

digestive tract are used most frequently for studying amphibian and reptilian diets. In the seventies and eighties sparing methods like stomach flushing, food bulk squeezing, tracing, studies on captive animals and feces analysis were tested for the first time for amphibians (BULAKHOV 1976; PISARENKO & VORONIN 1976) and reptiles (GORELOV 1973; KURANOVA & KOLBINTZEV 1983). A comparative presentation of some of these methods was given by BULAKHOV (1976). Diet composition is expressed most commonly by the percentage of individuals of each taxon represented in the diet and/or by the frequency of their occurrence (i. e. percentage of stomachs containing this taxon), rarely by proportional prey weights and/or volumes (KOROTKOVA & KOROTKOV 1974; ZLOTIN & PERESHKOLNIK 1977). In Caudata larvae the weight of some prey constituents may be estimated by their linear dimensions (KUZMIN 1984a, 1984b, 1985; KUZMIN & MESCHERSKY 1987; KUZMIN & TARKHNISHVILI 1987). To determine significance of prey weights, SHULGA (1979) proposed to calculate the product of frequency of occurrence in stomachs (%) and prey weight. For ecological characteristics, prey is divided into trophical and spatial groups. The most detailed scheme for terrestrial prey was proposed by MEDVEDEV (1974), who grouped invertebrate prey animals by their speed and mode of locomotion, spatial distribution, diurnal activity and agricultural utility. Prey size spectra are commonly described in terms of prey length (e. g. KOROTKOVA & KOROTKOV 1974). However, for Caudata - due to their morphology and foraging mode - the term $d_{\max} / Lt. or.$ was used, where d_{\max} = maximum diameter (width or height) of prey, and Lt. or. = predator's mouth width (KUZMIN 1985a).

Amphibians

The general feeding pattern of the amphibians of the USSR fauna is quite uniform: anuran larvae are detrito-, phyto- and zoophagous, while adult Anura and all Caudata are zoophagous, mainly arthropod feeders.

Amphibian feeding varies significantly according to habitat (KUZNETZOV 1926; KHONYAKINA 1961; RODIONENKO 1972; MAKAROV & ASTRADAMOV 1975; KUZMIN 1985b), season (KRASSAVTZEV 1939; ALEINIKOVA & UTROBINA 1951; MARKUZE 1964a; VERZHUTZKY 1978) and hour of the day (KUZNETZOV 1926; EKVTIMISHVILI 1948; RODIONENKO 1972; TARKHNISHVILI & KUZMIN 1987). This does not only allow

amphibians to be used as indicators of the invertebrate fauna, but also as estimators of its spatial distribution.

During the reproductive period feeding is not ceased, both in Caudata and some Anura (*Bufo viridis*, *Hyla arborea*, *Rana ridibunda* etc.)(IDELSON & VONOKOV 1938; KRASSAVTZEV 1939).

Among C a u d a t a changes in diet paralleling changes in age are less pronounced than in Anura. Such changes are described from 8 of 13 Caudata species in the USSR: *Salamandrella keyserlingii*, *Onychodactylus fischeri*, *Salamandra salamandra*, *Triturus vulgaris*, *T. vittatus*, *T. montandoni*, *T. alpestris*, *T. cristatus*, *T. karelini* (KUZMIN 1984a, b, c, 1985a, 1989 c, 1990, in press; KUZMIN & MESCHERSKY 1987; KUZMIN & TARKHNISHVILI 1987; TARKHNISHVILI 1988). These species show a period of mixed feeding when their larvae begin to forage (mainly upon small crustaceans) still having remnants of endogenous yolk in their digestive tracts. As the larvae grow, changes in morphology and behaviour allow them to catch more and more larger prey, whereas adaptations for using small one persist, leading to an ontogenetic widening of the spectrum of diet, mainly by molluscs and/or insects. During metamorphosis feeding either does not cease (Hynobiidae, *Salamandra salamandra*), or ceases for a very short period, coinciding with transition to terrestrial life (*Triturus* spp.). The trophic niches become narrow. During the postmetamorphic development a widening of the spectrum of prey takes place; in large species there is some displacement towards larger prey.

