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REVIEW

Physiological, behavioral, and ecological aspects of migration in reptiles

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Abstract Seasonal movements between foraging, breeding, and overwintering sites occur in a wide variety of reptile species. Terrestrial snakes, lizards, and turtles migrate short distances (<20 km) between seasonal habitats, whereas fully aquatic marine turtles migrate hundreds to thousands of kilometers between foraging and breeding areas. The purpose of this article is to summarize aspects of migratory physiology and behavior in reptiles, particularly with regards to energetics and sensory mechanisms for navigation and orientation. We discuss the influence of aerobic scope, endurance, and cost of transport on migratory capacity, the effects of temperature and circulating hormones on activity and behavior, and mechanisms of detecting and transducing environmental cues to successfully navigate and orient toward a goal during migration. Topics worthy of further research are highlighted in the text, and we conclude with a discussion of how information on migration patterns of reptiles may be used to manage and conserve threatened populations.

Keywords Physiology · Energetics · Ectothermy · Navigation · Orientation · Sensory

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Introduction

The feats of endurance associated with animal migration have fascinated people for many centuries. Scientists have sought to understand the mechanisms by which animals initiate and sustain movements between different habitats through field studies and laboratory investigations. The majority of work has focused on long-distance migrants, particularly birds, as the extreme nature and geographic scope of their extensive movements inspire curiosity and inquiry. Efforts have also been directed toward understanding movement patterns of animals that have economic, cultural, or conservation value. For example, the patterns and physiological mechanisms underlying migration of commercially valuable salmonid fishes and crop-threatening migratory insects have been well studied (Dingle 1996), as have the movements of terrestrial mammals of conservation concern (Berger 2004). Knowledge gained from understanding animal movement patterns has important applications for management and conservation strategies.

With the exception of sea turtles, reptile migrants have received relatively little attention compared with migrants in other taxa. This is likely due in part to the historical perception of migration as a long-distance, round-trip movement (Orr 1970) and the seemingly incompatible perception of reptiles as animals with low metabolic scope and limited capacity for sustained activity. Modern definitions of migration are more inclusive than past interpretations and acknowledge that directed movements of an animal out of its home range to exploit resources at another specific location may be classified as migration, regardless of the distance covered or whether the movement was unidirectional or bidirectional (Kennedy 1985; Dingle 1996). Dingle (1996) encourages an individual-based behavioral definition of migration that emphasizes migration as an adaptation driven by transitory availability and changing location of resources. Movements promote survival of the organism by insuring that it remains in suitable habitat year-round. Given the current criteria, the seasonal movements of many reptiles fall under the category of migration, despite the generally short distances travelled.

In this review, we will briefly summarize the role of migratory movements in the life history of reptiles and then focus on physiological aspects of migration for this group. Our goal is to provide a broad overview of the physiology underlying migration in reptiles, both in terms of energetics and locomotory performance (i.e. how reptiles sustain movements between habitats) as well as the sensory mechanisms associated with navigation and orientation (i.e. how they know where to go) (Fig. 1). A discussion of the physiological and ecological attributes that distinguish sea turtles from other reptiles will provide insight as to why they are the only long-distance reptilian migrants. Finally, we will discuss the conservation and management implications of migration in reptiles and highlight areas for future research.

Role of migration in the life history of reptiles

Several previous reviews have provided details regarding seasonal movements and the role of migration in the life history of reptiles (Gregory 1982; Gregory et al. 1987; Gibbons and Semlitsch 1987; Plotkin 2003; Luschi et al. 2003; Russell et al. 2005). Movements between distinct breeding, foraging, and overwintering sites have been documented for a wide variety of species. We present general information on migratory patterns for snakes, lizards, crocodilians, and turtles to provide a framework for interpretation of the physiological and behavioral aspects of migration in reptiles. Seasonal movement patterns of worm lizards (Amphisbaenians) and tuatara (Rhynchocephalians) have not been well-characterized and will not be included in this review.

Migratory movements of snakes have been reviewed by several authors (Gregory 1982; Gregory et al. 1987; Gibbons and Semlitsch 1987; Macartney et al. 1988; Reinert 1993), and continued interest in the spatial ecology of snakes has resulted in numerous recent publications on this topic (Madsen and Shine 1996; Heard et al. 2004; Brown et al. 2005; Marshall et al. 2006; Glaudas et al. 2007). Many species of snakes at temperate latitudes undertake seasonal movements between distinct foraging habitats and suitable overwintering sites (Gregory 1982; Reinert 1993). Snakes that take refuge in winter hibernacula are afforded protection from freezing temperatures and predators during the cold months when they are particularly vulnerable due to low metabolic rates and decreased responsiveness. Snake hibernacula are typically underground burrows or rock crevices with south-facing orientation for maximum solar exposure (Gregory 1982). Movements of up to 17 km between winter hibernacula and summer habitat have been documented for snakes (*Thamnophis sirtalis*, Gregory and Stewart 1975), but seasonal migratory movements to and from hibernacula are typically limited to distances of 1–10 km (Gregory 1982; Gibbons and Semlitsch 1987).

Snakes that inhabit warm climates at tropical and subtropical latitudes may migrate seasonally (Shine and Lambeck 1985; Gregory et al. 1987; Madsen and Shine 1996) as a result of water and food availability rather than thermal considerations. For example, water pythons

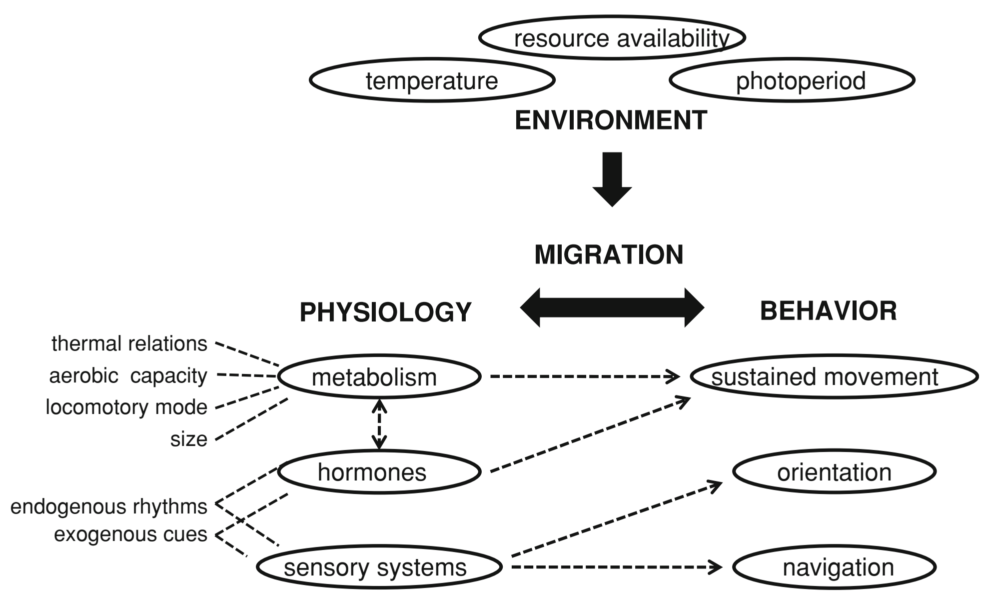

Fig. 1 Conceptual diagram illustrating the relationship between physiology and behaviors associated with migration

(*Liasus fuscus*) in the tropics of northern Australia exhibit movements between low-lying swamps in the dry season and woodlands or floodplains at higher ground up to 12 km distant during the wet season. Python movements are strongly correlated with movement patterns of their primary prey, the dusky rat (*Rattus colletti*) (Madsen and Shine 1996). Likewise, the Arafura file snake (*Acrochordus arafurae*) alters its movement patterns and habitat utilization between the dry and wet season in northern Australia (Shine and Lambeck 1985). This fully aquatic species is restricted to deep pools during the dry season, but moves into flooded grasslands to take advantage of previously unavailable resources as water levels rise during the wet season.

