

7 Migration in amphibians and reptiles: An overview of patterns and orientation mechanisms in relation to life history strategies

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7.1 Abstract

Differences in integumentary permeability dictate alternative life history strategies in amphibians and reptiles. Limiting resources for amphibians are chiefly associated with availability of water and, as a consequence, amphibian migrations are chiefly associated with movements to and from aquatic breeding habitats. These cyclic migrations from breeding to overwintering sites may be direct, or may be interrupted by periods of residence at foraging sites. In general, migrations take place over relatively short distances and are constrained by the problem of water balance associated with exposure during longer overland journeys. Many amphibians exhibit complex mechanisms of orientation involving multiple sensory modalities and are capable of precise homing abilities.

Among reptiles, migrations are chiefly associated with travel to and from egg laying sites, as displayed by turtles, or communal hibernacula, as is characteristic of some snakes. Marine turtles, in particular, undertake long distance migrations (up to thousands of kilometers) to reach nesting beaches and, sometimes, foraging grounds. In these chelonians, complex patterns of movement vary ontogenetically, as well as by gender and species. A variety of cues are used to locate destinations, including celestial, geomagnetic, olfactory, auditory, thermal, wave, and current pattern signals; however, evidence of a map-compass system of navigation is equivocal.

The migratory patterns of amphibians and reptiles often bring them into conflict with human resource utilization. For amphibians, breeding migrations that cross busy roads or areas turned over to agricultural

production lead to mass mortality. Marine turtle migratory pathways often result in conflicts with fishery activities. Knowledge of life history strategies and associated migratory behavior is essential for effective conservation measures.

Key words: Conservation, foraging, hibernation, homing, life history, orientation.

7.2 Introduction

Although amphibians and reptiles do not constitute a monophyletic group, they are often treated together under the rubric of herpetology because they are terrestrial vertebrates that share the plesiomorphic physiological traits of ectothermy and poikilothermy. Although they share some aspects of their general biology because of these traits, they also differ considerably in terms of basic aspects of anatomy, physiology, behavior and reproductive biology. One major contrast is associated with water balance and the range of habitats that can be occupied as a result of osmoregulatory constraints. Amphibians have an integument that is highly permeable to water, and the rate of evaporation from it is similar to that from a free water surface (Katz and Nagel 1994). It is also a route of water absorption and ion uptake, and plays a major role in osmoregulation. Such properties of the amphibian integument render them behavioral osmoregulators, largely controlling water flux across the skin by occupancy of appropriate microhabitats. Conversely, the integument of reptiles shows low permeability to water, ions, and gases, and forms an effective permeability barrier (Lillywhite and Maderson 1982) that allows them to be physiological osmoregulators.

The above-stated differences in integumentary function, coupled with the differences in breeding biology of amphibians and reptiles, place differing demands upon their ability and their requirements to migrate although, of course, different species in each taxon will manifest this in slightly different ways. Many species of amphibian have a biphasic lifestyle with typically an aquatic larval stage and a terrestrial adult stage. Although there are many exceptions to this, most amphibian species that undergo metamorphosis undertake breeding migrations (of short to relatively long distances) between foraging and/or overwintering sheltering sites and breeding sites, and back again. These migrations can be physiologically challenging, and are usually triggered by particular combinations of environmental circumstances. Distances traveled are

proportional to survivability in what can be osmotically very challenging conditions. Thus, although amphibian migrations may not encompass vast distances, they nonetheless require sophisticated behavioral and navigational mechanisms to undertake these repeated movements.

Reptiles, as amniotes, are able to cover considerably greater distances in migratory movements than amphibians, but their breeding biology, centered around the cleidoic egg or derivatives thereof (Russell and Bauer 2000) does not generally require migrations for reproductive purposes (although many of the longest and most spectacular reptile migrations are for reproductive purposes -- see below). Reptilian migrations are, therefore, much more likely to be based upon trophic resource exploitation, although common breeding sites may be the focus of periodic aggregations.

Dispersal and migration are two important and distinct types of animal movement. When an animal disperses it moves from one home range to another home range, and does not subsequently return to the original location. Furthermore, dispersal involves undirected movements of animals to unknown locations (Zug et al. 2001). Conversely, migration has been described as the movement of an animal from one location to another, followed by its subsequent return to the original location (Alcock 1975; Linzey 2001). Furthermore, migratory movements tend to be directed towards specific locations or goals. However, the migration of animals can be very complicated and highly variable between species, and thus broader definitions of migration as simply "the act of moving from one spatial-unit to another" (Baker 1978) or "a specialized behavior especially evolved for the displacement of the individual in space" (Dingle 1980) have also been adopted. These definitions indicate that migration occurs when the resources required by an animal are spatially or temporally separated, thus forcing movement in order to exploit these resources (Baker 1978; Semlitsch 1985; Pilliod et al. 2002). In this way migration also differs from the foraging movements of animals within their home range, as foraging involves movement within a home range from one feeding site to another, rather than movement between different types of resources (Baker 1978). Generally, migratory movements can be defined by five key features: 1) they are persistent and of greater duration than movements within the animal's home range; 2) movement is directional and takes place along relatively straight line paths (that is, having the properties of directed movement); 3) movements are purposeful and may be related to a scarcity of resources; 4) movements have a defined beginning and end; and 5) animals allocate energy specifically towards migratory movements (Dingle 1996). It is important to note that although these movements may be bidirectional, under this definition this is not necessary for a movement

to be considered a migration. Furthermore, although these five characteristics are common components of many migrations, they may not be evident in all examples (Dingle 1996).

Although migrations do not have to be extensive, they do involve the movement of an animal beyond the boundaries of its normal home range, and thus can be very strenuous and energetically expensive (Alcock 2001). Thus, if an animal can acquire all the resources it requires without leaving the boundaries of its home range it will not migrate. Animals will only migrate if the benefits of moving outweigh the costs of the migration (Alcock 2001), but distance alone may not be the only arbiter of such costs as some turtle and tortoise species bypass seemingly good nesting sites on the way to much more distant ones. There are three primary reasons that an animal will migrate. Firstly, animals may undertake annual migrations between feeding areas and breeding, nesting (Luschi 2003), or hibernation sites if the feeding area does not contain suitable breeding or overwintering sites, although an assessment of suitability is sometimes difficult to define. Secondly, animals may migrate in response to habitat changes. For instance, migrations may occur in order to avoid drought or flood conditions. Finally, animals may migrate in response to habitat shifts in their prey, although this is often related to climatic changes as well (Pough et al. 1998; Linzey 2001).

It is evident from the foregoing that migratory movements will have both life history and long-term populational influences as they play out over time and over changing landscapes at several scales. Over the short term, amphibians and reptiles (with the exception of marine turtles -- see below) generally cover only short distances in their migrations (in contrast to many fish, birds and mammals), so that the genetic consequences of these movements may well be swamped out by occasional migrants from adjacent breeding areas. Dispersal results in the establishment of metapopulations and promotes genetic variability (Kozlowski 1999; Brede and Beebee 2004). The potential for dispersal may differ between sexes in some taxa (for example in the frog *Rana temporaria*), in which males are more philopatric than females (Palo et al. 2004). Dispersal in the short term can thus influence the genetic structure of populations and alter the consequences of fundamental migratory patterns. Longer-term patterns are influenced by geologic history and the combined effects of vicariance and waif dispersal (Garcia-París et al. 2003; Vences et al. 2003, 2004; Martinez-Solano et al. 2004; Pauly et al. 2004). In this contribution, we focus on the life history strategies of migration in amphibians and reptiles, but recognize that there are additional short-term and long-term consequences of such behaviors.

7.3 Homing and Orientation

One of the most important aspects of migration is that it generally involves directed, goal-oriented movement. Furthermore, animals frequently return to the same location year after year with great accuracy. It is thus essential to understand how reptiles and amphibians are able to accomplish these feats, as well as why homing and orientation abilities have developed in these animals. It is likely that orientation behavior evolved in parallel with migratory behavior, as animals that are able to follow a direct course towards the destination expend fewer resources searching, and are less at risk of predation (Sinsch 1990a). In addition to this, the ability to home allows animals to return to a familiar, reliable area, and may even serve to stabilize and equalize the distribution of a population, thereby decreasing competition between individuals (Stebbins and Cohen 1995). There are, however, some disadvantages to homing behavior. For instance, animals are vulnerable to habitat destruction, and may decline in reproductive success if their natal breeding site is destroyed. An example of this is evident in a population of toads that was found to return to the same location for years after their breeding pond had been destroyed (Stebbins and Cohen 1995). In general, homing and orientation abilities are advantageous to migrating animals, although the mechanism by which they accomplish this is poorly understood.

One of the difficulties in studying the sensory basis of orientation in amphibians and reptiles is that new sensory capabilities are constantly being identified. For example, Twitty's (1966) work on olfaction in blinded newts and their homing ability did not consider polarized light effects because these had not yet been revealed. The effect of magnetic fields on orientation is another relatively new area of research. The precise system used to detect magnetic information is still being investigated.

In general, orientation can be broken down into three levels (Fig. 1) which show increasing complexity, and which probably function using different mechanisms. Depending on the distance, and the complexity of the migration an animal undertakes, it may employ only the simplest level of orientation, or any combination of the three levels. The first level of orientation is piloting. An animal that pilots uses a fixed reference, such as visual, auditory, or chemical cues to guide itself towards the destination.

