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Sympatric Amphibians of the Yew-box Grove, Caucasian State Biosphere Reserve, Sochi, Russia

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Abstract.-The Yew-box Grove of the Caucasian State Biosphere Reserve is home to seven species of amphibian. These species occur in a wide range of aquatic environments. The species composition, physical characteristics and history of each aquatic site was evaluated. The reproductive biology and food habits of each species was studied. These amphibians divide their niches on daily activity, seasonal activity, breeding site, microhabitat and food habits. The highest amphibian diversity and species overlap occurs in the most stable aquatic environments.

Key Words: Amphibia, Russia, Caucasus, ecology.

Introduction

It is important when studying the influence of environmental factors on life history characteristics to distinguish those factors that are significant and those that are part of the "neutral background" (Monchadsky, 1958). The study of environmental influences is accomplished on sympatric species, usually closely related species (Orr and Maple, 1978; Ananjeva, 1981) at the population level (Pianka, 1973; Schoener, 1974; Schoener, 1977; Lyapkov and Severtsev, 1981). This is the study of the ecological niche (Pianka, et al., 1979.

In the former Soviet Union one of the areas of highest amphibian diversity is found in the western Caucuses. The Yew-box Grove of the Caucasian State Biosphere Reserve is inhabited by eight amphibian species: *Triturus vulgaris lantzi, T. cristatus karelini, T. vittatus ophryticus, Pelodytes caucasicus, Bufo verrucosissimus, Hyla arborea schelkownikowi, Rana ridibunda,* and *R. macrocnemis.*

Methods

Field studies were conducted from 1980-1982 in the Yew-box Grove (approximate area 302 ha) in the Caucasian State Biosphere Reserve and on adjacent land. Transect routes and study sites were selected on the basis of local forest typography (Gulisashvili, et al., 1975). Observations on these study sites along the transects were made throughout the year (Fig. 1). The intensity of calls was recorded in spring (2-3 times per week), summer (1-2 times per month) and fall (2-3 times per week). Over 200 individuals were recorded.

FIG. 1. Study sites of sympatric amphibians in the Yew-box Grove, Caucasian State Biosphere Reserve. 1- Spring 118; 2- Opolznevaya Ravine; 3- Labirintovaya Ravine; 4- Glubokaya Ravine; 5- Khosta River; 6- Samshit Pond; 7- Pond on Malaya Khosta River.

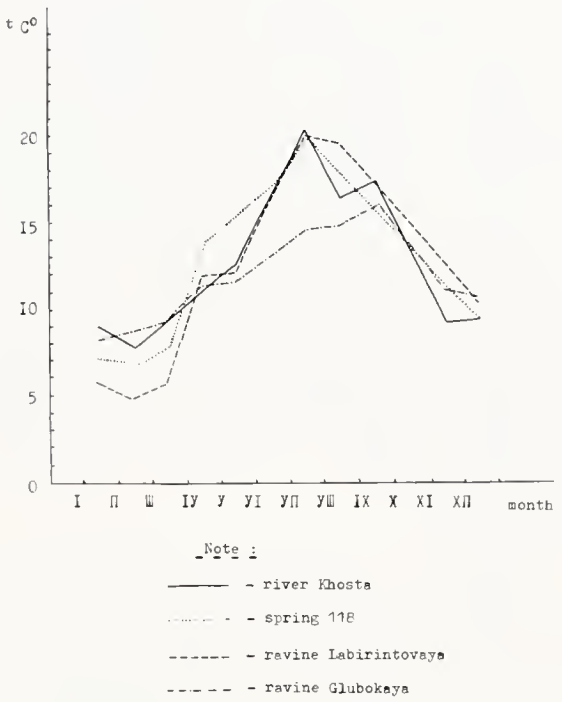

FIG. 2. Mean monthly temperatures of perennial bodies of water in the Yew-box Grove (1980-1982).

