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Feeding ecology of the adult Himalayan Salamander *Tylototriton verrucosus* ANDERSON, 1871 (Caudata: Salamandridae)

Nahrungsökologie des adulten Krokodilmolches
Tylototriton verrucosus ANDERSON, 1871
(Caudata: Salamandridae)

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KURZFASSUNG

In der Regenzeit (Juni bis September), in der *Tylototriton verrucosus* ANDERSON, 1871 überwiegend aquatisch lebt und zur Fortpflanzung schreitet, bestand die Nahrung adulter Salamander in Darjeeling (Indien) in beiden Geschlechtern sowohl aus aquatischen als auch terrestrischen Nahrungselementen. Da die Männchen bereits im August und September vermehrt wieder das Land aufsuchen, wiesen sie im Vergleich zu den Weibchen, die länger im Wasser bleiben, eine mehr aus terrestrischen Objekten zusammengesetzte Nahrung auf. Die Nahrung adulter Salamander bestand überwiegend aus unspezialisierten Elementen (Lumbriciden, Dipteren-Larven, Coleopteren-Larven, Lepidopteren-Larven, Odonaten-Larven, adulte Dytisciden, Rhacophoriden-Larven, konspezifische Gelege). Daneben fanden sich spezialisierte Nahrungsobjekte (Rhacophoriden-Schaumnester, Dipteren-Puppen und Lepidopteren-Puppen) sowie sich rasch bewegende terrestrische Invertebraten.

Magenfüllungs-Indices, Nahrungsnischenbreite und -überlappung zwischen den Geschlechtern waren am höchsten während der stärksten Regenperioden, der Zeit größter Primärproduktion und größten Beutedruckes.

ABSTRACT

In Darjeeling (India), *Tylototriton verrucosus* ANDERSON, 1871 lives predominantly aquatic in the monsoon months June through September. During this time of reproduction, the diet of adult male and female salamanders was found to comprise both aquatic and terrestrial elements. Males started to become terrestrial already in August/September and therefore had a more terrestrial diet than females which stayed longer in the water. Adult diet comprised mainly Lumbricidae, larval Diptera, larval Coleoptera, larval Lepidoptera, larval Odonata, adult dytiscid beetles, larval Rhacophoridae and cannibalized eggs while foam nests of Rhacophoridae, Diptera pupae, Lepidoptera pupae and fast moving terrestrial invertebrates were rare.

Digestive tract fill-indices, food niche breadth and niche overlap between sexes, were highest during periods of high rainfall and high primary productivity in the ponds.

KEY WORDS

Tylototriton verrucosus; feeding ecology, behaviour; India, Himalayas

INTRODUCTION

Knowledge on feeding ecology of the Himalayan Salamander, *Tylototriton verrucosus* ANDERSON, 1871 is fragmentary. DASGUPTA (1983) kept adult Salamanders alive in aquaria by feeding them with earthworms and noted (1988) that larval stages of this salamander fed upon microcrustaceans, chironomids, mosquito larvae, and various benthic prey while post-metamorphic juveniles preyed on small bivalves (*Sphaerium indicum*). According to KUZMIN & al. (1994), transition from feeding on endogenous yolk to exogenous diet occurred within stage II (sensu DASGUPTA 1983). Microcrustaceans were absent in the diet of larvae of stage IV and V, although they engorged themselves with aquatic insects and attacked syntopic crabs (*Potamon potamiscus sikkimense*). Adult diet was found to be highly variable depending on the study site. During reproductive peaks, adults preyed on a mixed diet of terrestrial and aquatic components.

The results of further work are presented here in view of the paucity of detailed knowledge on food and feeding habits of *T. verrucosus*, and lack of information on food niche breadth, food electivity and digestive tract fill index in relation to abiotic and biotic environmental factors.

Monsoon rain is the most important abiotic environmental factor in the Indian subcontinent. Amphibians and other amphibious organisms start to deposit eggs with the coming of monsoon rains (MALLICK & al. 1980). The level of primary productivity increases with rainfall and the level of predation pressure on *T. verrucosus* increases with increasing primary productivity (DASGUPTA 1995).

MATERIAL AND METHODS

Material

The present investigations were done from June to September 1994, at two study sites (26°27'10" N/ 87°59'30" E; 27°13' 04" N/ 88°53'00" E), at altitudes of 1350 m and 1200 m a.s.l., respectively, in Darjeeling Himalayas, India.

93 salamander specimens were sampled with the help of a throwing net during the entire study period (June: 42, July: 20; August: 18; September: 13).

