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Predator-prey size interaction in tropical ponds.

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ABSTRACT

An experiment was set-up to see in mortality inflicted by tadpole predators depends on prey and predator sizes. Fish and dragonfly larvae were used as predators and two size classes of **Osteocephalus taurinus** *tadpoles as prey. Results show that the effect of predators is dependent on the size structure of the prey population. Furthermore, dragonfly larvae are more voracious predators than the fish used in the experiment. Both predators occur in natural ponds where* **Osteocephalus taurinus** *lays its eggs. The timing of arrival of predators and prey, which determines the relative sizes of predators and prey, is an important factor determining the outcome of an episode of community interaction in tropical ponds, as in similar temperate systems.*

INTRODUCTION

The importance of predators in structuring larval amphibian communities has been demonstrated (MORIN, 1981, 1985, 1987; WOODWARD, 1983a; WILBUR, **et al.**, 1983). The impact of a predator on a tadpole population will obviously depend on the identity of both the predator and the prey. The temporal component of such a system (timing of arrival of the predator and the prey) is also extremely important and will determine the size structure of the predator and prey populations. For most species of larval anurans small tadpoles are most vulnerable to predators.

However, in many cases tadpoles can attain a size where the probability of being eaten decreases drastically (HEYER **et al.**, 1975; WOODWARD, 1983b; CRUMP, 1984; TRAVIS **et al.**, 1985; WOODWARD & JOHNSON, 1985; CRONIN & TRAVIS, 1986; FORMANOWICZ, 1986).

While predation of tappoles seems to be the overriding factor in most anuran communities (MORIN, 1987), most studies have looked at predation effects (and/or tested for a zise interaction) using insect larvae and adults (Odonata or Dytiscid beetles) or salamander larvae as the predator. Studies that have used fish as predators have either focused on the differential vulnerability of tadpole species occuring in temporary ponds (without fish) and those using permanente ponds (with fish) (WOODWARD, 1983a), or looked at the effect of predator and prey size structure on the mortality inflicted by the predator (SEMLITSCH & GIBBONS, 1988). Results of this latter study revealed significant size effects for both prey and predator sizes: larger tadpoles had higher survival than smaller ones and more tadpoles of all size classes survived in the presence of small fish than with large fish. Fish in

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that study seemed to be gape-limited predators due to the reduced biomas eaten in the large tadpole treatments than in the smaller ones. The importance of size determined by the timing of arrival of predator and prey species is, therefore, of major importance giving an early arriving prey a size advantage and a possible escape from fish predators. Available data do not seem to suport HEYER **et al.**, (1975) contention that fish are the top aquatic predator and can effectively wipe out entire cohorts of tadpoles in a pond regardless of tadpoles sizes. These authors suggest that in tropical systems, the more complex ponds will contain fish and that they will be able to eliminate many tadpole species from these ponds regardless of any advantage conferred to the prey by rapid growth or early arrival. The purpose of this study was to compare the voracity of two common predators in tropical ponds: fish and dragonfly larvae, and to test for an interaction between predator type and prey size to see if mortality inflicted by a predator was dependent on prey size.

NATURAL HISTORY

Osteocephalus taurinus

Osteocephalus taurinus is a large hylid with a widespread distribution in the Amazon basian of South America (DUELLMAN & LESCURE, 1973; BOCKERMAN, 1964). In a frog community under study (composed of over 45 species) in undisturbed primary tropical forest north of Manaus (Amazonas, Brazil), Which is part of the Biological Dynamics of Tropical Forest Fragments Project (formerly the Minimum Critical Size of Exosystems Project), it is the largest hydlid to occur and the only one known to deposit huge quantities of eggs as a surface film directly in ponds. In the study area breeding is year-round with the main burts of activity occurring during the rainy season (November-April). Frogs are either found calling solely or in small aggregations around breeding habitat (DUELLMAN & LESCURE, 1973; unpubl. data) although large choruses were reported by BOCKERMAN (1964). This species uses any terrestrial aquatic habitat as breeding ground from isolated forest pools to stream-side pools to areas of slow water current in streams. Egg masses are large (2 000 to 4 000 eggs; unpulb. data) and often cover the entire surface of small pools (BOCKERMAN, 1964; unpubl. data). Eggs hatch within 48 hours and tadpoles remain in the pools until metamorphosis which varies between 3 weeks and 2 months (unpubl. data).

Predators

Dragonfly larvae are a common and abundant tadpole predator in natural habitats of the study area. Both Aeshnidae and Libellulidae families are represented by various species and both families are known to be strong predators of tadpoles (unpubl. data). These predators are present in isolated forest pools and stream-side pools being much more abundant in the former.

Pyrrhulina sp. (Lebisianidae) is a small fish species that occurs throughout the study area occupying mostly streams and stream-side pools. Occurrence in upland sites was noted on an isolated basis (unpubl. data). Its occurrence in stream-side pools is subject to much variation and is dependent on periodic overflowing of the streams into adjacent pools on which occasions this fish species can invade those sites. Maximum total length encountered for this species was 6 cm.