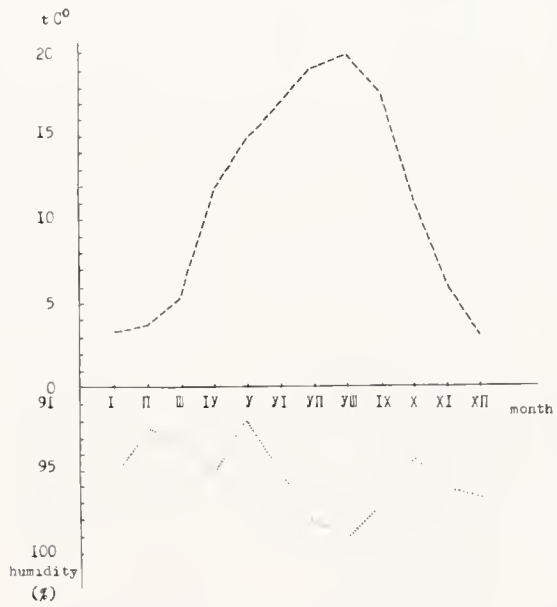

FIG. 3. Climatram of the Yew-box Grove (1982).

The location, weather conditions, air and body temperature, and behavior of each specimen was recorded. During 1982, detailed microclimate records were made in

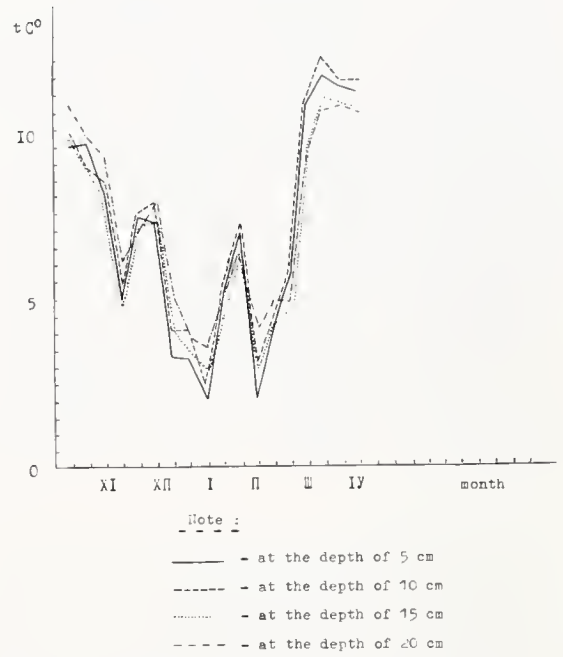

FIG. 4. Winter soil temperature in the Yew-Box Grove (1982-1983).

the Yew-box Grove (Fig. 2). Air temperature and humidity above the surface were recorded weekly by a thermograph (M-16AN) and a hydrograph (M-16AN) placed in a meteorological kiosk (Fig. 3). Soil temperatures were recorded at 5, 10, 15 and 20 cm depths (Fig. 4).

Water samples were taken periodically for chemical analysis by established methods (Anonymous, 1978). Ambient light was measured with a light meter and converted into percent relative illumination. Climagrams were made (Formozov, 1934).

Species composition of each biotope was calculated using conventional methods (Kashkarov, 1927; Dinesman and Kaletskaya, 1952). Food habits were studied using non-lethal methods (Verzhutsky and Zhuravlev, 1977).

Results

Description of Study Sites

Study Site 1. Spring 118. This site contains a small perennial stream running

TABLE 1. Some hydrochemical indices of the study sites.