Study site

At the head waters of Beltar (a tributary of the Balasone river) an elongated natural depression within the stream channel constitutes a small fluvio-lacustrine basin (5000 m^2) at an altitude of 1350 m. The actual water surface is confined by steep inward facing terraces. The superficial water supply is controlled by first and second order streams and fluctuates throughout the year. Two spring-initiated channels are mainly responsible for perennial water conditions during the dry post-monsoon periods. The second study site (Namthing lake, 1200 m a.s.l., 7700 m^2) is a typical structure of elongated valleys which are the results of faults; the lake is confined by a north and a south facing slope. Rain contributes to the water regime of this natural depression although ground water seepage is the main source of water; there is no natural outlet. With the end of monsoon rains, the water level drops, mainly due to decreasing ground water input. The landform characterized by multi-tiered terraces resulting from tectono-fluvial agencies. Submerged vegetation at both study sites comprise *Poa* sp., and *Hydrocotyle asiatica* while semi-submerged vegetation includes *Polygonum glabrum, P. aula, Cyperus cephalotes, C. rotundus, Scirpus articulatus, Acorus calamus, Cautleya hirta.*

T. verrucosus lives predominantly terrestrial in its non-reproductive period, and aquatic in its reproductive period. During June-July (courtship and egg-laying period) both sexes migrated into the water. In the post-breeding period (August-September) males moved back to land while females stayed in water. As a consequence, males were encountered more often on land, than females in August-September. Females were larger in length than males by 10-20%.

For the present paper, it turned out to be practical to subdivide the four monsoon months into a period of heavy rainfall (June and July, total precipitation in both months was 865 mm) and in a period with light rainfall (August and September, total precipitation in both months was 430 mm).

Methods

S t o m a c h f l u s h i n g. In the field, the broad end of a water filled pipette was inserted into the mouth of *T. verrucosus*. Water was pumped into the stomach by squeezing the rubber bulb gently three times, till the food items were displaced along the sides of the pipette and came to rest in the mouth. There was no overflow of water from the pipette outside the oral cavity. Items so stuck in the mouth and esophagus were removed gently with a pair of blunt forceps. This process was repeated three times for every specimen examined. The efficiency of this method was not checked by comparing its results with that of stomach contents obtained by dissection, because killing of this animal is prohibited in India. Similar methods of amphibian stomach flushing were used successfully in the former Soviet Union following recommendations given by BULAKOV (1976) and PISARENKO & VORONIN (1976). Caudata do not suffer any ill-effects after such stomach flushing (GRIFFITH 1986; JOLY 1987).

The stomach contents were placed on a waxed graph paper for measuring up to the nearest mm, prior to drying, sieving through a dry cheese cloth and weighing in a petri dish on a single pan balance in the field. The sieved sample was then fixed and preserved in 5% neutral formalin as recommended by JOLY (1987).

It was not possible to identify each of these stomach-flushed items up to generic level and so only the family names are mentioned. This is so, as the details of the fauna of the region still remain inadequately explored. E. g., gammarids which are usually common in lentic waters are still unknown from most of these habitats.

Volume of food items was calculated using the formulae described by GRIFFITH (1986). The formula was $2 \pi a b^2$ for cylindrical objects (Lumbricidae, Megascolecidae, adult Hymenoptera, larvae of the orders Diptera, Coleoptera, Trichoptera, Odonata and Ephemeroptera, pupae of Diptera and Lepidoptera, teleost hatchling); $\pi a b c$ for elliptical-cylindrical forms (Orthoptera nymphs, crab legs, Arachnida legs, adult Gastropoda without shells, Isopoda); $(4\pi/3)a^2b$ for oblate spheroid forms (Bivalvia, adult Gastropoda with shells, aquatic Coleoptera, Hemiptera nymphs); and $(4\pi/3)ab^2$ for prolate spheroid forms (eggs of Caudata, larval Anura), where 2a = length, 2b = width, c = depth of the prey item.

Stomach tract-fill index (J) in adults, is given as per mille of the stomach contents' wet weight (m) in the body weight of the salamander (M) without food (KUZMIN 1985, 1986).

$$J = 1000\, m / (M - m)$$

Total body wet weight of salamanders was taken prior to stomach flushing.

Food niche breadth (A) was calculated according to the methods of LEVINS (1968) by the formula

$$A = 1 / \sum (p_{xi})^2$$

where p_{xi} = percentage of the i-th component in the diet of predator species x (*T. verrucosus*). $[1 \leq A \leq +\infty]$

Food niche overlap: The method of SCHOENER (1970) was used to calculate food niche overlap between sexes by the formula

$$C_O = 1 - [0.5 \sum (p_{xi} - p_{yi})]$$

where p_{ix}, p_{iy} = percentage of the i-th component in the diet of predator species x (male) and y (female), respectively. $[0 \leq C_O \leq 1]$

Sampling of available food. The above methods for calculation of food niche breadth, food niche overlap and food electivity were selected, as it was not practical to estimate the abundance of terrestrial prey items.