Nesting migrations are also observed for snakes (Gregory et al. 1987; Gibbons and Semlitsch 1987; Brown et al. 2005). In many cases, nesting habitat differs significantly from foraging habitat with regards to thermal characteristics and availability of refugia, and gravid female snakes may travel 100–900 m from summer foraging grounds to access suitable nest sites (Madsen 1984; Reinert 1993; Marshall et al. 2006).

Migration is rare among lizards, but there are several interesting examples of movements associated with reproduction in large iguanid lizards. Green iguanas (*Iguana iguana*) on the island of Barro Colorado in Lake Gatun, Panama swim considerable distances (1–3 km) to access suitable nest sites on the adjacent island of Slothia (Rand 1968; Montgomery 1973; Bock 1989). These iguanas show strong nest site fidelity between years and return to the same home range along the shoreline of Barro Colorado post-nesting (Bock et al. 1985). The Galapagos land iguana (*Conolophus subcristatus*) covers even greater distances over land during their nesting migrations on the volcanic island of Fernandina. Werner (1983) used radiotelemetry to document movements of over 10 km distance between lowland foraging areas and nesting aggregations within the caldera of an active shield volcano at 1,400 m elevation.

There have been relatively few investigations of migration in crocodilians, perhaps due to the difficulties and dangers of working with these animals. Early radio-tracking studies with *Alligator mississippiensis* documented an increase in movements during the spring breeding season compared with the rest of the year, however, nesting sites for this species typically fell within the home range for activity (Goodwin and Marion 1979; Rootes and Chabreck 1993). Species within the genus *Crocodylus* display a greater propensity for long-distance movements. For example, female Nile crocodiles (*Crocodylus niloticus*) migrate between lakes to access nest sites with suitable soil composition and sufficient shade (Modha 1967). Recent studies of seasonal movements of estuarine crocodiles (*Crocodylus porosus*) in Australia showed that female crocodiles have very limited movements during the dry season but travel distances up to 62 km to reach nesting habitats during the wet season (Kay 2004).

The impressive nesting migrations made by turtles are among the most widely recognized migratory phenomena for reptiles. Terrestrial (*Geochelone* spp), freshwater (*Chelydra serpentina*, *Apalone spinifera, Podocnemis sextuberculata*), and estuarine (*Malaclemys terrapin*) species undertake relatively modest migrations of 1–27 km to reach oviposition sites (Rodhouse et al. 1975; Hurd et al. 1979; Obbard and Brooks 1980; Swingland et al. 1989; Brown and Brooks 1993; Bodie and Semlitsch 2000; Galois et al. 2002; Fachin-Teran et al. 2006), but it is the long-distance oceanic movements of sea turtles that piques the curiosity of scientist and layperson alike. The migratory patterns of adult sea turtles have been reviewed in detail most recently by Plotkin (2003), Luschi et al. (2003), and Russell et al. (2005). Adult sea turtles embark on migrations that cover thousands of kilometers distance between foraging areas and tropical or sub-tropical nesting beaches every 2–4 years. The majority of sea turtle species have distinct neritic foraging grounds to which they return after the nesting season, but the nomadic leatherback turtle (*Dermochelys coriacea*) and olive ridley turtle (*Lepidochelys olivacea*) wander widely throughout ocean basins seeking ephemeral patches of prey. All species of sea turtles are listed as either vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature and Natural Resources (IUCN, http://www.iucnredlist.org/), and an understanding of their movements and behaviors is critical for management and conservation efforts (Godley et al. 2008). The use of satellite telemetry to track sea turtles at sea has provided an enormous amount of information about the timing and pathways of migrations, but the mechanisms by which sea turtles accomplish directed, long-distance movements have been less studied.

Long-distance movements are undertaken at all stages in the sea turtle life cycle (Fig. 2). Upon emergence from nests, hatchling sea turtles display a period of intense activity fueled by yolk stores which is referred to as the hatchling “frenzy” (Wyneken 1997). During the frenzy stage hatchlings move off the beach, swim beyond the surf zone, and, with any luck, travel to prevailing currents that will deliver them to oceanic nursery habitats (reviewed by Musick and Limpus 1997). Movements of sea turtles during this pelagic stage are thought to be largely determined by currents. Young sea turtles spend approximately 3–7 years associated with sargassum mats and flotsam in open ocean convergence zones before recruiting to nearshore nursery grounds.

Juvenile and adult sea turtles display seasonal movements that are likely related to preferred thermal habitats and food availability. For example, Kemp’s ridley

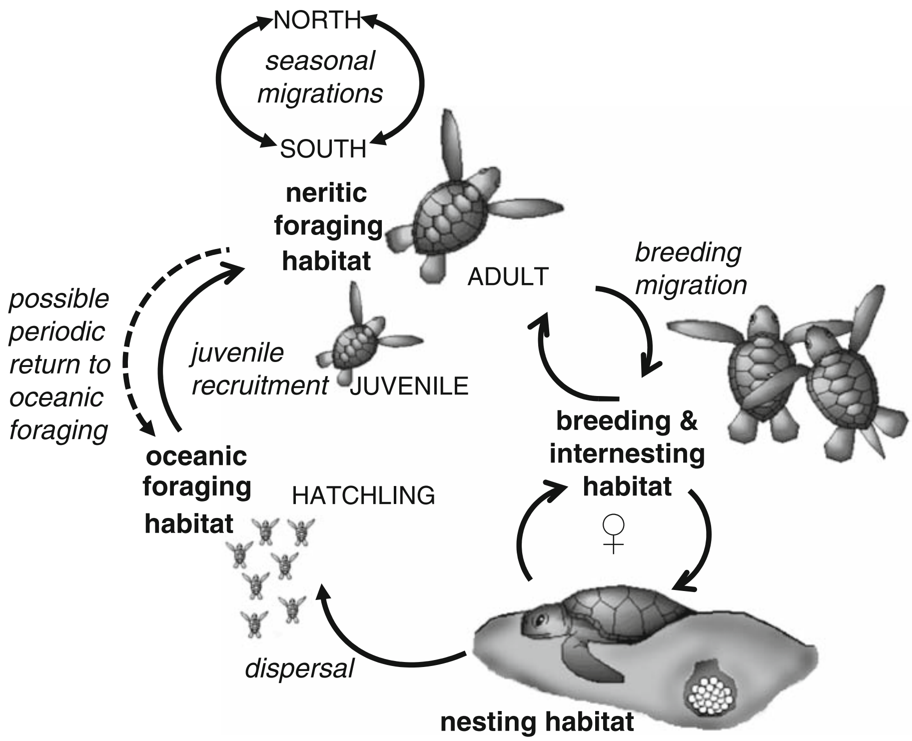

Fig. 2 Schematic diagram of the generalized sea turtle life cycle, with each species exhibiting variations on this central theme

(*Lepidochelys kempii*), loggerhead (*Caretta caretta*), and green (*Chelonia mydas*) sea turtles migrate northward along the eastern coast of the United States during the spring and summer to take advantage of nutrient rich waters during the warm months at higher latitudes (Epperly et al. 1995a, b; McClellan and Read 2007; Hawkes et al. 2007). As water temperatures decrease in late fall, turtles either return to more southerly latitudes or move offshore to the relatively warmer waters along the western edge of the Gulf Stream. Recent evidence from satellite telemetry studies has demonstrated that juvenile loggerhead and green sea turtles may also migrate back to open ocean habitats to overwinter (McClellan and Read 2007).