Sample site	pH	ions, total	total hardness		nitrogen		mineral
No. of samples	Mean	mg/l	mg-equiv/l	ammonium	nitrites	nitrates	phosphorous mg/l
Glubokaya	7.36-8.30	196.0-292.1	2.42-3.60	0.00-0.04	0.00-0.026	0.16-0.37	0.003-0.008
15	8.02	223.7	2.78	0.02	0..009	0.24	0.003
Labirintovaya	7.30-8.45	182.8-380.1	2.28-3.67	0.00-0.60	0.00-0.020	0.03-0.55	0.003-0.029
10	7.87	868.7	3.08	0.19	0.004	0.18	0.009
Opolznevaya	8.00-8.27	254.3-350.0	3.04-3.71	0.01-0.11	0.00-0.034	0.08-1.41	0.003-0.009
10	8.17	301.3	3.42	0.05	0.020	0.45	0.006
Spring 118	7.54-8.50	347.1-472.9	3.91-5.61	0.01-0.45	0.001-0.07	0.97-2.67	0.013-0.164
10	8.12	413.4	4.85	0.12	0.019	1.78	0.089
Khosta River	7.70-8.50	208.2-315.9	2.35-3.39	0.00-2.32	0.00-0.016	0.02-1.44	0.003-0.022
10	8.12	252.3	2.98	0.22	0.006	0.37	0.008

through a sub-tropical, mixed broad-leafed forest (*Fagus orientalis, Taxus baccata, Carpinus betulus*) with an evergreen understory (*Buxus colchicus, Ilex colchicus, Laurocerasus officinalis*) and lianas (*Hedera colchica, Smilax excelssior*). Relative illumination is 1-2%. The stream flows over a bed composed of clay and sandstone. The stream flow derives from runoff and a sub-surface aquifer. The water chemistry of the spring water was hydrocarbonic-calcic with moderate mineralization, and moderately hard (Table 1). Hydrogen ion concentration is neutral to slightly basic, pH ranges from 6.89-8.50. The concentration of nitrogen and nitrates (0.97-2.67 mg/l) is higher than in other waterways. This is a result of the subterranean flow. Ammonium concentration is normally low and increases during flash floods (up to 0.45 mg/l). Nitrites are also found in low concentrations except during flash floods (up to 0.08 mg/l). Phosphorus concentration is considerably higher than in other waterways (up to 0.16 mg/l). *Rana macrocnemis, R. ridibunda, Bufo verrucosissimus, Hyla arborea schelkownikowi , Pelodytes caucasicus,* and *Triturus vittatus ophryticus* are found at this study site and the latter two species breed there (Fig. 5, Table 2).

Study Site 2. Opolznevaya Ravine. A small intermittent waterway flows through an eroded ravine through carbonic rock and clay. The vegetational community is analogous to Study Site 1, but box yews and beeches are dominate. Relative illumination is 2%. Stream flow is derived from runoff and aquifer. The water chemistry of the spring water was hydrocarbonic-calcic with moderate mineralization, and soft. Hydrogen ion concentration is neutral to slightly basic, pH ranges from 8.0-8.27. No amphibians were observed at this study site.

Study Site 3 . Labirintovaya Ravine. A small intermittent, vernal-autumnal stream flows through an eroded, karst gorge with steep walls in a box yew forest. Relative illumination is 2%. Stream flow is derived from runoff and subsurface flow. During low waters periods the stream falls into a number of stagnant pools. The water chemistry of the spring water was hydrocarbonic-calcic with moderate mineralization, and soft. Hydrogen ion concentration is neutral to slightly basic, pH ranges from 7.3-8.45. Water content of nitrogen compounds is low but increases during flash floods. *R. ridibunda* is found here at this study site and *P. caucasicus* reproduces here.

Study Site 4. Glubokaya Ravine. This site is a small pond in a limestone gorge with steep walls and surrounded by a box yew forest. Relative illumination is 2-3%. The pond is fed by a small, relatively constant spring flowing from Karst.

