

OLFACTORY ORIENTATION IN ANURAN AMPHIBIANS

S. V. Ogurtsov¹

Submitted February 26, 2003.

Anuran amphibians are known to learn chemical stimuli in embryonic and larval development. Data on “kin recognition” and data on learning of native pond odor are considered as parts of complex chemical imprinting typical for other groups of vertebrates. It is rather probable that 2 sensitive periods of chemical learning exist in larval development. Imprinting, at least partly, determines species-specific strategy of dispersal in newly metamorphosed individuals. It is proposed that chemical stimuli learnt during larval development could be among cues that guide adult individuals to their native pond for breeding. Anuran olfactory abilities, such as discrimination of scent mixture components, seasonal changes and hormonal regulation of sensitivity, individual differences in perception are also discussed.

Keywords: amphibians, larval development, chemical imprinting, “kin recognition,” native pond odor, sensitive periods.

INTRODUCTION

Imprinting on environmental chemical stimuli seems to be a common feature of vertebrates. Memorization of chemical stimuli by young salmonid fish is a well-known example of imprinting. Adult salmonids use the learnt stimuli to locate their breeding stream, that is actually their birthplace (Hasler and Scholz, 1978). Sea turtles, that are known to lay eggs on the native beach, can memorize environmental odors while being in eggs and during several months after hatching. One year later turtles are able to discriminate between the water with sand from their native island and the water with sand from a strange island (Grassman, 1993). Thus chemical stimuli learnt early in ontogeny may help adult individuals of fish and reptiles to locate their birthplace.

Mammalian olfactory system becomes functioning prior to birth. Rat, rabbit, sheep and human newborns learn odors in utero (Hepper and Waldman, 1992; Lecanuet and Schaal, 1996). Rabbit pups learn the odor of the nipple-search pheromone before birth, and could memorize additional odors emanating from mother's body during a short period after birth. The memorization of mother's odor and preference for it are vitally essential for newborns (Hudson, 1999). Chicken embryo is able

to learn chemical cues present inside or outside the egg. Chick is attracted by these stimuli after hatching (Sneddon et al., 1998). Probably, it should be the reason why British storm-petrel chicks, *Hydrobates pelagicus*, can find their nest in a colony using olfactory cues (Minguez, 1997). The listed examples show that imprinting on environmental chemical cues enables a young individual to keep near mother or near the birthplace in its early age.

Experiments on vertebrate olfactory imprinting were successfully conducted using a variety of chemical stimuli, artificial as well as natural ones. It seems that the olfactory system of a young animal is potentially ready to learn all the chemical cues present around it. While in mammals imprinting is directed to a mother, in other vertebrates which grow without maternal care (fish, reptiles) it is addressed to stimuli marking the place of birth. In some species, the learnt stimuli help juveniles to survive being attached to their mother or to home, in others guide adult individuals to their first breeding site. Imprinting seems to give the answers on two vital questions: for a newborn — “what is good for me in this world?,” and for a newly matured individual — “where can I breed successfully?”.

Do amphibians possess any kind of olfactory imprinting? If so, what role does it play? Among urodelous amphibians terrestrial salamanders are known to recognize conspecifics by scent cues. Young juveniles of *Salamandra lanzai* are attracted by cues from older juveniles and,

¹ Dept. of Vertebrate Zoology, Faculty of Biology, M. V. Lomonosov Moscow State University, Leninskie gory, 1, korp. 12, Moscow 119992, Russia. E-mail: sk-ogurtsov@mtu-net.ru.

significantly greater, by that from adult females. Preference reverses with age. It is argued that a particularly long gestation period of this species may lead to an existence of olfactory imprinting that cause preferential spatial association between mothers and their offsprings. As adult individuals of terrestrial salamanders exhibit territorial defense, the difficulty of finding a suitable territory could make such association advantageous for young juveniles (Gautier et al., 2004). A similar mechanism was described for viviparous lizards (Léna and De Fraipont, 1998).

Chemosensory orientation of anuran amphibians is much less studied than that of mammals or even of urodela amphibians. Nevertheless, it seems to play an important role in their behaviour. By means of olfactory system tadpoles respond to food components, such as aminoacids (Kiseleva, 1995), avoid chemical stimuli from predators and the so-called “alarm substance” produced by a damaged conspecific (Kiesecker et al., 1996; Manteifel and Zhushev, 1998). The larvae of the common frog *Rana temporaria* are able to memorize chemical stimuli marking the environment (Kiseleva, 1984) and tadpoles of the spadefoot toad *Scaphiopus multiplicatus* can distinguish between water from various parts of the pool (Pfennig, 1990).