For determination of food electivity, food available in ponds was sampled with a playwood box with open ends, $1 m^2$ in size. The box was placed gently at twelve stations (six along the water edge, six in the middle of the lake) with minimum disturbance of the water. All larger animals encountered were scooped out with a tea strainer (72 meshes $/cm^2$) and preserved in 5% neutral formalin.

Food electivity. The method of IVLEV (1961) was used to assess food electivity (E) for aquatic prey items by the formula

$$E = (r_i - p_i) / (r_i + p_i)$$

where r_i = percentage of the i-th prey component in the diet and p_i = percentage of the i-th prey component in the environment (water body). $[-1 \leq E \leq +1]$

This method indicates differences between relative frequency of prey categories in a predator's diet and that in the environment by giving clearer upper and lower limits as compared to the electivity index of STRAUSS (1979).

Primary productivity. The method followed for the estimation of primary productivity (P) was the light and dark bottle method recommended by SANTANAM & al. (1989). Primary productivity was estimated by measuring the amounts of dissolved oxygen (DO) in two 250 ml reagent bottles. One of these bottles was dark and the other was transparent. The difference in DO between the transparent and dark bottle was used to estimate primary productivity (P) by converting the observed difference (A) to the equivalent of inorganic carbon that had been incorporated as organic carbon by multiplying with 0.375. This carbon equivalent was divided by the product of the photosynthetic quotient (PQ=1.2) and the period in hours (t) for which the bottle was kept

Table 1: Percentages of taxonomic categories according to number (n) and volume (v) found in stomachs of adult *Tylototriton verrucosus* during the monsoon months June through September. T - terrestrial taxa, A - aquatic taxa, (1) - legs only, (2) - hatchling, (3) -slough, (4) - eggs.

Tab. 1: Prozentueller Anteil verschiedener Taxa hinsichtlich Anzahl (n) und Volumen (v) am Mageninhalt adulter *Tylototriton verrucosus* während der Monsunmonate Juni bis September. T - terrestrischeTaxa, A - aquatische Taxa, (1) -nur Extremitäten, (2) -Schlüpfling, (3) -Häutung, (4) -Laich.

	Taxon			% (n)	% (v)
T	Gastropoda	Stylommatophora	Arionidae	1.12	0.42
T		Stylommatophora indet.		0.56	10.83
T	Clitellata	Oligochaeta	Lumbricidae	3.35	4.53
T			Megascolecidae	1.12	1.01
T	Crustacea	Isopoda	Oniscidae	0.56	0.49
T	Arachnida (1)	Araneae	Tetragnathidae	1.12	0.13
T			Cyclosidae	0.56	0.03
T			Theridiidae	0.56	0.03
T	Insecta	Orthoptera	Gryllidae	1.67	0.57
T			Tettigoniidae	0.56	0.06
T		Diptera (larvae)	Drosophilidae	4.46	0.03
T			Sciaridae	3.35	0.02
T			Tephritidae	3.91	0.03
T			Lonchopteridae	3.91	0.03
T			Phoridae	1.68	0.01
T			Asilidae	1.12	0.01
T		Diptera (pupae) indet.		1.12	0.01
T		Hymenoptera (imagines)	Braconidae	0.56	0.06
T			Formicidae	0.56	0.01
T		Coleoptera (imagines)	Lagriidae	0.56	0.08
T		Lepidoptera (larvae)	Bombycidae	2.23	2.36
T			Noctuidae	2.24	6.68
T			Saturniidae	2.23	7.00
T		Lepidoptera (pupae)	Satyridae	1.12	11.50
A	Bivalvia	Eulamellibranchiata	Euglesiidae, Pisidiidae	0.56	1.39
A	Crustacea (1)	Decapoda	Potamonidae	5.59	6.29
A	Insecta	Diptera (imagines)	Syrphidae	1.67	1.17
A			Tabanidae	1.12	0.38
A			Tipulidae	0.56	0.03
A			Chironomidae	9.50	1.38
A			Culicidae	7.82	0.44
A			Chaoboridae	0.56	0.01
A			Dolichopodidae	4.47	0.25
A			Ephydridae	2.23	0.28
A			Ceratopogonidae	2.79	0.04
A		Trichoptera (imagines)	Phryganeidae	4.47	0.50
A		Odonata (larvae)	Aeshnidae	1.68	0.49
A			Gomphidae	2.23	0.15
A			Pseudagrionidae	1.12	0.79
A			Crocothemidae	1.10	0.79
A		Coleoptera (larvae)	Dytiscidae	1.12	0.19
A		Coleoptera (imagines)	Gyrinidae	0.56	0.33
A			Laccophilidae	1.12	0.45
A			Hydaticidae	1.79	0.69
A			Dytiscidae	1.00	0.19
A	Osteichthyes	Teleostei	Siluridae (2)	0.56	0.03
A	Amphibia	Anura (larvae)	Rhacophoridae	4.47	36.78
A		Urodela	*T. verrucosus* (3)	0.56	0.00
A			*T. verrucosus* (4)	1.12	0.04