In A n u r a the same tendencies are observed. Growing tadpoles of *Rana ridibunda* widened their trophic spectra; animals are consumed more frequently, while foraging places are not changed (BELOVA 1964; DUSHIN 1974). For *Rana temporaria* and *Rana arvalis*, the metamorphic starvation period was demonstrated to be shorter than the duration of the metamorphosis proper (VERSHININ 1984). With the frog's size increasing, more and more large and diverse prey is consumed (DINESMAN 1952; KOROTKOVA & KOROTKOV 1974; ISZCZENKO & SKURYKHINA 1981).

Larger specimens may display cannibalism which is registered among 30 species making up 78% of the USSR batrachofauna (KUZMIN 1989b): *Salamandrella keyserlingii*, *Ranodon sibiricus*, *Onychodactylus fischeri*,

Salamandra salamandra, *Triturus vulgaris*, *T. vittatus*, *T. montandoni*, *T. alpestris*, *T. cristatus*, *T. karelini*, *Bombina bombina*, *B. variegata*, *B. orientalis*, *Pelobates fuscus*, *Pelodytes caucasicus*, *Bufo bufo*, *B. verrucosissimus*, *B. viridis*, *B. danatensis*, *B. calamita*, *Hyla arborea*, *H. japonica*, *Rana temporaria*, *R. arvalis*, *R. macrocnemis*, *R. amurensis*, *R. chensinensis*, *R. ridibunda*, *R. lessonae/esculenta*. Anuran cannibalism is performed in 9 combinations depending on the animals' stage and size: adult - small adult, adult - young-of-the-year, adult - metamorphosing specimen, young-of-the-year - metamorphosing specimen, adult - tadpole, adult - live spawn, tadpole - tadpole (live or dead), tadpole - spawn (live, dead), tadpole - adult (dead) (PISARENKO & USHAKOV 1985). The second of these combinations is most frequently mentioned in literature.

Reptiles

The reptiles of the USSR fauna may roughly be divided into the following groups by their predominate prey: plant feeders (*Agrionemys horsfieldi*, *Testudo graeca*, marine turtles); arthropod feeders (*Emys orbicularis*, Gekkonidae, Agamidae, Lacertidae, Scincidae, small snakes of the genus *Rhynchocalamus*, *Eirenis*, *Pseudocyclophis*, some snakes' young-of-the-year (see below)); earthworm feeder (*Amphiesma vibakari*); fish and anuran feeder (*Natrix tessellata*); anuran feeders (*Natrix natrix*, *Rhabdophis tigrina*, *Elaphe rufodorsata*); lizard feeders (*Psammophis* spp., *Lycodon striatus*, *Coronella austriaca*, *Coluber najadum*, *C. karelini*, *C. rhodorhachis*); homeotherms feeders (most species of *Elaphe*, *Coluber*, *Telescopus* and *Vipera*, as well as *Agkistrodon halys*, *A. saxatilis*); polyphagous forms (the rest of the snakes, *Mauremys caspica*, *Varanus griseus*, *Anguis fragilis* and *Ophisaurus apodus*). It must be noted that all of the USSR reptiles, excepting the specialized lizard-eater *Psammophis lineolatum*, are able to switch to secondary prey when the main food resource depletes.

As in amphibians, reptilian diets vary by habitats (ZINYAKOVA & SINDUKOV 1973; KOLBINTZEV 1986; and others), and time (FOMINA 1965, YADGAROV 1974b; DOTSENKO 1986; KOLBINTZEV 1986).

