Interference and exploitative competition in amphibian larvae

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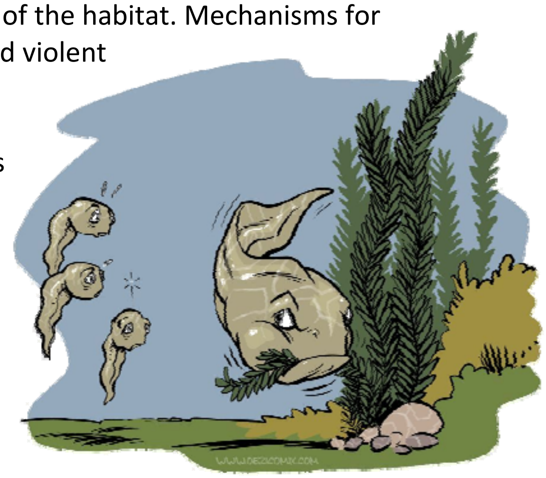
Competition can be defined as an interaction between species or individuals, in which the fitness of one is lowered by the presence of another. Through competition and a limited supply of at least one resource - such as food, water, and territory - used by competing entities required (Steinwascher 1978). Competition both within and between species is an important topic especially in community ecology. Competition is one of many interacting biotic and abiotic factors that affect community structure. Dramatic differences in growth and development rates (growth dispensation) between individual amphibian larvae are common in *ex situ* environments. These include mass rearing for conservation breeding programs and are consequently of high conservation significance. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Competition can occur by both direct and indirect behavior (Tilman 1982).

We consider two main categories of competition between amphibian larvae, these being interference and exploitative competion. Interference competition occurs *directly* between individuals when the individuals interfere with foraging, survival, reproduction of others, or by preventing their physical presence in a portion of the habitat. Mechanisms for interference competition include pheromones, and violent behaviors extending to cannibalism. Exploitation competition on the other hand occurs *indirectly* through a common limiting resource which acts as an intermediate. For example the use of the resource(s) depletes the amount available to others, or they compete for space (Van Kampen et al., unpublished).



Exploitative competition. The bigger tadpole is currently eating from the limited food source. And he is not letting the other tadpoles near. Therefore the smaller ones can not reach the food and will not be able to grow as well.

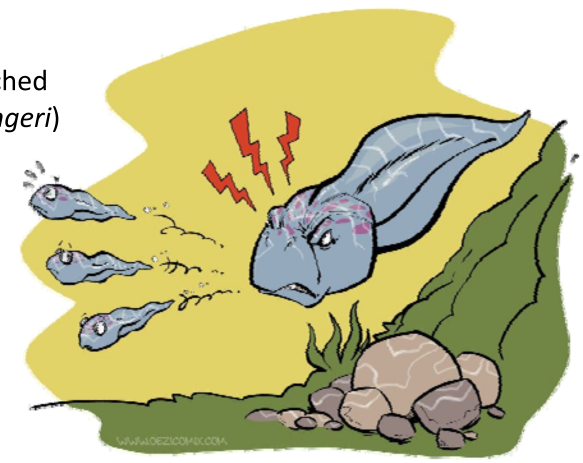
Therefore, both interference and exploitative competition may affect the growth and development of amphibian larvae in experiments or in conservation breeding programs. Steinwascher (1978) researched interference and exploitative competition among tadpoles of the Southern leopard frog (*Rana utricularia*). Steinwascher found that scarce resources can be distributed among individuals in a population by processes of intraspecific competition. Furthermore, Park 1954 showed that competitive interactions are mediated by: (1) interference mechanisms (such as allelopathy or territoriality), (2) differential consumptive abilities only, or (3) some combination of these two categories.

Interference competition must cost the individual more than exploitative competition per unit food value gained, because the total cost includes both the cost of the interference effect (i.e., the allelopathic chemical or that portion of time and energy spent in territorial defense) and the cost of collecting and consuming the food items. In this case the cost of collecting and consuming the food items exemplifies the the cost of exploitative competition.

The nature of these competitive interactions may change in response to environmental fluctuations of resources. For example, Gill and Wolf (1975) related the territoriality of sunbirds to the availability of the nectar resource outside of their territories. At high levels of undefended nectar, the interference mechanisms are replaced by a more exploitative form of competition. The effect of environmental fluctuations in resources is also is mirrored in amphibian larval rearing when limited food results in exploitative competition.