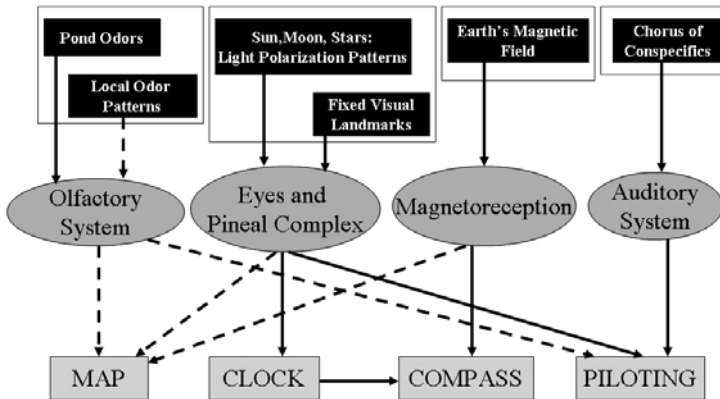


Fig. 1. Relationships between orientation cues (upper row, black boxes), perception systems (middle row, shaded ovals) and possible functional contributions to the map-compass concept (lower row, shaded boxes) for anuran amphibians. Solid arrows indicate demonstrated relationships; dashed arrows represent assumed relationships. After Sinsch (1990a, Fig. 4)

The second level of orientation involves compass orientation, which allows an animal to be aware of the direction in which it is moving. Finally the most complex level is map-compass orientation. This level of orientation involves a map-step, whereby the animal is able to determine its location relative to the goal, and a compass-step, whereby the animal determines the direction that will lead to the goal (Sinsch 1991; Phillips 1998). Map-compass orientation generally requires the use of more than one type of sensory input (Fig. 1), and an animal employing this orientation is capable of true navigation, meaning that it is able to orient towards a specific location even in the absence of familiar landmarks (Phillips 1987).

7.4 Patterns of Amphibian Migration

Short-distance, or microgeographic migrations, are fairly typical of amphibians including many salamanders and anurans (Glandt 1986; Linzey 2001), though nothing is known about the migratory habits of caecilians (Stebbins and Cohen 1995). Many salamanders and frogs require foraging areas, aestivation or hibernation sites, and are dependent upon water for reproduction. If these resources are spatially separated, then

an amphibian must migrate (Sinsch 1990a) (Fig. 2). However, the migratory behavior of amphibians is more constrained than that of other vertebrates, and they generally have much smaller migratory ranges (Sinsch 1990a). For instance, the migratory distance covered by amphibians may be as small as a few meters in some salamanders, and in some frog species like the arboreal *Hyla arborea* (Stumpel 1987). Migrations are generally not longer than 500m in salamanders, and not more than 1500m in anurans (Sinsch 1990a; Johnson 2003) (Fig. 2), and do not exceed speeds of 400m/night in salamanders (*Taricha rivularis*: Twitty et al. 1967) or 500m/night in anurans (*Bufo bufo*: Gelder et al. 1986). Even so, several anuran species, such as *Rana areolata aesopus* and *Bufo bufo*, have been observed to migrate up to 2-3km (Heusser 1968, Glandt 1986; Franz et al. 1988; Sinsch 1990b). The longest migration ever recorded for an amphibian is 15km for two species of European water frogs, *Rana lessonae*, and *R. esculenta* (Tunner 1992). However, most individuals of these species undertake much shorter migrations, and generally migrate only a few hundred meters (Tunner 1992). Even the longest amphibian migrations are very short compared to the much more extensive migrations of other vertebrates, including humpback whales (7000km), arctic terns (16000km), and sea turtles (2200km) (Sinsch 1990a).

The migrations of amphibians are limited for several reasons. Firstly, their skin is permeable to water, and thus they are highly susceptible to water loss. For this reason the migration of amphibians is limited to very humid periods, or they must stop frequently to rehydrate (Sinsch 1990a). Furthermore, amphibians are ectothermic, which further limits their migrations to a narrow range of environmental conditions (Sinsch 1990a).

The most common type of migrations among amphibians are seasonal breeding migrations from terrestrial habitats or hibernacula to aquatic breeding sites, and then back again (Martof 1953; Heusser 1968; Twitty et al. 1967; Orr 1982; Semlitsch 1985; Verrell 1987; Stebbins and Cohen 1995; Sinsch 1990a; Pough et al. 1998) (Fig. 2), although the occurrence of migration varies between species and populations. For instance, there is a great deal of variation in the migratory patterns observed among different groups of salamanders (Glandt 1986).

Breeding migrations are well documented for ambystomatids, salamandrids, and newts of the genera *Taricha* and *Notophthalmus* (Shoop 1965; Twitty et al. 1967; Hurlburt 1969; Gill 1978; Douglas and Munro 1981; Semlitsch 1985; Feldmann 1987; Petranka 1998; Johnson 2003), whereas most plethodontids do not migrate (Petranka 1998) and are not tied to water for reproduction.

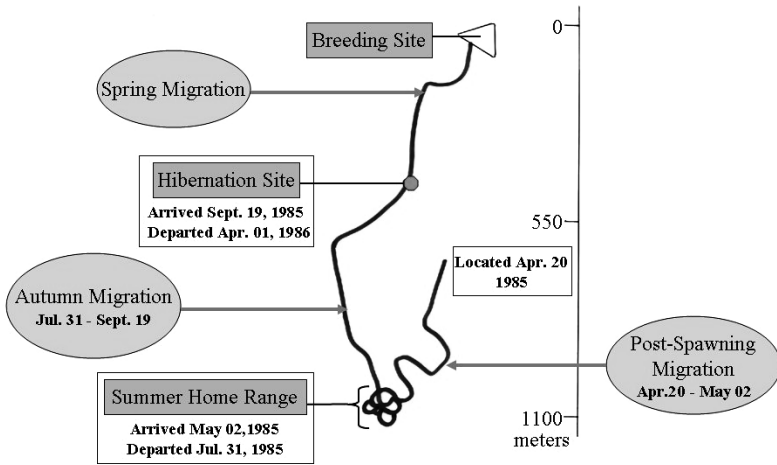


Fig. 2. Annual migrations of a male common toad (*Bufo bufo*) in Bavaria, Germany. Modified after Sinsch (1990a, Fig. 3)

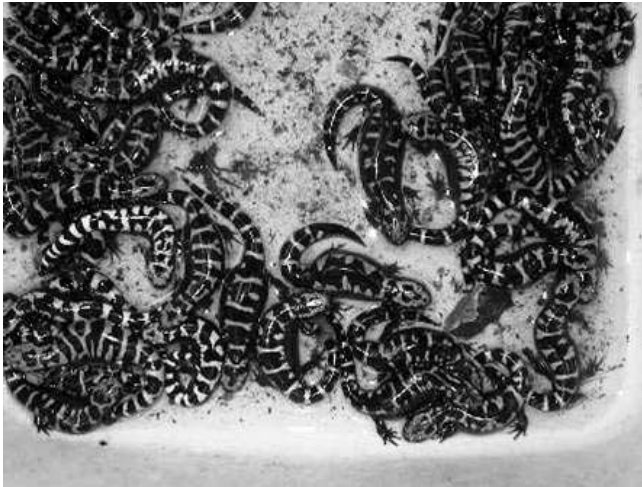


Fig. 3. Marbled salamanders (*Ambystoma opacum*) caught in a pitfall trap during their fall breeding migration at Jug Bay Wetlands Sanctuary, Maryland, USA. Picture reproduced with permission from Chris Swarth, Director and Karyn Molines, Sanctuary Naturalist, Jug Bay Wetlands Sanctuary

In amphibians that do migrate, breeding migrations are often highly synchronized, nocturnal, mass migrations (Fig. 3) that seem to be triggered

by certain environmental conditions (Sinsch 1990a; Pough et al. 1998), but some salamanders and newts may migrate during the day (Hurlburt 1969; Semlitsch and Pechman 1985). Precipitation is the primary environmental factor triggering the migration of many amphibians, although falling barometric pressure in the absence of precipitation may be a trigger for some. Temperature is of secondary importance (Hurlburt 1969; Healy 1975; Semlitsch 1985; Sinsch 1990a; Palis 1997), although the specific cues that trigger the onset of migration vary between species and populations. For example, although precipitation is the most important factor for most amphibian migrations, for the salamanders *Eurycea quadridigitata* and *Ambystoma maculatum*, a drop in air temperature plays a major role in triggering the onset of migration (Semlitsch and McMillan 1980; Sexton et al. 1990). Within North America, there is also some variation in the migratory cues of northern and southern salamander populations (Fig. 3). Southern species, like the Mole salamander (*Ambystoma talpoideum*) tend to migrate during the fall and winter, and the onset of migration is generally associated with decreased temperatures and sometimes with falling barometric pressure. Conversely, northern salamander species migrate during the spring, when temperatures increase (Semlitsch 1985). However, the migrations of both northern and southern species are associated with increased precipitation, and the breeding migrations of numerous other salamander species, including *Ambystoma talpoideum* (Semlitsch 1985), *Ambystoma macrodactylum* (Beneski et al. 1986), and *Ambystoma tigrinum*, have also been found to be limited to periods of increased rainfall (Semlitsch 1985; Beneski et al. 1986; Loredo et al. 1996). Precipitation has also been found to be an important factor in the migration of anurans. For example, the migration of the African ranid frog *Hoplobatrachus occipitalis* from permanent bodies of water to ephemeral breeding ponds corresponds to the arrival of the first rains of the wet season (Spieler and Linsenmair 1998).

Although many amphibians undertake breeding migrations, the pattern of these is not always consistent within populations, and thus migration in these animals may be a conditional tactic (Glandt 1986; Alcock 2001). For instance, among Columbian Spotted Frogs (*Rana luteiventris*) some individuals migrate while others do not (Pilliod et al. 2002). Whether or not an individual migrates seems to be related to the resources available to it. If a certain site has all of the resources that a frog needs to survive, such as food and breeding sites, then there is no necessity to expend energy migrating (Pilliod et al. 2002). Variability among migratory patterns has also been observed among Spotted salamanders (*Ambystoma maculatum*). This species exhibits facultative emigration, and thus the timing of the emigration of salamanders from the breeding ponds back to terrestrial

home ranges varies from year to year, and may occur in either the fall or spring, or may be split between them, depending on the environmental conditions (Madison 1997).

In some amphibian species, both adults and juveniles undertake migrations that may have different patterns. This is especially true for newts, which have both aquatic and terrestrial juvenile stages, and a terrestrial adult stage (Hurlburt 1969; Johnson 2003). Terrestrial juveniles, or efts, and adults of the species *Notophthalmus viridescens* both undertake migrations in the spring, but efts will also migrate in the fall (Hurlburt 1969). Furthermore, adult females generally migrate later than female efts (Hurlburt 1969). Conversely, in the anuran *Bufo hemiophrys* juveniles migrate later than adults (Kelleher and Tester 1969).

