Oecologia (1991) 86:310–318

Oecologia

Predation and the evolution of complex oviposition behaviour in Amazon rainforest frogs

William E. Magnusson[1] **and Jean-Marc Hero**[1,2,]*

[1] Instituto National de Pesquisas da Amazonia (INPA). Alameda, Cosme Ferreira 1756. Aleixo 69083, Manaus, AM, Brasil
[2] Division of Australian Environmental Studies, Griffith University. Nathan, Brisbane Queensland 4111 Australia

Received August 7, 1990 / Accepted in revised form November 22, 1990

Summary. Terrestrial oviposition with free-living aquatic larvae is a common reproductive mode used by amphibians within the central Amazonian rainforest. We investigated the factors presently associated with diversity of microhabitats (waterbodies) that may be maintaining the diversity of reproductive modes. In particular, desiccation, predation by fish, competition with other anurans and water quality were examined in 11 waterbodies as possible forces leading to the evolution of terrestrial oviposition. Predation experiments demonstrated that fish generally do not eat anuran eggs, and that predacious tadpoles and dytiscid beetle larvae are voracious predators of anuran eggs. The percentage of species with terrestrial oviposition was only weakly correlated with the occurrence of pond drying, pH and oxygen concentration, suggesting that anurans in this tropical community are able to use the range of water quality available for egg development. There was a tendency for terrestrial oviposition to be associated with the number of species of tadpoles using the waterbody, but we consider this to be spurious as there was no obvious competitive mechanism that could result in this relationship. The percentage of species with terrestrial oviposition was significantly positively related to our index of egg predation pressure, and negatively related to our index of fish biomass. Egg predation pressure was also negatively related to the index of fish biomass. These results allow us to discount as improbable the hypothesis that predation by fish on anuran eggs was an important selective pressure leading to terrestrial oviposition in this community. The strong positive relationship between terrestrial oviposition and our index of egg predation pressure indicates that these predators have exerted, and are exerting, a significant selective pressure for terrestrial oviposition. The strong negative relationship between the occurrence of fish and the egg predators suggests the surprising conclusion that the presence of fish actually protects aquatic anuran eggs from predation in this tropical system, and allows aquatic oviposition to dominate only in those waterbodies with moderate to high densities of fish. Our results suggest that terrestrial oviposition is a "fixed predator avoidance" trait.

Key words: Anura – Eggs – Palatability – Terrestrial oviposition – Amazon

Amphibians have many modes of reproduction (Duellman and Trueb 1986). Crump (1974) grouped them into three broad categories: (I) Eggs deposited in water, tadpoles develop in water (aquatic development); (II) Eggs deposited out of water, tadpoles develop in water (semi-terrestrial development); and (III) Eggs and young completely independent of standing water (terrestrial development). Type I development is generally considered to be primitive in relation to types II and III (Goin 1959; Tihen 1960; Goin and Goin 1962; Lynch 1973; Heyer 1975; McDiarmid 1978; Duellman and Trueb 1986; however see Bogart 1981 for an alternative view). Type II is regarded as the first step in the evolution of totally terrestrial development (Heyer 1969; McDiarmid 1978; Crump 1982; Scott and Limerick 1983; Duellman and Trueb 1986). Presumably the ancestors of species with terrestrial development (type III) had life history strategies similar to those of extant type II species (McDiarmid 1978). Most frogs with semi-terrestrial development occur in humid forested regions where aquatic habitats are continuously available (Tihen 1960; Lee 1967).

Several hypotheses have been proposed to explain the evolution of semi-terrestrial development from aquatic development. Terrestrial egg development may decrease the development time in water, and hence reduce mortality due to desiccation (Lee 1967; Crump 1974, 1982; McDiarmid 1978; Duellman and Trueb 1986).

Duellman and Trueb (1986) suggested that anurans evolved the ability to use ephemeral waterbodies as a response to predation on eggs and tadpoles in permanent

---

* *Present address and address for offprint requests:* Department of Zoology, The University of Melbourne, Parkville, Victoria 3052 Australia

waterbodies, even though periodic drying of this temporary environment may have led to increased mortality due to desiccation. Predation on aquatic eggs and larvae has been proposed as an important factor leading to terrestrial oviposition (Lutz 1948; Tihen 1960; Poynton 1964; Martin 1967; Coe 1974; Crump 1974, 1982; McDiarmid 1978; Scott and Limmerick 1983). Downie (1988) presented evidence to suggest that the primary function of the foam nest in *Physalaemus pustulosus* was to isolate eggs from predators. Fish (Noble 1927; Crump 1974; Kluge 1980; Scott and Limmerick 1983), and predacious tadpoles (Crump 1974, 1982; Kluge 1980; Polis and Myers 1985; Downie 1988) have been suggested as important egg predators. Some of these predators have been shown to eat anuran eggs in laboratory experiments (Dunn 1926, 1937; Laessle 1961; Licht 1968, 1969; Heusser 1970; Grubb 1972; Crump 1983; Downie 1988). Aquatic invertebrates are also cited as predators on amphibian eggs (Martin 1967; Crump 1974; Duellman and Trueb 1986); however these authors did not specify which invertebrates they considered important. Predation by leeches (Cory and Marion 1953; Cargo 1960; Licht 1969; Wilbur 1980) and caddis flies (Dalrymple 1970) on amphibian eggs has been documented. Downie (1988) found that odonate nymphs ate eggs of *Physalaemus pustulosus*. Salamanders are known to consume anuran eggs (Licht 1969; Heusser 1971; Walters 1975) but are not common in the humid tropics where most semi-terrestrial development occurs.