Tadpoles of Southern leopard frog (*R. utricularia*) also exhibit interspecific competition for food, which results in differing growth rates (Wilbur and Collins 1973). The difference in growth and development within a cohort – or group of the same age - is defined as growth depensation.

Kam et al. (2001) stuied the growth of newly-hatched oophagous rhacophorid tree frog (*Chirixalus eiffingeri*) larvae in bamboo stumps, that contained large tadpoles that hatched from earlier clutches. The growth of the small, late-hatching tadpoles in occupied nests was suppressed by the presence of large, early-hatching tadpoles. However, small tadpoles that were physically separated from large tadpoles in a perforated container grew at about the same rate as small tadpoles living in pools without large tadpoles. Thus, the slower growth of the late-hatching tadpoles was probably caused by behavioural interference competition with the early-hatching tadpoles.



Interference competition. The bigger tadpole is defending its own area of space, by actually scaring off the smaller ones using aggression. Therefore the other tadpoles are on the run an can not put their energy in growing, inherently keeping them smaller than the bigger and more aggressive ones.

Competition can occur at many different levels. It can be shown through physical engagement, and also manifested through food competition. Steinwascher (1978) showed the largest *R. utricularia* tadpole in each replicate successfully competed with other individuals for food. Body weights of single tadpoles raised in water conditioned by their siblings increased as the food level in the conditioning treatment increased. Greater dispersion of the food source in the conditioning treatment decreased the growth of single tadpoles. Interference competition replaced exploitative competition as food availability decreased. Other factors affected the growth of the single tadpoles by altering the food level in the conditioning treatments. The decreased growth in conditioned water was interpreted as resulting from chemical interference competition. However, the effect could be benign and due to metabolites or pathogen load.

Intraspecific competition can produce dramatic effects between populations of different species. Faragher and Jaeger (1998) showed that in natural ponds competition between two species of amphibians resulted in increased mortality of one of the species larvae. In this case both chemical and behavioural interference played a major role.

The degree of growth depensation is affected by population density, species, and food availability and type. In some species chemical signals have been implicated in interference competition. The effect of larval density on interference competition varies between species. Counter-intuitively, where adequate food is supplied, in amphibian larvae and fish, growth depensation declines or ceases at higher densities where individual recognition and therefore individually targeted interference competition ceases. Many species of amphibian larvae have been shown to exhibit growth depensation. It is not yet generally known at which point in the development of larvae this phenomenon sets in. With some species studies have shown that the basis of this process can occur within days after hatching.

In some fish species both growth depensation and stunted growth may be reversed through the removal of interference and exploitative competition (Jobling and Koskela (2005). Fish reared at optimal circumstances show regular growth, fish reared at poor circumstances over a few days or even weeks show growth depensation. However when the circumstance change to more optimal conditions of high density or individual rearing with feeding *ad libartum*, these fish show rapid growth and catch up in size to their faster growing siblings . This process is called compensatory growth. Browne et al. (unpublished) found the larvae of Amazonian milk frog (*Phrynohyas resinifictrix*) did not exhibit compensatory growth. Further, studies may elucidate the potential for compensatory growth in amphibian larvae.

High density rearing to reduce interference competition, fine food *ad libartum* to reduce exploitative competition, and 12hr water changes resulted in low growth dispensation in Green and golden bell frog (*Litoria aurea*) larvae. Densities of up to 80 larvae per liter maintained maximum size in metamorphs and minimum metamorphosis time. As densities reached 160 per liter metamorphosis size declined, and metamorphosis time and mortality increased. Similar results were found in studies with a range of species from the Peoples Republic of China (Browne et al. 2003).

Summary

Interference and exploitative competition have clearly been shown to affect amphibian larval growth and development. However, few definitive studies have elucidated these phenomenons. Studies of tadpole growth and development show frequent broad, and between studies, contradictory conclusions. Often these studies have not eliminated the possibility of confounding factors such as varying forms of competition. There are increasing needs to raise amphibian larvae in conservation breeding programs, to reduce harvest of amphibians for display, and to produce amphibians for micro-economic uses such as food. Within this scenario, the understanding and further study of interference and exploitative competition in amphibian larvae will make significant contributions to efficiency of production in reduced costs, and in healthier and more robust offspring.

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