Among amphibians, variation between the migratory patterns of males and females of a species is also common. In the salamanders *Ambystoma jeffersonianum* and *A. maculatum* males tend to migrate earlier than females (Douglas 1979; Sexton et al. 1990). Males seem to have a lower threshold for environmental cues, and will migrate as soon as the minimal conditions for migration are met. Females, on the other hand, will migrate only when conditions have improved and stabilized, such that there is reduced environmental danger during their migration (Douglas 1979). This difference in the migratory patterns of male and female salamanders relates to the differing reproductive strategies of the sexes. Females are a limiting resource to male reproductive success, and thus males arrive at the breeding site early in order to enhance their reproductive success by ensuring that they are present when the females arrive. Conversely, females do not need to compete for access to mates, and thus are able to arrive later, allowing them to travel when conditions are safer, and also allowing them to have a greater choice of mates when they arrive at the breeding pond (Douglas 1979). In the Chinhai salamander, *Echinotriton chinhaiensis*, only females migrate to spawning ponds, as fertilization appears to take place when the animals are dispersed (Xie et al. 2000).

Male and female migrations also differ in several species of anurans, including *Rana luteiventris*, *Rana clamitans*, *Bufo hemiophrys* and *Bufo microscaphus californicus* (Martof 1953, Sweet 1993; Pilliod et al. 2002). For instance, male *Rana clamitans* have been observed to visit more than one breeding area in order to meet reproductive demands, while females remain in only one breeding area (Martof 1953), and male *Bufo hemiophrys* and *B. bufo* have been found to migrate earlier than females (Kelleher and Tester 1969; Gittens 1983). Another example is evinced by Columbian Spotted frogs and Wood frogs, in which females are found to undertake longer migrations than males (Pilliod et al. 2002). This difference may be related to a physical limitation, as males of these species

tend to be smaller than the females, and thus may not be capable of long migrations; or it may be related to the differing reproductive strategies of males and females, with males remaining near breeding sites so that they can more easily compete for females in the spring. Another possible explanation is that males require less energy than females and thus they do not have to migrate to better foraging sites (Pilliod et al. 2002).

In addition to breeding migrations, some amphibians undertake migrations from summer feeding ranges or breeding areas, to overwintering or hibernation sites (Fig. 2). This behavior has been observed in numerous anuran species, including *Rana clamitans* (Martof 1953; Lamoreux and Maddison 1999), *R. sylvatica* (Bellis 1965), *Scaphiopus holbrookii* (Pearson 1955 1957) and *Bufo hemiophrys* (Kelleher and Tester 1969). *Rana clamitans* overwinters in streams, which have high oxygen levels, and which rarely freeze (Lamoreux and Maddison 1999). Other species, like *Bufo bufo*, which undertake relatively long breeding migrations, will overwinter in locations along the migratory route between their summer ranges and breeding ponds (Sinsch 1988) (Fig. 2). Generally the hibernacula of *Bufo bufo* are relatively close to their breeding sites (Sinsch 1990a) (Fig. 2). The newt *Notophthalmus viridescens* also overwinters at sites near the breeding pond (Gill 1978). Italian crested newts (*Triturus carnifex*) have been observed to migrate from their breeding site to hibernation sites in an old growth spruce forest, with individuals seeking refuge in small mammal burrows (Schabetsberger et al. 2004). Females migrated significantly further than males (median distance 168 m versus 53 m).

Other migrations may occur seasonally or sporadically in association with changing environmental conditions. Tailed frogs, *Ascaphus montanus*, may migrate along stream courses seasonally to avoid high water temperatures (Adams and Frissell 2001), and amphiumas may escape loss or degradation of their aquatic habitats by short overland migrations (Aresco 2002). Mass overland migrations of relatively long distance by aquatic frogs of the genus *Xenopus* have been observed in various parts of Africa and have been associated with the abandonment of drying ponds and dams (Hewitt and Power 1913; Loveridge 1953; Brass 1983). As these frogs are entirely dependent upon suitable aquatic habitats for feeding, breeding, development, and all other life functions, this represents perhaps the ultimate in resource-driven migration.

Despite the variation in migratory patterns that exist among amphibians, most species demonstrate a high level of fidelity to certain sites (Johnson 2003), often their natal pond, and are able to find these sites year after year. Some may even continue to return after the site has been destroyed (Twitty et al. 1967). This behavior is common in most groups of

amphibians. For example, marking experiments have shown that the newt *Taricha rivularis* returned to the same stream sections to breed for 11 years, even when numerous other, apparently suitable alternative streams exist in the area (Twitty 1966; Twitty et al. 1967). *Notophthalmus viridescens* shows fidelity to breeding sites, and adults will return to their natal pond to breed after spending 2-4 years on land (Hurlburt 1969; Gill 1978). A metapopulation of the crested newt (*Triturus cristatus*) in Germany was shown to display a high level of breeding pond fidelity, with a very low rate of inter-pond migration (1.3 - 9.0%). Exchange of first-time breeders provided the main source of interaction between breeding ponds within the metapopulation (Sinsch et al. 2003). Fidelity to breeding sites is also common among anurans. For example, *Rana sylvatica* has been found to be 100% faithful to its breeding ponds, even when other apparently suitable ponds occur in the vicinity (Berven and Grudzien 1990).

In addition to breeding site fidelity, some amphibians demonstrate hibernation site fidelity. This has been documented for *Salamandra salamandra*, which has been observed to return to the same hibernation site for 20 years (Feldman 1987), and for the toad, *Bufo hemiophrys* (Kelleher and Tester 1969). Many migrating amphibians also tend to enter and exit their breeding ponds in the same location (Shoop 1965; Douglas and Munro 1981; Phillips and Sexton 1989), although some species may show considerable annual variation that is dependent upon sex and life stage (Dodd and Cade 1998). Some species have been observed to follow relatively straight migratory courses (Twitty 1966; Douglas and Munro 1981; Sinsch 1988), even when displaced over great distances (Twitty 1966). For *Taricha rivulina* the return journey to the home site is very slow, and after displacements of several kilometers may take two or more years (Twitty 1966). These characteristics, and site fidelity exhibited by amphibians, indicate that these animals are capable of at least some degree of homing and orientation (Young 1981; Semlitsh 1985; Phillips 1987; Sinsch 1990a; Pasanen and Sorjonen 1995; Stebbins and Cohen 1995; Susuma et al. 1995; Pough et al. 1998).

7.5 Homing and Orientation in Amphibians

Experimental evidence of homing and orientation to breeding ponds or terrestrial sites has been documented for at least 13 species of salamanders, including ambystomatids, plethodontids, and salamandrids, and at least 16 species of anurans, including hylids, bufonids, pelobatids and the genus

Ascaphus. Since homing is common to both salamanders and anurans, it is possible that the common ancestor of lissamphibians was capable of homing, a postulate supported by the commonality of this behavior with fishes (Sinsch 1992). Even though many amphibians are capable of homing to and from their breeding ponds, most are not, however, able to home from outside their natural migratory range. This implies that most amphibians are not capable of true navigation, and that they must be familiar with an area in order to orient and home properly (Sinsch 1990a; Zug et al. 2001). One exception to this is *Taricha rivularis*, which has the ability to home from unfamiliar locations in excess of 30 km from their natural home range (Philips 1987). Experiments have shown that amphibians use a variety of cues for homeward orientation, and that the cues used may vary considerably between species (Sinsch 1987 1990b 1992; Papi 1992; Wilson 2001) (Fig. 1).

Olfaction is an important cue for most migrating amphibians (Fig. 1). Many species of amphibian, including newts (*Taricha rivularis*: Grant et al. 1968; *Notophthalmus viridescens*: Hershey and Forester 1980; *Triturus alpestris*: Joly and Miaud 1993), and anurans (*Bufo japonicus*: Susuma et al. 1995), are unable to orient, and show random movements, when their olfactory nerves are severed. Furthermore, when given a choice between foreign and home pond substrate, the salamanders *Ambystoma maculatum* and *Triturus alpestris*, and several anuran species, including *Bufo nebulifer* (as *B. valliceps*), *Pseudacris clarkii*, *Pseudacris streckeri*, and *Rana sphenoccephala utriculara*, preferred their home substrate, suggesting olfaction to be an important aspect of homing in these species (Martof 1962; Grubb 1973a 1975 1976; McGregor and Teska 1989; Joly and Miaud 1993). It is possible that these odor preferences develop in the embryonic stages and are retained into adulthood (Hepper and Waldman 1992). In the toad *Bufo nebulifer*, reproductive hormones may be responsible for triggering odor preferences (Grubb 1973b). It has also been suggested that amphibians establish an olfactory map of their migratory range (Fig. 1) based on a gradient of odors, which allows them to orient in familiar areas (Sinsch 1990a; Susuma et al. 1995). Therefore, an amphibians' ability to locate and perceive a pond depends on the intensity of the olfactory gradient (Ambrogio and Gillis 1998). For species such as *Ambystoma opacum*, however, which construct nests in dry vernal ponds that later fill with water, olfactory cues may be less important (Shoop and Doty 1972).

In general, olfactory cues seem to be more important in species that undertake long distance migrations, like those of the genus *Bufo*, than for those that live close to the breeding site (Semlitsch 1987; Sinsch 1987

1990b), and may play a role in the initial orientation towards the breeding pond (Grubb 1973a,b 1975; Sinsch 1987 1990a,b).