Adult individuals respond to odors of the common food (Khmelevskaya and Deulina, 1972). Toadlets of *Bufo cognatus* and *B. microscaphus* can recognize and avoid chemical substances from predators, snakes (Flowers and Graves, 1997). Using chemical cues adult individuals of *Hoplobatrachus occipitalis* (Ranidae) evaluate the presence and density of conspecific tadpoles in a pool and decide whether to spawn there or not (Spieler and Linsenmair, 1997). Males of the dwarf african clawed frog, *Hymenochirus* sp., and the magnificent tree frog, *Litoria splendida*, have specialized glands that produce chemosignals to attract females (Wabnitz et al., 1999; Pearl et al., 2000).

Anuran amphibians are known for their strong fidelity to breeding ponds and terrestrial summer home ranges (Sinsch, 1992a). During breeding migrations or while locating their terrestrial home ranges frogs and toads use olfactory cues to orient. Such an ability has been demonstrated in various species: *R. lessonae* and *R. ridibunda* (Vasiliev, 1967; Babenko et al., 1973); *R. arvalis* (Lyalyushko et al., 1972); *R. temporaria* (Lukianov et al., 1985); *B. viridis* and *Pelobates fuscus* (Khmelevskaya and Deulina, 1972); *B. valliceps* and *R. utricularia* (Grubb, 1973b, 1973c, 1975); *B. woodhousei*, *Pseudacris clarki*, and *Ps. streckeri* (Martof, 1962); *B. bufo*, *B. calamita*, and *B. spinulosus* (Sinsch,

1987, 1988, 1992b); and *Bombina variegata* (Babenko and Pashchenko, 1979).

WHAT IS “KIN RECOGNITION”?

A large field of study on anuran olfaction deals with the so-called “kin recognition.” It was shown that tadpoles of frogs and toads recognize individuals from the same sibship. “Kin recognition” is a result of learning of chemical stimuli marking the egg’s jelly. Learning occurs during the period between gastrulation and hatching, as shown in *R. temporaria* and *R. sylvatica* (Hepper and Waldman, 1992). In *R. cascadae* such stimuli could include maternal and paternal factors (Blaustein and O’Hara, 1986). However, tadpoles also learn chemical stimuli after hatching. For *Sc. multiplicatus* and *B. americanus* it is the period between hatching and the time when larvae disperse from oviposition sites (this time is usually associated with the beginning of active feeding). During this period the larvae sit on eggs jelly or stay near it (Waldman, 1981; Pfennig, 1990). If at that time tadpoles are kept with siblings they continue to recognize kin, if with nonsiblings — recognition disappears. Incubation in a different “company” during 6 weeks after the sensitive period does not modify the reaction — if kin recognition has formed it retains unchanged (Waldman, 1981). In *B. americanus* “kin recognition” is based on tadpoles’ metabolites that are perceived by olfaction (Waldman, 1985). These facts speak for the existence of a sensitive period for chemical learning in early embryonic and larval development (the period before the beginning of active feeding). Tadpoles of *B. boreas* could discriminate between kin and non-kin if they are exposed to kin individuals during the sensitive period. However, if after 75 days of such kin exposure, at the time of metamorphosis, tadpoles are transferred to a non-kin “company” within 2 – 6 days recognition disappears. This makes us think that there exist a second period in larval development, somewhere close to metamorphosis, when tadpoles’ reaction to surrounding chemical stimuli could be modified (Waldman, 1991).

It seems that during the sensitive period tadpoles are able to learn a variety of chemical cues, whether emanating from conspecifics or from the environment. Thus *R. sylvatica* could learn in embryonic development and later prefer chemical stimuli associated with surrounding algal cultures (Waldman, 1991). Larvae of *Scaphiopus multiplicatus* memorize the odors of the familiar foodstuff and are attracted by them later. At the same time they prefer kin. When forced to make choice between siblings, that were fed unfamiliar foodstuff, and

nonsiblings, that ate familiar foodstuff, tadpoles choose nonsiblings. That means that the use of familiar food odors dominates over kin cues in tadpoles' behaviour (Pfennig, 1990). That should be the reason why *B. americanus* tadpoles discriminate siblings better when nonsiblings (used for comparison in a test) are taken from a different pond, than if both originate from the same pool (Waldman, 1981).