Non-marine species of turtles also exhibit seasonal movements associated with temperature shifts or resource acquisition. Terrestrial and aquatic turtles at temperate latitudes typically enter a period of winter dormancy, during which time they seek refuge in subterranean or underwater hibernacula to avoid extremely cold temperatures and predators. Movements between summer active sites and suitable overwintering sites for tortoises and freshwater turtles vary between 0.1 and 13.7 km (Gregory 1982; Brown and Brooks 1994; Graham and Graham 1997; Galois et al. 2002). Large land tortoises on the island of Aldabra (*Geochelone gigantean*) and in the Galapagos (*Geochelone nigra*) move from inland areas to the coastline during the tropical wet season, presumably to take advantage of seasonal shifts in food availability (Rodhouse et al. 1975; Swingland et al. 1989). Similarly, map turtles (*Graptemys pseudogeographica*) and slider turtles (*Trachemys scripta*) demonstrate seasonal utilization of flooded wetlands that may provide large food resources that are not available year-round (Bodie and Semlitsch 2000).

Energetics of migration in reptiles

Aerobic metabolism and endurance

For most people, the term “migration” evokes images of animals sustaining high levels of activity for prolonged periods of time to travel extraordinary distances between habitats. Given this view, it is no wonder that reptiles do not leap immediately to mind when one considers animal migration. Fundamental aspects of reptile physiology present limitations to endurance activity and long-distance movements. Reptiles are ectotherms, and their metabolic and physiological processes are strongly affected by environmental temperatures. Although capable of using behavioral means to regulate body temperature, and thus metabolic rate, large diel and seasonal fluctuations in environmental temperature inevitably impact metabolism and activity capacity in reptiles. Furthermore, basal and maximal aerobic metabolic rates of ectotherms are typically 1/6 to 1/10 that of similarly sized endotherms at the same temperature (Hemmingsen 1960; Bennett 1978). The disparity in aerobic metabolic capacity between ectotherms and endotherms is evident from the level of basic metabolic machinery to organ systems involved in oxygen transport. Compared with endotherms, ectotherms have lower mitochondrial enzyme activity (Else and Hulbert 1981), lower mitochondrial volume and surface area (Else and Hulbert 1981), lower rates of mitochondrial and cellular oxygen consumption $\left(\dot{V}O_2\right)$ (Hulbert and Else 1981; Brand et al. 1991; Berner 1999), smaller pulmonary surface area for gas exchange (Perry 1983), and, with the exception of crocodilians, a three-chambered heart (two atria, one ventricle) that permits shunting of oxygenated and deoxygenated blood but limits generation of high blood pressures in the circulatory system (Shelton and Jones 1991). Morphological constraints on ventilation, specifically the necessity to use some of same muscles for locomotion and respiration, also place a ceiling on activity capacity, particularly among squamate lizards (Carrier 1987).

Prolonged activity in most vertebrates is fueled by aerobic metabolism, as it generates approximately 90% more ATP per substrate molecule than commonly used anaerobic pathways and produces chemical byproducts (i.e. CO_2 and H_2O) that are readily voided and, thus, do not build up to deleterious levels (Hill et al. 2008). There is a strong correlation between endurance (i.e. length of time an activity can be sustained or maximal sustainable speed) and maximal rates of aerobic metabolism (Bennett 1982, 1991). Constraints on aerobic means of ATP production prevent reptiles from achieving steady-state activity levels comparable to those of endotherms (Garland 1982) and, with the notable exception of sea turtles, restrict their ability to undertake migrations on the scale of that observed for endotherms.

Within the framework of generally low metabolism, there are several factors that may affect aerobic metabolic rates and capacity for sustained activity in reptiles, most notably temperature. Previous reviews of metabolism in a broad range of reptiles show that factorial aerobic scope (i.e. ratio of maximal to resting aerobic metabolic rates, Fry 1947) is typically maximized within the range of preferred body temperatures for a given species (Bennett and Dawson 1976; Bennett 1982). Optimization of aerobic work capacity during migration may be achieved if movements are timed to coincide with periods when preferred body temperatures are attainable. Temperature effects on migratory behavior of reptiles have not been well-investigated, but are likely to play an important role in the timing and duration of seasonal movements. Detailed studies on body temperatures and daily behavior patterns, including periods of basking and travel, during migration could provide insight as to the importance of achieving preferred body temperatures to support sustained movement in reptiles.

Levels of circulating hormones may also exert an effect on activity and aerobic capacity of reptiles. Supplemental injections of thyroxine (T4) increase resting and maximal levels of $\dot{V}O_2$, activity of aerobic metabolic enzymes, and heart mass in lizards (John-Alder 1983, 1990a), whereas thyroidectomy results in a significant decrease in resting $\dot{V}O_2$ and metabolic enzyme activity (John-Alder 1990b). Seasonal changes in plasma T4 levels have been documented for the iguanid lizard *Dipsosaurus dorsalis* under field conditions. Plasma T4 levels were highest in the spring and late summer and lowest during hibernation for this species (John-Alder 1984), and high levels of plasma T4 were associated with an increase in maximal $\dot{V}O_2$ and metabolic enzyme activities (John-Alder 1984). Seasonal trends in plasma T4 have also been observed in desert tortoises (*Gopherus agassizii*). This species has very low levels of T4 during winter dormancy and peak levels of T4 during the early spring when there is an increase in feeding, mating, and movements (Kohel et al. 2001). These results suggest that circulating levels of T4 may prompt an increase in aerobic capacity and endurance in reptiles, but the role of T4 in triggering or sustaining migratory activities has not been investigated.

Changes in plasma corticosterone levels are associated with migratory behavior of birds (reviewed in Wingfield et al. 1990; Dingle 1996), and appear to be involved in mobilization of fuel stores and activity levels of reptiles as well (Cash and Holberton 1999, 2005; Hamann et al. 2007). Red-eared sliders (*Trachemys scripta*) respond to treatment with corticosterone implants by increasing locomotor activity (Cash and Holberton 1999). Furthermore, increases in plasma corticosterone in red-eared sliders under field conditions are associated with emigration from sub-optimal habitats (Cash and Holberton 2005). Hatchling green sea turtles during the “frenzy” dispersal stage show elevated levels of corticosterone (Hamann et al. 2007), and corticosterone levels of red-sided garter snakes (*Thamnophis sirtalis parietalis*) captured while migrating from dens to summer foraging sites are higher than levels for pre-migratory snakes at the den (Cease et al. 2007). Elevated plasma corticosterone promotes fuel catabolism and may play a role in regulating the use of energy stores during seasonal movements. The role of the endocrine system in regulating metabolic rate, aerobic capacity, and activity levels during migration in reptiles deserves further investigation.

