

## MINI-REVIEW: THE ORIENTATION BEHAVIOUR OF AMPHIBIANS

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### INTRODUCTION

Migrations from one microhabitat to another, during development or reproduction, form part of the life history of most Amphibia. The embryonic and larval development often take place in bodies of water, and larvae regularly move between the sites which provide food, shelter, or other resources. During metamorphosis tadpoles of the terrestrial species orient towards the shore line. Juveniles disperse over the adjacent areas, sometimes reaching places several kilometres distant from their natal site. Adults return to specific breeding sites, sometimes in spectacular mass migrations. These examples demonstrate that amphibians migrate during all developmental stages, if important habitat resources such as food, shelter or mates are spatially separated.

During the past decades many studies presented evidence that migratory amphibians and even some sedentary species exhibit orientation behaviour (reviews: e.g. Adler, *Vertebrata Hungarica* 21, 7, 1982; Ferguson, *Ann. NY Acad. Sci.* 188, 30, 1971; Sinsch, *Ethology Ecology and Evolution* 2, 65, 1990). Displaced individuals are able to relocate known sites (e.g. ponds, home ranges) using a variety of directional cues to accomplish homing. This review summarises the present knowledge on the complex relationships between developmental stage, migratory range and preferred orientation cues.

### MIGRATORY BEHAVIOUR

Navigation means long-distance orientation independent of familiarity with the release site (Able, in: *Animal migration, orientation and navigation* (ed. Gauthreaux), 283, 1981). Therefore, the first step of analysis of orientation behaviour must be directed to the migratory experience obtained by larvae, juveniles and adults. Presently, our knowledge is limited to the scarce data on some terrestrial Anura and Urodela, whereas information on aquatic species and Gymnophiona are absent. The next step of analysis concerns the evidence that amphibians home to specific sites in their habitat. Site fidelity permits the experimental approach to orientation behaviour because the goal of displaced individuals can be predicted and the spatial range of homing response estimated.

*Natural migratory range:* The spatial experience obtained during larval development ranges from none

in terrestrial-brooding and viviparous species to the size of the natal pond. In stream-breeding species such as *Ambystoma texanum* (Petranka, *J. Herpet.* 18, 106, 1984) and *Ascaphus truei* (Landreth & Ferguson, *Herpetologica* 23, 81, 1967) drift may increase the area of familiarity considerably. Generally, the contribution to local knowledge gained during the larval stage appears to be small in most amphibians.

In contrast, dispersing juveniles move up to 800m per night (*Rana pipiens*; Dole, *Copeia*, 221, 1971) and maximally 35km away from their natal pond (*Bufo marinus*; Freeland and Martin, *Aust. Wildl. Res.* 12, 555, 1985). Juvenile *Bufo woodhousii* are about six times more vagile than conspecific adults (Breden, *Copeia*, 386, 1987). Observations on *Bufo calamita* (Sinsch, unpubl.) support this stage-specific difference in migratory activity. At least in these species the local map of adults mainly bases on the migratory experience obtained during the juvenile stage. Further quantitative studies should reveal whether the migratory range of juveniles is generally greater than that of adults.

The migratory range of adults ranges from a few metres in sedentary salamanders to 5.2km and 15km respectively in the frogs *Rana pipiens* (Dole, *Copeia*, 221, 1971) and *R. lessonae* (Tunner, Austria; pers. communication). The maximum speed of migration is 500m per night in *Bufo bufo* (Gelder, *Herpet. J.* 1, 111, 1986) and 400m in *Taricha rivularis* (Twitty *et al.*, *Proc. Nat. Acad. Sci. US* 56, 864, 1966). Thus, all maximum records of migrating adults are considerably lower than those of juvenile amphibians. Adults are undoubtedly able to cover large distances, but most individuals even of wide-ranging species such as *Bufo bufo* (Heusser, *Rev. Suisse Zool.* 75, 927, 1968) stay within a few hundred metres of their natal site during their whole lifetime.