“Kin recognition” could be ecologically advantageous for tadpoles of some anuran species, especially those that form aggregations or schools. But the retention of kin preference after metamorphosis seems to be useless as adult frogs are not known to aggregate. While in *R. aurora* the kin preference disappears during larval development, in *R. cascadae* it's still present, at least, 47 days after metamorphosis (Blaustein and O'Hara, 1986). In *R. temporaria* preference for artificial chemical stimuli marking eggs jelly is retained no less than 2 weeks after metamorphosis (Hepper and Waldman, 1992), though *R. temporaria* tadpoles are not known to recognize kin (Kiseleva, 1997).

In one of the most integrated reviews on anuran kin recognition it is mentioned that at present “we know considerably more regarding how frogs and toads recognize their kin than why they do so” (Waldman, 1991). There exists an opinion that “kin recognition” is a laboratory artifact, obtained when kin cues appear to be the only chemical stimuli in the environment (Blaustein et al., 1984; Pfennig, 1990). Chemical stimuli also could be learnt if they were present outside the eggs before hatching (Hepper and Waldman, 1992). In a series of publications a hypothesis was put forward presuming that memorized stimuli could be used in homing after metamorphosis (Blaustein et al., 1984; Pfennig, 1990; Hepper and Waldman, 1992). The fact that learning of surrounding chemical stimuli occurs at limited (sensitive) periods and that the memory about the stimuli retains long after metamorphosis makes us think that the process is analogous to chemical imprinting (Waldman, 1991).

IMPRINTING ON NATIVE POND ODOR

Young individuals of some anuran species appear to use odors emanating from the native pond for spatial orientation. The native pond is the place where tadpoles have passed their embryonic and larval development. Among substances that produce native pond odor are: ground from the pond's bottom and plants used by tadpoles as a foodstuff. The type of reaction to native pond odor largely depends on the biology of a species. Thus young-of-the-year of the common toad *B. bufo*, that

leave the native pond soon after metamorphosis, in laboratory tests try to avoid the native pond odor. On the contrary, froglets of the pool frog *R. lessonae*, that keep close to the native pond until wintering, in the same experiment are attracted by this odor for as long as 1.5 months after metamorphosis. It was shown that learning of the native pond odor could occur during larval development. The ecological basis of the process is that chemical cues learnt by tadpoles may later determine, at least partly, the strategy of dispersal of newly metamorphosed frogs (Bastakov, 1986, 1992).

We assume that “kin recognition” and learning of native pond odor should be viewed as a complex chemical imprinting. Some of the learnt cues could guide tadpoles to their relatives to form larval aggregations, other cues learnt at the same time could guide juveniles to or from the place of birth. The studies on “kin recognition” indicate that the sensitive period of chemical learning occupies the time from late embryonic development till the beginning of active feeding. The reaction that forms during this sensitive period cannot be modified until the beginning of hind limb toes differentiation (Waldman, 1981) and in some species it is retained after metamorphosis. The results obtained in our research group showed that anuran amphibians can also learn odors after the beginning of active feeding. Thus young-of-the-year of *B. bufo* and *R. lessonae* remember odors of the familiar foodstuff that was present in the water during the mentioned period (Bastakov, 1992). These facts gave us an assumption about the existence of more than one sensitive period in larval development, the second taking place somewhere close to metamorphosis. In a preliminary study this appeared to be true with the pool frog *R. lessonae*. Incubation of tadpoles during the two periods — stages 18 – 21 and 32 – 43 (Gosner, 1960) — in natural pond water, as well as in artificial stimuli, morpholine, and β -phenylethanol, led to preference for them after metamorphosis. Those froglets who were not exposed to the stimuli or those exposed to them during the time intermediate between two sensitive periods were indifferent to the same chemical stimuli (Ogurtsov and Bastakov, 2001). It is worth mentioning that the morphological development of the frog's olfactory system also have 2 stages of intensive neurogenesis (Spaeti, 1978), and these stages appear to be correlated with the described periods of learning. In fish and mammals olfactory imprinting also occurs at the time of active neurogenesis in olfactory system (Apfelbach and Weiler, 1985; Nevitt et al., 1994).