Competition has also been suggested as a factor influencing the evolution of terrestrial oviposition (Lutz 1948; Savage 1961; Martin 1967; Coe 1974; Crump 1974, 1982; Duellman and Trueb 1986). Savage (1961) proposed that larvae which hatch as soon as the pond fills will be more advanced in development, and thus competitively superior, by the time those resulting from post-rain breeding have hatched.

Several authors (Alcala 1962; Goin and Goin 1962; Scott and Limerick 1983) have proposed that the predominance of frog species with either semi-terrestrial or totally terrestrial development at high altitudes is due to the physical difficulties of embryonic and larval life in swift streams. Additionally, eggs may be placed terrestrially to avoid waterbodies with unfavourable chemical or physical conditions (e.g., low oxygen, extreme temperatures and low pH).

In this study, the ecological factors presently associated with the local distributions of aquatic and semi-terrestrial development in a community of Amazonian rainforest frogs is investigated. Desiccation, predation, competition and water quality are examined as forces maintaining, and possibly leading to the evolution of, terrestrial egg deposition.

Methods

Study site

The study was carried out in Reserva Florestal Adolfo Ducke (RFAD), a 10 000-ha forestry reserve 25 km northeast of Manaus, Amazonas, Brasil. The vegetation consists of "terra firme" rainforest, a well drained forest not subject to seasonal inundation (Guillaumet 1987). The climate is dominated by distinct wet and dry seasons, most of the rain falling between December and May; the mean annual rainfall for RFAD between 1965 and 1980 was 2362 mm (Marques Filho et al. 1981).

General methods

During this study, we encountered 35 of the 42 species of Anura known to reproduce in primary rainforest in the central Amazon region (Hero 1990). For each species we determined from field observations whether development of eggs and tadpoles occurred in aquatic or terrestrial environments. Egg deposition by frogs of the genus *Leptodactylus* was always terrestrial (with the exception of the *Leptodactylus ocellatus* "group"; Heyer 1969), even though subsequent flooding sometimes resulted in floating foam nests. Eggs develop in the foam nest, and following rains the tadpoles swim into the pond or stream. Therefore, we consider this reproductive mode to be terrestrial oviposition followed by aquatic tadpole development (i.e. semi-terrestrial).

To determine the local distributions of frog species, detailed observations were made on ten ponds (sites A–J) and one section of stream (site L). Sites were located in undisturbed rainforest, and were formed naturally, with the exception of pond J which was formed by wheel ruts on a disused road. Sites were selected to cover the range of habitats available, and contained most of the species with aquatic tadpoles known to occur in the Reserve (Hero 1990).

Eggs were identified either by observing oviposition or by culturing eggs to the tadpole stage, which could then be identified using a key to tadpoles of the central Amazon rainforest (Hero 1990). The 12 waterbodies were visited in daylight hours at approximately weekly intervals and the following observations were recorded: presence or absence of egg/tadpole species, depth of water, presence or absence of potential egg-predators (fish, naiads, aquatic beetles, turtles, snakes, etc.).

To quantify the density and abundance of predators in each habitat, we returned to ponds A–I at night at approximately weekly intervals between January 1986 and November 1987. During night-time visits, the presence or absence of eggs or tadpoles of anuran species and the number, estimated body length and species of suspected predators were recorded. Water temperature and dissolved oxygen levels were measured in each waterbody at approximately 6-week intervals using a YSI model 80 portable dissolved oxygen and temperature meter.

Predation experiments

Anuran eggs were offered to potential predators in controlled experiments. Predators used were species commonly encountered in the waterbodies under investigation and taxa found to eat anuran eggs in previous studies.

Experiments were conducted in the field to minimize differences in temperature and water quality and to minimize transportation effects on predators and eggs. Predator and prey sizes (TL, total body length) were recorded and egg specimens preserved. Freshly collected predators and eggs were used in each experiment. Experiments were done in plastic basins of five colours: red, yellow, blue, cream and grey. Replicates were distributed evenly among colours. Individual predators were placed in a container and left without food for 12 h. Twenty anuran eggs were then added and the number of eggs remaining after 12 h was recorded. The percentage of eggs eaten by the end of each experiment was used as a measure of palatability. Experiments were conducted between 29 March 1985 and 13 May 1989. The numbers of experiments performed with each potential predator is given in Table 3.

Two species of fish (*Aequidens* cf. *tetramerus* and *Pyrrhulina* sp.), odonate naiads (*Gynacanther* sp.), water beetles (Dytiscidae and

Hydrophylidae) and several species of tadpole were tested. Fish were collected by dipnetting the streams at night, and transported to the campsite in plastic bags where they were placed individually in 35 cm by 25 cm rectangular plastic basins with 10 cm depth of water. For *Pyrrhulia* sp. (TL 55–98 mm), eggs of six anuran species were tested in 33 experiments; and for *Aequidens* cf. *tetramerus* (TL 73–143 mm), eggs of three anuran species were tested in 12 experiments (Table 3). These species were chosen because they are common in ponds and streams respectively, and readily eat many species of tadpole in the field and under similar experimental conditions (Hero et al., unpublished).