In addition to olfactory cues, visual cues also play an important role in amphibian orientation and migration. There are two main types of visual cues: celestial cues and fixed visual landmarks (Sinsch 1990a) (Fig. 1). Fixed visual landmarks are probably important for short-distance piloting (Sinsch 1987; 1990b). For instance, Great Crested Newts (*Triturus cristatus*) use cues in the vicinity of their breeding pond to orient (Malmgren 2002), and *Bufo bufo* uses visual landmarks to help it maintain a straight course (Heusser 1969). On the other hand, celestial cues may be used by amphibians for compass or Y-axis orientation (Sinsch 1990a). The home shore is an important landmark for amphibians, and many tend to orient 90 degrees to it. This is Y-axis orientation, and it allows amphibians to orient along the most direct route to and from the shore, which is important for breeding migrations (Taylor and Auburn 1978; Stebbins and Cohen 1995; Zug et al. 2001). This type of orientation has been observed in numerous amphibian species, including the newt, *Notophthalmus viridescens* (Philips 1987). The establishment of an X-Y compass for Y-axis orientation requires light information from the sky, a familiarity with the home shore, and an internal clock phased to local time (Newcomer et al. 1974; Stebbins and Cohen 1995). However, the type of celestial cues used varies between species; light information may be received from the sun or stars using the eyes, or polarized light may be perceived by extraocular photoreceptors in the upper part of the brain, such as the pineal or frontal organ (Taylor and Ferguson 1970; Taylor 1972; Adler 1976; Demian and Taylor 1977) (Fig. 1). Some amphibians require a clear sky to orient, whereas others do not, and amphibians may or may not (depending upon species) be able to orient when blinded (Twitty et al. 1967; Stebbins and Cohen 1995). Many species, including *Notophthalmus viridescens* and *Ambystoma tigrinum*, are able to orient when blinded, but become disoriented when their pineal organ is covered (Taylor and Adler 1978; Hershey and Forester 1980; Hairston 1994; Stebbins and Cohen 1995), suggesting that these species use polarized light perceived by extraocular photoreceptors for orientation. This is also the case in eyeless red-spotted newts (Demian and Taylor 1977).

Furthermore, experiments have suggested that some species of amphibians use visual cues in conjunction with olfactory cues to orient. For example, with its pineal gland covered, *Notophthalmus viridescens* is unable to orient, but still exhibits directional movement. However, when its olfactory nerves are severed, this species exhibits random movements, suggesting that both senses in combination are important for orientation (Hershey and Forrester 1980). Furthermore, *Bufo valiceps* is able to orient

if either its vision or olfactory sense is impaired, but not if both are damaged, indicating that it can use either sense for orientation (Grubb 1970). It is possible that visual cues are less important in amphibian species that migrate over the course of a single rainy or overcast night (Duellman and Trueb 1986).

For anurans, short-distance orientation to the breeding pond may be accomplished using acoustic cues (Bogert 1947; Brattstrom 1962; Sinsch 1990a). For example frogs may use the calls of conspecifics to guide them to the pond (Fig. 1). These cues are generally only useful for short distance movements of 10-100m, although the calls of chorus frogs (*Pseudacris triseriata*) and natterjack toads (*Bufo calamita*) can be heard from up to 1km away (Sinsch 1990a). Studies of natterjack toads have shown that displaced females will orient towards the nearest pond that has calling males, and are unaffected by a deprivation of olfactory cues. Conversely, males were found to return faithfully to the original breeding pond, and were disoriented when deprived of olfactory or visual cues (Sinsch 1992). Thus, in this species, auditory cues seem to play an important role in the orientation and piloting of females, whereas males use a different set of cues, including magnetic, olfactory and visual cues, to orient (Sinsch 1992). However, since calling is energetically expensive, and since these cues cannot be used for orientation during migration away from the breeding pond, acoustic cues are probably of secondary importance in the orientation of most anurans.

Some amphibians may use magnetic cues for orientation (Phillips and Adler 1978; Phillips 1986a,b) (Fig. 1), this ability being found in widely disparate taxa of amphibians, and vertebrates in general (Phillips 1977; Sinsch 1990a). The ability to detect magnetic fields was first identified in the salamander, *Eurycea lucifuga* (Phillips 1977), and has since been found in other salamanders, newts and in some frogs. For instance, male natterjack toads were disoriented when bar magnets were glued to their heads, disrupting the magnetic field (Sinsch 1992). Magnetic cues are likely used for simple compass orientation in such species, and are probably used in conjunction with other sensory information, including visual and olfactory cues (Phillips 1986a; Diego-Rasilla 2003). However, in *Notophthalmus viridescens* this ability may be related to their capability of using true navigation (Phillips 1986a,b 1987; Pough et al. 1998; Zug et al. 2001). Newts of this species are capable of orienting towards their home pond after being displaced 30km away in the absence of all types of cues during the displacement (Phillips 1987; Phillips et al. 1995). They are able to detect the earth's magnetic field, and may form a magnetic map based on the spatial variation in the magnetic field, which, combined with a compass sense, allows them to navigate (Phillips and Borland 1992a,b

1994; Phillips et al. 2001; Zug et al. 2001). This species may detect the magnetic field either via visual centres in the brain, a trigeminal nerve system or a magnetite-based receptor in the head (Zug et al. 2001). Recent work has suggested that these newts have two separate magnetic receptors, with one being sensitive to changes in the wavelength of ambient light and related to the visual system, and the second a non-light dependent detector sensitive to the polarity of the magnetic field (Phillips and Borland 1994). It is possible that both types of receptors are necessary for true navigation (Deutschlander et al. 1999).

The newt *Taricha torosa* is the only species so far that has been shown to use kinesthetic senses in migration. Newts that were spun around showed erratic migratory courses, indicating body position is important for maintaining a straight migratory course (Endler 1970). Geotactic and hygrostatic responses may also be important, as some amphibians, including juvenile *Notophthalmus viridescens*, have been shown to migrate along depressions, following humidity gradients (Hurlburt 1969; Duellman and Trueb 1986). However, these senses probably play only a secondary role in the homing and orientation of most amphibians.

Overall, amphibians employ a multisensory system of orientation that involves the complex integration of many different cues (Sinsch 1991) (Fig. 1). They most likely use olfactory or visual cues, and in the case of newts, magnetic cues, to determine their location, and then use celestial cues to establish a compass direction (Sinsch 1990a 1991). However, it is important to note that amphibians are likely capable of using alternate cues if the preferred cue is unavailable (Sinsch 1987 1990b 1992; Papi 1992), and that cues are used in combination, but with one assuming dominance over others in a pattern that varies by species.

7.6 Patterns of Reptilian Migration

The scale of reptile migrations varies dramatically, from a few hundred metres to thousands of kilometers. Unlike amphibians, few reptiles migrate to common areas to breed, and most do not migrate at all (Cogger and Zweifel 1998; Pough et al. 1998). This is because reptiles do not depend upon water for reproduction, and thus most terrestrial reptiles do not need to travel long distances and instead generally lay their eggs at nesting sites within their normal home range (Pough et al. 1998). However, there are many other reasons for which reptiles may migrate. For instance, they may migrate in response to seasonal habitat changes, or to follow their prey. Migration may also be a consequence of laying their eggs on land, with

journeys being undertaken to reach suitable, terrestrial nesting sites (Pough et al. 1998), as is the case for many aquatic reptiles, including sea turtles, freshwater turtles, and some crocodylians. The most extensively studied of these nesting migrations are those of sea turtles.

Sea turtles often undertake resource-driven migrations of several thousand kilometers between nesting and feeding grounds (Meylan 1982) (Fig. 4). Marine turtles undertake these long-distance, or macro-geographic, migrations, because their nesting sites are often distantly separated from their feeding grounds (Bowen et al. 1989; Linzey 2001). Different species of sea turtles exhibit different migratory patterns (Luschi et al. 2003) (Fig. 4). For example, Green Turtles (*Chelonia mydas*) from various colonies in the Indian and Pacific oceans regularly migrate over 1000 km between their feeding grounds and nesting beaches; Olive Ridley turtles (*Lepidochelys olivacea*) tagged in Surinam have been found up to 1900 km away; and Loggerhead turtles (*Caretta caretta*) tagged in South Africa have been observed in Zanzibar, almost 3000 km away (Hughes 1974; Pough et al. 2002). Highly nomadic Leatherback sea turtles (*Dermochelys coriacea*) tagged in French Guiana have been recaptured in a variety of locations up to 5000 km away, including Texas, Mexico, New Jersey, New England, Nova Scotia and Africa (Luschi et al. 1996; Pough et al. 2002). The migratory patterns of these species may be fixed or not, depending on whether they exploit predictable or unpredictable resources. However, one common characteristic of marine turtle migrations is that despite the enormous spans of open ocean they traverse, these turtles are able to return with great precision to the same nesting beaches year after year (Meylan 1982) (Fig. 5).

The most well studied of these migrations is that of Green Sea Turtles (*Chelonia mydas*) (Fig. 4A). These turtles inhabit tropical and subtropical waters, where they forage in the neritic zone of inshore waters (Carr 1965; Luschi et al. 1998; Godley, Lima et al. 2003). Every 2-4 years these turtles traverse the open ocean, using fast, directed movements along migration corridors to reach nesting sites thousands of kilometers away (Miller 1998; Luschi et al. 1997; Luschi et al. 2001). In the Caribbean Sea and North Atlantic Ocean, Green Turtles utilize four major nesting sites located on Tortuguero, Aves Island, the Surinam coast, and Ascension Island. Post-nesting females migrate hundreds or thousands of kilometers to return to foraging areas, although some may remain near the nesting beach for a time (Luschi et al. 1998; Garduno et al. 2000; Papi et al. 2000; Hays et al. 2001). Females from distantly separated nesting beaches may use the same feeding grounds (LeGall and Hughes 1987).