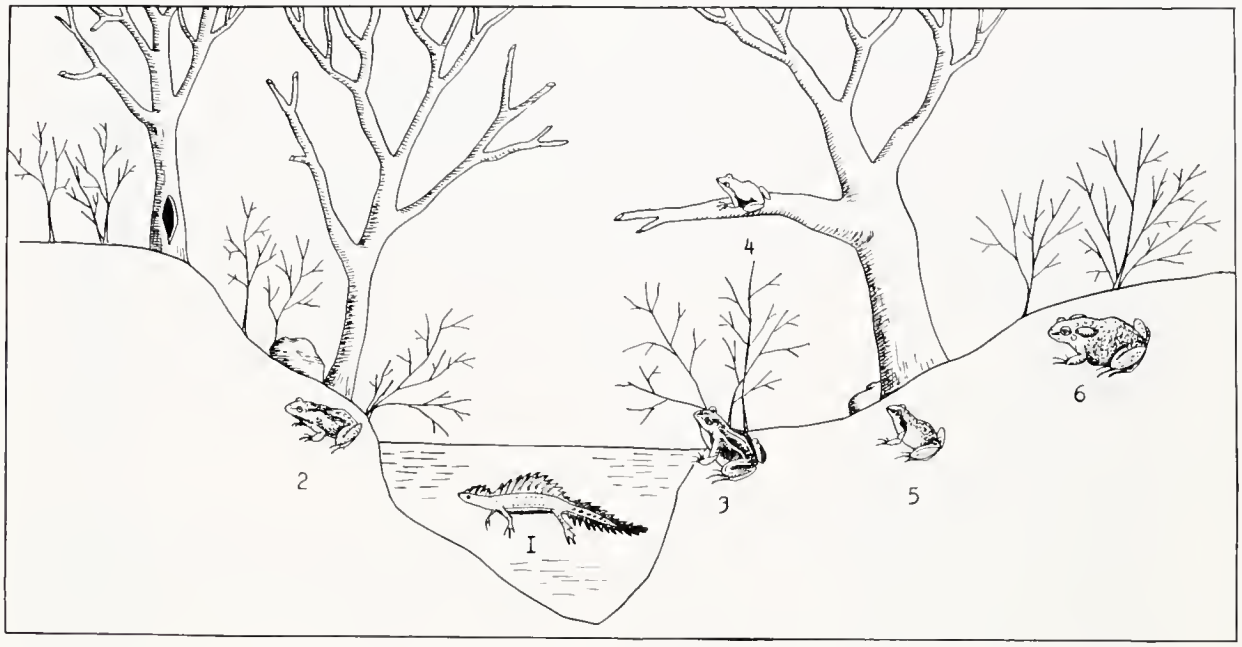

FIG. 5. Distribution of sympatric amphibians at Spring 118 in the Yew Box Grove. 1- Triturus vittatus ophryticus; 2- Pelodytes caucasicus; 3- Rana ridibunda; 4- Hyla arborea schelkownikowi; 5- Rana macrocnemis; 6- Bufo verrucosissimus.

Spring temperature ranges from 11-16° C. The water chemistry of the spring water was hydrocarbonic-calcic with moderate mineralization, and moderately hard (2.42 - 3.6 mg-eq/l). Ammonium concentration is low (maximum = 0.04 mg/l) and in winter drops to 0. Nitrates are highest during summer low water period (up to 0.37 mg/l). Phosphorus concentration is very low (>0.01 mg/l). *Bufo verrucosissimus*, *R. macrocnemis*, *P. caucasicus*, *R. ridibunda* and *T. v. ophryticus* are found living at this study site and the last three species breed here.

Study Site 5. Khosta River. This site is a small mountain stream 21 km long that drains a watershed of approximately 96 km^2. The stream flows through a canyon formed in Cretaceous limestone at an average of 5 m^3/sec. Water flow is derived from runoff and springs arising in karst rock formations. Vegetation is a broad-leafed, subtropical Colchis type forest. Relative illumination is as high as 100%. The water chemistry of this stream is hydrocarbonic-calcic with moderate mineralization and basic pH (7.7-8.5). Ammonium concentration is not high and varies from 0 to 0.07 mg/l, but during floods it can reach 2.32 mg/l. This stream is subject to occasional flooding. Concentration of nitrates reaches a maximum during floods of 1.44 mg/l. Dissolved oxygen is 10-15mg/l and carbonic acid is 10mg/l.