Odonate naiads (*Gynacanther* sp. TL 33.5–41.0 mm) were dipnetted from a series of ponds along an access road within the rainforest. Individual naiads were placed in round plastic basins of 22 cm diameter, with 6 cm depth of water. Eggs of two anuran species were tested in ten experiments (Table 3).

Water beetles (Dytiscidae and Hydrophylidae, TL 13.4–15.5 mm) were collected from a series of ponds along an access road within the rainforest. Three beetles were placed in round glass jars of 6 cm diameter, with 10 cm of water. For dytiscids, eggs of three species of anuran were tested in 18 experiments; and for Hydrophylids, eggs of one anuran species were tested in two experiments (Table 3).

Tadpoles were collected in various waterbodies throughout the reserve. Ten free-swimming tadpoles (Gosner 1960: stage 25) were placed in round plastic basins of 22 cm diameter, with 6 cm depth of water. Tadpoles of fourteen anuran species were tested in a total of 255 experiments (Table 3).

Variables used in the analyses

The biotic and abiotic characteristics of each waterbody were monitored between August 1985 and November 1987. The data were then summarized for each waterbody in order to test the effects of predator levels (fish, dytiscid beetles and egg-eating tadpoles), potential competition levels (number of sympatric species) and, the physical and chemical characteristics of the water (temperature and dissolved oxygen). The variables used in the analyses are as follows:

1. The percentage of species with terrestrial oviposition per waterbody: the number of species with terrestrial oviposition divided by the total number of tadpole species encountered.
2. Index of fish biomass per waterbody: the mean of the sum of the estimated lengths (cm) of all fish observed on each nocturnal visit.
3. The number of tadpole species encountered in each waterbody.
4. The percentage dry days per waterbody: the percentage of visits that the pond was dry.
5. An index of egg predation pressure in each waterbody: the sum of the percentage of visits when each predator (tadpoles and Dytiscidae) was present multiplied by the mean egg palatability for each predator (mean % of aquatic anuran eggs eaten by that predator in palatability experiments – see Table 4). Other, and perhaps more precise, indices of predation pressure can be formulated, but we retain our *a priori* index to maintain the validity of the statistical tests. There is no reason to believe our index of egg predation pressure would be correlated with any confounding factors.
6. Minimum oxygen level recorded per waterbody.
7. Mean of the water temperatures recorded per visit, per waterbody.

Statistical analysis

We were specifically interested in testing hypotheses relating to predation and the evolution of terrestrial oviposition. For these analyses we used regression analyses and their associated statistical tests (Wilkinson 1986). Due to the years of work necessary to estimate predation pressure and the composition of the tadpole community in each waterbody, it was not possible to obtain sufficient replication to statistically test all possible alternative hypotheses relating to the distribution of terrestrial oviposition. However, we present a matrix of Pearson correlations including all probable confounding variables so that the reader can make sensible decisions as to the possibility of spurious results due to confounding factors. Presenting the level of significance for each correlation in a correlation matrix is statistical nonsense (Wilkinson 1986) but the sample sizes are given so that significance levels may be calculated for any *a priori* hypotheses that may be tested with our data.

Results

Distributions of anuran eggs and tadpoles

Thirty-five anuran species were found to reproduce in rainforest habitat at RFAD (Hero 1990). Of the 25 species with aquatic tadpoles, 18 reproduced in the 12 waterbodies surveyed in this study (Table 1). Of these species, 11 had terrestrial egg-development and 6 had aquatic egg-development. Life-history information on *Chiasmocleis* cf. *ventrimaculata* is lacking, so this species was not included in the analyses.

Waterbody characteristics

The biotic and abiotic characteristics varied greatly among waterbodies, representing a wide range of habitats available to anuran eggs and larvae. Ponds had usually dried by the end of the dry season (August-October) yet the shortest-lived waterbody held water continuously for at least 8 months of the year, and all other waterbodies contained water for at least 9 months of the year (Table 2). Mean water temperatures in the ponds ranged from 23.98 to 25.10° C (Table 2). Dissolved oxygen content was low for all of the pond sites, with the exception of pond B which approached the levels observed in the stream (Table 2).

Distribution of potential egg-predators

The index of egg-predation pressure observed in the waterbodies varied from 635 to 10390 (Table 2). Fish were found in all waterbodies except I and J. The index of fish biomass ranged from 0 to 131.33 (Table 2).

Palatability of anuran eggs

Fish ate few aquatic eggs, yet terrestrial eggs of *Phyllomedusa vaillanti* were readily accepted by *Pyrrhulina* sp. (Table 3). Odonate naiads and hydrophylid beetles ate few eggs (Table 3). The predacious diving beetles (Diticidae), and tadpoles of *Leptodactylus pentadactylus, L. knudseni, L. rhodomystax* and *Osteocephalus taurinus,* ate most eggs offered to them (Table 3). While *Leptodactylus pentadactylus* tadpoles were only found in isolated terrestrial holes (Hero and Galatti 1990), and are thus unlikely to eat eggs of other anuran species, oophagy in this species may be important for survival in a terrestrial