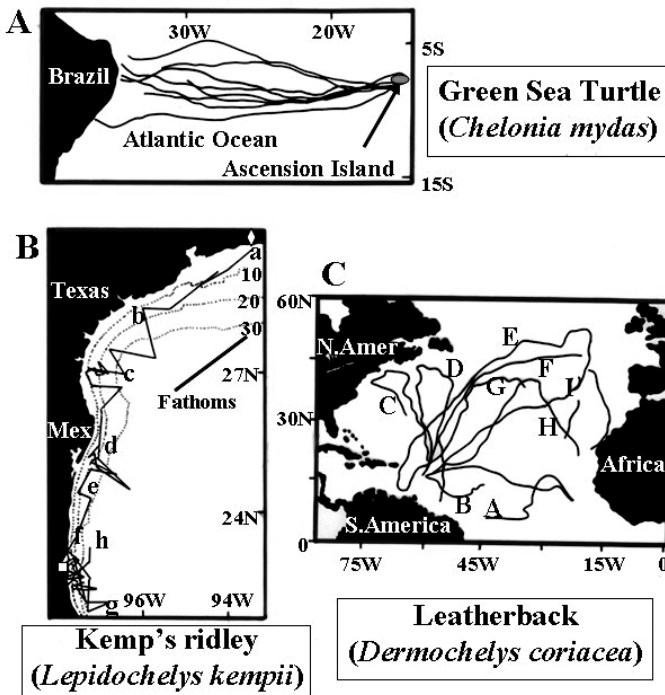


Fig. 4. Representative migration patterns of marine turtles. **A.** Routes of eight Ascension turtles (*Chelonia mydas*) undertaking a transoceanic shuttling migration from their breeding grounds on Ascension Island to their feeding grounds along the Brazilian coast. Modified from Luschi, Hays and Papi (2003, Fig. 1). Elapsed time for the journey between 33 and 74 days. **B.** Movement of a satellite-tracked Kemp's ridley (*Lepidochelys kempii*) from Cameron, Louisiana (a, white diamond) to a nesting site at Rancho Nuevo, Mexico (white square). The tracking period lasted from 13 August 1994 (Cameron, Louisiana -- a) to May 16 1995 (point h). The time course of the migration is indicated by the letters a-h: a - August 13 1994; b - December 10 1994; c - December 18 1994; d - January 17 1995; e - March 8 1995; f - March 10 1995; g - March 18 1995; h - May 16 1995. Modified from Renaud et al. (1996, Fig. 1). **C.** Pan-Atlantic foraging movements of nine leatherback turtles (*Dermochelys coriacea*) tracked after nesting in the Caribbean. Individuals A and B were tracked for 12 months (July 2002 - July 2003). Individuals C to I were tracked for 6-8 months (May-July 2003 to January 2004). Modified after Hays, Houghton and Myers (2004, Fig. 1a)

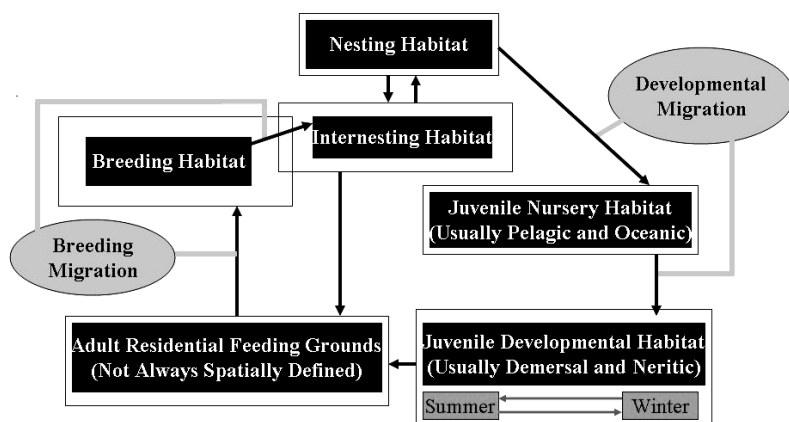


Fig. 5. Conceptual model of a generalized sea turtle life cycle, after Luschi (2003, Fig. 6.1) and Musick and Limpus (1997, Fig. 4.1)

As many as 50,000 *Chelonia mydas* come ashore to nest on the beaches Tortuguero, Costa Rica each year. Tens of thousands of these turtles have been tagged, and have been recovered at feeding grounds as far away as Panama, Colombia, Venezuela and the Yucatan Peninsula (Carr et al. 1978). The reproductive circuits identified for this Tortuguera – Western Caribbean population of Green Turtles (Carr and Giovannoli 1957) are very similar to other populations located near Yemen in the Western Indian Ocean (Hirth and Carr 1970), the central South Pacific (Craig et al. 2004), the Mediterranean (Godley et al. 2002), and southern Chinese waters (Cheng 2000).

The Ascension Island population of *Chelonia mydas* has also been extensively studied (Fig. 4A). These turtles migrate 2200 km from their feeding grounds off the coast of Brazil, where their population mixes with turtles that nest on the coast of Surinam and French Guiana, to their nesting beaches on Ascension Island (Carr 1962; Mortimer and Carr 1987). Ascension Island is a tiny island of only 20 km diameter located along the mid-Atlantic ridge (Pough et al. 2002), and does not possess adequate resources for feeding (Rebel 1974). Turtles return to it with incredible precision every 2-3 years in order to breed and lay their eggs, a journey which takes six weeks to complete (Bowen et al. 1989; Luschi et al. 1998; Pough et al. 2002). Females demonstrate nest site fidelity, and return to the same beach, which is often their natal beach. This has been confirmed using mitochondrial DNA evidence (Meylan et al. 1990).

It has been suggested that the isolated breeding population of turtles on Ascension Island is the result of sea-floor spreading (Carr and Coleman 1974). This hypothesis indicates that historically, Ascension Island was located much closer to the coast of Brazil, and that sea floor spreading at the mid-Atlantic ridge has slowly moved the island farther from Brazil, requiring the Ascension Island turtles to migrate across increasingly greater distances to their nesting beach (Carr and Coleman 1974). However, examination of the mitochondrial DNA of female Green turtles from three separate Atlantic rookeries has revealed that the genetic divergence between the populations is too small to support this hypothesis, and instead suggests a more recent origin of the Ascension Island population of turtles, probably in the past few thousand years (Bowen et al. 1989). Thus the question of how turtles began to nest on this remote island remains unanswered. However, although the females from the three rookeries are closely related, the rookeries are genetically distinct from each other (Bowen et al. 1989; Avise and Bowen 1994). This suggests that not only do females show nest site fidelity, but that they return to their natal beach year after year (Bowen et al. 1989; Avise and Bowen 1994).

The range of Eastern Pacific Green Turtles (*Chelonia mydas agassizi*) is restricted to the west coast of the Americas, from Baja California to southern Peru. Females migrate from foraging grounds to nesting sites along the Mexican coast every 3-4 years (Alvarado et al. 2003). The primary nesting site of these turtles is Michoacan. After breeding the turtles undertake a return migration to their foraging grounds in the Gulf of California and coastal Central and South America (Byles et al. 1995).

Hawksbill turtles (*Eretmochelys imbricata*) show a similar migratory pattern to that of Green Turtles. These turtles are widely distributed, and generally inhabit coral reefs. This species was originally thought to be non-migratory, but radio-telemetry studies have revealed that hawksbill turtles may migrate long distances (Parmenter 1993; Meylan 1999; Horrocks et al. 2001; Buitrago and Guada 2002). There is evidence that males of the species are also highly migratory (Nietschmann 1981). The nesting migrations of this species are not well understood, but it appears that females return to their natal beaches to nest every 2-3 years (Witzell 1983; Bass 1999), and that females inhabiting the same foraging areas do not migrate to the same nesting beaches. After laying their eggs Hawksbill turtles immediately migrate back to their foraging grounds (Horrocks et al. 2001). There is some variation in the length of migration that the females undertake; females nesting on the same beaches exploit different foraging areas that may be either very close to, or a long distance from the nesting beach, and thus migrations may take place across deep oceans or through shallow water (Ellis et al. 2000).

Kemp's ridley turtles (*Lepidochelys kempii*) exhibit a different migratory pattern from that of Green Turtles or Hawksbill turtles (Fig. 4B). These turtles have a restricted range in the Gulf of Mexico and the western Atlantic, and migrate in shallow waters along the United States and Mexican coast along a well-defined migration corridor (Byles and Plotkin 1994; Marquez 1994). Mature females migrate to, and aggregate at the nesting beaches prior to the breeding season, whereas males appear to be non-migratory, and remain at the nesting beach year round (Plotkin 2003). The migration of females takes place annually, and the majority of the population of Kemp's ridley turtles migrates to the same beach at Rancho Nuevo, Mexico (Fig. 4B), although some turtles nest at a few adjacent beaches in Vera Cruz, as well as in Texas and other areas of the southern United States (Renaud et al. 1996). After breeding, females migrate back to their restricted feeding ranges (Marquez 1994; Byles and Plotkin 1994; Renaud et al. 1996).

Adult Loggerhead turtles (*Caretta caretta*) inhabit subtropical and temperate waters (Polovina et al. 2004) around continental shelves and estuarine areas, and spend the majority of their time in near shore and inshore waters (Dodd and Byles 2003; Godley, Broderick et al. 2003). Unlike some other marine turtle species, female loggerhead turtles are not restricted to any one, fixed foraging area, but instead move continuously between a series of foraging areas (Dodd 1988; Papi et al. 1997; Plotkin and Spotila 2002). Females migrate hundreds to thousands of kilometers (Limpus and Limpus 2001; Bentivegna 2002) to breeding sites approximately once every three years, and generally migrate in inshore waters, with only brief offshore movements (Papi et al. 1997; Plotkin and Spotila 2002), although some populations may undergo trans-Pacific migrations along specific migratory corridors with particular thermal characteristics (Resendiz et al. 1988; Nichols et al. 2000). Male and female Loggerhead turtles migrate asynchronously, with males arriving at the breeding site weeks in advance of the females (Limpus 1985; Dodd 1988). However, it is possible that some males are non-migratory, and remain near the nesting beaches year round (Henwood 1987).

Another species of turtle that exhibits primarily inshore migrations is the Flatback turtle (*Natator depressus*). These turtles have the most restricted migratory range of all sea turtles. They have feeding grounds around Indonesia and New Guinea, and migrate with a high degree of fidelity to the nesting beaches on the northern coast of Australia every 1-3 years (Limpus et al. 1981 1983 1984; Parmenter 1994). Postnesting migrations may be hundreds to thousands of kilometers in length, and are generally restricted to inshore waters around northern Australia, and as far as Papua (western New Guinea).