The Nizhe-Khostinsky Spring, flowing out of a karst formation, contributes 1-1.5 m^3/sec of flow at 11-13° C to the Khosta River. In low water periods the Khosta River above the spring nearly dries up and its temperature ranges from 0.6 (the river freezes) - 26° C. During low waters on the Khosta River the Nizhe-Khostinsky Spring provides a relatively stable flow and temperature regime. This spring serves as a barrier for dispersal of amphibians at this study site. *Rana ridibunda* and *Hyla arborea schelkownikowi* live and reproduce above the spring. *Pelodytes caucasicus* and *Bufo verrucoisissimus* live and breed below the spring.

Study Site 6. Samshit Pond. This site is a small pond with flowing water in a stand of hornbeam (*Carpinus betulus*) in the broad-leafed forest. Relative

TABLE 2. Diversity of amphibian species at the study sites.

Species	Study Sites						
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No.7
Triturus vulgaris						X	X
Triturus vittatus	X			X		X	X
Bufo verrucosissimus	O			O	X		O
Pelodytes caucasicus	X		X	X	X		
Hyla arborea	O					O	X
Rana ridibunda	O		O	X	X	O	
Rana macrocnemis	O	O		O	O	X	X

NOTE: X- reproduce, O- inhabit

illumination is 100%. The pond flow is feed by run off and flow from the aquifer. The water chemistry of this pond is hydrocarbonic-calcic with moderate mineralization, moderately hard and alkaline. *Hyla arborea schelkownikowi, Triturus vulgaris lantzi, Triturus vittatus ophryticus, Rana ridibunda,* and *R. macrocnemis,* are found living at this study site and the last three species breed here.

Study Site 7. Pond on the Malaya Khosta River. This site is a small stagnant pond located in the flood plain forest. The pond is filled by runoff and flow from the aquifer. Relative illumination is 50%. *Bufo verrucosissimus, T. vulgaris lantzi, T. v. ophryticus ,H. a. schelkownikowi* and *R. macrocnemis,* are found living at this study site and the last two species breed here.

Species Accounts

Triturus cristatus karelini. This newt is an extremely rare and declining species along the Caucasian Black Sea coast. It was observed only once, at Study Site 1, in the box yew forest.

Triturus vulgaris lantzi. This species exclusively inhabits stagnant ponds and ponds with flowing water, in well illuminated stands of hornbeam in broad-leafed forests, and adjacent areas. These newts are found in the ponds beginning in early March. Reproductive activity begins when water temperature reaches 10° C (usually from mid-March to early April. Females lay their eggs in shallow, thoroughly warmed waters at a depth of 5 cm and remain in the pond until the end of June. The newts over-winter in forest leaf litter and underground (Table 3).

Triturus vittatus ophryticus. This species is found in both well illuminated broad-leafed flood plain forests and thick yew-box groves. It appears in bodies of water from the end of November through January. Reproduction occurs from January until the middle of April at water temperatures of 7-9° C. Females lay their eggs at depths of 5-10 cm. The adults stay in the water until the end of May. The newts over-winter in forest leaf litter.

Bufo verrucosissimus. This toad is found throughout the Yew-box Grove with the exception of the steeper parts of the Khosta Canyon. Reproduction takes place in well illuminated running water in the Khosta River from February until May at water temperatures from 9.5-16° C. Eggs are deposited at a depth of 20-70 cm in strings through vegetation and other underwater objects. These toad over-winter in forest leaf litter beginning in December.

Pelodytes caucasicus. This species inhabits back-water vegetation communities with flowing water. Reproduction lasts from the end of May until the end of October at water temperatures of 13-16° C. Females lay their eggs at a depth of 10-20 cm. These anurans over-winter in forest leaf litter.