There is a substantial amount of interspecific variation in maximal aerobic metabolic rates and the scope for sustained activity among reptiles which may reflect differences in phylogeny or behavioral differences in foraging (i.e. active vs. ambush) (Ruben 1976; Andrews and Pough 1985; Secor and Nagy 1994) or defense strategies (i.e. flight vs. static defense) (Tucker 1967). One might assume that the propensity for a species to undertake seasonal migrations might also be reflected by differences in aerobic capacity, but no clear association between aerobic scope and migration emerges from currently published data. Among snakes, active foragers with comparatively high field metabolic rates (i.e. *Masticophis flagellum*, *Coluber constrictor*, Colubridae) and sit-and-wait predators with comparatively low field metabolic rates (i.e. *Crotalus viridis*, *Crotalus cerastes*, Viperidae) both display seasonal migration (Ruben 1976; Gregory 1982; Gibbons and Semlitsch 1987; Secor and Nagy 1994). Migrating lizards (*Iguana iguana*) fall mid-way along the continuum of activity and aerobic capacity observed for lizards (Tucker 1967), and migration among crocodilians is rare, despite possession of anatomical features (diaphragmaticus, 4-chambered heart) seemingly well-suited to support enhanced ventilation and high activity levels (Farmer and Carrier 2000; Claessens 2009). Sea turtles exhibit factorial aerobic scopes (2–10) within the range observed for other reptile species (Prange 1976; Prange and Jackson 1976; Bennett and Dawson 1976; Jackson and Prange 1979; Butler et al. 1984; Bennett 1985), even though they migrate distances at least one order of magnitude larger than those observed for any other reptile. Enhanced aerobic capacity may be advantageous during migration, but it is not a prerequisite, nor is it a good predictor of which reptile species will undertake migrations. Multiple other factors, including mode of locomotion, cost of transport, and ecological requirements, impact the migratory behavior and capacity for sustained activity of species.

Whereas most reptiles traverse distances of hundreds to thousands of meters during migration, sea turtles migrate hundreds to thousands of kilometers. Important insights regarding the metabolic and physiological characteristics that support sustained movements in sea turtles have emerged over the last several decades. Laboratory experiments to assess effects of swimming activity on $\dot{V}O_2$ in hatchling and immature sea turtles have demonstrated that sustained active aerobic metabolic rates are 2–4 times higher than resting rates at these life stages (Prange 1976; Wyneken 1997), there is good correlation between activity level and $\dot{V}O_2$ (Prange 1976; Jones et al. 2007; Booth 2009), and immature green sea turtles (0.25–1.32 kg) can sustain high swim speeds (0.1–0.6 m s^{-1}, $\geq$1.5 body lengths s^{-1}) without resorting to anaerobic metabolism (Prange 1976; Butler et al. 1984). Field studies of aerobic metabolic capacity in adult female green and leatherback sea turtles on nesting beaches showed that $\dot{V}O_2$ during vigorous activity (walking on beach) was 4–10 times higher than resting rates (Prange and Jackson 1976; Jackson and Prange 1979; Paladino et al. 1990); aerobic factorial scopes in green turtles were larger in adults than in smaller, immature turtles (Wyneken 1997). Prange and Jackson (1976) studied the effects of body size on $\dot{V}O_2$ for green sea turtles (size range 0.03–141.50 kg) and found a divergence in scaling of resting and active aerobic metabolism, such that an increase in body size resulted in an increase in capacity for aerobic activity. The slope for the least squares power regression relating mass specific $\dot{V}O_2$ to body mass was -0.17 for resting green turtles and -0.06 for active green turtles. This pattern has important implications with regards to ontogenetic habitat shifts (i.e. timing of recruitment of juvenile sea turtles to neritic foraging grounds from open ocean nursery grounds) and the ability of adult sea turtles to undertake open ocean migrations, often moving against prevailing currents, to reach breeding or foraging destinations.

The combined evidence from studies of sea turtle metabolism suggests that sea turtles are capable of meeting the metabolic demands of prolonged activity during migration using primarily aerobic metabolism at all life history stages. Reliance on aerobic metabolic pathways insures efficient use of limited yolk energy reserves during the hatchling frenzy stage (Jones et al. 2007) and of lipid reserves during nesting migrations of capital breeding adult sea turtles (Carr and Goodman 1970; Prange and Jackson 1976). Morphological and physiological studies have demonstrated that the cardio-pulmonary system of sea turtles is well-equipped to meet oxygen demands of long-distance migration. There is a linear relationship between heart rate and $\dot{V}O_2$ in exercising immature green turtles (Butler et al. 1984), and increased $\dot{V}O_2$ during activity is well-matched by increased ventilation and pulmonary blood flow (West et al. 1992). Sea turtles possess multi-cameral lungs with extensive surface area to promote efficient gas exchange (Jackson and Prange 1979; Lutcavage et al. 1987) and reinforced large diameter primary and secondary airways that permit exceptionally high ventilatory flow rates (Tenney et al. 1974). Sea turtles also have large tidal volumes compared with other reptiles, exchanging up to 80% of lung air volume during a respiratory cycle (Berkson 1967; Tenney et al. 1974; Lutcavage and Lutz 1997). The rapid, forceful expiratory-inspiratory breathing cycle of sea turtles while at the water surface or on the beach is quite audible and has been described as “dramatically dynamic” (Tenney et al. 1974). Blood oxygen transport properties are highly variable among sea turtles species and depend on whether oxygen for breath-hold dives is stored primarily in the blood (i.e. Dermochelyidae) or in the lungs (i.e. Chelonidae) (Lutcavage and Lutz 1997).

Among reptiles, only varanid lizards (monitors or goannas) are comparable to sea turtles with regards to high aerobic capacity and corresponding adaptations of the cardio-pulmonary system to support high rates of oxygen consumption (Wood et al. 1978; Gleeson et al. 1980;

Bickler and Anderson 1986; Thompson and Withers 1997; Frappell et al. 2002). Interestingly, varanids are not known to undertake migrations of any considerable distance. Ecological needs of these tropical to temperate lizards appears to be fully met within their home range of activity, and enhanced aerobic capacity is primarily a reflection of their active foraging strategy rather than an adaptation to support prolonged migratory movements (Clemente et al. 2009).

Cost of transport

One of the criteria used to define migration is that movements are undeterred by resources, such as food or mates, that might otherwise be utilized (Dingle 1996). To the best of our knowledge, most reptiles conform to this criterion and do not eat during seasonal migrations between habitats. For movements fueled by on-board energy reserves, it is advantageous to use those energy reserves in the most efficient manner to insure that the destination is reached. Energetic efficiency may be accomplished by traveling at speeds that minimize the mass-specific cost of transport, i.e. the metabolic cost of moving a given mass a given distance (Tucker 1970; Schmidt-Nielsen 1972). The cost of transport for reptiles is typically reported as the net cost of transport (*NCT*), which is equivalent to the slope of the relationship between aerobic metabolic rate and speed and does not include metabolic costs associated with maintenance and posture (Schmidt-Nielsen 1972).