Leatherback turtles (*Dermochelys coriacea*) demonstrate a completely different migratory pattern to those of the species of marine turtles discussed above. This species is highly nomadic, undertakes transoceanic migrations, and is capable of diving to great depths (Goff et al. 1994; Morreale et al. 1996; Eckert 1998; Hays, Houghton et al. 2004). Leatherback turtles do not exploit fixed feeding grounds (Hays, Houghton and Myers 2004, but some areas of the North Atlantic may be regularly visited as feeding grounds); instead they migrate widely between sites (Keinath and Musick 1993; Steyermark et al. 1996; Hays, Houghton et al. 2004) (Fig. 4C), and are often found in cold northern waters far from their nesting sites (Pritchard 1976; Hays, Houghton and Myers 2004). The pre-nesting migrations of leatherback turtles are not well understood; however, females are known to migrate to nearshore waters adjacent to nesting beaches a few weeks prior to the nesting season every 2-3 years. Unlike other marine turtles, female leatherbacks do not demonstrate strong nest site fidelity, although they do return to the same general nesting area. After nesting, females migrate extremely long distances, sometimes across oceanic basins (Morreale et al. 1996; Eckert 1998; Hughes et al. 1998). It is not known, however, whether or not these long distance movements follow generalized tracks. Indeed, major oceanographic processes, such as main currents and eddies, have been shown to have a major influence on Leatherback movements, placing into question whether these journeys are really migrations or just prolonged stays in vast feeding areas (Luschi et al. 2003b).

Like Leatherback turtles, Olive ridley turtles (*Lepidochelys olivacea*) are highly migratory (Polovina et al. 2004), and spend most of their non-reproductive life in the open ocean (Beavers and Cassano 1996; Plotkin 2003). During the nesting season reproductively active males and females migrate towards the coast, and aggregate in breeding grounds near the nesting beaches. Females then emerge onto the beaches to lay their eggs, although they do not exhibit strong nest site fidelity (Kalb 1999). Some males of this species appear to be non-migratory, and instead attempt to intercept females along their migratory route to the nesting beaches, and thus different males utilize different reproductive strategies (Plotkin et al. 1995; Kopitsky et al. 2000). After mating, females remain in the breeding area for several weeks or even months. The post-nesting migration of Olive ridley turtles is unique and complex. The routes taken by individual females and by groups of females vary annually, and do not seem to follow any sort of migratory corridor (Plotkin 2003). Olive ridley's are highly nomadic, and traverse vast stretches of open ocean without exploiting any specific, fixed feeding grounds.

Overall, sea turtles demonstrate three distinct migratory patterns (Fig. 4). Some species, including Leatherbacks and Olive Ridley turtles, do not have a fixed foraging area, and roam widely and unpredictably before returning to their breeding areas (Fig. 4C). Conversely, Kemp's ridley turtles, Loggerheads, and Flatback turtles migrate between breeding areas and highly productive neritic foraging areas on continental shelves (Fig. 4B). Finally, Green turtles and Hawksbill turtles exploit well established, fixed foraging areas, with very little variation (Fig. 4A). Superimposed upon this are smaller migratory movements made by marine turtles on a seasonal basis as they travel to warmer foraging grounds during winter periods (Gitschlag 1996).

Many aspects of marine turtle migrations remain uncertain. For instance, studies have focused primarily on postnesting migrations, as these are easier to study than prenesting migrations. Furthermore, the movements of male sea turtles are not well understood, because they do not come ashore, and are thus difficult to tag. Limited radiotracking studies of males indicate that they return faithfully to the same breeding areas each year (FitzSimmons et al. 1997). However, other studies have revealed that the males of some species may be non-migratory (Henwood 1987; Plotkin et al. 1994; Kopitsky et al. 2000). Finally, the movement patterns of young turtles after hatching are not very well understood (Fig. 5). It is thought that hatchlings of some species drift around gyres, or circular current systems, that serve as moving, open ocean nursery grounds (Luschi, Hughes et al. 2003). Hatchlings thus gradually migrate around the Atlantic Ocean, a round trip that takes up to 12 years, and eventually return to their natal beaches to breed (Hairston 1994; Lohmann et al. 2001; Pough et al. 2002). Juveniles and subadults of many populations reside in coastal feeding areas located hundreds or thousands of kilometers from their natal beaches (Fig. 5). For example, juvenile Loggerhead turtles from nesting beaches in Japan and Australia traverse the entire Pacific Ocean (Bowen et al. 1995), and young Loggerheads from nesting beaches in the western Atlantic will traverse the entire Atlantic Ocean in the course of their developmental migrations (Bolten et al. 1998).

Some other types of chelonians also undertake nesting migrations, although they are not as extensive as those of sea turtles. For instance, European Tortoises (*Testudo hermanni*) (Swingland et al. 1986), and some freshwater turtles, such as *Glyptemys insculpta* (Quinn and Tate 1991), *Kinosternon* (Gibbons et al. 1990), *Chelydra serpentina* (Gibbons et al. 1990), and *Chelodina longicollis* (Graham et al. 1996) have been found to undertake seasonal migrations of 50m to 5km from ponds or forested areas to nesting sites. Females of some species exhibit strong fidelity to general nesting areas, and will return to the same aquatic habitats year after year

(Lindeman 1992; Dodd 2001). However, turtles have also been observed to migrate for reasons other than finding suitable nesting sites. For example, Snapping Turtles (*Chelydra serpentina*) may migrate up to 4 km beyond their normal home range to find suitable overwintering sites in flowing water (Cagle 1944; Brown and Brooks 1994). Aldabra Giant Tortoises (*Geochelone gigantea*) migrate from inland areas to coastal regions during the rainy season to gain access to high quality food resources available on the coast (Swingland and Lessells 1974; Swingland et al. 1989). Galapagos Tortoises also migrate between different habitats (Rodhouse et al. 1975). Many freshwater turtles have been observed to migrate to new ponds as a result of fluctuating environmental conditions such as droughts (Bennett et al. 1970; Yeomans 1995; Graham et al. 1996). However, as in amphibians, there is some degree of variation in the migratory patterns within populations and between species of turtles. For instance, if suitable nesting sites are available nearby, European Tortoises will not migrate (Swingland et al. 1986). Furthermore, as migration can be dangerous, energetically expensive, or both, only about 20% of the Aldabra Giant Tortoise population studied migrated to the coast to exploit rich food resources (Swingland et al. 1989).

In addition to turtles, some crocodylians also undertake regular, seasonal migrations. Some species, including Nile crocodiles (*Crocodylus niloticus*) may swim great distances to find suitable nesting sites (Chelazzi 1992). Females of this species have been observed to swim to breeding beaches on Central Island, Lake Rudolf to lay their eggs (Modha 1967 1968). However, this type of behavior is rare among crocodylians, and most species, including the Australian *Crocodylus johnstoni*, remain within their home range to nest (Webb et al. 1983a,b). Some species of alligator and caiman may increase their home range during the breeding season, but like crocodiles, their nesting sites are generally located within the home range, and the animals do not undertake nesting migrations (Pough et al. 1998). Furthermore, although some crocodylians travel very long distances, for example the island hopping behavior exhibited by saltwater crocodiles, these movements are not considered migrations (Rodda 1985). Among some crocodylians, migrations in response to environmental changes are more common than are nesting migrations. Some species of crocodiles (*Crocodylus johnstoni*), caimans (*Caiman crocodilus*), and alligators migrate seasonally from drying swamps to more permanent bodies of water (Neill 1971; Pough et al. 1998).



Fig. 6. Part of a massive accumulation of red-sided garter snakes (*Thamnophis sirtalis parietalis*) emerging from a communal den in the spring in the Interlakes region of Manitoba, Canada. Photograph courtesy of Dr. Herb Rosenberg

Most oviparous squamates lay their eggs within their normal home ranges, and thus do not undertake breeding migrations, although a few species of snakes have been reported to make directional movements to specialized oviposition or breeding sites (Pough et al. 2002). For example, *Vipera berus* in Finland moves from basking sites to a common breeding area several hundred metres away (Pough et al. 2002). Many species of snakes also exhibit dramatic migrations between summer feeding ranges and winter denning sites. This is common in northern temperate zone snakes, including garter snakes (*Thamnophis*) (Fig. 6) and some rattlesnakes (e.g. *Crotalus atrox*) (Landreth 1973; Klauber 1982; Lawson 1989; Lawson and Secoy 1991; Bauer and Russell 2001; LeMaster et al. 2001; Linzey 2001). These snakes generally migrate about 1-10km to their dens in the fall for winter hibernation. Snakes congregate at the denning sites, and mating occurs at the dens before the snakes migrate back to their summer feeding areas in the spring (Klauber 1982; Lawson 1989; LeMaster et al. 2001) (Fig. 6), although the patterns of seasonal movement may differ between males and females (King and Duvall 1990). Like other migrating reptiles and amphibians, garter snakes and rattlesnakes tend to show fidelity to both their den sites and their feeding areas, returning to the same locations year after year (Lawson 1989). The sea snake, *Pelamis*

platyrus, also undertakes long distance breeding migrations in the Indian and Pacific oceans (Graham et al. 1971).

Other types of snakes demonstrate different migratory patterns. For example, water pythons (*Liasis fuscus*) in Australia migrate considerable distances each year to follow their most important source of prey, the dusky rat (*Rattus colletti*). Although many large mammals migrate to follow their prey, this type of migration is difficult for terrestrial ectotherms because they are generally small, have a limited capacity for sustained activity, and are often inactive for much of the year due to thermal constraints (Madsen and Shine 1996). However, water pythons are large animals that live in a tropical environment, and are thus able to undertake long migrations to track their prey. These snakes have been observed to follow their primary prey up to 12km from the backswamp area to the floodplain during the wet season (Madsen and Shine 1996). Other types of aquatic snake, like Arafura filesnakes (*Acrochordus arafurae*), also undergo seasonal migrations, moving from restricted ponds to flooded grasslands at the onset of the wet season. They thus show a strong seasonal shift in habitat utilization which may be due to the snakes following their prey (fish) out of the ponds, or may simply be a result of changing environmental conditions (Shine and Lambeck 1985).