TABLE 3. Ecological characteristics of sympatric species of the Yew-box Grove amphibians

DISTRIBUTION:	SPECIES: *Triturus vulgaris*	*Triturus vittatus*	*Bufo verrucosissimus*	*Pelodytes caucasicus*	*Hyla arborea*	*Rana ridibunda*	*Rana macrocnemis*
at summer biotopes:							
flood plain forest	x	x	x	x	x	x	x
box tree forest		x	x	x		x	x
hornbeam forest	x	x	x	x	x	x	x
ash and oak forest			x				x
yew and cherry laurel forest			x				x
agrocenocis			x		x	x	x
at spawning site:							
river			x	x		x	
pools (rain)							x
lotic streams		x		x		x	
semi-lotic streams		x		x		x	
ponds	x	x		x	x	x	
at hibernation sites:							
stagnant, semi-lotic body of water						x	x
soil and litter	x	x	x	x	x		x
Breeding periods:							
January		x					
February		x	x			x	x
March	x	x	x			x	x
April	x	x	x			x	x
May			x	x	x		
June-October				x	x		
Depth of egg-laying from water surface:							
0-5 cm	x						x
5-10 cm		x					
10-20 cm				x	x	x	
20-50 cm			x				
over 50 cm			x				
Preferable water temp. for breeding:							
4-5 degrees Celcius							x
5-7 degrees Celcius							x
7-9 degrees Celcius		x				x	
9-18 degrees Celcius	x		x	x	x	x	

TABLE 4. Comparison of development periods of *Triturus vittatus ophryticus* and *Pelodytes caucasicus*.

SPECIES:	MONTHS: XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Triturus vittatus (ad.)	x	x	x	x	x	x						
Triturus vittatus (larvae)				x	x	x	x	x	x			
Pelodytes caucasicus (ad.)						x	x	x	x	x	x	
Pelodytes caucasicus (larvae)	x	x	x	x	x	x	x	x	x	x	x	x

* Note: Shaded area represents the periods of mutual number limitation

Hyla arborea schelkownikowi. This species is found in open, well illuminated ecotones throughout the grove. Reproduction take place from March until October in warm (>11° C), stagnant waters. Eggs are laid at a depth of 10-12 cm. These frogs over-winter in the forest leaf litter.

Rana ridibunda. This frog is numerous in Khostinsky Canyon in open, well illuminated areas in the water-box yew forest ecotone. Reproduction last from January until March at water temperatures from 5-9° C. Frogs over-winter at the bottom of stagnant bodies of water.

Rana macrocnemis. This frog is found in low numbers in all areas of the grove except in the rocks. Reproduction takes place from February to March in warm (4-9° C), shallow water. Eggs are laid at 0-5 cm depth. During cool winters this frog over-winters in the forest leaf litter and during warm winter it remains abroad.

Discussion

During the summer all of the species of amphibians in the Caucasian Biosphere Reserve are broadly sympatric. However, during reproduction and winter retreat there is habitat segregation (Table 3). The highest level of overlap occurs in the summer in the flood plain forest where all of the above are found. The lowest level of overlap occurs in the box yew-cherry laurel stands with only *B. verrucosissimus*, and *R. macrocnemis* present. The box yew-cherry laurel stands are the most ancient forest type preserved in the Yew-box Grove. This ancient forest is dominated by box yew trees ranging from 500 to 2000 years old and has been virtually unchanged in appearance during that time. It is interesting that this ancient forest is inhabited by the indigenous Caucasian species *B. verrucosissimus*, and *R. macrocnemis.*

The hornbeam tree is a pioneering species that invades disturbed areas such as those that have burned or been logged. It also grows in barren areas. The diversity of amphibian species in the hornbeam forest is caused by a number of factors: 1) secondary character of hornbeam forest; 2) relatively higher illumination (compared to the box yew forest; 3) presence of suitable water conditions for reproduction. When the hornbeam trees are young and the habitat is still open, such species as *R. ridibunda, T. v. lantzi,* and *H. a. schelkownikowi* are found. Later, when the trees become mature and the forest more closed and less illuminated, *B. verrucosissimus*, *R. macrocnemis* and *P. caucasicus* become established. This environment supports the highest level of sympatry of amphibian species in the Yew-box Grove. In box yew stands *T. v. lantzi* and *H. a. schelkownikowi*, the most illumination tolerant species, are not represented. These two species appear in

TABLE 5. Daily activity of amphibians of the Yew-box Grove.