Table 2: Percentages of terrestrial (TERR.) and aquatic (AQUAT.) food components in adult male (M) and female (F) *Tylototriton verrucosus* during the monsoon months June through September. SPEARMAN rank correlation between % numbers (%n) and % volumes (%v) of prey items was significant ($p<0.001$, $n=14$) in all cases. Differences in diet between males and females during monsoons were significant (KRUSKAL-WALLIS ANOVA: $p<0.001$, $n=14$)

Tab. 2: Prozentanteile terrestrischer (TERR.) and aquatischer (AQUAT.) Nahrungskomponenten bei adulten Männchen (M) and Weibchen (F) von *Tylototriton verrucosus* während der Monsunmonate Juni bis September. SPEARMAN Rangkorrelation zwischen % Anzahl (%n) und % Volumen (%v) der Nahrungsobjekte war in allen Fällen signifikant ($p<0.001$, $n=14$). Die Unterschiede in der Nahrungszusammensetzung bei Männchen und Weibchen während der Monsunmonate waren signifikant (KRUSKAL-WALLIS ANOVA: $p<0.001$, $n=14$).

Month/Monat	Sex	TERR.		AQUAT.	
		% n	% v	% n	% v
June/Juni	M	26.58	33.18	73.42	66.82
	F	26.54	33.20	73.46	66.80
July/Juli	M	1.03	3.57	98.97	96.43
	F	0.00	0.00	100.00	100.00
August	M	67.86	57.01	32.14	42.99
	F	30.34	41.51	69.66	58.49
September	M	85.26	91.66	14.74	8.34
	F	0.00	0.00	100.00	100.00

submerged at that time of measurement (i. e., 2 hours). The photosynthetic quotient is the proportion involving the amount of carbon uptake to the equivalent amount of oxygen discharged during the process of photosynthesis. Primary productivity has been expressed as mg-carbon/litre/hour.

$$P=A * 0.375 / PQ * t$$

Predation pressure (PP) was estimated as a proportion involving the number of predators of *T. verrucosus* eggs and larvae to the actual number of eggs and larvae of *T. verrucosus* present in each m^2. Predators belonging to different taxa have been assumed to be equivalent predators.

$$PP= \frac{No.Prd./m^2}{No.Pry./m^2}$$

where No.Prd. = number of aquatic predators (invertebrates + vertebrates), No. Pry. = number of juveniles and eggs of *T. verrucosus*.

In a rather unconventional way and as a rough approach, it was tried to estimate predation pressure against adult salamanders by using the formula

$$PP= \frac{No.Prd./hr}{No.ad.Pry/hr}$$

where No.Prd./hr=number of snakes (*Oligodon arnensis*) caught in an hour by 240 villagers; No.ad.Pry./hr = number of adult salamanders caught by a throwing net.

Statistics. A Kruskal-Wallis ANOVA was performed to detect differences in the diet of adults during the monsoons, comparing the stomach flushes with the samples from the water bodies. Spearman rank correlation coefficient was determined between numbers and volumes of food items of the stomach-flushed material each month during the monsoons. Nonparametric tests like this, were performed due to non-occurrence of normal distribution and small sample size ($n=14$).

Table 3: Comparison of mean stomach-fill indices [J ($\bar{x}$)] for adult male (M) and female (F) *Tylototriton verrucosus* during the monsoon months June through September. SD - standard deviation.

Tab 3: Vergleich der mittleren Magenfüllungs-Indices [J ($\bar{x}$)] von adulten Männchen (M) und Weibchen (F) von *Tylototriton verrucosus* während der Monsunmonate Juni bis September. SD - Standardabweichung.