In conclusion, the natural migratory range of Amphibia amounts to 35km at most, which is far smaller than that of any other vertebrate class. Ectothermy and the water permeability of skin limit locomotory activity to periods of favourable temperatures and humidity and so constrain the migratory range.

*Site fidelity:* Adults of many salamander and anuran species annually return to the same pond for reproduction, others prefer specific parts of their habitat as home ranges, and some even hibernate at the same site during their whole lifetime. These examples illustrate the meaning of site fidelity; voluntary homing to specific sites following active or passive displacement.

Experimental evidence for homing to breeding ponds or terrestrial nests has been presented in 13 species of Urodela (*Ambystoma maculatum*, *A. opacum*, *Aneides aeneus*, *Desmognathus auriculatus*, *D. fuscus*, *D. ochrophaeus*, *Notophthalmus viridescens*, *Taricha granulosa*, *T. rivularis*, *T. torosa*, *Triturus alpestris*, *T. cristatus*, *T. vulgaris*), and in 16 anurans (*Acris gryllus*, *Ascaphus truei*, *Bufo americanus*, *B. boreas*, *B. bufo*, *B. calamita*, *B. japonicus*, *B. spinulosus*, *B. terrestris*, *B. valliceps*, *B. woodhousii*, *Hyla regilla*, *Pelobates fuscus*, *Pseudacris triseriata*, *Rana clamitans*, *R. temporaria*, *Scaphiopus bombifrons*). In many species reproductive adults return to their natal pond as shown in *B. woodhousii* (Breden, Copeia, 386, 1987). The homing response seems widely independent of information obtained during experimental displacement provided that the release site is located within the migratory range. Such strong attachment to a specific site indicates that breeding places are a scarce resource in the habitat. In fact, following the construction of an artificial pond within the migratory range of a *B. bufo* population, a large number of individuals broke their former breeding site fidelity and headed directly to the new pond (Schlupp *et al.*, Informationsdienst Naturschutz Niedersachsen 10, 12, 1990). This study shows that breeding site fidelity is not unalterable. The fact that new ponds are rapidly colonised by species with a rather strict breeding site fidelity supports this view.

Home site fidelity has been reported for an additional number of species (Urodela: *Ambystoma talpoideum*, *A. tigrinum*, *Eurycea lucifuga*, *Plethodon cinereus*, *P. jordani*, *Salamandra salamandra*; Anura: *Atelopus varius*, *Bufo hemiophrys*, *B. marinus*, *B. punctatus*, *Dendrobates pumilio*, *Hyla cadaverina*, *R. pipiens*). The motivation to return towards a home area may last a few days (*B. hemiophrys*; Breckenridge and Tester, Ecology 42, 637, 1961), one season (*B. bufo*; Heusser, Rev. Suisse Zool. 75, 927, 1968) or a lifetime (*B. woodhousii*; Ferguson, Herpetologica 16, 112, 1960). The extent of home site fidelity is probably a function of the number of suitable home ranges in the habitat.

Finally, there are two well-documented cases of hibernation site fidelity. Several individuals of *Salamandra salamandra* hibernated in the same cave for 20 years (Feldmann, Jahrb. Feldherpet. 1, 33, 1987), and some *B. hemiophrys* in the same mould for at least 6 years (Kelleher and Tester, Ecology 50, 1040, 1969).

In conclusion, selection has favoured homing behaviour to specific parts of the habitat instead of random search for new resources by adults. Basic to homing, however, is exploratory behaviour at the juvenile stage to get an idea of the distribution of resources. Considering the scarcity of appropriate localities for reproduction, nutrition, and shelter, homing is obviously a strategy to minimise energetic expenditure for locomotory activity.

*Spatial range of homing response:* Individuals of several species have been passively displaced to estimate the range of their homing response. The extensive field studies on the newt *T. rivularis* revealed a range exceeding 12.8km (Twitty *et al.*, Proc. Nat.