Among reptiles, migration is least common among lizards. These terrestrial animals often show strong, territorial attachments to specific sites, and their small size and ectothermic nature tends to preclude migration (Madsen and Shine 1996). However, a few species of lizards have been observed to migrate. Large iguanids that live in environments where nesting sites are scarce may migrate up to 15km to reach suitable nesting sites (Pough et al. 1998). For example, Green Iguanas on Barro Colorado Island swim to small offshore islands to nest, although most move less than 1km beyond their normal home range (Rand 1968; Bock et al. 1985). A similar pattern is seen among female Ground Iguanas (*Cyclura spp.*), which migrate up to 6.5 km to reach suitable nesting sites (Wiewandt 1982). Galapagos Land Iguanas (*Conolophus subcristatus*) also migrate to reach nesting sites, and some females have been observed to climb 1400m to the rim of a volcanic crater, and then descend 900m into the crater to nest (Werner 1983).

Somewhat unusual migratory behavior has also been observed in *Ctenophorus* lizards in Western Australia. Juveniles emigrate away from rock outcrops when they are 2-3 months old to avoid harassment by adult males. Once the juveniles reach sexual maturity they migrate back to the main outcrop (Bradshaw 1971). Most other lizards do not migrate, but many lacertids and iguanids exhibit homing abilities (Mayhew 1963; Weintraub 1970).

7.7 Homing and Orientation in Reptiles

Homing and orientation play very important roles in the migration of reptiles, and particularly in the very long-distance migrations of sea turtles. The lives of sea turtles consist of a series of migrations beginning with hatchlings swimming from their natal beaches to the open sea, and then later the migrations of adult turtles between foraging areas and their nesting beaches (Fig. 5). These animals migrate long distances in the open ocean where landmarks are largely unavailable, yet they demonstrate very precise orientation to specific locations, including some very small islands (Zug et al. 2001). The lifestyle of sea turtles is thus inextricably linked to the ability to orient accurately across spans of seemingly featureless ocean, indicating that these animals possess a sophisticated orientation system.

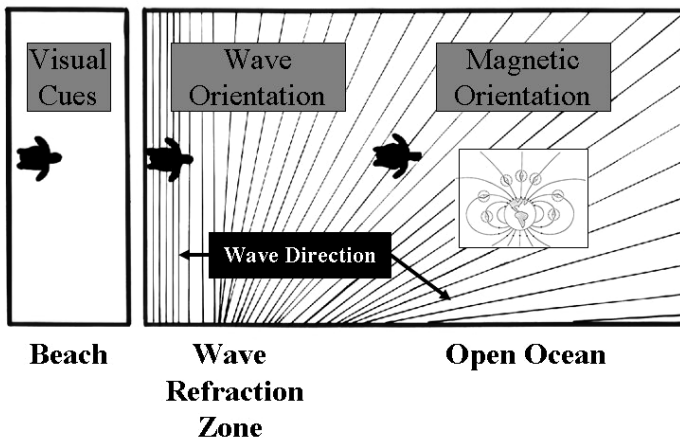


Fig. 7. Sequential orientation cues hypothesized to guide hatchling Loggerhead turtles from the nesting beach to the open ocean. Modified after Lohmann et al. (1997, Fig. 5.8)

The migratory movements of hatchling sea turtles are no less impressive than those of adults (Fig. 7). These small animals crawl to the sea, and immediately establish an offshore heading which is maintained long after the sight of land has been lost. After hatching, young sea turtles use three different types of cues to orient (Pough et al. 2002) (Fig. 7). First, upon emerging from the nests, hatchlings use visual cues to orient towards the sea. Studies have shown that hatchling Loggerhead and Green Turtles

exhibit a strong phototropotactic response, and will orient towards the brightest light in the vicinity, which, in the absence of artificial lights, is the horizon over the ocean, highlighted by the reflection of light off the ocean (Carr 1962; Kingsmill and Mrosovsky 1982; Mrosovsky and Kingsmill 1985; Salmon and Wyneken 1990; Peters and Verhoeven 1994) (Fig. 7). The color or wavelength of light is also used by hatchling turtles to help them find the sea. For this reason, artificial lighting near beaches can be a problem for hatchlings, causing them to become disoriented and disrupting their sea-finding ability (Salmon 2003). Green turtles exhibit a preference for blue or purple wavelengths over red, orange or yellow light (Witherington and Bjorndal 1991; Lohmann et al. 1997). This preference causes them to avoid orienting towards the rising or setting sun. Polarized light may also be used by hatchlings to orient towards the sea. Finally, hatchlings tend to avoid dark, elevated silhouettes, which may be caused by dunes or vegetation, objects typically located in a direction opposite to that of the shoreline (Godfrey 1995; Lohmann et al. 1997). This behavior also helps to guide hatchlings towards the sea, and similar cues may be used by nesting adults to return to the sea following oviposition (Caldwell and Caldwell 1962).

Once they have reached the ocean, hatchlings begin to swim vigorously, and are carried 5-10m from the beach by the wave undertow. When they surface, hatchlings establish a course towards the open ocean, using wave propagation direction to orient (Fig. 7). They swim perpendicular to the waves, which leads them out into the ocean and toward the global current systems (Salmon and Lohmann 1989; Lohmann et al. 1990 1995; Lohmann 1992; Pough et al. 2002; Nagelkirken et al. 2003).

However, further from shore, wave direction no longer provides a reliable indication of the offshore direction, yet hatchlings continue to follow the same seaward course. Furthermore, hatchlings carried thousands of kilometers from their natal beaches find their way back to breed, sometimes 30-50 years later. This indicates that they use other, more complex sources of directional information. Studies have shown that hatchling Loggerhead and Leatherback sea turtles are sensitive to the earth's magnetic field, and it has been suggested that they develop a magnetic compass as they leave their natal beaches (Lohmann 1992; Lohmann et al. 1997; Irwin et al. 2004) (Fig. 7). For example, hatchlings trained to swim in a particular direction, towards a light will maintain the same compass direction even in the dark. Furthermore, if the magnetic field is reversed, the turtles will reverse their swimming direction (Lohmann et al. 1997).

Young turtles at sea also show abilities beyond a simple sensitivity to the earth's magnetic field. There is evidence that they are capable of

detecting changes in the inclination angle of the earth's magnetic field relative to the earth's gravitational field (Light et al. 1993), as well as changes in the local intensity of the magnetic field. For example, hatchling turtles with no migratory experience have been shown to orient relative to a magnetic field in a direction that would keep them within the warmer North Atlantic Gyre current system, and on a safe migratory route (Lohmann and Lohmann 1998; Lohmann et al. 2001). The ability to detect both the inclination angle and the intensity of the earth's magnetic field would allow turtles to approximate the latitude and longitude of their global position, providing them with a bi-coordinate geomagnetic map sense (Lohmann et al. 1997).

These studies on hatchlings may provide insight into the navigational cues employed by adult sea turtles, although it is possible that juveniles and adults respond to different types of cues. The migration of adult sea turtles has been extensively studied over the past 10 years, but the mechanism of orientation and navigation employed by these animals remains uncertain (Papi and Luschi 1996; Papi et al. 2000), although it likely involves a variety of sensory cues, as is the case for amphibians (Hays et al. 2002; Pough et al. 2002). There is even some debate over whether or not these animals are capable of true navigation. It has been suggested that since they follow fairly straight routes to their goal, simple compass orientation is adequate to guide their migrations (Luschi, Hughes et al. 2003). This may be true for migrations towards large targets, such as the return migration of Green Sea Turtles to the Brazilian coast (Fig. 4A), but probably not for the nesting migration, which is directed towards a very small target. Displaced adult Loggerhead turtles in the Indian Ocean were found to be unable to compensate for the post-nesting displacement and appeared to rely on simple orientation mechanisms, such as the coastline, as a guide (Luschi, Hays and Papi 2003). The nesting migration is much more complex, and probably requires the animals to have a map-sense, and true navigational abilities (Papi et al. 2000; Hays et al. 2002). Furthermore, the ability of displaced turtles to return to or orient towards their original location (Papi and Luschi 1996; Luschi et al. 1998; Avens and Lohmann 2004), and the ability of turtles to correct deviations in their migratory course caused by ocean currents (Luschi et al. 1998; Papi et al. 2000), suggest that simple compass orientation is not adequate, and that a more sophisticated mechanism is being used.

If the ability to detect magnetic fields that has been identified in hatchlings is retained in adults, then it is likely that adult sea turtles also use a magnetic map for orientation and navigation (Lutcavage 1996; Lohmann et al. 1997; Papi et al. 2000; Lohmann et al. 2004). However, if such an ability exists, it is not yet known if it provides very precise or only

approximate information about the natal beach, with other types of cues being used closer to the natal beach. Furthermore, a study tracking the migration routes of Green Sea Turtles found that the routes taken by magnetically disturbed turtles did not differ significantly from those of the control turtles, suggesting that magnetic cues are not essential for the migration of sea turtles (Papi et al. 2000). On the other hand, this study focused on the return migration of the sea turtles, and thus it is possible that turtles rely more heavily on magnetic cues while undertaking the much more complex pre-nesting migration (Papi et al. 2000).

In addition to magnetic cues, many other mechanisms have been proposed to explain the orientation abilities of sea turtles. For instance, as in amphibians, olfaction may play an important role in the migration of these animals (Carr 1967; Manton et al. 1972; Bowen et al. 1989; Chelazzi 1992; Papi et al. 2000). Carr (1967) found evidence that sea turtles have an odor memory of at least one year, which led others to suggest that juvenile sea turtles imprint on chemical cues associated with natal beaches, and then use a chemical plume along ocean currents, combined with compass orientation, to guide them to their beach when they return as adults (Lohmann et al. 1997; Papi et al. 2000). However, the role of chemical cues in long-distance navigation is almost unknown, and there is no convincing experimental evidence to support this hypothesis. Furthermore, the straight migration routes of adults are not consistent with tracking a chemical plume, and oceanic currents resulting from trade winds may disrupt chemical cues, thus preventing the formation of chemical trails that turtles could follow (Brown 1990). It is also debatable whether the time of exposure to natal beach odors is long enough for their imprinting on hatchlings to occur. Åkesson et al. (2003) reviewed the evidence relating to the methods Green Sea Turtles (*Chelonia mydas*) may use to locate Ascension Island in their migration from the Brazilian coast. Investigating the behavior of displaced females, they concluded that chemical information transported by ocean currents did not account for navigation, nor did bi-coordinate geomagnetic methods, other magnetic gradients or celestial cues. Instead, females found the island by searching and beaconing, and then used wind-borne cues for final location.