In zoophagous reptiles the change of the diet correlated with age generally means an increase of prey size and, as a consequence, a shift to larger species of prey. For example, young *Mauremys caspica* exclusively prey upon

animals; as they grow, they consume more and more plants making up the main food of the largest specimens (SEREGIN & TROPHIMOV 1979). Some lizards exhibit similar patterns. Adults of *Phrynocephalus mystaceus* differ from the young by eating not only insects, but also plants (KHONYAKINA 1965; POLYNOVA 1982). Smaller *Phrynocephalus*-species, typically not feeding on plants, display myrmecophagia, and younger specimens were observed to feed upon smaller ant species than adults (*Ph. reticulatus*: KAMALOVA 1970). Young *Lacerta vivipara* consume relatively more collembolans and small spiders than adults (GLAZOV & ZAMOŁODCHIKOV 1985). Insects (mainly Acridodea) are the main food items of *Vipera ursinii*, which transfers to vertebrates as its age advances (FOMINA 1965). Arthropods disappear from the food of *Elaphe dione* (KOROTKOV 1985), and *Agkistrodon halys* (LESNYAK 1964) in process of ontogenesis. Young *Eryx miliaris*, *Spalerosophis diadema*, *Coluber rhodorhachis* and *Vipera lebetina* prey upon lizards and widen their food spectra when they grow; *Psammophis lineolatum* eats lizards during its whole life (BOGDANOV 1965).

Unlike amphibians, USSR reptiles display cannibalism exclusively at adult stages. This is known from 23 species - about 15% of the USSR reptilian fauna: *Tenuidactylus fedtschenkoi* (YADGAROV & DAVLETSHINA 1979), *T. caspius*, *Stellio caucasius*, *Trapelus sanguinolentus* (ATAEV 1985), *Phrynocephalus mystaceus* (KHONYAKINA 1965), *Mabuya aurata* (ATAEV 1985), *Ablepharus deserti* (ERIOMTSHENKO & SZCZERBAK 1986), *A. pannonicus*, *Varanus griseus*, *Eremias nikolskii*, *E. velox*, *E. intermedia* (BOGDANOV 1965), *E. grammica* (PARASKIV 1956), *E. arguta* (SZCZERBAK 1974), *Lacerta agilis* (PARASKIV 1956), *L. viridis* (SZCZERBAK & SZCZERBAN 1980), *Malpolon monspessulanus* (ALEKPEROV 1978), *Coronella austriaca* (PIKULIK & al. 1988), *Ptyas mucosus*, *Elaphe dione*, *Agkistrodon halys*, *Echis carinatus* (BOGDANOV 1965), *Vipera berus* (PIKULIK & al. 1988).

Thus, cannibalism occurs less frequently in USSR reptiles than in amphibians. This could be explained by higher densities, more generalized feeding spectra and more pronounced intraspecific size differences in the latter. In reptiles larger specimens devour smaller ones more frequently than eggs and autotomized tails.

FOOD ELECTIVITY

Methods

For a given species food electivity is commonly estimated by the comparison of the spectra of animals forming the diet and of those forming the environment. The latter are established using collecting techniques like nets, biocenometers, ditches, pitfall, traps, digging and/or plotting. Desert invertebrates are collected by hand. As measures of electivity both the simple proportion of the number of prey groups in the diet and in the environment (SHVARTZ 1948, 1950; DAREVSKY 1953; MARKUZE 1964a; GLAZOV 1975; NOVRUZOV 1981; ISZCZENKO & SKURYKHINA 1981) and IVLEV's index (INOZEMTZEV 1969; ZELLARIUS 1982; ZELLARIUS & CHERLIN 1981; ZELLARIUS & al. 1983; KUZMIN 1986, 1989c; KUZMIN & MESCHERSKY 1987; KUZMIN & TARKHNISHVILI 1987; TARKHNISHVILI 1988; TARKHNISHVILI & KUZMIN 1988) are used. Sometimes electivity is estimated by comparison of the prey distributions in the diet and in the environment (ALEINIKOVA & UTROBINA 1951).

