

THE PROBLEM OF FOOD COMPETITION IN AMPHIBIANS

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Competition occurs when resources are limited and may be determined only by its effects on the component species. It must change the condition of resources and the fitness of competitors (or at least part of them) so that both are negatively affected. Original data and analysis of the literature revealed that food competition in amphibians is usually discussed in terms of (1) negative interactions between individuals; (2) density-dependent responses of individuals; (3) density-dependent responses without estimation of food resources; (4) differences in the biology of syntopic species; (5) feeding rate variability; (6) the impact of amphibians on their food resources; and (7) density-dependent responses with estimation of food resources. Food competition can only be identified in the last case, where depletion of food resources is demonstrated together with negative interactions between species. Such events have been demonstrated in some laboratory or microcosm experiments, but not in nature. Food competition appears to be rather rare in natural guilds of amphibians.

INTRODUCTION

According to Darwin, competition is regarded as one of the main forces of organic evolution. However, scientists vary in their interpretation of competition, its mechanisms and how it manifests itself in nature. Nowadays, Milne's (1961, p.67) definition of the term "competition" appears to be the most precise. According to Milne (1961), competition may be identified only by its effects in nature. These effects are reflected by both competitors and the resources upon which they rely. To become a potential subject of competition, the usable part of the resource spectrum must be limited in abundance and in its availability to consumers. In addition, the "contest" for resources must influence the condition of the competitors. Establishing a relationship between the condition of consumers and their resources is, therefore, the only practical indicator of the presence of competition between species. If resources are not limited, they can be used without competition and no negative effects on the component species will occur. If competition occurs, one or more of the competing species will suffer reduced fitness as a result of (1) less resources being available, and (2) energy used up in direct contests or interference with other competitors. Competition for limited resources may therefore result in reduced fitness of consumers. Such reduced fitness may affect all or only some of the consumers, depending on differential competitive abilities between species.

Thus, the following modification of Milne's (1961) definition has been proposed (Kuzmin & Tarkhnishvili, 1990a, p.47): "Competition is the endeavour of two or more organisms to use the same part of the resource spectrum, when resource supply in this part of the spectrum fails to meet the requirements of both or more organisms, and the endeavour leads to reduced fitness of one or more competitors".

So, there are three main criteria for identifying the presence of competition: (1) food limitation; (2) reduced fitness of consumers; and (3) a relationship between these two parameters. If one or more of these three condition cannot be identified, then competition is not unequivocally demonstrated.

Food is considered to be one of the main resources that animals compete for in nature (e.g. Schoener, 1974). Among amphibians, the presence of food competition is frequently assumed to apply. In this paper, I analyse the main evidence for this supposition in the context of the definition proposed above.

EVIDENCE FOR THE PRESENCE OF FOOD COMPETITION

The evidence for food competition in amphibians may be divided into six main types of study (Table 1). Studies which analyse similarities and/or differences in the biology of syntopic species, infer the presence of competition as a structuring force most frequently. For example, morphological, spatial, and feeding relationships (Szymura, 1974; Miller, 1978; Shlyakhtin, 1986) are often interpreted as indicators of the presence of food competition. Differences between species in these parameters are explained as evidence of past competition or as a way of avoiding competition in the present (Anderson & Graham, 1967; Passmore & Carruthers, 1979; Okochi & Katsuren, 1989, etc.). On the other hand, similarity in feeding may be interpreted as an evidence for the lack of food limitation and competition (e.g. Licht, 1986).

Such relationships may be related to food competition but cannot be regarded as unequivocal evidence for competition, because of the lack of data on resource supply or its depletion by consumers. In the absence of food limitation, amphibian trophic niches may completely overlap without competition (e.g. Kuzmin & Tarkhnishvili, 1987, 1990a,b, 1991, 1992). Food and

TABLE 1. Arguments for presence of food competition among amphibians

Argument	Taxa	Stages	Conditions	References
(1) Similarities/differences in biology of syntopic species	Ambystomatidae Plethodontidae Salamandridae Discoglossidae Bufonidae Pelobatidae Ranidae	Larvae and Adults	Natural	2/11/12/13/16/20
(2) Negative interactions of individuals	Plethodontidae Bufonidae Ranidae	Larvae and Adults	Natural and Experimental	3/4/9/14
(3) Density-dependent reactions without estimation of food resources	Ambystomatidae Plethodontidae Salamandridae Bufonidae Ranidae	Larvae and Adults	Natural and Experimental	1/10/23/24/25
(4) Feeding rate variability	Plethodontidae	Adults	Natural and Experimental	8
(5) Amphibian influences on food resources	Salamandridae Bufonidae Ranidae	Larvae	Natural and Experimental	6/15/22
(6) Density-dependent reactions in relation to food resource limitation	Ambystomatidae Plethodontidae Bufonidae Hylidae Ranidae Leptodactylidae	Larvae and Adults	Experimental	5/7/17/18/19/21/26/27/28

