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TROPHIC STRUCTURE OF AMPHIBIAN AND REPTILE COMMUNITIES IN TERRESTRIAL AND AQUATIC ECOSYSTEMS OF BELARUS

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In the article, data on the dietary habits, food relations and trophic structure of amphibian and reptile communities in the ecosystems of Belarus are analyzed. The study has revealed that natural herpetofaunal communities emerging and functioning in diverse terrestrial and aquatic ecosystems include several different groups of species located at 7 trophic levels: detritophages, phytophages, and consumers of 1-5 levels. In the structure of herpetocomplexes four mayor trophical and functional groups (guilds) are clearly distinguished, specialized in diets and habitats: detritus-phytophages of aquatic ecosystems, consumers of zoobenthos, entomophages of land ecosystems, and terrestrial predators of higher (4-5) levels. Guilds form stable «elementary units» of larger supraspecific associations of the food web of ecosystems. The trophic structure of amphibian and reptile communities is realized in two main options of organization corresponding to the main types of ecosystems (biocycles): terrestrial and aquatic. The transformation of organic matter and energy along trophic chains through the link of reptiles is most intense in terrestrial ecosystems, amphibians – equally in terrestrial and aquatic. The trophic structure of communities of the researched vertebrate groups, which includes differ functionally blocks, diverse trophic niches of species, groups of similar species that compete for food resources, as well as predator-prey relationships, is characterized by high complexity and a certain order of organization.

Key words: Amphibians, reptiles, community, nutrition, food interspecies relations, trophic structure, Belarus.

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INTRODUCTION

Trophic structure is defined as a fundamental property and the most important characteristic of biotic communities, a certain ratio of living organisms of different trophic levels, a complex system of food relationships between species, and the interaction of energy processes in food chains of ecosystems (Pianka 1981, Giller 1988, Shenbrot 1986, Whittaker 1980).

Amphibians and reptiles are an important component of terrestrial and aquatic ecosystems of the forest zone the temperate climate belt of Europe. Due to wide range of habitats and high population number and biomass, these lover

vertebrate animals play a significant and often key role in the transformation of biogenic matter and energy in ecosystems (Gilmanow 1987, Pough 2008, Herpetological communities 1982, Scheibe 1987, Drobenkov et al. 2006).

At the same time, many issues related to nutrition, bioenergetics, and structural and functional organization of faunistic complexes of amphibians and reptiles in the forest zone have not been sufficiently studied to date (Gilmanow 1987, Herpetological communities 1982). The significant similarity of food requirements, habitat distribution of populations, and temporal activity indicates a close relationship between the ecological niches of these heterothermal herpetobiont animals, which gives reason to consider them as a natural community.

A comprehensive comparative analysis of the taxonomic composition of food rations, biocenotic relationships, and other aspects related to the nutrition of amphibians and reptiles has not yet been conducted in Belarus. The purpose of this work is to analyze the trophic structure of amphibian and reptile communities (herpetocomplexes) that function in a diverse terrestrial and aquatic natural little human-modified ecosystems in Belarus.

MATERIAL AND METHODS

The work is based on materials collected in 1982-2017 during of field research conducted by the author in various natural-climatic and landscape zones of Belarus. Part of data collected generalized and partially published earlier (Drobenkov 1999, 2000, 2005, 2006, 2015, Drobenkov et al. 2001, Yasula & Drobenkov 1999).

At the collecting and analyzing of the data most traditional approaches and methods described in a number of reports were used (Bulakhov, 1976, Legler 1977, Legler & Sulivan 1979, Darevskij 1987, Kuzmin 1992). The taxonomic spectrum and quantitative ratio of amphibian and reptile food items were identified by analyzing the contents of the digestive tract (Legler 1977, Legler & Sulivan 1979). The contents of snakes' stomachs were evaluated by intravital method using squeezing out a food lump (Darevskij 1987). The sample size for assessing the taxonomic composition of food consumed in the habitat, according to the available methodological recommendations, was 18-25 individuals (Kuzmin 1992).

To analyze the systematic affiliation of amphibian food items 1850 trophic samples were collected, in which more than 6700 specimens of prey were presented. The material for studying the food relations of reptiles was a sample of 6230 specimen victims, which received from 1230 individuals of different species.

To assess the systematic affiliation of amphibian nutrition components 1850 food samples were collected, in which more than 6700 specimen of prey were presented. The material for studying the food relations of reptiles was a sample of 6230 specimen victims, which received from 1230 individuals of different species.

The width of trophic niche was estimated by the Simpson's Index, the overlap between niches of different species was assess in Index Similarity of Morisita (Kuzmin 1992).

