSC). At the end of the hour, the small tadpoles were untied and their condition noted. The videotapes were then watched by an observer who noted the number of attacks and bites the test tadpole inflicted on each of the smaller animals. To control for any a priori assumptions about outcome, the observer did not know the relatedness of the tadpoles when scoring the videotapes.

Experiment 2: Timed cannibalism trials

To determine if relatedness of tadpoles affected the amount of time for a large tadpole to consume a small tadpole, we conducted paired trials with animals in small containers. These experiments also controlled for the effect of tethering in the first experiment, ensuring that the attacks on the small tadpoles in the first experiment did not occur simply because the tadpoles were tethered. Two tadpoles, again one larger than the other, were placed together in small plastic containers containing 75 mL of dechlorinated water. Each paired trial consisted of a container holding a large and small, related tadpole and a container holding a large and small, unrelated tadpole. In each set of trials, large and small animals were carefully matched for size, both in wet weight and snout-vent length. After measuring, all tadpoles were placed individually into clean containers with water and left for the 24 hr prior to the experiment. After the 24 hr, the large and small, related animals were put together and the large and small, unrelated animals were put together in a separate container. A pellet of goldfish food was added to each container with the pair of tadpoles. This was done to give the big tadpole a choice of foods and eliminate the possibility that a starving tadpole would indiscriminately eat any tadpole in the same pool. Containers were checked every 12 hr and the time taken for the large tadpole to kill the small tadpole was noted.

Statistical analysis

Statistical analyses were carried out using Systat Version 8.0 (SPSS Inc., 1998). Data were tested for normality of distribution (Kolmogorov-Smirnov normality test) and for homogeneity of variances (Bartlett's test). Proportional data were arcsine–square root transformed to meet parametric assumptions of normality (Zar 1999).

In experiment 1, body length and mass differences were examined with two-sample t-tests. Kruskal-Wallis one-way analysis of variance was used to determine if the test tadpoles were significantly larger than the tethered tadpoles. To determine if the number of attacks and bites were based on kinship, a Mann-Whitney U-test was used. To take into consideration the range in attack behavior of the different test tadpoles, we analyzed, with t-tests, the proportion of attacks and bites inflicted on related and unrelated small tadpoles.

In experiment 2, body length and mass differences were examined with two-sample t-tests. To determine if kinship influenced the time to cannibalism, a Mann-Whitney U-test was used (Zar 1999).

Results

Experiment 1: Kin discrimination trials

There were no significant differences in the sizes of the small tadpoles used in each kin discrimination trial (mean ± standard deviation; small tadpoles related to the test tadpole 0.065 ± 0.0184 g wet weight, 6.5 ± 0.704 mm body length, N = 19; small tadpoles unrelated to the test tadpole 0.064 ± 0.0165 g, 6.49 ± 0.603 mm, N = 19; two-sample t-test for mass: $t36 = 0.315$, $P = 0.754$; two-sample t-test for body length: $t36 = 0.025$, $P = 0.98$). The test tadpoles were significantly larger than the small tadpoles (0.12 ± 0.0435 g wet weight, 7.97 ± 0.986 mm body length, N = 13; Kruskal-Wallis one-way analysis of variance for mass: $H = 16.11$, $k = 3$, $P \ll 0.05$; analysis of variance for SVL: $F = 15.94$, df(factor) = 2, df(residual) = 36, $P \ll 0.05$). The test tadpoles were almost twice the weight and on average 1.5 mm longer than the small tadpoles.

There was no significant difference in the number of attacks on the small tadpoles based on kinship (mean number of attacks on kin 8.89 ± 9.73 and on nonkin 4.63 ± 6.73, Mann-Whitney U-test: $U = 235$, $N1 = N2 = 19$, P