ADULT FROGS ALSO USE POND ODORS IN ORIENTATION

It is very likely that anuran amphibians come to breed for the first time into their native pond as shown in *R. sylvatica*, *R. temporaria*, *B. valliceps*, and *B. woodhousei fowleri* (Blair, 1953; Breden, 1987; Khmelevskaya, 1989; Waldman, 1991). That is why imprinting on native pond odor could provide an orientational cue to guide adult frogs and toads to breeding sites (Grubb, 1973b). Whether sexually mature individuals still remember olfactory cues learnt early in ontogeny is not known. Nevertheless, adult *R. arvalis*, *R. lessonae*, *R. ridibunda*, *Bombina bombina*, and *B. bufo* use olfaction to orient toward their breeding pond at distances 100–300 m away from it (Vasiliev, 1967; Lyalyushko et al., 1972; Babenko et al., 1973; Sinsch, 1987). When *B. japonicus* moves towards its breeding pond the olfactory epithelium activates. The maximum amplitude of EOG is registered in toads which have reached the pond (Kaji et al., 1997). The wind from the pond increases the accuracy of orientation in breeding *R. lessonae* and *B. bufo* (Lyalyushko, 1972; Sinsch, 1987).

What sources of the pond odor do adult amphibians use for orientation? *R. temporaria* is attracted by the water from its breeding pond (Lukianov et al., 1985). *R. utricularia* and *B. valliceps* recognize water with plants and bottom components taken from their breeding site. This sample of water is still recognizable after it has been stored in low temperature for 2 months (Grubb, 1973b, 1975). Such species as *B. woodhousei*, *Pseudacris clarki*, and *Ps. streckeri* are attracted by the water with ground taken from their breeding pool. They do not orient toward chemical cues from conspecifics (Grubb, 1973c). Thus the pond odor, probably, emanates from the water body of the pond: water itself, ground from the bottom, aquatic plants. We should point that nearly the same components are memorized by amphibians during their larval development.

ANURAN OLFACTORY SENSITIVITY

Undoubtedly, the pond odor should be a complex stimulus. The mechanism of perception of scent mixtures is being discussed. As for amphibian tadpoles, it seems they can distinguish single components in a mixture. The wood frog *R. sylvatica* learns and later recognize both the stimuli from the siblings and the artificial chemicals injected at the same time into the eggs (Hepper and Waldman, 1992). Soon after hatching tadpoles of a spadefoot toad *Sc. multiplicatus* learn and later rec-

ognize the stimuli from siblings and the stimuli from the familiar foodstuff (Pfennig, 1990). *R. temporaria* tadpoles memorize single artificial chemicals when the food components could be present in water at the same time (Kiseleva, 1984). That means that olfactory system of anuran amphibians is able to discriminate, at least, 2 components in a scent mixture.

The olfactory sensitivity of adult frogs changes seasonally. In *R. ridibunda* the olfaction is more sensitive in summer than in autumn. The length of olfactory cilia in *R. temporaria* is 2 times larger in spring than in autumn (Kruzhalov, 1980). According to electrophysiological studies, the olfactory system of *R. temporaria* undergoes functional changes in spring. It seems the majority of neurons of the olfactory bulb becomes highly specific and responds only to some biologically relevant stimuli; other odors are not detected (Ghuselnikova et al., 1979). Summarising, in autumn the anuran olfactory sensitivity decreases, in spring it becomes highly specific.

Seasonal changes also occur in the reaction of adult amphibians to the odor of their breeding pond. Strong preference is exhibited during the breeding period in spring and it completely disappears in summer. These changes are under hormonal control. In *B. valliceps* the injection of chorionic gonadotropin increases the attractiveness of the pond odor. Two–three days of handling of toads in laboratory also decrease preference and that seems to be associated with the decline in gonadotropin secretion (Grubb, 1973b). One can assume an increase in preference for the native pond odor in individuals reaching sexual maturation, should the memory about it retain. It is known that *B. valliceps* breeds in the native pond (Blair, 1953). Young toads do not respond to the native pond odor (Grubb, 1973a), but adults are attracted by it (Grubb, 1973b).