The *NCT* for animals varies predictably with body size, mode of locomotion, and temperature (Schmidt-Nielsen 1972; Tucker 1975; Taylor et al. 1982; Bennett 1982). Measurements of *NCT* in reptiles are usually reported for animals at their preferred body temperature (Gleeson 1979; John-Alder et al. 1986; Walton et al. 1990; Secor et al. 1992). As body size increases, the mass-specific *NCT* decreases such that larger animals can travel a given distance at a lower energetic cost per unit mass than smaller animals (Taylor et al. 1982; Bennett 1985). In general, body size of reptiles is smaller than that of birds and mammals (Pough et al. 2004), and the high mass-specific *NCT* associated with small size contributes to their limited ability to travel long-distances. It should come as no surprise that most reptile species that migrate tend to attain relatively large body size as adults. The most obvious examples of this are the sea turtles, which, depending on species, may weigh as much as 100–900 kg as adults. Other examples include the large boid (*Liasus fuscus*) and viperid (*Crotalus* spp.) snakes that undertake seasonal migrations (Hirth et al. 1969; Landreth 1973; Madsen and Shine 1996).

The mode of locomotion employed by an animal has a large impact on the *NCT*: swimming is the least costly form of locomotion, terrestrial walking or running are the most expensive forms of locomotion, and flying is intermediate (Tucker 1970; Schmidt-Nielsen 1972). The relationship between *NCT* and mode of locomotion exerts a stronger effect on locomotory energetics than does taxonomic status. In other words, the cost to move given mass a given distance is comparable for terrestrial reptiles and mammals of similar size, and this cost is higher than that of a similarly sized animal that uses swimming as its primary mode of locomotion (Tucker 1975). John-Alder et al. (1986) reviewed *NCT* for a broad size range of lizards, and found that larger lizards had a lower *NCT* than did smaller lizards (Fig. 1) and the few species of large iguanid lizards known to migrate had *NCT* within the range of 0.26–1.07 ml O_2 g^{-1} km^{-1} (mass range 0.6–4.6 kg). Interestingly, the cost of transport for terrestrial locomotion in *Iguana iguana* was twice that of the land iguana *Conolophus cristatus* (Moberly 1968; Gleeson 1979). Migratory movements in *Iguana iguana* are less extensive than those of *C. cristatus* and are accomplished primarily by swimming between islands rather than terrestrial locomotion.

The energetic cost of terrestrial limbless locomotion has been a topic of interest and debate for many years. Snakes exhibit several different types of locomotory modes depending on species, habitat, and substrate composition, and the energetic cost of movement varies depending on locomotory mode. For black racers (*Coluber constrictor*) weighing approximately 100 g, the mean *NCT* for concertina locomotion, a locomotory mode that involves static points of contact with substrate, was 8.49 ± 1.68 (SEM) ml O_2 g^{-1} km^{-1}, whereas the mean the *NCT* for lateral undulation, in which snakes experience only sliding contact with the ground, was just 1.15 ± 0.21 ml O_2 g^{-1} km^{-1} at 30°C (Walton et al. 1990). The *NCT* for sidewinding locomotion in similarly sized viperid snake *Crotalus cerastes* at 30°C was 0.41 ml O_2 g^{-1} km^{-1} (Secor et al. 1992). If a snake is capable of utilizing multiple locomotory modes, it seems reasonable to assume that given the appropriate habitat and substrate conditions the locomotory mode with the lowest *NCT* would be used for migratory movements. This aspect of snake migration has not been well-investigated. Factors other than energetic efficiency, such as risk of predation, may also affect the mode of locomotion used by snakes during migration.

Chodrow and Taylor (1973) noted that *NCT* for small garter snakes (*Thamnophis sirtalis*, 25 g) was 0.52 ml O_2 g^{-1} km^{-1}, only 30% of the value predicted for a lizard of similar size (Fig. 1). This led to the conclusion that limbless terrestrial locomotion was less energetically costly than limbed terrestrial locomotion, a conclusion that has been both refuted (Walton et al. 1990) and supported (Secor et al. 1992) by later studies. From a biomechanics point of view, factors contributing to a low *NCT* in snakes could include the elimination of vertical displacement of the center of gravity, low cost of body support, and lack of energetic cost to lift and protract limbs (Walton et al. 1990). Data from a wider variety of species may help resolve this issue.

The *NCT* for terrestrial locomotion has been reported for a limited number of chelonians. The available data show that energetic cost of terrestrial locomotion in turtles is actually lower than predicted by scaling relationships of *NCT* and body size (Baudinette et al. 2000; Zani and Kram 2008). The *NCT* for Murray short-necked turtles (*Emydura macquarii*, 535–620 g) and ornate box turtles (*Terrapene ornate*, 173–431 g) walking on a treadmill was less than half the values predicted by previously published allometric equations (Fig. 1) (John-Alder et al. 1986; Full 1991; Baudinette et al. 2000; Zani and Kram 2008). Low metabolic costs of locomotion in turtles may be due to their unique limb girdle morphology, very slow rates of movement, and high efficiency of muscles (Woledge 1968; Zani and Kram 2008). A broader investigation of energetics of locomotion may provide important insight as to the mechanisms supporting terrestrial migratory movements of turtles.

Cost of transport for semi-aquatic species of reptiles is 2–4 times lower while swimming compared with walking, although this has only been investigated in a few species (*Amblyrhynchus cristatus*, Gleeson 1979; *Emydura macquarii*, Baudinette et al. 2000). Fully aquatic reptiles that swim as their primary form of locomotion have very low *NCT* compared with terrestrial forms (Fig. 3). For example, the *NCT* of immature green sea turtles (mass $\approx$ 735 g) is 0.11 ml O_2 g^{-1} km^{-1} and *NCT* of sea snakes (mass $\approx$ 400 g) is 0.06 ml O_2 g^{-1} km^{-1} (Prange 1976; Seymour 1982; Butler et al. 1984). Although the *NCT* of fully aquatic reptiles is low compared with terrestrial reptiles, it is still considerably higher than *NCT* of fish (Brett 1964; Prange and Jackson 1976; Gleeson 1979; Butler et al. 1984). The discrepancy may be due to the necessity of reptiles to return repeatedly to surface to breathe and the energy expended to overcome surface turbulence and buoyancy upon descent (Gleeson 1979; Hays et al. 2007).