Amphibians

During the ontogenesis of Caudata food electivity is clearly shifted towards larger prey (KUZMIN 1986; KUZMIN & MESCHERSKY 1987). The different sensory systems in larvae and adults used for prey detection result in selection of larger objects in adults (KUZMIN 1989c). Electivity concerning prey taxa is unstable: index values vary considerably depending on the mobility, mode of locomotion, relative abundance, diurnal activity, size, coloration and protectability of the prey and environmental conditions (SHVARTZ 1948, 1950; INOZEMTZEV 1969; GLAZOV 1975; KUZMIN 1986; TARKHNISHVILI 1988). Electivity is quite passive (ZLOTIN & PERESHKOLNIK 1977; KUZMIN 1989c).

Reptiles

In both amphibians and reptiles electivity is less pronounced than in homeotherms (SHVARTZ 1950). Electivity in reptiles depends on the prey's coloration, contrast, mobility, size, taste, spatial distribution and abundance (DAREVSKY 1953; ALEKPEROV 1963; NOVRUZOV 1981; ZELLARIUS

1982, 1986; ZELLARIUS & CHERLIN 1981; GLAZOV & ZAMOLODCHIKOV 1985). In some cases large forms (*Ophisaurus apodus*, some snakes) are able to gather prey (birds, insects) in order to hunt within higher concentrations (ALEKPEROV 1963; ZINYAKOVA & SINDUKOV 1973; KOTENKO 1985). Thus, electivity in reptiles is more active than in amphibians, i. e. rather determined by preferences than by availability of prey.

TROPHIC NICHES AND RESOURCE PARTITIONING

Amphibians

Although amphibian diet depends rather on the habitat than on the predator itself, coexisting species frequently partition their food resources. Thus, in *Triturus*, interspecific differences in larval diets were found to be increasing during ontogenesis, both in syn- and allotopic situations. These differences are not correlated with food competition, but with inheritedly fixed specific morphophysiological and behavioural peculiarities (KUZMIN 1989c; KUZMIN & TARKHNISHVILI 1987). At the same time, peculiarities in ontogenesis may play a role in the reciprocal predatory limitation of species. In the end of July - beginning of August *Pelodytes caucasicus* preys upon young-of-the-year of *Triturus vittatus*, while adult newts, entering their reproductive ponds in December, feed on small toad tadpoles (TUNIYEV & BEREGOVAYA 1986). During the terrestrial life interspecific differences are also displayed. Thus, the species of the genus *Bufo* are consuming more ants relative to the other members of the guilds - *Pelobates*, *Rana* and *Hyla* (ALENIKOVA & UTROBINA 1951; MEDVEDEV 1974; PLESHANOV & POPOV 1981; SHLYAKHTIN 1986). The slow moving *Bufo* and *Pelobates* take soil dwellers rather than phyllobionts and fast flying forms. The trophic niches of the semiaquatic *Bombina bombina* and *Rana ridibunda* are shared mainly by flying insects, prey size and the connection with water (SHLYAKHTIN 1986). In terrestrial species there is more trophic niche overlap than in aquatic. All differences described are clearly explained by the species' morphology and behaviour. However, SHLYAKHTIN (1986) believes that they reduce competition, which is measured by the degree of diet overlap (not considering the food resources).

Reptiles

In reptilian assemblages food is more partitioned than in those of amphibians. In the USSR herpetofauna resource partitioning is best investigated in 19 desert lizard species (ZELLARIUS 1981, 1982, 1986; ZELLARIUS & al. 1983; ANANJEVA & TSELLARIUS 1986; MISHAGINA 1988). The average prey sizes turned out to be correlated with those of the lizards. Their electivity is weak. The spatial distribution of the lizards could not be explained by the abundance or scarcity of the prey, whereas trophic niche differences were found to be determined by the lizards' spatial distribution, activity and morphology, but not by their electivity or feeding competition. Similar explanations may be applicable to dietary differences in snake assemblages described in the literature (YADGAROV 1974a; KOROTKOV 1978, 1985; DOTSENKO, 1986). However, snakes may rather compete for food than lizards, due to less resource supply. KOROTKOV (1985) noted that food competition is considerably strong in certain snakes of the Far Eastern region because many sorts of animals of prey are accepted by the majority of snake species. On the other hand he noted food supply to be sufficient for the number of snakes occurring.