References: 1 - Alford & Wilbur, 1985; 2 - Anderson & Graham, 1967; 3 - Bastakov & Mantefel, 1987; 4 - Boice & Williams, 1971; 5 - Dash & Hota, 1980; 6 - Dickmann, 1968; 7 - Hota & Dash, 1981; 8 - Jaeger, 1972; 9 - Jaeger, 1979; 10 - Kleeberger, 1985; 11 - Miller, 1978; 12 - Okochi & Katsuren, 1988; 13 Passmore & Carruthers, 1979; 14 - Pisarenko, 1987; 15 - Seale, 1980; 16 - Shlyakhtin, 1986; 17 - Steinwascher, 1978a; 18 - Steinwascher, 1978b; 19 - Steinwascher, 1979; 20 - Szymura, 1974; 21 - Travis, 1984; 22 - Viertel, 1981; 23 - Wilbur, 1971; 24 - Wilbur, 1972; 25 - Wilbur, 1977a; 26 - Wilbur, 1977b; 27 - Wilbur, 1987; 28 - Wiltshire & Bull, 1977

spatial differences may result from historically fixed morphological and behavioural differences which are independent of present or past competition, e.g. in larval newt (*Triturus* spp.) and terrestrial anuran guilds (e.g. Kuzmin, 1992; Kuzmin & Tarkhnishvili, 1987, 1990a, 1992).

Evidence from studies in groups 2-4 (see Table 1), are discussed frequently. Differential density-dependent responses of amphibian larvae (Wilbur, 1971, 1972, 1977a; Alford & Wilbur, 1985); frog aggressive behaviour during feeding, and hierarchical feeding behaviour (Boice & Williams, 1971; Bastakov & Mantefel, 1987); cannibalism (Pisarenko, 1987); and feeding rate variability (Jaeger, 1972) are frequently explained in terms of food competition. Some authors (e.g. Jaeger, 1979; Kleeberger, 1985) explain salamander territoriality as the defence of food territories, i.e. the places with the highest concentration of prey in a

patchy environment. However, all these events can be sufficiently explained in other ways: density-dependent responses may, for example, be related to metabolic and behavioural regulation (Shvarts *et al.*, 1976). Different types of behavioural interactions may not depend on food supply, but may be explained in terms of territoriality, dominance behaviour, displacement responses, mistakes in feeding strikes, or defence of refugia (Wrobel *et al.*, 1980; Kuzmin & Tarkhnishvili, 1990b, 1992). Such interactions may negatively affect foraging and the physiological condition of amphibians (e.g. Grant, 1955). Cannibalism can arise when there is a rapid appearance of juveniles, which provide a short-term but more profitable food resource than other unlimited prey. Similarly, variation in feeding rate is influenced by temperature, humidity and aggressive interactions (Kuzmin & Tarkhnishvili, 1990b).

Thus, arguments presented in groups 2-4 (Table 1) are no more persuasive than non-competitive explanations, because these studies do not include data on resource depletion or consumer fitness.

Evidence from studies within group 5 (see Table 1) are more important for our discussion. Anuran tadpoles, for example, have been shown to influence the amount and diversity of periphyton and phytoplankton both in experimental (Dickmann, 1968) and natural conditions (Seale, 1980). This corresponds with data that shows that tadpole growth and developmental rates are higher in ponds with maximum phytoplankton and periphyton concentrations (e.g. Viertel, 1981). However, even in these studies, part of the food resource spectrum (e.g. bottom debris) invariably remains unestimated. In addition, density-dependent interactions between the consumers and their food supply may be unknown. Some experiments have revealed that under certain conditions, tadpoles do not compete for food even if the latter is sharply limited (e.g. De-Benedictis, 1974; Steinwascher, 1979).