Acad. Sci. U.S. 57, 342, 1967) and a speed of homing of up to 8km per year (Twitty *et al.*, 56, 864, 1966) which have not been matched by any other amphibian. In anurans the range seems smaller: 7 out of 10 displaced toads *B. bufo* oriented towards the 3km distant breeding pond (Sinsch, J. Comp. Physiol 161A, 715, 1987). In both studies the release sites were far outside the adults' migratory range. Nevertheless, it cannot be excluded that migrations during the juvenile stage (*B. bufo*: 2-4 years; *T. rivularis*: 5 years) extended to the release site. Displaced individuals of several other anuran species did not show homeward orientation, if the release site was outside their migratory range.

Amphibians share some common features of homing behaviour: (1) the number of individuals which do not intend to home increases with the displacement distance; (2) the time to determine the correct home direction or to initiate homing also increases with the displacement distance; (3) the motivation to home can persist several years. Nevertheless, it will remain doubtful that amphibians are able to navigate from unfamiliar sites towards a home site, unless the previous migratory experience of the displaced individuals is exactly known.

#### SENSORY BASIS OF ORIENTATION

Amphibia use a number of different ways to accomplish homing. Path integration as evidenced in the newt *Taricha torosa* (Endler, Behaviour 37, 15, 1970) relies entirely on the uninterrupted flow of information during the outward movement. However, it is probably of little importance because the absence of outward journey information does not impair homing. Piloting towards a fixed reference (e.g. breeding chorus) is a form of homing based exclusively on cues which are perceived at the release site. Another possibility which does not require a geographically fixed reference is compass orientation along a preferred direction ('y-axis': Ferguson and Landreth, Behaviour 26, 105, 1966). However, this behaviour only results in homing, if the compass direction leads to a familiar area. The most complex way to home is the map-compass orientation which relies on (1) the determination of the exact position relative to the goal (map-step), and on (2) the calculation of the direction which leads directly to the goal (compass-step; Able, in: Animal migration, orientation and navigation (ed. Gauthreaux), 283, 1981).

Amphibians employ acoustic, magnetic, mechanical, olfactory and visual cues for orientation. The present knowledge mainly bases on studies of those species mentioned before, that means on more or less terrestrial salamanders and anurans, and, with a few exceptions, on adults. The following sections summarise the classes of cues as well as their possible function in the orientation system.

*Acoustic cues:* Short-distance acoustic communication is widespread among anurans. However, wide-ranging vocalisation is restricted to few species such as *Bufo calamita* (Arak, Nature 306, 261, 1983), *Dendrobates histrionicus* (Zimmermann, Fortschr. Zool. 38, 61, 1990), and *Pseudacris triseriata*

(Ferguson, *Ergeb. Biol.* 26, 128, 1963). Choruses produce advertisement calls which are audible at 500–1000m distance. Nevertheless, homing of *B. calamita* is neither influenced by misleading acoustic information nor by the absence of choruses (Sinsch, *Fortschr. Zool.* 38, 75, 1990). Moreover, the acoustic transmission of the position of a potential breeding site over large distances implies great energetic expenditure. Therefore, this strategy probably is only used by species which reproduce at unpredictable sites (e.g. temporary ponds). Even in species which employ phonotaxis for long-distance piloting acoustic cues can be replaced by other cues.

**Magnetic cues:** Orientation based on earth's magnetic field was first demonstrated in *Eurycea lucifuga* (Phillips, *J. Comp. Physiol.* 121, 273, 1977), later also in *Notophthalmus viridescens* (Phillips, *J. Comp. Physiol.* 158A, 103, 1986), *Bufo bufo* (Sinsch, *J. Comp. Physiol.* 161A, 715, 1987), *B. calamita* (Sinsch, *Fortschr. Zool.* 38, 75, 1990), *B. spinulosus* (Sinsch, *Boletin de Lima* 57, 83, 1988), and *Xenopus laevis* (Leucht, *Fortschr. Zool.* 38, 321, 1990). Evidence in adults is based on deprivation experiments in the field and controlled alterations of magnetic parameters in the laboratory, and in tadpoles of *X. laevis* just on the latter. The effects range from complete disorientation to predictable false directional choice. The inclination of the magnetic field (vertical component) serves as reference for a compass system (Phillips, *J. Comp. Physiol.* 158A, 103, 1986). Moreover, there are recent indications that magnetoperception may be related to the map-step (Phillips, *Science* 233, 765, 1986). Yet evidence is still too weak to attempt a final evaluation of the function of magnetic parameters in the orientation behaviour of amphibians. Since toads deprived of magnetic information still home successfully, there obviously exists an alternative map to the proposed magnetic one (Sinsch, *Fortschr. Zool.* 38, 75, 1990).