It's worth mentioning that some individuals in the population can respond indifferently to pond odors. Though the majority of frogs of *R. utricularia* prefer breeding pond odor, some individuals are indifferent to it (Grubb, 1975). Not all embryos of *R. temporaria* can learn chemical stimuli. Nearly 70% do remember them. These individual differences pass through metamorphosis (Hepper and Waldman, 1992). "Kin recognition" (viewed in the context of chemical imprinting) is characteristic to nearly 80% of *R. cascadae* individuals tested (Blaustein et al., 1984). As amphibians possess a metapopulation structure (Sjögren, 1994), the mentioned variability in the response to a native odor may give some individuals (indifferent ones) an opportunity to inhabit distant ponds, while the majority of population is attached to the native one.

CONCLUSION

Amphibians thus join the row of vertebrates that possess chemical imprinting. In anurans imprinting determines the strategy of dispersal of newly metamorphosed individuals. Metamorphosis draws them into a completely new, terrestrial environment and imprinting should provide cues for a starting point in animal's orientation. After all, it is very likely that cues learnt early in ontogeny guide adult individuals to their birthplace for breeding. Olfactory cues could be among them.

Acknowledgments. I wish to thank Claude Miaud from Université de Savoie (France) for useful comments on the manuscript.

REFERENCES

- Apfelbach R. and Weiler E. (1985), "Olfactory deprivation enhances normal spine loss in the olfactory bulb of developing ferrets," *Neurosci. Lett.*, **62**, 169 – 173.
- Babenco L. A. and Pashchenko Yu. I. (1979), "Some features of orientation of the yellow-bellied toad in homing experiments," *Vestn. Zool.*, **5**, 61 – 65 [in Russian].
- Babenco L. A., Pashchenko Yu. I., and Lyalyushko D. M. (1973), "Role of sense organs in orientation "by homing" in constant-water amphibians," *Vestn. Zool.*, **2**, 30 – 32 [in Russian, with an English abstract].
- Bastakov V. A. (1986), "Preference by young-of-the-year of the edible frog (*Rana esculenta* complex) for their own reservoir ground smell," *Zool. Zh.*, **65**(12), 1864 – 1868 [in Russian, with an English abstract].
- Bastakov V. A. (1992), "Experimental study of the memorizing of pond odor during larval development of two anuran species," *Zool. Zh.*, **71**(10), 123 – 127 [in Russian, with an English abstract].
- Blair W. F. (1953), "Growth, dispersal and age at sexual maturity of the Mexican toad (*Bufo valliceps* Wiegmann)," *Copeia*, **1953**(4), 208 – 212.
- Blaustein A. R. and O'Hara R. K. (1986), "Kin recognition in tadpoles," *Sci. American*, January, 90 – 96.
- Blaustein A. R., O'Hara R. K., and Olson D. H. (1984), "Kin preference behaviour is present after metamorphosis in *Rana cascadae* frogs," *Animal Behav.*, **32**, 445 – 450.
- Breden F. (1987), "The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*," *Copeia*, **1987**, 386 – 394.
- Flowers M. A. and Graves B. M. (1997), "Juvenile toads avoid chemical cues from snake predators," *Animal Behav.*, **53**(3), 641 – 646.