Given their anguilliform mode of locomotion, morphological adaptations for efficient swimming (paddle-shaped tail, ventral body keel), very low *NCT*, and capacity for non-pulmonary gas exchange while submerged, sea snakes appear to be well-equipped for accomplishing long-distance migrations. Movements of sea snakes are difficult to study, but the limited amount of research conducted on this topic show that sea snakes are primarily surface dwellers and horizontal movements are greatly influenced by currents (Graham et al. 1987; Rubinoff et al. 1988). Nevertheless, the ability to dive fairly deeply (50 m) and for prolonged periods of time (>200 min) may permit sea snakes to avoid surface turbulence and move against currents. The limited data on movements of hydrophiid sea snakes (*Aipysurus laevis* and *Emydocephalus annulatus*) show a tendency for limited home range, strong site fidelity, and slow swimming speeds (Burns and Heatwole 1998; Shine et al. 2003; Lukoschek et al. 2007), but Lynch (2000) suggested that male snakes may undertake seasonal movements between reefs to mate. Laticaudid sea snakes (sea kraits) forage in water, but periodically return to land to court, mate, and lay eggs. The distances travelled between foraging and breeding sites have not been documented for this group. Movements, behavior, and energetics of sea snakes are topics worthy of future investigations.

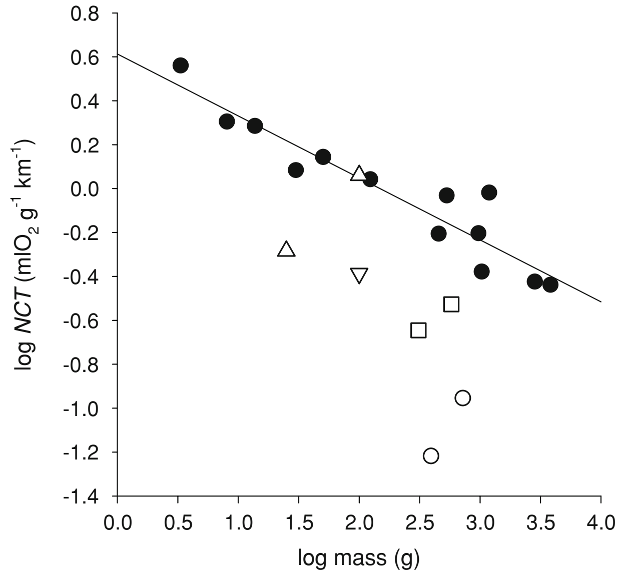

Fig. 3 Mass-specific net cost of transport (*NCT*) for various reptiles. *Closed circles* and *regression line* are for 13 species of diurnal lizards (3–3,885 g) while walking (*NCT* (ml O_2 g^{-1} km^{-1}) = $-0.2822 \times$ mass (g) + 0.6134, $r^2 = 0.8855$) (data reviewed by John-Alder et al. 1986). *Open circles* represent *NCT* of fully aquatic reptiles swimming (*Chelonia mydas*, Prange 1976; Hydrophiid spp., Seymour 1982), *open up triangles* represent *NCT* of snakes moving by lateral undulation (*Thamnophis sirtalis*, Chodrow and Taylor 1973; *Coluber constrictor*, Walton et al. 1990), *open down triangle* represents snakes moving by sidewinding (*Crotalus cerastes*, Secor et al. 1992), and *open squares* represent *NCT* of turtles walking on land (*Emydura macquarii*, Baudinette et al. 2000; *Terrapene ornata*, Zani and Kram 2008)

Morphological and behavioral adaptations for aquatic existence may enhance efficiency of swimming locomotion, a point made evident by considering the anatomical features and locomotory gait of sea turtles. Sea turtles have a streamlined body form to minimize drag, rigid wing-like fore flippers for propulsion, and rudder-like hind limbs that serve either as elevators or a steering mechanism during routine swimming (Davenport et al. 1984; Wyneken 1997). Sea turtles swim by synchronously moving their forelimbs in a motion (i.e. the "powerstroke") that has been compared to the flapping of bird wings (Davenport et al. 1984). Forward thrust is generated during all phases of the powerstroke, by lift-based mechanisms during the upstroke and by drag-based mechanisms during the downstroke. Sea turtles may also glide through the water for considerable distances by holding forelimbs close to the horizontal plane to reduce drag and create hydrodynamic lift (Davenport et al. 1984; Wyneken 1997). In comparison, semi-aquatic freshwater turtles typically swim by protracting and retracting diagonally opposite limbs synchronously while paddling. This form of drag-based locomotion generates less thrust and lower swim speeds than the powerstroke used by sea turtles (Davenport et al. 1984; Wyneken 1997).

Fuel storage and utilization

Migrating birds, mammals, fish, and invertebrates depend on lipid stores to fuel long-distance movements, and extensive feeding and lipid deposition is a common premigratory behavior (Orr 1970; Blem 1980; Dingle 1996; Weber 2009). Catabolism of lipids yields more ATP per gram fuel than catabolism of either carbohydrates or proteins, so storing energy in the form of lipids is the best way to maximize on-board fuel reserves. Reptiles typically store lipids either subcutaneously or in visceral fatbodies, and the degree to which a given species stores lipid is determined by food availability (Derickson 1976). Lipid reserves of reptiles are relied upon to provide energy during hibernation and to fuel activities associated with reproduction (Derickson 1976; Scott et al. 1995).

Lipid utilization in the context of migratory movements has not been specifically addressed for this group, although several studies have considered use of lipid stores for nesting migrations as part of the overall cost of reproduction (Kwan 1994; Aubret et al. 2002; Hamann et al. 2002; Jessop et al. 2004; James et al. 2005). The strategy of capital breeding, i.e. fueling reproductive activities using energy stores rather than resources gathered during the reproductive period, is common in reptiles (Bonnet et al. 1998) and exemplified by sea turtles. Sea turtles periodically undertake breeding migrations from foraging areas to nesting areas (Miller 1997), and generally do not eat during the nesting season (for exceptions see Hochscheid et al. 1999; Myers and Hays 2006; Fossette et al. 2008). The length of the interval between nesting years (i.e. remigration interval) varies depending on environmental conditions and food availability at the foraging grounds (Wallace et al. 2006). Hatase and Tsukamoto (2008) found that variation in remigration intervals for a nesting population of loggerhead sea turtles in Japan could be explained by differences in foraging strategies, food quality, and habitat. Smaller females that foraged on oceanic planktonic prey had longer remigration intervals compared with larger females that foraged on nutrient-rich benthic prey (Hatase et al. 2004; Hatase and Tsukamoto 2008). Correlations between the number of nesting green turtles in a given year and major fluctuations in the Southern Oscillation have been documented on nesting beaches in the Great Barrier Reef (Limpus and Nicholls 1988). Likewise, climate variability due to the El Nino Southern Oscillation has been shown to have significant impacts on remigration intervals and number of nesting females in populations of Pacific leatherback turtles (Saba et al. 2007; Reina et al. 2009). These observations suggest that resource availability and the ability to acquire sufficient fuel reserves on the foraging grounds play a critical role in the timing of breeding migrations and reproductive success for endangered species of sea turtles.

Evidence of the importance of lipid storage and mobilization during migration and reproduction in sea turtles has been provided by studies of blood chemistry and body condition (Kwan 1994; Hamann et al. 2002; Jessop et al. 2004). Plasma triglycerides, indicative of mobilized lipids, of female green sea turtles are highest during pre-migratory vitellogenesis (13.11 ± 1.40 mmol l^{-1}), intermediate during the first two-thirds of the nesting season (7.54 ± 1.68 mmol l^{-1}), decline toward the end of the nesting season (4.90 ± 0.79 mmol l^{-1}), and are at lowest levels in post-breeding turtles at foraging areas (1.22 ± 0.19 mmol l^{-1}). Similarly, plasma triglycerides and body condition index (a measure of fat stores) of male green turtles prior to migration to breeding areas are significantly higher than values for males engaged in courtship behaviors at the breeding grounds (Jessop et al. 2004). Although both female and male sea turtles migrate to breeding and nesting areas, fat reserves in females are typically greater than those of males due to the additional energetic costs associated with egg production and nesting (Kwan 1994).