Table 1. Distribution of tadpoles of eight anuran species and two families of water beetle (Dytiscidae / Hydrophylidae) in the 12 waterbodies (A–L) sampled in this study. Each number represents the percentage of visits during which tadpole species were recorded. The * column represents the known oviposition site: terrestrial (T) or aquatic (A)

Species		Waterbody												*
		A	B	C	D	E	F	G	H	I	J	K	L	
Centrolenella oyampiensis	(C o)											59	66	T
Hyla boans	(H b)												29	A
Osteocephalus buckleyi	(O b)												4	A
Hyla granosa	(H gr)			1	2	1								A
H. geographica	(H ge)	56	30	74	66			32	70					A
Phyllomedusa vaillanti	(P v)		5	39	32			6	68					T
P. bicolor	(P b)								38		24			T
Dendrophryniscus minutus	(D m)	6	1	6	6	26	23	3						T
Colostethus marchesianus	(C m)					45	54	47	11	63	5			T
Leptodactylus rhodomystax	(L r)					7	11	9						T
Osteocephalus taurinus	(O t)	11				19	13	15	3	19	4			A
Chiasmocleis cf. *ventrimaculata*	(C v)							10	8					?
Hyla cf. *nana*	(H n)							14						A
Phyllomedusa tomopterna	(P to)									4	84			T
P. tarsius	(P ta)										84			T
Leptodactylus knudseni	(L k)								11		55			T
Epipedobates femoralis	(D f)										40			T
Leptodactylus wagneri	(L w)										4			T
Dytiscidae / Hydrophylidae		9	0	9	0	27	24	14	27	85	69	0	0	

Table 2. Summary of waterbody characteristics (for explanations of variables refer to the Methods section in the text)

Waterbody	% Terr. Ovipos.	Egg Predator Index	Index Fish Biomass	No. Tad. Spp.	% Dry Days	Mean D.O. Conc.	Mean Temp. (°C)
A	33	2680	41.6	3	0	0.925	24.05
B	67	635	131.3	3	0	4.35	24.26
C	50	2079	40.7	4	0	1.34	24.36
D	50	1516	62.5	4	0	5.35	24.33
E	60	4096	9.0	5	22	1.66	24.20
F	75	3759	9.7	4	23	2.03	24.21
G	43	3918	15.0	8	21	0.80	23.98
H	67	4350	25.7	7	21	0.62	24.00
I	67	6172	0	3	40	0.84	25.10
J	88	10390	0	8	0	1.93	24.31
L[a]	33	1322	150	3	0	6.57	24.23

[a] The true index of predation pressure in the stream is several orders of magnitude above the ponds but to avoid having to transform fish densities in all ponds, and an undue influence of site L on the statistical analyses, we arbitrarily set the index of fish biomass at 150

environment where food resources are probably limited. Tadpoles of *Hyla boans* ate 20–100% of eggs offered to them (Table 3). However these tadpoles are normally found on the bottom of streams (pers obs.) and are unlikely to encounter frog eggs. Tadpoles of the remaining species *Colostethus marchesianus Dendrophryniscus minutus, Epipedobates femoralis, Hyla geographica, H. granosa, Phyllomedusa bicolor, P. tarsius, P. tomopterna* and *P. vaillanti* ate few eggs, and are probably not important predators of anuran eggs in this system (Table 3).

Factors Affecting the Distribution of Terrestrial Oviposition

The proportion of species with terrestrial oviposition was significantly ($P=0.027$, adj. $r^2=0.373$) and positively associated with the index of egg predation pressure (Fig. 1) and, significantly ($P=0.033$, adj. $r^2=0.347$) and negatively associated with the log index of fish biomass (Fig. 2).

The index of egg predation pressure was significantly ($P=0.00$, adj. $r^2=0.82$) and negatively associated with the log-index of fish biomass (Fig. 3).

The physical factors mean temperature, dissolved oxygen and % dry days, were not highly correlated with the percentage of species with terrestrial oviposition (Table 4). The number of species per waterbody was highly correlated with the index of egg predation pressure and the index of fish biomass, but was only weakly correlated with the percentage of species with terrestrial oviposition (Table 4). The partial correlation between the percentage of species with terrestrial oviposition and the number of species per waterbody independent of the effect of egg predation pressure was 0.31. The partial

Table 3. Palatability of aquatic and terrestrial anuran eggs to potential predators. Numbers indicate the percentage of eggs consumed after 12 h (rounded to the nearest %) with the number of replications indicated below in brackets ( ). Palatability is expressed as the mean % of aquatic eggs eaten for the experiments with eggs that are aquatic. Blank spaces indicate that no data are available. Abbreviations for anuran species are as in Table 1