- Gautier P., Léna J. P., and Miaud C. (2004), "Responses to conspecific scent marks and the ontogeny of territorial marking in immature terrestrial salamanders," *Behav. Ecol. Sociobiol.* (in press).
- Ghuselnikova K. G., Korolev A. M., and Pletnev O. A. (1979), "Identification of odors by neural networks of olfactory bulbs of amphibians and reptiles," in: *Vopr. Kibernetiki*, No. 53, 58 – 88 [in Russian].
- Gosner K. L. (1960), "A simplified table for staging anuran embryos and larvae with notes on identification," *Herpetologica*, **16**(2), 183 – 190.
- Grassman M. (1993), "Chemosensory orientation behaviour in juvenile sea turtles," *Brain Behav. Evol.*, **41**(3 – 5), 224 – 228.
- Grubb J. C. (1973a), "Orientation in newly metamorphosed Mexican toad, *Bufo valliceps*," *Herpetologica*, **29**(2), 95–100.
- Grubb J. C. (1973b), "Olfactory orientation in the breeding Mexican toad, *Bufo valliceps*," *Copeia*, **1973**(3), 490–497.
- Grubb J. C. (1973c), "Olfactory orientation in *Bufo woodhousei fowleri*, *Pseudacris clarki* and *Pseudacris streckeri*," *Animal Behav.*, **21**, 726 – 732.
- Grubb J. C. (1975), "Olfactory orientation in the southern leopard frog, *Rana utricularia*," *Herpetologica*, **31**(2), 219 – 221.
- Hasler A. D. and Scholz A. T. (1978), "Olfactory imprinting in Coho Salmon (*Oncorhynchus kisutch*)," in: *Animal Migration, Navigation and Homing*, Springer-Verlag, Berlin, pp. 356 – 369.
- Hepper P. G. and Waldman B. (1992), "Embryonic olfactory learning in frogs," *Quart. J. Exp. Psychol. Sec. B. Comp. Phys. Psych.*, **44B**(3 – 4), 179 – 197.
- Hudson R. (1999), "From molecule to mind: the role of experience in shaping olfactory function," *J. Comp. Physiol. A*, **185**, 297 – 304.
- Kaji S., Nakazawa H., and Ishii S. (1997), "Changes in the electro olfactogram during breeding migration in the Japanese toad, *Bufo japonicus*," in: *Herpetology'97. Abstrs. of the 3rd World Congr. Herpetol., Prague, August 2 – 10, 1997*, p. 248.
- Khmelevskaya N. V. (1989), "Spatial structure of the common frog *Rana temporaria* population and its dynamics," in: *Zemnovodnye i Presmykaushchiesya Moskovskoi oblasti. Materialy soveshchaniya po gerpetofaune Moskvyy i Moskovskoi oblasti [Amphibians and Reptiles of Moscow Region. Materials of Meeting on Herpetofauna of Moscow and Moscow Region]*, Nauka, Moscow, pp. 124 – 133 [in Russian].
- Khmelevskaya N. V. and Deulina T. O. (1972), "On the role of the sense of smell in the life of Anura," *Zool. Zh.*, **51**(5), 764 – 767 [in Russian, with an English abstract].
- Kiesecker J. M., Chivers D. P., and Blaustein A. R. (1996), "The use of chemical cues in predator recognition by western toad tadpoles," *Animal Behav.*, **52**(6), 1237 – 1245.
- Kiseleva E. I. (1984), "Responses of behavioural reactions in the *Rana temporaria* tadpoles to chemical stimuli under the conditions of pretreatment," *Zool. Zh.*, **63**(7), 1046 – 1054 [in Russian, with an English abstract].
- Kiseleva E. I. (1995), "Natural amino-acids as effective stimuli, causing chemoreceptorally directed behaviour in anuran tadpoles," *Zh. Obshch. Biol.*, **56**(3), 329 – 345 [in Russian, with an English abstract].
- Kiseleva E. I. (1997), "Kin recognition in European anuran tadpoles and their sociality," in: *Herpetology'97. Abstrs. of*