= 0.104). Similarly, there was no significant difference in the number of bites inflicted by the test tadpole on the small related or unrelated tadpoles (mean number of bites to kin 49.63 ± 159.831 and to nonkin 11 ± 16.9345; Mann-Whitney U-test: $U = 224$, $N1 = N2 = 19$, $P = 0.195$). The large variance in numbers of bites was attributable, in particular, to one test tadpole that attacked the related small tadpole 23 times, biting the small tadpole 707 times. This value is an order of magnitude greater than the next highest number of bites (65). The test tadpoles displayed a significant preference for attacking kin (proportion of attacks on kin, 0.74 ± 0.302; one sample t-test: $t15 = 2.821$, $P = 0.013$). There was no significant preference, relative to a baseline of 50%, found when the proportion of bites inflicted was examined (proportion of bites to kin 0.676 ± 0.358; one sample t-test: $t15 = 1.670$, $P = 0.116$). There were however significantly greater proportions of both attacks and bites made to kin tadpoles when compared to the proportion of attacks and bites to nonkin (two-sample t-test for attacks: $t30 = 3.99$, $P = 0.000$; two-sample t-test for bites: $t30 = 2.361$, $P = 0.025$).

The use of the observed condition of the tadpoles as they were removed from the setup proved problematic as the test tadpole often continued to attack tadpoles during the dismantling of the arena. The end result was that during the 19 trials, three kin and three unrelated small tadpoles were fatally wounded by the time they were removed from the test arena. From the videotapes, only the three related and one of the unrelated small tadpoles were attacked during filming meaning that enough injuries were sustained during the dismantling period to kill an additional two unrelated tadpoles.

There was no significant tendency for the test tadpole to preferentially attack or bite the tadpole on a particular side of the test arena (one-sample t-test for attacks: $t15 = -1.833$, $P = 0.087$; one-sample t-test for bites: $t15 = -1.796$, $P = 0.093$).

Experiment 2: Timed cannibalism trials

The large tadpoles in the timed kin trials (0.14 ± 0.038 g; 8.29 ± 0.887 mm, N = 10) and the large tadpoles in the timed unrelated trials (0.14 ± 0.0370 g; 8.49 ± 1.01 mm, N = 10) were not significantly different in size (two-sample t-test for mass: $t18 = 0.254$, $P = 0.802$; two-sample t-test for body length: $t18 = -0.470$, $P = 0.644$). There was also no significant difference in size of the small tadpoles (small tadpoles in kin trials 0.061 ± 0.0147 g, 6.41 ± 0.499 mm body length, N = 10; small tadpoles in unrelated trials 0.061 ± 0.0141 g, 6.22 ± 0.657 mm, N = 10; two-sample t-test for mass: $t18 = -0.015$, $P = 0.988$; two-sample t-test for body length: $t18 = 0.727$, $P = 0.476$). The large tadpoles were significantly larger than the small tadpoles (two-sample t-test for mass: $t38 = 8.71$, $P = <<0.05$; two-sample t-test for body length: $t38 = 8.47$, $P = <<0.05$).

It took large tadpoles less than 12 hours to up to two weeks to fully consume the smaller tadpole in the container. The majority of large tadpoles took less than 24 hours to consume the smaller tadpole (70%, N = 20). In four of 10 paired trials, the time that it took for the large tadpole to kill the small tadpole was the same. In three trials, the small tadpole in the related container died first and in three trials the unrelated small animal died first. There was no significant difference between the mean time until cannibalism between trials with kin and trials with non-kin (Mann-Whitney U test, N = 10, Xkin = 42.8 hr, SE = 14.6 hr, Xnonkin = 22.8 hr, SE = 3.3 hr, U = 41, P = 0.496).

Discussion

In some species, tadpoles recognize their kin and modify their cannibalistic behavior in order to avoid a reduction of inclusive fitness (Crump 1990). We found no evidence that *Dendrobates auratus* tadpoles avoid cannibalizing their kin. Our results demonstrated that the test tadpoles directed a higher proportion of both attacks and

bites toward related, rather than unrelated tadpoles, although tadpoles in both groups ultimately suffered the same fate. The numbers of attacks and bites directed at unrelated tadpoles were not significantly different than those directed at related tadpoles, and an equal number of unrelated and related small tadpoles ultimately died in the preference trials. In experiment 2, the similar speed with which large tadpoles killed and consumed unrelated or related smaller tadpoles confirms that even if tadpoles are able to discriminate kin from unrelated tadpoles this does not modify their cannibalistic behavior.