Snakes also exhibit a strategy of capital breeding, and fuel reserves for species that undertake reproductive migrations must be sufficient to cover the cost of movements and nesting or brooding activities. Resource availability may influence the frequency of reproduction and reproductive episodes are often separated by several years (Seigel and Ford 1987). For females of many snake species, reproduction only occurs after a critical body condition threshold is met, insuring that sufficient energy reserves are available to meet costs of reproduction (Nalleau and Bonnet 1996; Madsen and Shine 1999; Bonnet et al. 2001; Aubret et al. 2002; Shine 2009). The literature on lipid reserves in snakes focuses primarily on the relationship between reserves and reproductive output (Plummer 1983; Madsen and Shine 1999; Bonnet et al. 2001), and the amount of reserves allocated to travel to nesting or brooding sites has received less attention.

Analyses of fat stores, body condition, and lipid mobilization prior to, during, and after completion of reproductive activities could provide insight regarding the relative contribution of migratory costs to the overall cost of reproduction in snakes and other reptiles.

Many temperate species of reptiles undertake migrations from overwintering sites to foraging or breeding sites in the spring. Reptiles experience metabolic downregulation and typically do not eat while overwintering, so metabolic needs, albeit low, must be met using energy reserves during this time (Gregory 1982). Metabolic depression and rates of energy store depletion vary greatly for overwintering reptiles, depending on species and thermal conditions in the hibernacula (Gregory 1982). The amount of fuel reserves remaining at the end of the overwintering period may be an important factor in determining migratory and reproductive behavior during the spring.

Migrating reptiles may use fuels other than lipid to reach their destination. Plasma concentrations of glucose, non-esterized free fatty acids, and protein were elevated during natal dispersal of hatchling green sea turtles, indicating that hatchlings were mobilizing a variety of fuel sources (Hamann et al. 2007). Lipids are the primary source of energy for long-distance movements in birds and mammals, and are assumed to be of primary importance for reptiles as well, however, the degree to which other types of fuel are utilized during seasonal migrations in reptiles has not been studied in detail.

Sensory mechanisms for navigation and orientation

The migrations of reptiles occur over a range of scales, which in turn can potentially require different approaches to orientation, resulting either in use of different guidance cues or perhaps use of the same cues in different ways, to locate the intended goal (Able 1991; Cheng et al. 2007; Rozhok 2008). Within the fairly small, familiar ranges traversed by some reptile species over the course of a lifetime, piloting using familiar visual, chemical, or magnetic landmarks (Griffin 1952; Åkesson and Wehner 2002) may provide sufficient guidance for their movements. Directional information for orientation over both short and long distances can also be obtained from exogenous compass cues (e.g. celestial, magnetic), which allow organisms to set and maintain a course in a particular direction without use of landmarks (Able 2001). Reptile species whose movements take them over longer distances, most notably sea turtles (Lohmann et al. 2008b), may possess the capability of true navigation, whereby they are able to use "map" information to determine geographic position based on local cues (Able 2001). Once global location relative to a goal has been assessed, then compass and/or landmark cues can be used to set and maintain a course to the destination (Able 2001).

Typically, organisms do not rely solely on one or even just a few types of guidance cues for directional information and any available cues may be used, perhaps calibrated against one another, to ensure that the intended destination is reached (Able 1991; Cheng et al. 2007). Given that migratory movements are resource-driven and failure to acquire those necessary resources can ultimately reduce fitness, selection for efficient and precise navigational skills should be expected (Papi 1992; Dingle 1996). Investigation of the cues underlying orientation and navigation has most often been accomplished by means of artificial displacement, in which animals are taken some distance from a capture location and then released and monitored to evaluate homing ability (Papi 1992). Alternatively, directional orientation is elicited in a laboratory setting so that available guidance cues can be carefully controlled to determine which are integral to the navigation and/or orientation process (Wiltschko and Wiltschko 1995). Although using these approaches has certainly yielded valuable information regarding cue detection, investigation of integrated use of multiple cue types under natural conditions is an area where additional study is needed (Åkesson and Hedenström 2007).

Chemical cues

During smaller-scale movements, use of chemical cues seems to be prevalent among various reptile groups. Many snake species have demonstrated the capability of following conspecific trails (Ford 1986) that consist of pheromones laid down with skin lipids on substrate during locomotion (LeMaster et al. 2001), although these chemicals may also persist in the air, including at the water's surface (Aldridge et al. 2005). These pheromones are detected by the snakes' highly sensitive vomeronasal system (LeMaster et al. 2001; Shine et al. 2005). Young snakes appear to follow conspecific scent trails to locate suitable foraging areas and both juveniles and adults utilize pheromone trailing to find hibernacula (Brown and MacLean 1983; Burger 1989; Costanzo 1989; Cobb et al. 2005). Males of diverse snake species have been documented to sense and follow along pheromone trails deposited by females during the vernal breeding migration (LeMaster et al. 2001).

Some terrestrial and semi-aquatic turtles may also use chemical cues to guide their movements. Hatchling wood turtles (*Glyptemys insculpta*) exhibited movements that closely tracked those of conspecifics, suggesting trail following behavior (Tuttle and Carroll 2005). Interestingly, during choice experiments, painted turtles (*Chrysemys picta*) did not prefer water containing the odor of pond plants to tap water, suggesting that perhaps chemical cues are not a significant source of information for these turtles (Ortleb and Sexton 1964). However, during similar laboratory trials, eastern long-necked turtles (*Chelodina longicolla*) preferred water containing odors that under natural conditions would signify appropriate habitat (Graham et al. 1996). Furthermore, *Testudo hermanni* made anosmic by application of ZnSO4 to the nasal epithelia displayed reduced homing ability (Chelazzi and Delfino 1986), also supporting use of chemical information for orientation.

It has been proposed that sea turtles might imprint to the chemical signature of their natal beaches and upon reaching maturation, use chemical gradients to guide their long-distance movements to return to these areas in a manner similar to that demonstrated for salmon returning to their natal streams (Hasler and Scholz 1983). This idea was first suggested for green turtles that migrate thousands of kilometers against a prevailing westward current from foraging areas in Brazil to nesting beaches on tiny Ascension Island, in the middle of the South Atlantic (Koch et al. 1969). During conditioning trials, juvenile green turtles demonstrated the ability to distinguish among various chemical stimuli at low concentrations, indicating that they might be capable of recognizing familiar odors during orientation (Manton et al. 1972). To further investigate the possibility of chemosensory imprinting, Grassman et al. (1984) conducted laboratory experiments in which captive-reared juvenile Kemp's ridley sea turtles were able to choose among compartments filled with water that was untreated or solutions of sand and water acquired either at the natal beach or a beach near the rearing location. Although the turtles entered the natal water compartments less frequently than the others, they cumulatively spent more time in those compartments, suggesting the existence of a preference (Grassman et al. 1984). Green turtles incubated in environments containing the chemicals morpholine or 2-phenylethanol (the same chemicals used for salmon imprinting experiments) did not exhibit a preference for water containing the chemicals as opposed to untreated water (Grassman and Owens 1986). However, juvenile green turtles incubated and then reared for several months in water containing these chemicals did preferentially enter water-filled compartments containing the chemicals during choice experiments (Grassman and Owens 1986). As hatchlings are typically only exposed to natal beach cues for a period of several days prior to emergence from the nest and at the beginning of the offshore migration, additional experiments are needed to determine if chemosensory preferences can also develop within this abbreviated time frame (Lohmann et al. 1996).