Potential	Eggs						Mean Palatability
	Terrestrial		Aquatic				
Predators	*P.v.*	*L.k.*	*H.b.*	*H.ge.*	*O.b.*	*O.t*	
TADPOLES							
Dendrophryniscus minutus						1 (10)	0.5
Colostethus marchesianus			3 (3)	5 (4)			4.3
Epipedobates femoralis				29 (5)			29.0
Hyla boans			20 (11)	100 (5)	55 (1)		45.6
H. geographica	38 (5)		0 (5)	14 (16)	84 (5)	12 (12)	20.9
H. granosa				43 (6)			42.9
Osteocephalus taurinus	73 (10)		98 (10)	96 (10)	100 (5)	100 (9)	98.1
Phyllomedusa bicolor				2 (11)		0 (5)	1.6
P. tarsius				0 (5)		0 (5)	0.0
P. tomopterna				0 (5)		0 (5)	0.0
P. vaillanti	15 (1)		3 (3)			1 (10)	1.5
Leptodactylus knudseni	100 (5)		100 (8)	100 (11)	100 (12)	100 (9)	100.0
L. pentadactylus			96 (5)	93 (5)		95 (5)	94.7
L. rhodomystax		100 (3)		100 (10)			100.0
INSECTS							
Hydrophylidae				3 (2)			2.5
Dytiscidae			39 (4)	40 (4)		64 (4)	47.5
Odonate naiads			6 (5)	18 (5)			12.0
FISH							
Aequidens tetramerus			7 (5)	18 (2)		0 (5)	5.8
Pyrrhulina sp.	100 (3)		0 (11)	0 (7)	0 (9)	3 (6)	0.5

correlation of the percentage of species with terrestrial oviposition and egg predation pressure was 0.51 (independent of the number of species).

Some of the residual variance in the relationship between terrestrial oviposition and egg predation pressure may be due to the influence of other selective pressures. However, most can be attributed to errors in estimating predation pressure, the small number of species (and hence high coefficient of variation in some waterbodies), and unique conditions, unrelated to terrestrial oviposition, in our sample of waterbodies. The clear trend is strong evidence that predation pressure from tadpoles

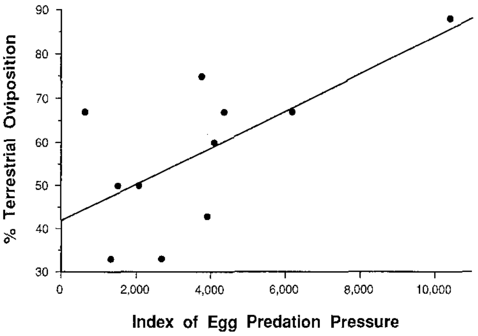

Fig. 1. The relationship between the percentage of species with terrestrial oviposition (*STO*) and the index for egg predation pressure (*EPP*) in each waterbody ($n = 11$ waterbodies). The *line* represents the least squares regression: STO = 41.9 + 0.004 EPP (adj. $r^2 = 0.373$, $P = 0.027$)

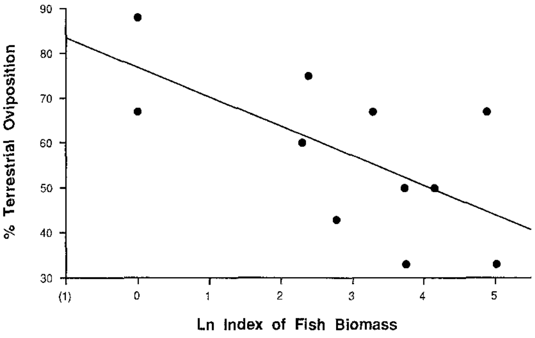

Fig. 2. The relationship between the percentage of species with terrestrial oviposition (*STO*) and the log index of fish biomass for each waterbody ($n = 11$ waterbodies). The *line* represents the least squares regression: STO = 76.8 − 6.6 ln IFB (adj. $r^2 = 0.47$, $P = 0.033$)

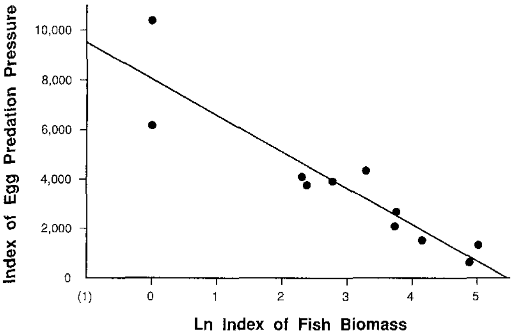

Fig. 3. The relationship between index for egg predators (*EPP*) and the log index of fish biomass ($n = 11$ waterbodies). The *line* represents the least squares regression: EPP = 8038.3 − 1471.9 ln IFB (adj. $r^2 = 0.820$, $P = 0.000$)

Table 4. Matrix of Pearson correlation coefficients for the waterbody characteristics ($n = 11$ waterbodies): STO = % of Species with Terrestrial Oviposition; EPP = Index of Egg Predation Pressure; IFB = Index of Fish Biomass; NOS = Number of anuran Species; DD = % Dry Days; DOC = Dissolved Oxygen Content; and, MT = Mean Temperature

	STO	EPP	IFB	NOS	DD	DOC
EPP	0.660					
IFB	−0.447	−0.700				
NOS	0.356	0.616	−0.512			
DD	0.292	0.320	−0.589	0.128		
DOC	−0.259	−0.496	0.830	−0.424	−0.541	
MT	0.278	0.256	−0.155	−0.409	0.413	−0.012

and dytiscids is a major factor affecting the evolution of terrestrial oviposition in this system.

Discussion

Abiotic waterbody characteristics

The physical characteristics temperature, dissolved oxygen, and the percentage of dry days were not highly correlated with the distribution of aquatic ovipositors, indicating that anurans in this tropical community are able to utilize the wide range of water quality available for egg development.