RESULTS AND DISCUSSION

Position in the food web

Analysis of the obtained data showed that the communities formed by amphibians and reptiles in terrestrial and aquatic ecosystems of Belarus are represented by several trophic-functional groups combining species located at several levels. In herpetocomplexes next groups are clear identified: detritophages (larvae of tailless amphibians), phytophages (larvae of tailless amphibians), entomophages-consumers of 1-2 levels (larvae of tailed amphibians, all amphibian species in the land phase, adult tailed amphibians during the breeding period, pond turtle and lizards) and consumers of medium and higher (3-5) trophic levels (snakes) (Drobenkov 1993,

1994, 1995, 2005, 2015, Drobenkov et al. 2006, Yasula & Drobenkov 1999).

As shown in the generalized scheme of food relations between amphibians and reptiles in ecosystems of study area (Fig. 1), these groups of vertebrates are part of different parts of the food pyramid, where they perform diverse functions. It is characteristic that most species of the studied community occupy two or more ecological niches (or sub-niches) during their lifetime, which are often quite different. Such very different position in ecosystems is occupied by amphibians, which distinct on the stages development and are characterized by habitat change during ontogenesis during the transposition from the aquatic to the terrestrial phase of the life cycle.

Functional feeding-groups (guilds)

Identification and analysis the system organization of guilds (groups of taxonomically close species, using a particular resource or set of resources in a functionally similar way) is the most productive approach to studying the trophic structure of natural communities (Giller 1988). It is the guilds whose components are most closely interconnected are the scene of the most intense interspecific interactions and the evolution of species (Pianka 1981).

In ecosystems of Belarus in natural communities of amphibians and reptiles 4 main functional feeding-groups-guilds specialized in the utilization of certain living organisms clearly stand out: 1) entomophages present in terrestrial ecosystems (13 species of amphibians in the land phase of the life cycle and 3 species of lizards); 2) phyto-detritophages of aquatic ecosystems (all species of tailless amphibians Anura at the larval stage, as well as young pond turtles optionaly); 3) consumers of hydrobionts (larvae and adult newts in ponds during the breeding season, adult pond turtles); 4) consumers of the 3-5th levels (3 species of snakes). Quantitatively, in the communities the consumers of terrestrial invertebrates (16 species) and consumers of vegetation and detritus (13 species) are dominated.

The trophic structure of amphibian and reptile assemblages in the natural ecosystems of study area is a rather complex system of closely co-operative groups of species populations that function due to various food relationships (Table 1).

Designating the guilds in the community is based on the results of the analysis of feeding

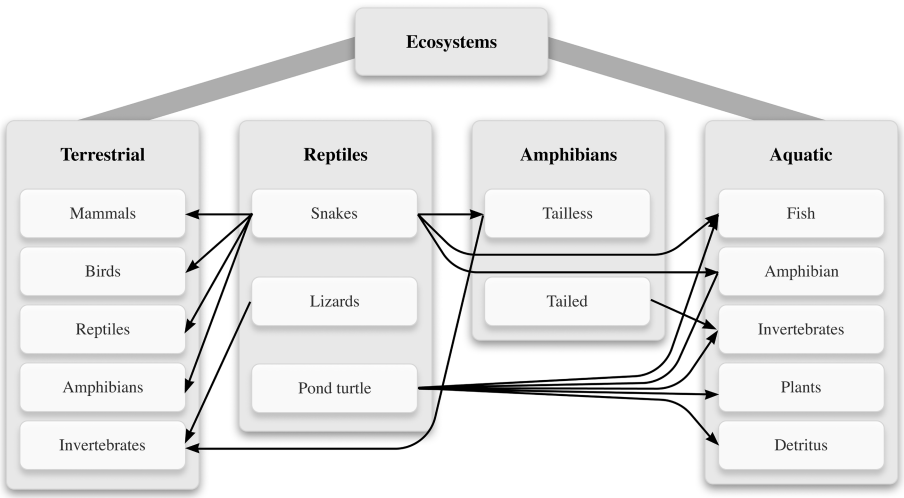

Fig. 1. Scheme of food relations of amphibians and reptiles in communities of terrestrial and aquatic ecosystems of Belarus.