Month/Monat	Sex	n	J ($\bar{x}$)	SD
June/Juni	M	12	43	0.36
	F	30	48	0.39
July/Juli	M	4	43	0.59
	F	16	46	0.34
August	M	4	25	0.42
	F	13	16	0.18
September	M	4	24	0.37
	F	9	13	0.64

Table 4: Food niche breadth (A) in adult male (M) and female (F) *Tylototriton verrucosus* calculated according to LEVINS (1964), based on number (n) and volume (v) of prey items.

Tab 4: Nahrungsnischenbreite (A) bei adulten Männchen (M) und Weibchen (F) von *Tylototriton verrucosus* auf Grundlage der Anzahl (n) und des Volumens (v) der Nahrungsobjekte; berechnet nach der Methode von LEVINS (1964).

Month/Monat	Sex	A (n)	A (v)
June/Juni	M	0.052	0.053
	F	0.055	0.056
July/Juli	M	0.052	0.053
	F	0.055	0.056
August	M	0.030	0.033
	F	0.031	0.034
September	M	0.015	0.016
	F	0.016	0.018

Table 5: Food niche overlap between sexes (C_O) of adult *Tylototriton verrucosus*, according to number [C_O (n)] and volume [C_O (v)] of food items, during the monsoon months June through September. Indices calculated according to SCHOENER (1970).

Tab 5: Überlappung der Nahrungsnischen der Geschlechter (C_O) bei adulten *Tylototriton verrucosus* auf Grundlage der Anzahl [C_O (n)] und des Volumens [C_O (v)] der Nahrungsobjekte, während der Monsunmonate Juni bis September; berechnet nach der Methode von SCHOENER (1970).

Month/Monat	C_O (n)	C_O (v)
June/Juni	0.6962	0.6319
July/Juli	0.3481	0.1265
August	0.0201	0.0196
September	0.0201	0.0201

RESULTS

Primary productivity

Primary productivity was high (maximum 26.23 mg/l/hr) during June and July (rainfall 582 mm and 283 mm, respectively) at 1350 m. With progress of monsoons, a decline in primary productivity (maximum 24.32 mg/l/hr) in August and September (rainfall 222 mm and 208 mm, respectively) was recorded at 1350 m. At 1200 m, the highest levels of primary productivity recorded were 26.23 mg/l/hr for June-July and 26.00/l/hr for August-September.

Food during different months of the monsoon period (tables 1 & 2)

In the monsoon period, food items obtained by stomach flushing comprised both aquatic and terrestrial elements; planctonic crustaceans and other microarthropods were absent in the stomach-flushed material. Aquatic prey taxa predominated in the stomachs during times of heavy rainfall (June-July), and concomitant high levels of primary productivity.

During periods of low rainfall (end of monsoon rains, August-September), terrestrial prey taxa predominated in the stomach-flushed samples obtained from males and aquatic prey taxa in that obtained from females. Compared to the females' diet, the diet of males was more terrestrial at any time and included Lepidoptera (larvae and pupae of Noctuidae, Saturnidae, Bombycidae) and larval Diptera. Food of females included rhacophorid foam nests.

In males, diet was mainly aquatic in June, almost exclusively aquatic in July, mainly terrestrial in August and predominantly terrestrial in September. In females, diet was mainly aquatic in June, exclusively aquatic in July, predominantly aquatic in August and exclusively aquatic in September.

Differences in the bulk, number and composition of the diet during different months of the rainy season was significant ($P<0.001$; Kruskal-Wallis ANOVA).

Stomach-fill index (table 3)

Stomach-fill indices were highest during periods of heavy rainfall (June: 43-48 ‰; July: 43-46‰) and subsequent high levels of primary productivity. Stomach-

Table 6: Predation pressure (PP) on adults, eggs and larvae of *Tylototriton verrucosus* in the monsoon months June through September.

Tab 6: Beutedruck (PP) auf adulte, Eier und Larven von *Tylototriton verrucosus* in den Monsunmonaten Juni bis September.

Stage/Stadium	PP			
	June / Juni	July / Juli	August	September
Adults/Adulte	0.05	0.03	0.00	0.00
Ova + Larvae	0.17	0.05	0.03	0.03

fill indices were lower when rainfall was low (August: 16-25 ‰; September: 13-24 ‰). Females had higher stomach-fill indices than males during the egg-laying period (June-July), males had higher stomach-fill indices than females during the post-reproductive period (August-September.

Food niche breadth (table 4)

Food niche breadth was largely the same in males and females. Indices were twice as high in August and September than in June and July. During the post-reproductive period (August-September) females were mostly sampled from water and males from land.

Food niche overlap between sexes (table 5)

Food niche overlap between sexes (Co) was clearly expressed during reproductive peaks when both sexes were in the water (June-July, beginning of strong monsoon rains, high primary productivity).