	TIME OF ACTIVITY:																							
SPECIES:	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	3
Triturus vittatus		x	x	x	x		x	x	x	x	x	x	x	x										
Triturus vulgaris		x	x	x	x	x	x	x	x	x	x	x	x	x										
Pelodytes caucasicus	x																		x	x	x	x	x	x
Bufo verrucosissimus																	x	x	x	x	x			
Hyla arborea				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		
Rana ridibunda		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						
Rana macroenemis		x	x																x	x	x	x	x	x

the ecotone adjoining the southwest boundary of the grove (Table 3).

It is interesting to note that *B. verrucosissimus* and *R. macrocnemis* have very specific breeding requirements in terms of the aquatic environment required, but they occur over a large area during the terrestrial stages of their life history. They can be termed stenotopic or very restricted in terms of the reproductive requirements (*B. verrucosissimus* lays its eggs in rivers and *R. macrocnemis* in small pools) and eurytopic in terms of their general distribution (Dazho, 1975). These two species are autochthones or indigenous to the broken country Caucasian region and reproduce in rapid mountain stream and ephemeral pools. The majority of lakes in this region are of recent origin and formed by glaciation, karst or from landslides. As this range of aquatic environments became available at the end of the last glacial period, amphibians successfully colonized those environments which met their reproductive requirements (Monchadsky, 1958).

Bufo verrucosissimus lays its eggs in strings and wraps them around aquatic vegetation and other anchored objects in the water. This allows the toad to lay its eggs in fast flowing mountains streams which are generally unsuitable for other species. It lays its eggs at depths of 20 to 70 cm thus providing some protection from flash floods though many eggs perish in such floods. *Pelodytes caucasicus* and *R. ridibunda* are found sympatric with *B. verrucosissimus*. *Rana ridibunda* lays its eggs in the shallow, slow-moving sections of the river or in pools formed by floods. Reproduction in *R. ridibunda* is limited to the short period of winter low water and lasts from the end of January to the end of March.

Pelodytes caucasicus is isolated from other breeding anurans temporally. It attaches its eggs to thin roots (2-10 cm) beginning in mid-June, when other species have finished breeding. Typically breeding sites are in the backwaters of streams, under vegetation canopies where temperatures are moderate. In small streams *R. ridibunda* and *T. v. ophryticus* are sympatric with *P. caucasicus* .

At Glubokaya Ravine, Study Site 4, there is a high level of sympatry among the amphibian species. There is significant temporal segregation. Adult *T. v. ophryticus* remain in the water from the end of November to the end of May. Larval

TABLE 6. Faeces compostion of sympatric amphibian species of the Yew-box Grove

	SPECIES:					
	Triturus cristatus	*Triturus vittatus*	*Bufo verrucosissimus*	*Pelodytes caucasicus*	*Rana ridibunda*	*Rana macrocnemis*
COLEOPTERA:						
Curculionidae			x	x	x	x
Carabidae		x	x	x	x	x
Cerambycidae			x		x	
Chrysomelidae			x	x	x	
Coccinelidae					x	x
Scarabaeidae			x			
Lucanidae			x			
Silphidae			x			
Elateridae			x			
non det.	x		x			
DIPTERA:						
Tipulidae			x			
Muscidae					x	
non det.	x					x
HYMENOPTERA:						
Apidae				x		
Vespidae			x	x	x	
Formicidae			x			
HEMIPTERA:						
Pentatomidae			x	x	x	
Pyrrhocoridae			x	x		
ANNELIDES:						
Hirudinea		x				
Oligochaeta		x				
ARTROPODA:						
Lepidoptera			x			
Scorpiones			x			
Amphipoda		x				
Isopoda			x	x	x	
MOLLUSCA:						
Pisidium	x					
Oxychilus						x

development occurs from March until August (Table 4). *Pelodytes caucasicus* can be heard calling from May until the middle of October.

The adults of *T. v. ophryticus* and *P. caucasicus* prey upon each others larval stages. When post metamorphic *T. v. ophryticus* begin leaving the water in late July they are prey upon by adult *P. caucasicus* . In December when adult newts enter the water to breed they capture the smaller sizes of *P. caucasicus* tadpoles. During these periods of intense competition and predation both species adopt several strategies for preying upon the other for avoiding predation (Smith 1981).