Table 1. Ecological and biological characteristics of the food amphibians and reptiles in ecosystems in Belarus

Species	Food characteristics			
	Ontogenetic		Ecological	
	Adult	Immature (larvae)	Ecosystems	Rhythm of food activity
Amphibian				
Common newt *Lissotriton vulgaris*	ent	pl	tw	tn
Crested newt *Triturus cristatus*	ent	pl	tw	tn
Fire-bellied toad *Bombina bombina*	ent	phb	w	rc
Common spadefoot *Pelobates fuscus*	ent	phb	tw	tn
Common toad *Bufo bufo*	ent	phb	tw	tn
Green toad *Pseudepidalea viridis*	ent	phb	tw	tn
Natterjack toad *Epidalea calamita*	ent	phb	tw	tn
Tree frog *Hyla arborea*	ent	phb	tw	tn
Moor frog *Rana arvalis*	ent	phb	tw	tn
Common frog *Rana temporaria*	ent	phb	w	tn
Marsh frog *Pelophylax ridibundus*	ent	phb	w	rc
Pool frog *Pelophylax lessonae*	ent	phb	w	rc
Edible frog *Pelophylax esculentus*	ent	phb	tw	rc
Reptile				
Pond turtle *Emys orbicularis*	ent	ent	w	d
Slow-worm *Anguis fragilis*	ent	ent	t	rc
Sand lizard *Lacerta agilis*	ent	ent	t	d
Common lizard *Zootoca vivipara*	ent	ent	t	d
Grass snake *Natrix natrix*	batr	batr	tw	d
Smooth snake *Coronella austriaca*	herp	saur	t	d
Common viper *Pelias berus*	saur	myo	t	d

Designation: ent – entomophage, ph-b – phyto-bentosphage, p – planktonphage, batr – batrachophage, herp – herpetophage, myo – myophage, saur – saurophage, t –terrestrial, tw – terrestrial and water, w – water, tn – twilight and night, rc – round clock, d – daily

and habitat preferences of the species, which represents their position in the system of diverse interspecific relationships in the ecosystem. As found on the models of several taxonomic groups (lizards, brown frogs, snakes), the position of a particular species in a group in different types of ecosystems is characterized by a certain constancy, which almost does not change depending on the species diversity or taxonomic composition of the community (Drobenkov 1993, 1995, Drobenkov et al. 2006).

The entire diversity of amphibian and reptile food relationships in communities can be represented as several main forms of interaction. Fig. 2 shows the scheme of food relations between consumers of the lowest trophic levels (excluding snakes) in the natural ecosystems of Belarus.

Indifferent relations

Possibly, there are no absolutely indifferent relations between the members of the studied community. Uncharacteristic food that are consumed accidentally or in very small quantities are found in all species. The most different diets were observed at the pond turtle, which feeds on hydrobionts, and members of the terrestrial consumers group.

Even in the absence of direct trophic connection (as in successive links in the feeding chain), all components of the ecosystem are integrated into a unified structure through intermediate links or shared resources. For example, a rare fact of a common adder eating a young pond turtle has been established, indicating atypical, but possible relationships between members of very different guilds. An uncharacteristic case of a common adder eaten by a smooth snake, a specialized herpetophage, was also noted (Drobenkov 1995). Lizards are sometimes disposed of as occasional or substitute food by the common grass snake. The stomachs of most entomophages contain fragments of plants that are accidentally captured during foraging.

The relative indifference (mutually independence) of food different species as no direct nutritional relationship (or facts their observations) characteristic for pairs or groups of species next members of different guilds: common viper – sand lizard, common grass snake – sand and viviparous lizards, common smooth snake – amphibians (Drobenkov 1995), pond turtle and terrestrial reptiles and amphibians. It is obvious that the expansion of materials on the food spectrum of various members of herpetocomplexes will somewhat expand the understanding of their feeding links and relationships in natural communities.