During the course of field surveys in 1987 and 1988 *Osteocephalus taurinus* was found to occur in habitats where fish and larval dragonfly were present. Very large tadpoles and emerging metamorphs of this species were found in these same sites. These observations cast doubt on the fact that predators are imposing an overwhelming pressure on larval anurans in tropical systems capable of eliminating entire cohorts of most species. Two possible explanations exist: 1) fish (and dragonfly larvae) are in too low abundance in certain sites to completely eliminate some cohorts of some species or, 2) these predators are size limited and that whether some individual anuran larvae metamorphose is dependent on their attaining refuge from predators through large size (i.e. by arriving a system before any predators and growing beyond the threshold size). This paper presents results of an experimente that was set up to test this second hypothesis. Data show that there is an interaction between predator type and prey size indicating that dragonfly larvae are size limited predators for *Osteocephalus taurinus* meaning that mortality inflicted by aeshnid naiads on *Osteocephalus taurinus* tadpoles depends on tadpole size: smaller tadpoles having a greater probability of being eaten than larger ones. Furthermore, results indicate that dragonfly larvae eat significantly more larvae of *O. tautinus* than do fish for both prey size classes.

MATERIAL AND METHODS

An experiment investigated the effects of predator type and prey size on the mortality inflicted by these predators on tadpoles of *Osteocephalus taurinus*. A two factor design was used; each prey size and predator species was an independent factor. Small, and large fish as well as one species of dragonfly larvae were used (small and large fish were considered differente "species"). A treatmente of no predator served as a control. The fish species used was *Pyrrhulina* sp. (Lebisianidae). The small fish were $<$ 3cm (2.7–3.0cm) whereas the large category included fish that were $>$ 4cm (4.5–5.2cm). This is the size range most commonly found in the natural sites that are surveyed as part of another study.

The dragonfly larvae were of the family Aeshnidae and naiad size varied between 2 and 4 cm. Two sizes of *Osteocephalus taurinus* tadpoles were used: small stage 25 (mean total length 1.3cm [1.1–1.6cm]) and large stage 30-38 (mean total length 3.0cm [2.4–3.5cm]) according to GOSNER (1960). Fifty tadpoles of either size were placed in plastic basins (30 cm width by 11 cm deep) followed by one individual of each of the appropriate predator.

A total of 16 basins were used (2 tadpole sizes X 4 predator treatments X 2 replicates). All basins were covered with nylon screening to prevent entry of other predators. The experiment was run for 25 days. Survival was determined at the end of the experiment. Trials were run out in the field. A small area close to camp was cleared of ground vegetation and basins were set out directly on the ground. Forest canopy cover remained intact. Treatments were randomly assigned to each basin.

RESULTS

A 2-way ANOVA showed a significant interaction term (table I), indicating that the effect of predator type depended on the size of the tadpoles. In this case, only simple effects can be investigated (predator effects within small and large tadpoles; STEEL & TORIE, 1960). ANOVA for only the small tadpoles showed a significant effect of predators on mortality (table I).

TABLE I. Summary of results of predator type and prey size experiment. Underscore connects indistinguishable averages.

1. Analysis of variance

	SS	DF	MS	F-Ratio	P
Prey size	.274	1	.274	5.151	0.053
Predator	4.712	3	1.571	29.521	0.001
Interaction	1.003	3	.334	6.285	0.017
Error	.426	8	.053		

2. ANOVA for simple effects of predator types

A. Within small prey size

		Predator type			
		Absent	Small flish	Large fish	Odonate
Mortality out of 50	X	3.5	3.5	6.0	48.5
	Sx	3.5	4.9	7.1	2.1

$F(3,4) = 19.640$
$p < 0.05$

B. Within large prey size

		Predator type			
		Absent	Small flish	Large fish	Odonate
Mortality out of 50	X	7.5	2.0	8.0	35.0
	Sx	6.4	0.0	5.7	7.1

$F(3,4) = 10.912$
$p < 0.05$

Multiple comparison tests show that mortality caused by odonates was significantly higher than in the other treatments. Both fish types (small and large) were not significantly different from the control treatment (no predator). Whitin the large tadpoles results show the same trends, the impact of odonate predators, however, being lower than in the small tadpole basins (table I).

DISCUSSION

Data from this experiment clearly show: 1) that at least one predator common in tropical aquatic communities is size limited with respect to predation on *Osteocephalus taurinus* within the size range used and, 2) dragonfly larvae are more voracious predators of *O. taurinus* tadpoles than are *Pyrrhulina* sp. In the case of Aeshnid predators it is probably that when very abundant and present at the time of egg laying of *Osteocephalus taurinus* naiads could wipe out entire cohorts. Whether *Osteocephalus taurinus* can attain a size refuge will probably depend on a combination of both density and timing of arrival of naiads and tadpoles into a pond.

Although only larval anuran species was tested with one fish species these results do not support the contention by HEYER **et al.**, (1975) that fish are the top predators in tropical systems and are capable of eliminating entire cohorts of larval anurans. Althoug *O. Taurinus* does nor always occur with fish these results demonstrate that under favorable circumstances some larvae could metamorphose from sites that contain fish. There is a possibility that very large fish could occasionally enter sites where *O. taurinus* or another species has laid eggs and wipe out entire cohorts. The fish species used in this experiment are, however, well within the size range of those normally encountered in natural ponds and such a possibility, if it occurs, remains a rare event.

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