Drying of ponds has been proposed as a major factor in the evolution of terrestrial oviposition (Lee 1967; Crump 1974, 1982; McDiarmid 1978; Duellman and Trueb 1986), yet in this study, little relationship was found between the percentage of days when a pond was dry and the percentage of terrestrial ovipositors. The most ephemeral pond in this study contained water for over 8 months of the year, which is more than enough time for all the species in this community to complete metamorphosis (observed egg and larval growth periods in this study varied from 6 weeks to 6 months). The lack of a relationship between terrestrial development and the permanence of a pond is not surprising due to the high rainfall experienced in tropical rainforest. Terrestrial oviposition is widespread in the tropics where drying of ponds is probably not an important characteristic of the available waterbodies (Tihen 1960; Lee 1967; Coe 1974; this study). Terrestrial oviposition is probably limited to wet terrestrial environments because desiccation of eggs is not a problem there.

Competition

The number of species using a waterbody was positively associated with the percentage of terrestrial ovipositors, indicating possible competitive interactions. The competition hypothesis was proposed by Savage (1961) for ephemeral ponds where early tadpole arrival may be crucial to avoid desiccation and ensures a competitive advantage over other species. However, most terrestrial oviposition occurs in the humid tropics where desiccation is generally not a critical problem and egg development is rapid. As eggs that develop terrestrially generally take longer to hatch than those laid in water (pers obs.), there is no reason to expect that tadpoles from eggs laid terrestrially would gain a temporal advantage over those laid in water.

Predation

Many tadpoles are known to eat eggs of anurans (Baldauf 1947; Taylor 1954; Heusser 1970; Heyer et al. 1975;

Seale 1980; Waldman 1982; Crump 1983; Polis and Myers 1985; Downie 1988). The tadpoles investigated in many of these studies are obligatory camivores living in isolated waterbodies where alternative food is not available (Crump 1983). In the waterbodies investigated in this study, three species of tadpole were voracious anuran egg-predators (*Leptodactylus knudseni, L. rhodomystax* and *Osteocephalus taurinus)*. Tadpoles of both *L. knudseni* and *O. taurinus* were regularly observed eating anuran eggs in the field, suggesting that predation by tadpoles is an important component of anuran egg mortality in this system.

Predacious diving beetles (Dytiscidae) were also found to be efficient egg predators. We have been unable to find any reference in the literature to these beetles preying on anuran eggs, although they are known to eat tadpoles in other systems (Brodie et al. 1978). Dytiscids commonly occur in ponds without fish (Macan 1974) and are potentially an important group of predators on anuran eggs.

Dragonfly naiads did not eat the anuran eggs offered to them even though they readily ate tadpoles under similar experimental conditions (Hero et al., unpublished). These results are not surprising as naiads are primarily visual and/or tactile predators, and normally consume mobile prey (Pritchard 1965).

The rejection of anuran eggs by fish in this and other studies (Licht 1968; Werschkul and Christensen 1977; Grubb 1972) indicates that fish are not important anuran egg predators. This may not apply to all systems as Licht (1969) reported that eggs of four species of *Rana* and eggs of *Hyla regilla* were readily eaten by stickleback *Gasterosteus aculeatus* and cutthroat trout *Salmo clarkii.* In this study, the terrestrial eggs of *Phyllomedusa vaillanti* were readily eaten by the fish tested, demonstrating that the rejection of aquatic eggs was the result of an active defense mechanism rather than an experimental artifact.

Rejection of anuran eggs by vertebrate predators has been explained by unpalatability (Licht 1968, 1969) and the physical protection of the egg capsule (Grubb 1972). The effects of unpalatable chemicals on invertebrate predators, however, are obscure. Choice tests have clearly demonstrated that invertebrate predators prefer tadpole species without distasteful chemicals to those species that are unpalatable (Formanowicz and Brodie 1982; Formanowicz 1986). However, in a "no choice" situation, odonate naiads ate equal amounts of tadpole species that clearly demonstrated a wide range of palatability for fish predators (Hero et al., unpublished). Dytiscid beetles and predacious tadpoles ate anuran eggs indiscriminately, suggesting that unpalatability of anuran eggs has minimal effects on some predators (dytiscid beetles and tadpoles) but is an important defence mechanisms to deter fish.

Egg predators and the distribution of species with terrestrial oviposition

Predation has been suggested as an important factor in the evolution of terrestrial oviposition. The significant positive relationship between egg predation pressure in each pond and the proportion of frog species with terrestrial oviposition strongly supports the contention that predation by aquatic predators has been a major factor in maintaining, and probably in the evolution of, semi-terrestrial development in this tropical anuran community.

Aquatic oviposition dominated in those waterbodies with high fish biomass. The major tadpole predators of eggs in this system have intermediate to high palatability for fish, and are generally restricted to waterbodies with low fish abundance (Hero et al., unpublished). Egg predation pressure decreased as fish biomass increased, suggesting that fish actually protect the eggs of some anuran species by eliminating their predators, allowing aquatic oviposition to predominate in waterbodies with high fish biomass.

Community ecology

Predation and competition are known to have a major influence on community structure in some systems (Paine 1966; Connell 1975; Wilbur 1987; Sih et al. 1985; Sih 1987; Martin 1988). Morin (1983, 1987), Wilbur (1987) and Alford (1989) have demonstrated the importance of predation in reducing the effects of competition in experimental studies on amphibian larval assemblages, and have emphasized that interactions between predation and competition are a key to understanding community dynamics. However, in many studies it is difficult to distinguish between the effects of competition and predation without rigorous experimentation (Connell 1980; Sih et al. 1985; Wilbur 1987).