Overlap in diet was almost absent during August-September (periods of low rainfall) in the post-reproductive period when males were leaving or had already left the water and primary productivity was low.

Predation pressure (table 6)

Predation pressure on adults, eggs and larvae of *T. verrucosus* varied seasonally. Predation pressure decreased from June through September in response to gradual lowering of primary productivity and rainfall with progress of monsoons.

Food niche overlap and breadth, stomach-fill index, and their relation to rainfall and primary productivity (table 7)

Stomach-fill indices, food niche overlap and breadth between sexes were highest during periods of heavy rainfall, coinciding with the time of oviposition, high level of primary productivity and high predation pressure.

Food electivity (table 8)

Despite the great abundance of *T. verrucosus* eggs in the ponds during June and July, conspecific eggs contributed only very little (1.12 %, negative electivity indices) to the female stomach contents and were never found in males. A teleost hatchling (*Neomacheilus* sp.) was detected in the stomach of a female in June (period of maximum rainfall) (table 1).

In June, aquatic dipterous larvae (Chironomidae, Culicidae, Chaoboridae, Tabanidae, Tipulidae, Syrphidae) and larval Anura were present in the stomach contents, while aquatic Coleoptera, Bivalvia, Trichoptera and Odonata nymphs were absent. Cannibalized eggs were obtained only from female stomachs.

In July, Odonata nymphs (Aeshnidae, Gomphidae, Pseudagrionidae, Crocothemidae), Chironomidae, Tipulidae, Culicidae, Chaoboridae, adult aquatic Coleoptera (Dytiscidae, Hydaticidae, Laccophilidae, Gyrinidae), and larval Anura were the dominating prey taxa in the stomach contents, while larval Tabanidae and Syrphidae were absent.

In August, Phryganeidae (Trichoptera), Tabanidae, Syrphidae, and other larval Diptera, Odonata nymphs, larval Anura, adult and larval Dytiscidae were present in the stomach flushes while Tipulidae were not detected.

In September, Tabanidae, Syrphidae, Bivalvia, adult aquatic Coleoptera, and Odonata nymphs dominated in stomach-flushed samples, whereas Chironomidae, Culicidae, Chaoboridae, Tipulidae, and larval Anura were absent.

Differences in food electivity values by numbers and volumes are due to variation in the relative size and proportion of individual food items at different altitudes during different monsoon periods. This is reflective of differences in trophic structure and spatial distribution of the prey at different altitudes during different monsoon months.

Food quantity (table 9)

There were clear differences between months concerning the mean quantity of food found in the stomachs of adult *T. ver-*

Table 7: Relation between rainfall, food niche breadth (A), food niche overlap (C_O), stomach fill index (J), primary productivity (P) and predation pressure (PP) in adult *Tylotriton verrucosus* at 1350 m altitude in the monsoon months June through September.

Tab. 7: Beziehung zwischen Niederschlagsmenge, Nahrungsnischenbreite (A), und -überlappung (C_O), Magenfüllungsindex (J), Primärproduktion (P) und Beutedruck (PP) bei adulten *Tylotriton verrucosus* an einem Fuindort in 1350 m Höhe während der Monsunmonate Juni bis September.

Month/Monat	Rain/Regen (mm)	A	C_O	J	P	PP
June/Juni	582	0.055	0.696	0.91	26.23	0.17
July/Juli	283	0.052	0.348	0.89	26.00	0.05
August	222	0.031	0.020	0.41	24.44	0.03
September	208	0.016	0.020	0.37	24.32	0.03

Table 8: Food electivity (E) in male (M) and female (F) *Tylototriton verrucosus*, in the monsoon months June through September. Electivity indices are calculated according to IVLEV (1961) and given as E∗100 to reduce the number of decimal scores. A slash separates electivity indices based on food item number (left) and food item volume (right).

Tab. 8: Nahrungselektivität (E) bei Männchen (M) und Weibchen (F) von *Tylototriton verrucosus* in den Monsunmonaten Juni bis September. Elektivitätsindices berechnet nach der Methode von IVLEV (1961) und in der Form von E∗100 angegeben, um die Anzahl der Dezimalstellen zu verringern. Schrägstriche trennen die Indices, die auf Grundlage von Anzahl (links) und Volumen (rechts) der Nahrungsobjekte berechnet wurden.