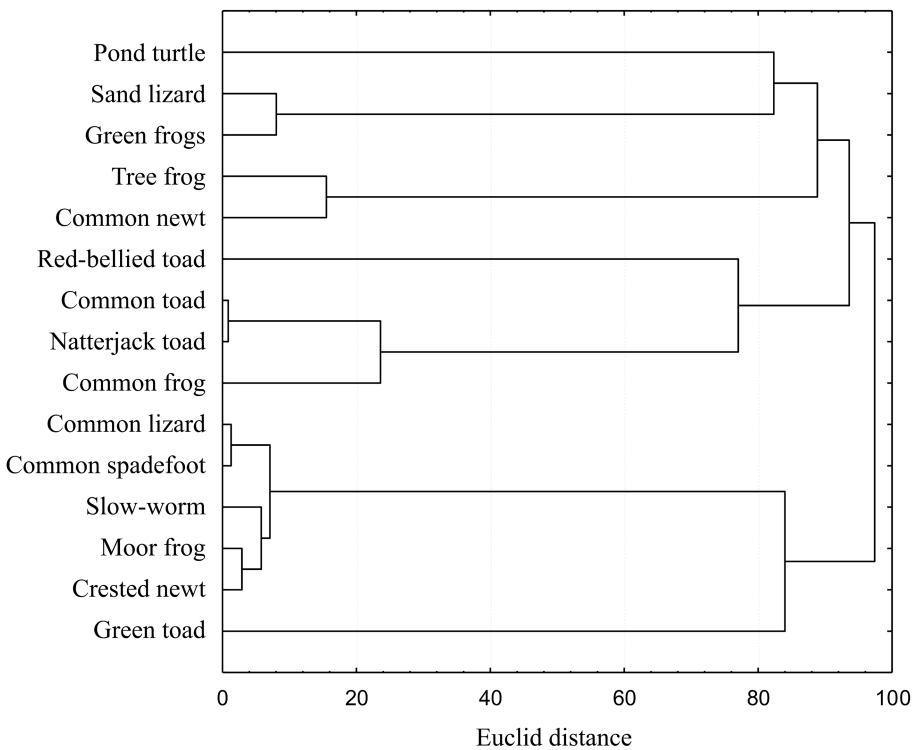

Fig. 2. Degree of similarity of taxonomic composition of food ration of amphibians and reptiles-entomophages in natural ecosystems of Belarus.

Trophic differentiation of species (interference) is usually already initially determined by their differences in requirements to environmental conditions. The narrow food specialization of species is usually associated with their stenotopicity, which is well clear, for example, in the common smooth snake and some other species and groups of the studied community (Drobenkov 1995).

b) Predation

Predator-prey relationships in the herpetofauna community are established for common grass snake and amphibians, common smooth snake and lizards (Drobenkov 1995), common viper and all the lizards and frogs. The pond turtle optionally eats amphibian larvae of many species during the season of their mass development in ponds. Large individuals of some amphibian species (adults and larvae) often consume smaller specimens of other species.

c) Cannibalism

Conspecific individuals are often found in the stomachs of the larvae of most amphibians. This type of feeding relationship is also characteristic for one species of snake (common smooth snake), one species of lizard (sand lizard), and adult green frogs (all three species) (Drobenkov 1993, 1995, 1996).

When analyzing trophic relationships in communities, this special form of feeding relations probably have an intermediate connecting position between competition and predation, as the cause and effect of one and the same process. Cannibalism in the condition of strong intraspecific competition and limited ecological resources can cause the effect of reduction in populations of such spatial conservative species as the common smooth snake and sand lizard (Drobenkov 1995, 1999).

d) Competitive relations

In varying degrees, competitive relations for food are characteristic of many species belonging to the same guild: to a large extent for many syntopic amphibian species (both adults and larvae), to an average for more segregated lizards, and to a very small extent for well differentiated topically snakes.

Interspecific competition is the most powerful factor in shaping the structure of communities of living organisms (Giller 1988). According to the hypothesis of E. Pianka (1981), who studied relationships beetween desert lizards, guilds naturally arise in the process of community evolution, as an adaptation directed at decrease competitive interactions within one small group of species with unidirectional elimination of adverse effects from members of other guilds. Various diets of amphibians and, to a lesser extent, of lizards at condition of abundance of resources and habitat segregation of similar species can almost completely neutralize the stress of competitive relations within these groups.

Spatial differentiation of the two species of snakes, common viper (numerous species, wide spectrum of diet) and common smooth snake (rare species, narrow diet spectrum) in their sympatric area in Belarus is likely to be a consequence of displacement of one species by another. Another pair of snakes, the common grass snake and the common viper, in common habitats at mixing living, such as in floodplain landscapes, can perform a similar function and act as potential competitors for a common food supply – anurans (Drobenkov 1995, 1999).

Significance of trophic differentiation in processes of formation and development of nature community probably is increasing with the complexity of their structure and increasing species diversity.

Generalized scheme of trophic relationships in communities

Among the main characteristics of the trophic organization of biological communities are: a) a set of food relationships and their interactions, and b) new (emergent) properties that are

manifested at the supraspecific level due to these interactions.

It is the trophic factor that most often underlies the regulation of the structural organization of zoocenoses. Feeding relationships such as competition and predation among many biotic factors most strongly affect interspecific relationships and assemblage structure (Drobenkov 1996, 2015, Drobenkov et al. 2006). The abundance of prey not only determines the ability of the consumer to develop new habitats, but also determines its number. This relationship is well evident between the consumers of higher levels - snakes and the groups of animals they use for food-small vertebrates. The most characteristic in this respect are the common viper and the common smooth snake, which in the early stages of ontogenesis specialize in a single food object – the viviparous lizard. The spatial correlations of habitat adder and viviparous lizard in the study area account for 48.0% (24 of 50), common smooth snakes and common lizard – 100% (9). The dependence of the spatial distribution of populations of the common viper and the primary trophic resource (amphibians) is also very high (93%).