Individuals can respond to predators or competitors through "fixed avoidance traits" (Sih et al. 1985; Sih 1987) which can consist of either *habitat selection,* where species use a habitat free of predators/competitors (Petranka 1983; McPeek 1990), or *evolutionary shifts* in life history traits where species can avoid predators/competitors through an inherent aspect of their life history, such as nesting site selection for birds (Martin 1988), or nocturnal drift of stream invertebrates (Allan 1978). Individuals can also respond to the presence of a predator/competitor by short term responses, such as alterations in microhabitat use, activity period, and/or behavioural avoidance (Alford 1986; Morin 1986; Sih 1986, 1987; Semlitsch 1987; Kats et al. 1987).

The diversity of reproductive modes in tropical anuran assemblages is ideal for studying the effects of predation on life history traits. As anuran eggs are unlikely to compete *per se*, we consider that competition is unlikely to be a factor affecting the evolution of reproductive modes in our system. Our results suggest that terrestrial oviposition is a "fixed predator avoidance" trait (Sih 1987).

Acknowledgements. This research was partially funded by grant no. 301299-86/ZO from the Brazilian Conselho Nacional de Desenvolvimento Cientifico e Tecnologico to W.E. Magnusson. We are especially grateful for the support provided by the Instituto National de Pesquisas da Amazonia, Brasil. Jill Windle, Albertina Lima, Neusa Hamada and many people assisted in the fieldwork and we thank them all. Constructive comments on draft manuscripts were gratefully received from C. Catterall, B. Forsberg, R. Cintra, P. Becker, C. Gerhart, B. Pusey, M. Wong, M. Littlejohn and several anonymous reviewers. JMH wishes to thank C. Catterall for her support, encouragement and advice at Griffith University, and A.A. Martin and M.J. Littlejohn for their support at The University of Melbourne, Australia.

References

Alcala AC (1962) Breeding behavior and early development of frogs of Negros, Philippine Islands. Copeia 1962:679–726

Alford RA (1989) Variation in predator phenology affects predator performance and prey community composition. Ecology 70:206–219

Allan JD (1978) Trout predation and the size composition of stream drift. Limnol Oceonogr 23:1231–1237

Baldauf R (1947) *Desmognathus f. fuscus* eating eggs of its own species. Copeia 1947:66

Bogart JP (1981) How many times has terrestrial breeding evolved in anuran amphibians? Monitore Zool Ital XV:23–28

Brodie ED Jr, Formanowicz DR Jr, Brodie ED III (1978) The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. Herpetologica 34:302–306

Cargo DG (1960) Predation of eggs of the spotted salamander, *Ambystoma maculatum*, by the leech, *Acrobdella decora*. Chesapeake Sci 1:119–120

Coe M (1974) Observations on the ecology and breeding biology of the genus *Chiromantis* (Amphibia, Rhacophoridae). J Zool Lond 172:13–34

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Mass., pp 460–490

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138

Cory L, Marion JJ (1953) Predation on eggs of the wood frog, *Rana sylvatica* by leeches. Copeia 1953:66

Crump ML (1974) Reproductive strategies in a tropical anuran community. Univ Kansas Mus Nat Hist Misc Publ 61:1–68

Crump ML (1982) Amphibian reproductive ecology on the community level. In: Scott NJJr (ed) Herpetological communities. Wildl Res Rept No 13, pp 21–36

Crump ML (1983) Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. Am Nat 121:281–287

Dalrymple GH (1970) Caddis fli larvae feeding upon eggs of *Ambystoma t. tigrinum*. Herpetologica 26:128–129

Downie JR (1988) Functions of the foam in the foam-nesting Leptodactylid *Physalaemus pustulosus*. Herp J 1:302–307

Duellman WE, Trueb L (1986) Biology of amphibians. McGraw-Hill, New York Dunn ER (1926) The frogs of Jamaica. Proc Boston Soc Nat Hist 38:111–130

Dunn ER (1937) The amphibian and reptilian fauna of bromeliads in Costa Rica and Panama. Copeia 1937:163–167

Formanowicz DR Jr (1986) Anuran tadpole/aquatic insect predator prey interactions: tadpole size and predator capture success. Herpetologica 42:367–373

Formanowicz DR Jr, Brodie ED Jr (1982) Relative palatabilities of members of a larval amphibian community. Copeia 1982:91–97

Goin CJ (1959) Amphibians, pioneers of terrestrial breeding habits. Annual Smithsonian Report 1959:427–445

Goin OB, Goin CJ (1962) Amphibian eggs and the montane environment. Evolution 16:364–371

Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190

Grubb JC (1972) Differential predation by *Gambusia affinus* on the eggs of seven species of Anuran amphibians. Am Midl Nat 88:102–108

Guillaumet J-L (1987) Some structural and floristic aspects of the forest. Experientia 43:241–251

Hero J-M (1990). An illustrated key to tadpoles occurring in the central Amazon rainforest, Manaus, Amazonas Brasil. Amazoniana 11(2) (in press)

Hero J-M, Galatti U (1990) Characteristics distinguishing *Leptodactylus pentadactylus* and *L. knudseni* in Central Amazon rainforest. J Herpetol 24(2):226–228