Another possibility is that turtles orient using wave direction or ocean currents, as observed in hatchling Loggerhead sea turtles, and that they calibrate this system using celestial cues such as the stars or the sun (Morreale et al. 1996; Papi et al. 2000). Other potential mechanisms of navigation include information from the wind above the ocean surface (Luschi et al. 2001; Åkesson et al. 2003; Hays et al. 2003), bathymetric features of the ocean floor (Morreale et al. 1994), or water temperature (Plotkin 2003). However, evidence is sparse to support these mechanisms,

and some have been shown to be unimportant in the migrations of some species of sea turtles. For instance, Green Sea Turtles do not rely on ocean surface temperatures while migrating (Hays et al. 2001). Overall, much more research is necessary before any definite conclusions can be drawn regarding the orientation and navigation system of sea turtles.

In addition to sea turtles, orientation and homing mechanisms are also used by other types of reptiles including freshwater and terrestrial turtles, snakes, crocodylians and some lizards. Although few species of freshwater and terrestrial turtles undertake extensive migrations, many have been found to possess impressive homing abilities. For example, map turtles (*Graptemys pulchra*) returned home after being displaced up to 24km along a river, which puts them far beyond the boundaries of their natural home range (Shealy 1976). However, the total number of turtles that returned successfully was low. Many other freshwater turtle species, including *Clemmys guttata*, *Chrysemys picta*, *Glyptemys insculpta* and *Apalone mutica*, have been shown to demonstrate good homing performance following displacement (Cagle 1944; Ernst 1968 1970; Plummer and Shirer 1975; Carroll and Ehrenfeld 1978). The mechanism by which freshwater turtles orient is not well understood. Experiments have shown that the orientation abilities of turtles of the genera *Terrapene* and *Chrysemys* are reduced on overcast days, although some are still able to home for short distances under cloudy skies (Emlen 1969; Yeomans 1995; Graham et al. 1996). These results indicate that these turtles orient using a sun compass calibrated with an internal clock (Gould 1957; DeRosa and Taylor 1980 1982; Yeomans 1995; Graham et al. 1996). However, olfactory cues may also play an important role in homing and orientation of freshwater turtles. Olfaction has been suggested as an important factor in the homing ability of *Glyptemys insculpta* (Carroll and Ehrenfeld 1978), and olfaction and geotaxis could not be ruled out as factors in the homing of *Chrysemys picta* (Ernst 1970). Furthermore, the Australian Snake-necked Turtle, *Chelodina longicollis*, has been found to orient towards its home substrate in laboratory experiments (Graham et al. 1996), suggesting that olfaction also plays a key role in the orientation of these animals. It has furthermore been suggested that some freshwater turtles have the ability to detect and orient towards water, indicating that they may be using surface-reflected polarized light to orient, as polarization tends to be higher over moist surfaces (Yeomans 1995; Zug et al. 2001). Finally, the species *Terrapene carolina* has been shown to use both local visual cues (Lemkau 1970) and magnetic cues to aid in orientation (Mathis and Moore 1988).

The mechanism of homing and orientation of tortoises is even less well understood. The tortoise *Testudo hermanni* is capable of orienting at

distances up to 1560m outside its home range (Calzolari and Chelazzi 1981; Chelazzi and Calzolari 1986). It has been suggested that tortoises use olfactory cues to orient towards their home ranges, and to locate bodies of water following displacement (Chelazzi and Delfino 1986; Pough et al. 2002). Tortoises may also utilize visual cues based on topographic relief (Auffenberg and Weaver 1969; McCoy et al. 1993), but for the most part no definitive conclusions about tortoise orientation have been reached.

Homing behavior has also been demonstrated among crocodylians. The most impressive of these abilities have been observed in juvenile alligators. In general, alligators are fairly sedentary animals, but will migrate in order to avoid unfavorable environmental conditions. Studies have shown that alligators are able to home from over 5km away from their capture site, and are able to orient towards home from up to 34km away (Rodda 1985). Like sea turtles, alligators are able to detect magnetic fields, and thus they use magnetic cues for orientation (Rodda 1984). Furthermore, they are able to home from unfamiliar areas, suggesting that they are capable of true navigation (Rodda 1984 1985). Other species of crocodylians, including *Caiman crocodilus* and the saltwater crocodile (*Crocodylus porosus*) have also been found to return home following displacements of 2km and 30km respectively (Gorzula 1978; Ouboter and Nanhoe 1988; Pough et al. 2002).

Homing abilities also appear to be common in some snakes, but results regarding homing in North American snakes have been contradictory. Homing behavior has been observed in several species of garter snake (*Thamnophis sirtalis*, *T. radix*), water snakes (*Nerodia sipedon*, *Regina septemvittata*) and a rattlesnake (*Crotalus atrox*) when they are displaced from their den sites or from rich food sources (Landreth 1973; Newcomer et al. 1974; Brown and Parker 1976; Lawson 1989 1994; Lawson and Secoy 1991). However, garter snakes did not demonstrate the same evidence of homeward orientation when displaced from their normal home ranges (Lawson 1994). Other species of snake, including *Sistrurus catenatus* and *Carphophis amoenus*, also do not exhibit homing behavior, and will establish new home ranges when displaced (Barbour et al. 1969; Reinert and Kodrich 1982). Based on these results it is possible that some snakes may be capable of homing, but they may not always be motivated to use these abilities.

Some snakes that do exhibit homing behavior are able to orient along a specific compass direction, even when displaced great distances from their home range or den sites (Landreth 1973; Newcomer et al. 1974; Brown and Parker 1976; Lawson 1989 1994; Lawson and Secoy 1991). Furthermore, studies have shown that the orientation direction taken by snakes shifts if they are transported in the dark, suggesting that these

animals use celestial cues for orientation (Newcomer et al. 1974; Gregory et al. 1987; Lawson 1989; Lawson and Secoy 1991). The type of celestial cue used is likely solar, as there is no evidence that nocturnal snakes utilize lunar or stellar cues for orientation (Chelazzi 1992). Finally, there is some evidence to suggest that some snake species use olfactory cues for short-distance orientation (*Diadophis punctatus*: Dundee and Miller 1968), and that juvenile *Thamnophis* and *Crotalus* follow the pheromone trails of conspecifics to guide them towards their goals (Ford 1986; Graves et al. 1986; Lawson and Secoy 1991; Ford and Burghardt 1993; Pough et al. 1998).

Among lizards, migratory behavior is very rare and very little is known about their homing and orientation. Homing abilities in lizards are found almost exclusively in lacertids and iguanids (Mayhew 1963; Weintraub 1970). Several species of *Sceloporus*, *Phrynosoma* and *Uta* are capable of homing following displacements of less than 300m from their normal home ranges (Spoekker 1967; Guyer 1978; Bissinger 1983; Ellis-Quinn and Simon 1989; Chelazzi 1992). Some other lizard species have demonstrated the ability to return home following short displacements (*Dipsosaurus dorsalis*: Krekorian 1977; *Takydromus takydromoides*: Ishihara 1969; *Podarcis sicula*: Foà et al. 1990; *Tilqua rugosa*: Freake 1998). However, many other lizards are not capable of homing from similar distances (*Anolis lineatopus*: Rand 1967; *Sceloporus occidentalis*: Fitch 1940; *Uta stansburiana*: Tinkle 1967). It has been suggested that the strength of attachment to a home range affects the homing ability of lizards. For example, male and female *Sceloporus jarrovi* are both territorial, and demonstrate similar homing abilities. Conversely, non-territorial female *Sceloporus orcutti* exhibit poorer homing abilities than territorial conspecific males (Ellis-Quinn and Simon 1989; Weintraub 1970). Sex-based differences in homing behavior have also been observed in *Tilqua rugosa* (Freake 1998). Similarly, the territorial species *Sceloporus graciosus* has better homing abilities than the non-territorial species *Phrynosoma douglasii*, even though they occupy the same habitat (Guyer 1991).

The mechanism of orientation employed by lizards is not well understood. Experiments using directionally trained lizards have suggested the use of a celestial compass in *Lacerta viridis* (Fischer 1961), *Uma notata* (Adler and Phillips 1985) and *Tiliqua rugosa* (Freake 1999). It is possible that the pineal organ of lizards acts as a polarized light detector, and thus some lizards may be able to orient using polarized light, as is the case for some species of salamanders (Ellis-Quinn and Simon 1991; Freake 1999; Zug et al. 2001). However, although many lizard species are

capable of homing and orientation, most do not undertake migrations, and these abilities may be useful for some other function in these animals.

7.8 Conclusion

Migration plays a very important role in the lives of many amphibians and reptiles, as it allows them to acquire the resources they need to survive, or to avoid unfavorable environmental conditions. In order to undertake these migrations amphibians and reptiles employ a wide variety of orientation mechanisms, which likely involve the use of olfactory, visual, celestial and magnetic cues. However, the exact mechanisms used by many of these animals are still poorly understood. Furthermore, the migratory routes and patterns of many amphibians and reptiles are not completely known. Such patterns are strongly dependent on a diversity of factors, including phylogeny, body size, physiological and energetic constraints, and especially life history traits. As numerous amphibian and reptile species are highly endangered, it is essential that we develop an understanding of the migratory patterns of these species. This is especially crucial for some taxa, such as sea turtles, whose extensive marine migrations increase their likelihood of interactions with longline fishing operations (Plotkin and Spotila 2002; Luschi 2003; Hays, Houghton and Myers 2004) or fishing weirs (Godley, Lima et al. 2003), or many amphibians, whose migrations cross busy roadways (Langton 1989; Laufer 1997; Scoccianti 2000; Clavenger et al. 2001), or areas subject to habitat fragmentation as a result of human activities (de Maynadier and Hunter 1999). Without this knowledge, and that of the consequences of and potential for dispersal (Farrier et al. 2000; Lehtinen and Galatowitsch 2001), it is impossible to adequately protect and conserve these animals.

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