Only the arguments based on studies in group 6 (Table 1), i.e. amphibian density-dependent reactions in relation to food resource limitation, may serve as evidence for the presence of food competition. Such events have been demonstrated experimentally for many urodele and anuran species. In these experiments, the influence of amphibian density has been distinguished from density-dependent food limitation. Stewart (1956) first demonstrated more rapid growth and development of well-fed *Ambystoma opacum* larvae than poorly-fed specimens reared at the same population density. Petranka (1984) demonstrated the lack of density-dependent regulation of the growth and development of *Ambystoma texanum* larvae reared with excess food and a regular change of water. In other trials, food was supplied in proportion to the density of larvae, i.e. on a per capita basis. Under such conditions larval growth and development were reduced by the low food levels, but growth inhibition was independent of larval density. It is interesting to note that variation in larval size under food competition was lower than at higher food levels (Petranka, 1984: Fig. 6). Thus interspecific competition for food did not lead to a differentiation in the size of competitors, which is the basis of trophic niche divergence in syntopic amphibians. Fraser (1976) found similar negative effects of food limitation on competing *Plethodon cinereus* and *Plethodon hoffmani*.

Competition for food has also been clearly separated from other mechanisms in laboratory trials (Wilbur, 1977b, 1987; Steinwascher, 1978a,b, 1979; Dash & Hota, 1980; Hota & Dash, 1981; Travis, 1984) and field experiments (Wiltshire & Bull, 1977) in ten species of anuran tadpoles. These experiments showed that food competition extends the duration of larval development and reduces size at metamorphosis. Variation in larval size, growth and developmental rates

has been increased, or decreased, according to species and density.

THE ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF COMPETITION

The problem of food competition has been discussed in many previous studies (e.g. Toft, 1985). However, it has been demonstrated clearly only in laboratory or microcosm experiments but not in nature. All the attempts to explain some natural situations as resulting from food competition were more or less speculative, and did not bring clear evidence for the unequivocal role of competition. Moreover, it is simpler to demonstrate the lack of food competition than its presence. The latter may be demonstrated only if all three conditions stated in the definition (see above) are met. If one or more of these conditions cannot be demonstrated then competition may not be in operation. For example, in many natural situations food resources may be unlimited (Degani, 1982, 1986; Kuzmin & Meschersky, 1989; Kuzmin & Tarkhnishvili, 1987; Taylor *et al.*, 1988). In such cases there will be no competition for food between amphibians.

At low population densities of amphibians, their interactions do not lead to competition. Moreover, there is some indirect evidence of the low influence (or even absence) of food limitation upon amphibian life-history regulation. For example, density-dependent effects in some situations may be sufficiently explained by abiotic factors (Travis & Trexler, 1986) or metabolic influences (Shvarts *et al.*, 1976). The density of *Ambystoma maculatum* eggs in different ponds is not correlated with the amount of food therein (Albers & Prouty, 1987). Moreover, ambystomatid salamanders can change from living in ponds to living in streams, where the food resources are scarcer (Petranka, 1984; Smith & Petranka, 1987). Studies on newts of the genus *Triturus* revealed a convergence rather than a divergence in their trophic niches (Griffiths, 1986; Kuzmin & Meschersky, 1989; Kuzmin & Tarkhnishvili, 1987); such a pattern would not be observed if food competition was operating.

Although competition for food in amphibians has never been unequivocally demonstrated in nature, it appears to be possible in some situations. Theoretically, it is most likely to occur in larvae which have a highly specialised diet, such as the "embryos" of *Salamandra* spp., oophagous tadpoles of Dendrobatiidae, and so on. In such situations food competition may be a by-product of specialised reproductive strategies and must ultimately be controlled by them. However, in natural assemblages of opportunistic amphibians, food competition appears to be an unusual event, which plays a minor, or insignificant, role in their structure and dynamics.

This feature of amphibian population interactions may be related to general traits in their evolutionary ecology; those of opportunistic and unspecialised feed-

ing. This feature is based on general morphological and functional similarities in feeding mechanisms in different amphibian taxa. Probably, the main trends in resource use by amphibians have remain unchanged during the course of their evolutionary history. Indeed, an opportunistic feeding strategy may be one of the adaptations which has allowed amphibians to exploit unstable environments. In an environment consisting of a mosaic of small suitable and unsuitable microhabitats, each prey group may be limited in any one patch, but the total prey spectrum as a whole may be not limited. This would obviate selection towards food specialization and perhaps explain the scarcity of this trait in living amphibians.

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