	June/Juni		July/Juli		August		September	
Taxon	F	M	F	M	F	M	F	M
Bivalvia	-	-	-	-	-	-	66/54.4	-
larval Chironomidae	88/97.8	72/97.1	87/92.5	81/94.6	89/77	88/77	-	-
larval Culicidae	78/99.8	63/99.1	73/99.7	75/99.8	78/99.7	76/99.7	-	-
larval Chaoboridae	90/93.2	96/97.5	97/97.9	95/94.1	98/97.3	97/96.5	-	-
larval Tabanidae	95/98.2	92/96.2	-	-	94/96.3	93/63.3	-	92/95.2
larval Tipulidae	69/17	33/1	50/16	25/2	-	-	-	-
larval Syrphidae	90/93.9	37/85.6	-	-	88/92.2	86/91.2	98/97.4	96/85.2
larval Phryganeidae	-	-	34/41	32/42.6	31/32.4	23/39.8	-	-
larval Odonata 1)	-	-	44/88.2	38/94	10/60	10/60	28/57	7/78
larval Dytiscidae	-	-	-	-	-	64/65	-	-
adult aquat. Coleoptera 2)	-	-	38/97	36/83.5	29/85	29/83.3	2/95	22/94.9
eggs (*T. verrucosus*)	-33/-12.6	-	-30/-13.6	-	-	-	-	-
larval Anura (mostly Rhacophoridae)	57/61.1	64/73	80/75.3	73/79.2	81/66.1	40/79.4	-	-

1) - Aeshnidae, Gomphidae, Pseudagrionidae, Crocothemidae.
2) - Dytiscidae, Hydaticidae, Laccophilidae, Gyrinidae.

Table 9: Mean food wet weight (gr) in the stomachs of adult *Tylototriton verrucosus* in the monsoon months June through September, with data on specialized food items. n - sample size; SD - standard deviation.

Tab. 9: Mittleres Naßgewicht der Nahrung (g) in Mägen adulter *Tylototriton verrucosus* in den Monsunmonaten Juni bis September, mit Angaben zu spezialisierten Nahrungsobjekten. n - Stichprobenumfang; SD - Standardabweichung.

Month/Monat	n	Food weight (gr) Gewicht der Nahrung (g)		Specialized food items found in n adults Spezialisierte Nahrung bei n Adulten		
		mean/Mittel	SD	foam nest pieces Teile von Schaumnestern	Lepidoptera pupae	Diptera pupae
June/Juni	42	13.53	5.23	12	9	6
July/Juli	20	12.83	0.94	2	4	2
August	18	10.56	0.87	1	-	-
September	13	6.00	0.61	-	-	-

rucosus (P< 0.0001; Kruskal-Wallis ANOVA) indicating increased food ingestion by both sexes during the reproductive period in June and July.

DISCUSSION

Diversity of food items

SATTMANN (1989) found that the diet of *Triturus alpestris* comprised aquatic and terrestrial prey. The diet was predominantly aquatic during the aquatic breeding phase of this newt. Towards the end of its reproductive period, food became increasingly composed of terrestrial prey, especially in males. He further noted negative food electivity indices for cannibalized eggs.

As was found earlier as well as in the present study, the diet of adult *T. verrucosus* comprised both aquatic and terrestrial elements. In stomach contents at different habitats in Darjeeling, KUZMIN & al. (1994) found Lumbricidae (16.7% - 85.7%), Chironomidae (*Cryptochironomus* and *Tanytarsus*, 17.7% - 95.2%), aquatic Diptera other than Chironomidae (7.1% - 66.7%), imagines of Hydrophilidae (19% - 25%), terrestrial gastropods (16.7%), and eggs of Amphibia (25% - 66.7%). Terrestrial prey items included larval Diptera. Furthermore, these authors mentioned the presence of low percentages of puparia of aquatic Diptera (4.8%), larval *T. verrucosus* of 13 mm SVL (4.8%), shed skin of *T. verrucosus* (4.8%) and anuran larvae (11.8%). They further reported on larval *T. verrucosus* attacking syntopic crabs (*Potamon potamiscus sikkimense*).

Arthropod remains obtained from stomach flushed material during the present study additionally comprised Oniscidae, Drosophilidae, Sciaridae; Tephritidae, Lonchopteridae, Asilidae, Phoridae, Lagriidae, Bombycidae, Noctuidae and Saturniidae. Crabs were not likely to be swallowed entirely, since only crab legs (*Potamon potamiscus sikkimense*) were flushed from the stomachs of *T. verrucosus*. Mollusk remains included Arionidae and other Stylommatophora.

A hatchling of *Neomacheilus* sp. obtained from stomach flushed material during the present study represents an unusual instance of ingestion of a lotic organism by a lentic caudate; possibly after the former had either accidentally strayed or drifted (monsoon rain) from an adjoining stream into the lentic habitat occupied by the adult *T. verrucosus* during its breeding period. There appears to be no earlier record of *T. verrucosus* feeding on teleost hatchlings.