ROLES IN THE TROPHIC NET

Methods

Herps' feeding rates are estimated commonly by the stomach- (or whole digestive tract-) fill index (J) given in per cent or per mille of the total prey weight per unit of the body weight (without the weight of the food). Daily food consumption is commonly accepted to be equal to the weight of the stomach contents at maximum feeding rate (e. g. DAREVSKY 1953; GLAZOV 1975; LEONTJEVA 1988). Data from experiments (IDELSON & VONOKOV 1938; MARKUZE 1964a, 1964b; INOZEMTZEV 1969) and literature (e. g. ISZCZENKO & SKURYKHINA 1981) are consulted. A "natural" method is based on the estimation of the difference between the food quantities consumed and digested within a certain time (KUZMIN & MESCHERSKY 1989). In *Rana* spp. it was found to equal about 1.5 of the total weight of the stomach contents at its maximum fullness (MARKUZE 1964a, 1964b; INOZEMTZEV 1969). Data on daily food consumption as

well as species density, metabolism and caloric content are used to estimate population energetics (APOSTOLOV & al. 1977; GOROVAYA & DJANDAROV 1985; GOROVAYA & al. 1987). Exponential equations describing the food consumption of amphibian larvae and young-of-the-year were recently proposed by IGROPOULO & TERTYSHNIKOV 1987.

Amphibians

Amphibian feeding rates are not constant all over the day. Thus, *Bufo bufo* larvae have maximum rates between about 11.00 a. m. and 8.00 p. m., *Triturus* larvae at about 3.00 a. m. (MURKINA 1973, 1983; TARKHNISHVILI & KUZMIN 1987). Adult *Rana ridibunda* most intensively feed in the morning, *Rana macrocnemis* and *Bufo viridis* in the morning and evening (MURKINA 1973; USHAKOV & TUSNOLOBOVA 1987). Amphibian feeding rate is maximum at the larval stages, minimum at metamorphosis (KUZMIN 1989b). Food intake in female amphibians is frequently larger than in males due to higher reproductive expenses (reviewed by KUZMIN 1989a).

During their terrestrial life amphibians are commonly II-III level consumers. GOROVAYA & DJANDAROV (1985) estimated the annual flux of energy through the populations of 9 amphibian species in Precaucasia to equal 0.067 - 192 J/1000 m² (minimum in *Triturus vittatus*, maximum in *Rana ridibunda*). Populations' contributions to the ecosystem vary with their age (GOROVAYA & al. 1987; IGROPOULO & TERTYSHNIKOV 1987), the ecology of the prey (MAKAROV & ASTRADAMOV 1975) and habitat (APOSTOLOV & al. 1977). The annual consumption of invertebrates by amphibians is about 2-5% of the production of different ecosystems (GILMANOV 1987).

Reptiles

Carnivorous reptiles, being II-V level consumers, apparently influence the communities different from carnivorous amphibians, due to the more pronounced electivity and shorter active period. Thus, lizards may be important regulators of the abundance of some invertebrate groups (GLAZOV & ZAMOLODCHIKOV 1985; BULAKHOV 1986; ZELLARIUS 1986). In deserts removal of prey by lizards may come to 200 000 specimens/km², or more than 81 kg/km² per summer (STALMAKOVA & RZHEPAKOVSKY

1981). In general, lizards consume 1-10% of the resource production, which is as much as turtles do; snakes' influence is more important (4-20%)(GILMANOV 1987).

CONCLUSIONS

The main fields of the trophological research in USSR batracho- and herpetology were briefly characterized. The bulk of these publications (ca. 90%) are dedicated to food composition and its variation in space and time. In the most recent years stress is laid on energetics and ecology of assemblages, where trophology is integrated providing with data on life history and population ecology. These works centered mainly on anurans of the temperate zone and on desert lizards, the latter having been studied more detailed. Problems of food competition, diurnal dynamics and changes of feeding correlated with age are so far poorly investigated but progress in this fields is to be expected in the near future.

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SERGIUS L. KUZMIN

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A review of studies on feeding ecology in the USSR

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