Heusser H (1970) Laich-Fressen durch Kaulquappen als mogliche Ursache spezifischer Biotoppraferenzen und kurzer Laichzeiten bei europaischen Frochlurchen (Amphibia, Anura). Oecologia 4:83–88

Heusser H (1971) Differenzierendes Kaulquappen-Fressen durch Molche. Experientia 27:475

Heyer WR (1969) The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution 23:421–428

Heyer WR (1975) A preliminary analysis of the intergeneric relationships of the frog family Leptodactylidae. Smithson Contrib Zool 199:1–54

Heyer WR, McDiarmid RW, Weigmann DL (1975). Tadpoles, predation and pond habitats in the tropics. Biotropica 7:100–111

Kats LB, Petranka JW, Sih A (1988) Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1865–1870

Kluge AG (1980) The life history, social organisation, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. Misc Pub Mus Zool Univ Michigan 160:1–170

Laessle AM (1961) A micro-limnological study of Jamaican bromeliads. Ecology 42:499–517

Lee AK (1967) Studies in Australian amphibia. II Taxonomy, ecology and evolution of the genus *Helioporus* Gray (Anura: Leptodactylidae). Aust J Zool 15:367–439

Licht LE (1968) Unpalatability and toxicity of toad eggs. Herpetologica 24:93–98

Licht LE (1969) Palatability of *Rana* and *Hyla* eggs. Am Midl Nat 82:296–299

Lutz B (1948) Ontogenetic evolution in frogs. Evolution 2:29–39

Lynch JD (1973) The transition from archaic to advanced frogs. In: Vial JL (ed) Evolutionary biology of the anurans. Contemporary research on major problems. University of Missouri Press, Columbia, Missouri, pp 133–182

Macan TT (1974) Freshwater ecology. London, Longmans

Marques Filho AM, Nazare Goes Ribeiro, Menezes dos Santos H, Marden dos Santos J (1981) Estudos climatologicos da Reserva Florestal Ducke- Manaus- Amazonas. IV Precipitacao. Acta Amazonica 11:759–768

Martin AA (1967) Australian life histories: Some evolutionary and ecological aspects. In: Weatherly AH (ed) Australian inland waters and their fauna. Canberra Nat. Univ. Press, Canberra, pp 175–191

Martin TE (1988) Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol. 2:37–50

McDiarmid RW (1978) Evolution of parental care in frogs. In: Burghardt G, Bekoff M (eds) The development of behavior. Garland, New York, pp 127–147

McPeek MA (1990) Determination of species composition in the *Enallagma* Damselfly assemblages of permanent lakes. Ecology 71:83–98

Morin PJ (1983) Predation, competition, and the composition of larval anuran guilds. Ecol Monogr 53:119–138

Morin PJ (1986) Interactions between intraspecific competition and predation in an amphibian predator-prey system. Ecology 67:713–720

Morin PJ (1987) Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. Ecology 68:675–683

Noble BG (1927) The value of life history data in the study of the evolution of the amphibian. Ann NY Acad Sci 30:31–128

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Petranka JW (1983) Fish predation: a factor affecting the distribution of a stream-breeding salamander. Copeia 1983:624–628

Polis GA, Myers CA (1985) A survey of intraspecific predation among reptiles and amphibians. J Herpetol 19:99–107

Poynton JC (1964) Relationships between habitat and terrestrial breeding in amphibians. Evolution 18:131

Pritchard G (1965) Prey capture by dragonfly larvae (Odonata; Anisoptera). Can J Zool 43:271–289

Savage RM (1961) The ecology and life history of the common frog *Rana temporaria temporaria).* Pitman and Sons, London

Scott NJ, Limerick S (1983) Reptiles and amphibians, In: Janzen DH (ed) Costa Rican natural history. Univ Chicago Press, Chicago, pp 351–367

Seale DB (1980) Physical factors influencing oviposition by the wood frog *Rana sylvatica* in Pennsylvania. Copeia 1982:627–635

Semlitsch RD (1987) Interactions between fish and salamander larvae. Costs of predator avoidance or competition? Oecologia 72:481–486

Sih A (1986) Antipredator responses and the perception of danger by mosquito larvae. Ecology 67:434–441

Sih A (1987) Predator and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect effects on aquatic communities. Univ. Press of New England, Hanover, NH, pp 203–224

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Ann Rev Ecol Syst 16:269–311

Taylor EH (1954) Frog-eating tadpoles of *Anotheca coronata* (Steineger) (Salienta, Hylidae). Univ Kansas Sci Bull 36:589–596

Tihen JA (1960) Comments on the origin of the amniote egg. Evolution 14:528–531

Waldman B (1982) Sibling association among schooling toad tadpoles: field evidence and implications. Anim Behav 30:700–713

Walters B (1975) Studies of interspecific predation within an amphibian community. J Herpetol 9:267–279

Werschkul DF, Christensen MT (1977) Differential predation by *Lepomis machrochirus* on the eggs and tadpoles of *Rana.* Herpetologica 33:237–241

Wilbur HM (1980) Complex life cycles. Ann Rev Ecol Syst 11:67–93

Wilbur HM (1987) Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452

Wilkinson L (1986) SYSTAT: The system for statistics. SYSTAT Inc., Evanston IL