At the same time, the habitat similarity of some herpetofauna species is sometimes explained not by the food relations formed between them (predator-prey, competition), but by a simple coincidence of environmental requirements.

The data obtained confirm the general ecological rule that any species in biotic communities adapts to serve as a food source itself (Pianka 1981, Giller 1988, Emelianov 1994). As a result of mutual coadaptation of food partners (located in successive links of the trophic chain), a certain mutual dependence of the populations of the predator and its prey is developed. According to the hypothesis of natural equilibrium (Whittaker, 1980), predators prevent the depletion of the biomass consumed by their victims by utilizing food resources only to a certain limited level.

Brown frogs (genus Rana) and lizards are one of the most widespread and important components of natural ecosystems in Belarus, which utilize the most numerous and diverse groups of invertebrates, on the one hand, and serve as food for animals of higher trophic levels (snakes, predatory birds, and mammals), on the other (Drobenkov 1993, Drobenkov et al. 2006).

The trophic structure of communities formed by amphibians and reptiles, in which various functional blocks, independent trophic niches of species, groups of similar species are distinguished, between which competition for food resources and predator-prey relationships are manifested, is characterized by a fairly high complexity and a certain order of organization. The orderly in the structure of trophic relationships are manifested in the form of certain quantitative rations between different components of herpetocomplexes. For instance, according to the data obtained, in terrestrial ecosystems, 5-7 species of amphibians and reptiles are usually integrated at the lower (2-3) trophic levels, including tailless and tailed amphibians and lizards, and 1-2 species of consults of higher (4-5) trophic levels, represented by snakes. These patterns indicate the systemic organization of communities, which determines the natural variability and certain stability of the structure to influence of environmental factors. Such clear relationships between the components of successive trophic levels allow us to assess the scale and rate of transfer the matter and energy in ecosystems. Qualitative characteristics of the food intake these groups of animals based on data on the spectrum and composition of the diets make it possible to move to a quantitative assessment of energy flows in populations and ecosystems.

The trophic structure of amphibian and reptile communities in Belarus is implemented in two main options of the guild organization, relevant to two basic types of ecosystems (biocycles): terrestrial and aquatic. The first includes all terrestrial forms of herpetofauna - amphibians (out of the breeding phase), lizards and snakes, the second – amphibian larvae, pond turtle, and (optionally) – common grass snake. The transformation of organic matter and energy

through trophic chains through the link of reptiles, according to data on their distribution, abundance, and diet, is most intense in terrestrial ecosystems, and amphibians – equally in both types ecosystems.

The most significant role in the formation trophic structure of communities of vertebrate groups under study is played by interspecific differences in food associated with the taxonomic spectrum of groups being eaten. Thus, comparing most plastic and the most specialized species, we can see that eurythrophic forms have a wider topical niche and are more often present in natural communities than stenotrophic ones. In mixed interspecies assemblages, in condition of the competition for a common trophic resource, a specialized species has fewer advantages and is usually replaced by a generalist species.

The wide range of animal and plant taxa used for food, and also detritus, high abundance of populations, spatial differentiation of habitats into functionally different areas (forage, reproductive, wintering, basking), characteristic of many amphibian and reptile species, indicate the high importance of these groups of lower vertebrates as a significant link in the transfer of matter and energy between land and water, as well as forest and open ecosystems of Belarus.

CONCLUSIONS

Analysis of the data obtained showed that natural communities of amphibians and reptiles formed in the land and water ecosystems of Belarus are represented by several very distinct groups of species located at seven trophic levels: detritophages, phytophages and consumers of 1-5 levels. As part of herpetocomplexes, four major trophic functional groups (guilds) are clearly stand out, specialized in nutrition and habitats): detritus-phytophages of aquatic ecosystems, zoobenthos eating, entomophages of land ecosystems and terraneous predators of higher (4-5) levels. Guilds represent stable «elementary units» of larger supraspecific associations of communities.

The trophic structure of herpetocomplexes is realized in two main options of organization corresponding to two main types of ecosystems (biocycles): land and water one. The transformation of organic matter and energy along trophic chains through the link of reptiles is most intensive in terrestrial ecosystems, amphibians is equally in both types of ecosystems.

As shown by the research results the organization of natural communities of vertebrate groups under study, which includes various functional blocks, various trophic niches of species, groups of similar species that compete for food resources, and predator-prey relationships, is characterized by high complexity and a certain order of organization.

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