Our results raise several questions. First, why did large tadpoles not discriminate in favor of their kin, as has been observed in other species? Most anuran species that possess kin discrimination live in temporary or permanent ponds (e.g., *Spea bombifrons,* Pfennig *et al.* 1993). Because these ponds contain large clutches of related and unrelated larvae, there are typically many individuals from which to choose and a cannibal can be selective and avoid eating a relative. This is not the case for *Dendrobates auratus* tadpoles which are deposited into small, nutrient-poor pools. Indiscriminate killing of related and unrelated conspecifics occurs in other species that utilize small pools (e.g., *Adelphobates castaneoticus* [Caldwell and Araújo 1998] and mosquito larvae [Sheratt *et al.* 1999]). In such pools, competition for severely limited resources may make the costs of altruism toward kin (e.g., refraining from cannibalism) too high (Pfennig 1997). Given the small size of the pools utilized by *D. auratus,* there may simply not be enough food available for a tadpole to allow even a small full sibling to survive and compete for resources. Hence, the best strategy may be to eat all small tadpoles introduced into the pools.

It is possible that cannibalism in *Dendrobates auratus* occurs as a result of completely indiscriminate predation, in which all competitors and potential predators are attacked, and no distinction is made between different species (Crump 1992, Caldwell and Araújo 1998). *D. auratus* tadpoles are efficient predators of the tadpoles of sympatric species of frogs (Summers 1990, Caldwell and Araújo 1998). *D. auratus* tadpoles also attack invertebrate larvae (Finke 1994). Other than some of these larvae which become predators when large, the greatest threat to *D. auratus* tadpoles are conspecifics, which may explain why the large tadpoles in experiment 2 chose to kill and consume the smaller tadpole in preference to eating the fish food. The drive to attack was not simply a consequence of hunger, implying that the calories and nutrients gained from cannibalism are not the immediate motivator of the behavior. Instead, the elimination of a potentially long-term competitor (or predator) may be the most important benefit.

A second reason that large tadpoles did not discriminate in favor of kin may be that the risk of attacking close relatives is comparatively low. The tadpoles of *Dendrobates auratus* are transported individually by their male parent to a pool. The male chooses where to deposit each of his offspring. Male *D. ventrimaculatus* have been shown to avoid placing young into pools which already contain a large tadpole (Summers 1999), and the same may be true for *D. auratus.* Male *D. auratus* spend substantial amounts of time evaluating and searching for suitable pools to deposit tadpoles (Summers 1990). Part of this evaluation may involve the number and the size of other tadpoles, as well as the presence of previous offspring in the pool. Males transport tadpoles of the same clutch to different pools (Summers 1990). These deposition strategies of male *D. auratus* may reduce the probability that tadpoles will encounter and consume close relatives, and hence decrease the indirect fitness costs of indiscriminate predation of conspecifics.

Another question is why did kin receive a greater proportion of attacks? One possibility is that tadpoles were able to recognize kin as potential competitors more quickly and

efficiently than they were able to recognize non-kin. It is not known what cue tadpoles use to determine either relatedness or conspecific status. Other species of amphibians have been shown to use chemical cues (olfactory) to recognize kin (Pfennig and Collins 1993). Adult *Dendrobates pumilio* have been shown to use olfactory cues in territory identification (Forester and Wisnieski 1991), and tadpoles of *Dendrobates* species may also have well-developed chemosensory reception. The *D. auratus* tadpoles may be using olfactory cues to identify another tadpole in the pool. As the experimental tadpoles were raised in isolation, the test tadpole may recognize a tadpole that smells like itself as a conspecific competitor more quickly and this may explain the initial preference for kin. This use of self to develop a standard for comparison is described by Grafen (1990), who posited that kin recognition (and discrimination) might be an artifact of species recognition. Specifically, he proposed that, if the cues used for species recognition are perceived by matching those cues to a template derived from the animals' own phenotype, then individuals may tend to recognize closely related individuals more effectively, simply as a byproduct of the recognition system. This could produce non-adaptive biases in recognition and discrimination that are associated with kinship.

Acknowledgements

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