TABLE 7. Size limits of feeding objects of sypatric amphibians in the Yew-box Grove

SPECIES:	SIZE OF FEEDING OBJECTS (in mm)								
	up to 3	3-3. 5	3. 5-4	4-4. 5	4. 5-5	5-5. 5	5. 5-14. 5	14. 5-19	19-36
Triturus vulgaris					x	x			
Triturus vittatus							x	x	
Bufo verrucosissimus		x	x	x	x	x	x	x	x
Pelodytes caucasicus	x	x	x	x	x	x	x		
Rana macrocnemis				x	x	x	x	x	
Rana ridibunda						x	x	x	

The highest population densities of *T. v. ophryticus*, *T. v. lantzi* and *T. c. karelini* occur in small forest lakes. Much lower population densities are found in mountain streams. Recently formed lakes are apparently the most suitable habitat for these species of newts. As lakes mature, sediments accumulate and they become less suitable habitat and populations decline and are preserved at low levels in nearby streams.

The highest level of sympatry occurs in lakes during breeding season (Table 3). There is, however, very little competition because of temporal and microhabitat segregation for egg deposition and deposition sites.

Lakes and deep pits (Study Site 7) are breeding sites for *H. a. schelkownikowi* where it is spatially segregated from other amphibians but overlaps temporally with *P. caucasicus* (Table 3) and activity patterns (Table 5).

In the Yew-box Grove *P. caucasicus* and *H. a. schelkownikowi* are allopatric at breeding sites. On the Caucasian Black Sea Coast they are sympatric at breeding sites. The interrelationships of these populations in the zones of sympatry have not been studied.

On the Caucasian Black Sea Coast winters are mild with abundant precipitation. Most amphibians remain active and abroad through the winter. Though, on the occasional cold days they become torpid. The exceptions are adult *P. caucasicus* and *H. a. schelkownikowi*. During some cold winters when night temperatures fall to -10 to -12° C all amphibian species enter hibernation.

Bufo verrucosissimus, *P. caucasicus*, *H. a. schelkownikowi*. and *T. v. lantzi* pass hibernation hidden in the soil and leaf litter. *Rana macrocnemis* hibernates in the soil, leaf litter and in the water. Winter soil temperatures at 20 cm depth ranges from 3.5 - 7.2° C. In the spring the water warms more quickly than the soil and this may explain why the those amphibians hibernating in the water breed earlier than those hibernating in the soil.

The mechanism of niche isolation of symbiotopic species includes layering, or the formation of adaptive groups (Dinesman 1948a) and differences in daily and seasonal activity. For example, at Study Site 1, *T. v. ophryticus* occupies the deepest aquatic level, *R. ridibunda* and *P. caucasicus* are found in the lower intermediate levels, *R. macrocnemis* and *B. verrucosissimus* occupy the higher intermediate levels and *H. a. schelkownikowi* is found at the shallowest level and onto land (Fig. 4). Some of the pattern of species distribution can be explained by varying tolerance of desiccation among the different species (Dinesman, 1948b). Those species that are found at the same level are active at different times of the day (Table 5).

The amphibians of the Yew-box Grove can be divided into three groups based on their food habits: 1) feeding on hydrobionts (newts), 2) feeding on arboreal invertebrates (tree frogs), 3) feeding on

terrestrial invertebrates (all other species). *Rana ridibunda* feeds on both aquatic and terrestrial invertebrates (Table 6, 7).

In a given area species diversity is dependent upon niche separation (Pianka, 1981). The seven amphibian species studied here are characterized by biotopic (including breeding site choice, hibernation sites and summer activity ranges), seasonal activity period, daily activity period and food habits isolation. In the Yew-box Grove the highest level of species diversity is achieved in the most stable aquatic environments. Water temperature during the breeding season, level of illumination and water chemistry appear to be an important characteristics.

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