Different sensory systems in larvae and adults used for prey detection resulted in selection for larger objects in the latter (KUZMIN 1986). Small prey items (microarthropods) were absent from the diet of adult *T. verrucosus* (KUZMIN & al. 1994; this paper) but occurred in the diet of larvae and metamorphs (KUZMIN & al. 1994). Adults may ingest such items accidenally.

According to KUZMIN (1991), stomach contents of caudate amphibians did not only allow for indication of the local invertebrate fauna but also served as an estimator of its spatial distribution. The results of stomach flushes obtained from the present study have added Tephritidae (Diptera) to the faunal list of the study site. The absence of gammarids in stomach contents in the previous (KUZMIN & al. 1994) and in the present study, suggests that Gammarids might not occur in the habitats under study.

Sex-specific oophagy

There is a number of observations published concerning oophagy in salamanders: Intrauterine cannibalism of the oophagous type viz., epitheliophagy and adelphophagy of *Salamandra s. terrestris* embryos was thought to be responsible for deposition of larger but fewer young by females of this species at higher altitudes as compared to females from the foothills (JOLY 1961). WOOD & GOODWIN (1954) reported on *Notophthalmus viridescens* feeding on conspecific eggs; larval and adult *N. viridescens* and larval *Ambystoma opacum* fed on eggs of several anuran and caudate species (WALTERS 1975); KAPLAN & SHERMAN (1980) recorded *Taricha* preying on conspecific eggs, and KUZMIN & al. (1994) reported on egg cannibalism in *T. verrucosus*. According to DUELLMAN & TRUEB (1986), newt eggs are hidden singly or in clumps amidst aquatic vegetation because adults are known to consume eggs with moving embryos. Salamanders which guard their clutches do not forage actively during this time, nevertheless, eggs could serve as an important energy source for these adults (HARRIS & GILL 1980; POLIS & MYERS 1985; SOLANO 1987). Attending female *Desmognathus ochrophaeus* fed on dead or infected eggs from their clutches (FORESTER 1979, 1986). Oophagy in newts was considered indiscriminate cannibalism (DUELLMAN & TRUEB 1986) because individuals may not recognize their own eggs. The same authority considered preying on conspecific eggs to represent just exploitation of an available food resource. Amongst Dendrobatidae, feeding on eggs laid by other females was interpreted as an example of competition (SUMMERS 1989). MARSHALL & al. (1990) reported that only males cannibalized eggs in *Bombina orientalis* and only females in case of *Taricha torosa*. KUZMIN (1989, 1991a) listed 59 amphibian species that were oophagous and noted (1991a) that cannibalism was a simple manifestation of polyphagy.

In the present study, only female *T. verrucosus* cannibalized eggs. Detection of cannibalized eggs in females at times of high levels of food availibility (June, July) suggests that oophagy in this species was not a consequence of depletion of food resources. The high abundance of eggs appeared to have induced oophagy. Thus, oophagy in case of this species is in accordance with the optimal foraging theory: the electivity of polyphages increases in step with improvement in feeding conditions.

Food niche breadth and overlap

There appears to be little divergence in the diet between sexes which is not uncommon and is known in case of some species of *Triturus*, where male-female diet overlap is sometimes high. According to GRIFFITHS (1987) a high degree of food niche overlap is known to occur e.g. between *Triturus vulgaris* and *Triturus helveticus* and such co-existence between species with nearly identical food niches is explained by unlimited food resources or extremely high rates of predation.

Female *T. verrucosus* were larger in length than males by 10-20%. So it is not surprising that different sexes actually consumed prey of different mean size and quantity.

Stomach-fill index

In both sexes, stomach fill indices were higher in June-July (period of heaviest rainfall and highest levels of primary productivity) than in the post-breeding period (August-September).

Males had lower stomach fill indices throughout the breeding period (June-July) and higher stomach fill indices during the post-breeding period (August-September), as compared to the females. This may be explained by the females' higher reproductive expenses in June-July (KUZMIN 1989a) and by the males' more terrestrial life in August-September.

During the post-breeding period till hatching of the young, the females apparently did not forage actively.

Prey composition in relation to precipitation

Seasonal differences in diet reflect prey availibility and selectivity (TOFT 1985).

In adult *T. verrucosus*, stomach-fill indices, food niche breadth and overlap between sexes were highest, largest and widest respectively, during the peaks of rainfall, primary productivity and predation-pressure, thus, coinciding with the breeding period in June-July when both sexes migrated into the water.

In the post-breeding period (August-September), males moved away from the water. This was reflected in their having a more terrestrial diet than females.

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