- the 3rd World Congr. Herpetol., Prague, August 2 – 10, 1997, p. 112.
- Kruzhalov N. B.** (1980), “Natural aminoacids as olfactory stimuli for some amphibians,” in: *Sensornye Sistemy. Obonyanie i Vkus [Sensory Systems. Olfaction and Taste]*, Nauka, Leningrad, pp. 60 – 72 [in Russian].
- Lecanuet J.-P. and Schaal B.** (1996), “Fetal sensory competencies,” *Eur. J. Obstet. Gyn. Rep. Biol.*, **68**, 1 – 23.
- Léna J. P. and De Fraipont M.** (1998), “Kin recognition in the common lizard,” *Behav. Ecol. Sociobiol.*, **42**, 341–347.
- Lukianov A. S., Potapov A. A., and Khmelevskaya N. V.** (1985), “On possible involvement of smelling in spring spawning migrations of *Rana temporaria* L.,” *Zh. Obshch. Biol.*, **46**(6), 786 – 793 [in Russian, with an English abstract].
- Lyalyushko D. M.** (1972), “Orientation of *Rana esculenta* L.,” *Vestn. Zool.*, No. 4, 41 – 45 [in Russian, with an English abstract].
- Lyalyushko D. M., Pashchenko Yu. O., and Babenko L. A.** (1972), “Orientation of amphibians when excluding some sense organs,” *Vestn. Zool.*, No. 6, 90 – 91 [in Russian, with an English abstract].
- Manteifel Yu. B. and Zhushev A. V.** (1998), “Behavioral reactions of larvae of four anuran species on chemical stimuli from predators,” *Zh. Obshch. Biol.*, **59**(2), 192 – 208 [in Russian, with an English abstract].
- Martof B. S.** (1962), “Some observations on the role of olfaction among salientian amphibia,” *Phys. Zool.*, **35**(3), 270 – 272.
- Minguez E.** (1997), “Olfactory nest recognition by British storm-petrel chicks,” *Animal Behav.*, **53**(4), 701 – 707.
- Nevitt G. A., Dittman A. H., Quinn T. P., and Moody W. J., Jr.** (1994), “Evidence for a peripheral olfactory memory in imprinted salmon,” *Proc. Natl. Acad. Sci. USA*, **91**, 4288 – 4292.
- Ogurtsov S. V. and Bastakov V. A.** (2001), “Imprinting on native pond odor in the pool frog, *Rana lessonae* Cam.,” in: *Chemical Signals in Vertebrates. Vol. 9*, A. Marchlewskaja-Koj, J. J. Lepri, and D. Müller-Schwarze (eds.), Kluwer Academic/Plenum Publishers, New York, pp. 433 – 441.
- Pearl Ch. A., Cervantes M., Chan M., Ho U., Shoji R., and Thomas E. O.** (2000), “Evidence for a mate-attracting chemosignal in the dwarf african clawed frog *Hymenochirus*,” *Hormones Behav.*, **38**, 67 – 74
- Pfennig D. W.** (1990), “‘Kin recognition’ among spadefoot toad tadpoles: a side-effect of habitat selection,” *Evolution*, **44**, 785 – 798.
- Sinsch U.** (1987), “Orientation behaviour of toads (*Bufo bufo*) displaced from the breeding site,” *J. Comp. Physiol. A*, **161**(5), 715 – 727.
- Sinsch U.** (1988), “El sapo andino, *Bufo spinulosus*: análisis preliminar de su orientación hacia sus lugares de reproducción,” *Bol. Lima*, **57**, 83 – 91.
- Sinsch U.** (1992a), “Amphibians,” in: *Animal Homing*, F. Papi (ed.), Chapman & Hall, London, pp. 213 – 233.
- Sinsch U.** (1992b), “Sex-biased site fidelity and orientation behaviour in reproductive natterjack toads (*Bufo calamita*),” *Ethol. Ecol. Evol.*, **4**, 15 – 32.
- Sjögren P.** (1994), “Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*,” *Ecology*, **75**, 1357 – 1367.
- Sneddon H., Hadden R., and Hepper P. G.** (1998), “Chemosensory learning in the chicken embryo,” *Physiol. Behav.*, **64**(2), 133 – 139.
- Spaeti U.** (1978), “Development of the sensory systems in the larval and metamorphosing European grass frog (*Rana temporaria* L.),” *J. Hirnforschung*, **19**(6), 543 – 575.
- Spieler M. and Linsenmair K. E.** (1997), “Choice of optimal oviposition sites by *Hoplobatrachus occipitalis* (Anura: Ranidae) in an unpredictable and patchy environment,” *Oecologia*, **109**(2), 184 – 199.
- Vasiliev B. D.** (1967), “On adaptive value of differences in the function of olfactory system of three species of frogs searching ‘home’,” in: *Issledovanie Adaptivnogo Povedeniya i Vyshei Nervnoi Deyatel'nosti. Referaty Dokladov k III Soveshchaniyu po Ékologicheskoi Fiziologii, Biologii i Morfologii [Research on Adaptive Behaviour and Supreme Neural Activity. Report Materials for III Meeting on Ecological Physiology, Biology, and Morphology]*, Novosibirsk, pp. 34 – 36 [in Russian].
- Wabnitz P. A., Bowie J. H., Tyler M. J., Wallace J. C., and Smith B. P.** (1999), “Aquatic sex pheromone from a male tree frog,” *Nature*, **401**(6752), 444 – 445.
- Waldman B.** (1981), “Sibling recognition in toad tadpoles: the role of experience,” *Zeitsch. Tierpsychol.*, **56**(4), 341–358.
- Waldman B.** (1985), “Olfactory basis of kin recognition in toad tadpoles,” *J. Comp. Physiol. A*, **156**, 565 – 577.
- Waldman B.** (1991), “Kin recognition in amphibians,” in: *Kin Recognition*, P. G. Hepper (ed.), Cambridge Univ. Press, Cambridge, pp. 162 – 219.