**Mechanical cues:** Water surface-waves (Walkowiak and Münz, *Naturwissenschaften* 72, 49, 1985), seismic signals (Lewis and Narins, *Science* 227, 187, 1985) and rheotaxis (Durand and Parzefall, *Behav. Processes* 15, 285, 1987) are used in several species for short-distance orientation. However, there is no indication that mechanical cues provide directional information for long-distance orientation.

**Olfactory cues:** Many adult salamanders and anurans use odours as directional cues. However, the effect of anosmia on homeward orientation differs considerably among the species: (1) homing is completely impaired in *Desmognathus fuscus* (Barthalmus and Bellis, *Copeia*, 632, 1972) and *Plethodon jordani* (Madison, *NASA SP* 262, 485, 1972); (2) initial orientation towards home is greatly reduced, but homing is still possible in *Taricha rivularis* (Grant *et al.*, *Science* 160, 1354, 1968), *Notophthalmus viridescens* (Hershey and Forester, *Can. J. Zool.* 58, 266, 1980), *Bufo boreas* (Tracey and Dole, *Copeia*, 693, 1969), and *B. bufo* (Sinsch, *J. Comp. Physiol.* 161A, 715, 1987); (3) homeward orientation is only affected during the simultaneous absence of visual cues in *B. valliceps* (Grubb, *Copeia*, 674, 1970). In toads of the

genus *Bufo* the importance of olfactory cues for initial orientation increases with the size of the migratory range (Sinsch, *Fortschr. Zool.* 38, 75, 1990).

The chemical nature of the olfactory cues is completely unknown. During the breeding migration guiding odours originate at least partly from the breeding pond itself as evidenced in *Rana temporaria*, *Bufo bufo*, *B. woodhousii*, *Pseudacris clarki*, and *P. streckeri* (e.g. Grubb, *Anim. Behav.* 21, 726, 1973). Although olfaction is undoubtedly involved in the orientation of many amphibians, its specific function is unclear. Odours may serve for piloting along gradients of familiar odours (Adler, *Photochem. and Photobiol.* 23, 275, 1976) or as sources of a local map (Sinsch, *Ethology Ecology and Evolution* 2, 65, 1990).

**Visual cues:** Vision is used for the perception of directional cues in tadpoles (Justis and Taylor, *Copeia*, 98, 1976), in juveniles (Tracy, *Copeia*, 145, 1971), and in adults (Landreth and Ferguson, *Nature* 215, 516, 1967). The cues involved are either fixed visual landmarks (e.g. shore lines, forest silhouettes) or periodically 'moving' celestial cues (e.g. sun, moon, stars, skylight polarisation patterns). In Amphibia, not only the lateral eyes perceive such cues but also extraocular photoreceptors of the pineal complex (Adler, *Photochem. and Photobiol.* 23, 275, 1976). The interaction of both sensory systems has been demonstrated in *Acris gryllus* (Taylor and Ferguson, *Science* 168, 390, 1970): eyeless frogs and frogs with covered pineal complex orient as untreated individuals, whereas eyeless frogs with covered pineal complex orient randomly. Analogous experiments with *Ambystoma tigrinum* (Taylor, *Anim. Behav.* 20, 233, 1972) yielded the same result indicating similar sensory mechanisms in Urodela and Anura.

The role of visual cues in homeward orientation apparently differs among the species and depends on the class of cues. Fixed visual landmarks can serve for piloting as evidenced in the toad *B. bufo* (Heusser, *Rev. Suisse Zool.* 76, 444, 1969). Celestial cues are used as references for time-compensated compass systems (Adler, *Vertebrata Hungarica* 21, 7, 1982). The ability of larval and adult amphibians to use the axis (e-vector) of linearly-polarised light for orientation and the visibility of skylight polarisation even when the sun's position cannot be determined directly suggest that the reference of the sun compass probably is the e-vector and not the sun itself. In nocturnal amphibians star or lunar compasses have been demonstrated (Plasa, *Z. Tierpsychol.* 51, 112, 1979), but their contribution to orientation is probably low because most individuals migrate in rainy nights under cloud cover. Finally, fixed visual landmarks are potential map sources as indicated by the findings that (1) visual landmarks can apparently supplant olfactory cues in *B. valliceps* (Grubb, *Copeia*, 674, 1970), and that (2) blindfolded *B. spinulosus* were completely disoriented, although they were not deprived of magnetic and olfactory cues (Sinsch, *Boletin de Lima* 57, 83, 1988). Generally, visual cues are more important for the orientation of species with a small migratory range than for that of wide-ranging species.

*Multisensory system of orientation:* An important feature of the orientation behaviour of amphibians is the integration of many potential cues into a redundant system which leads them safely to their goal even if the availability of cues changes during migration. The apparent contradiction to the principle of parsimony is probably consequence of (1) differences in the availability of potential cues among different biotopes inhabited by the same species, (2) the necessity to reach a breeding site at a fixed time (e.g. explosive breeders), and (3) the increased risk of losing life during a prolonged search for the goal. The natural migratory range, the diel activity period and the type of breeding site influence considerably the selection of normally-used cues for initial orientation. The ranking of the sensory input obtained from the potential cues into a specific hierarchy optimises the available information in every habitat. Thus, the interspecific differences in orientation behaviour are probably modifications of the same basic system.

## PROSPECT

The concept of a multisensory orientation system in Amphibia (Ferguson, Ann. NY Acad. Sci. 188, 30, 1971) has stimulated research specifically with regard to the identification of directional cues and perceiving sensory systems. Presently, we know that amphibians usually prefer certain cues for initial orientation but also that they use every available source of information to back up their orientation system. A major future task will be the analysis of the neuronal base of ranking the sensory input to filter out reliable directional information. Moreover, the system of magnetoperception has still not been identified. Besides the neurophysiological approach, future field studies will contribute considerably to our understanding of orientation, if they consider the interactions of migratory range, habitat and preferred orientation cues during the complete life history of the studied species.

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## SUMMER ACTIVITY PATTERNS AND THERMOREGULATION IN THE WALL LIZARD, *PODARCIS MURALIS*

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### ABSTRACT

Body temperature of active *Podarcis muralis* from Noreña (Asturias; Northern Spain) during summer averages 33.8°C (SD = 2.0, n = 116), and similar values were found in other close populations (grand mean: 33.8°C, SD = 2.3, n = 171). There were no significant differences neither in body temperatures between populations nor between sex/age groups within populations. Daily activity pattern is bimodal, with depressed activity during the warmer hours at the midday. This pattern of activity, as well as the significant negative correlation between the percentage of lizards at sun and the environmental temperatures, are indicative of behavioural thermoregulation. The standard deviations of the mean body temperature and the slopes of the regressions of body temperature on environment temperatures are indicative of a relatively imprecise thermoregulation. Populations from the highest altitudes show a higher variability in body temperature and a greater dependence on the thermal environment.

### INTRODUCTION

Since the pioneer study by Cowles and Bogert (1944), finding that desert reptiles behaviourally regulate body temperature, many aspects of reptilian thermoregulation have been examined, so that thermal ecology represents currently a major topic in reptilian research. Many studies have shown that, under a

variety of environmental conditions, most diurnal lizards are able to regulate their body temperature within relatively narrow limits during the active periods (see review in Avery, 1982).

The mean body temperature, calculated by averaging the temperatures recorded from active animals in the field, is commonly used as a measure of the thermal status of a species. However, field body