In addition to these laboratory experiments, various field studies have attempted to elucidate the role of chemosensory cues in sea turtle navigation. Oceanic currents did not appear to provide directional information for green turtles displaced from the island of Europa, in the Mozmbique channel (Girard et al. 2006). Similarly, comparison of return paths for satellite-tagged adult female green turtles displaced in various directions from Ascension Island indicated that chemical information carried by prevailing westward currents was not used during homing (Luschi et al. 2001). However, green turtles released to the northwest, downwind of the island, returned more rapidly and along straighter paths than those turtles released to the southeast (Hays et al. 2003). As a result, the authors of the study propose that the turtles homing from this location were able to orient using chemical information carried on the prevailing winds (Hays et al. 2003).

In summary, sea turtles are able to detect chemosensory cues (Bartol and Musick 2003) and it is possible that in some cases this type of information could influence their orientation (Lohmann et al. 2008a). Although chemical gradients are thought to perhaps lack sufficient stability to guide migrations over the long distances transited by sea turtles (Able 1996, but see DeBose and Nevitt 2009), it is possible that these gradients could provide directional information in the vicinity of a goal. Alternatively, chemical information could be incorporated into a "mosaic map" (Papi 1992), whereby odors are associated with specific locations and the spatial relationship among those locations is learned as compass directions.

Inertial cues

Although use of inertial cues for orientation has been demonstrated in organisms as diverse as arthropods and rodents (Samu et al. 2009), experiments exploring this possibility for reptiles have been limited. Hatchling sea turtles are able to use inertial information to detect both the direction of wave surge (Wang et al. 1998) and orbital motion (Manning et al. 1997), which allows them to establish and maintain an offshore bearing during the first stage of their migration to the open ocean (Avens et al. 2003; Lohmann et al. 1996). This inertial information can also be used to set their magnetic compass sense, which can continue to provide information about the offshore direction after the turtles move beyond the zone of wave refraction where the axis of wave propagation no longer lies perpendicular to the shoreline (Lohmann et al. 1996). As wave movement varies depending upon water depth and current speed, the magnitude of orbital motion may provide oceanic animals such as sea turtles with information regarding geographic location and position within water currents (Sand and Karlsen 2000). However, it has been suggested that as during terrestrial locomotion, aquatic migrants would need to reference inertial cues against external information to accurately calculate the magnitude of displacement (Montgomery et al. 2000). Studies involving other taxa indicate that such external information may include landmark cues learned during previous explorations (Samu et al. 2009), as well as celestial (Wehner et al. 1996) or magnetic (Wiltschko and Wiltschko 1982) compass cues.

Visual cues

There are many different ways in which visual information might be used to guide organisms during their movements, one of the most basic of which is phototaxis, or movement relative to a light stimulus (Burger 1976). Sea turtle hatchlings emerging during the night from their nests on coastal beaches use a combination of positive phototropotaxis and orientation away from dark, elevated shapes, to determine the seaward direction (reviewed by Lohmann et al. 1996). Positive phototactic responses thought to relate to water-finding ability have also been observed in hatchlings, juveniles, and adults of many aquatic turtle species (Ortleb and Sexton 1964; Mrosovsky and Boycott 1965). It has also been proposed that aquatic turtles might orient toward areas of increasingly polarized light (Yeomans 1995), as sunlight becomes polarized parallel to the surface of a body of water as it is reflected (Wehner 2001) and therefore might serve as an indirect cue denoting appropriate habitat.

Pilotage refers to the guidance of movements using knowledge of the spatial relationship among landmarks within a familiar area, sometimes termed a "cognitive map" (Papi 1992; Rozhok 2008). The possibility of cognitive map use has been extensively investigated for invertebrates (Wehner et al. 1996) and small mammals (Etienne et al. 1996) and in this context landmarks might function to guide movements through scene recognition, eliciting biased detours during locomotion, beaconing from a distance, and goal identification through image matching (Collett 1996). Alternatively, animals are also thought to use landmarks to orient as part of a "mosaic map" where the spatial relationship among familiar features is learned as compass directions (Wiltschko and Wiltschko 2003). Studies investigating landmark use in reptiles are sparse (Wilkinson et al. 2009). However, corn snakes (*Elaphe guttata guttata*) appear to possess the ability to locate goals using distant landmarks, or beaconing (Holzmann et al. 1999). Also, both red-footed tortoises (*Geochelone carbonaria*; Wilkinson et al. 2009) and red-eared sliders (López et al. 2001) trained to locate goals within mazes were able to use landmark cues to accomplish the task.

Nocturnally migrating birds have been demonstrated to use a star compass based on star patterns and/or the axis of star rotation to guide their movements (Wiltschko et al. 1998) and sandhoppers orient along the water–sea interface by referencing the moon (Papi et al. 2007). However, few data are available to indicate that reptiles might use nocturnal celestial cues for orientation. Murphy (1981) found that juvenile alligators were able to orient when stars were the only available cue. While it has also been suggested that perhaps sea turtles might use star patterns to orient, their visual acuity out of water is thought to be insufficient to accomplish this task (Ehrenfeld and Koch 1967).

Conversely, many studies of reptile behavior have provided indications that solar cues provide directional information during movements. For example, during displacement experiments, Gould (1957) found that the homing ability of box turtles (*Terrapene carolina*) decreased under overcast skies. When displaced from capture locations and tested in orientation arenas where the view of the immediate surroundings was blocked, rattlesnakes (*Crotalus atrox*) transported in darkness were randomly oriented, while those relocated with a view of the sky exhibited homeward orientation (Landreth 1973). Fischer (1964) reported that although post-hatchling green sea turtles swimming in an experimental arena were significantly (but bi-modally) oriented under sun, they exhibited random orientation when celestial cues were blocked. During laboratory trials in which magnetic, visual, and then both magnetic and visual cues were disrupted for juvenile loggerhead sea turtles, the turtles were able to orient in the absence of one or the other cue, but not both, suggesting use of solar cues (Avens and Lohmann 2003).

Use of a time-compensated sun compass for orientation is prevalent in both invertebrate and vertebrate taxa (reviewed in Avens and Lohmann 2003) and reptiles have proven to be no exception. The location of the sun relative to the earth's horizon can impart directional information provided that an animal is able to compensate for the changes in the sun's position throughout the day, approximately 15° of movement along its path (azimuth) per hour (Schmidt-Koenig et al. 1991). Due to the temporal component of this directional sense, use of a sun compass is typically demonstrated by shifting an organism's internal clock by a given period of time (via alterations in photoperiod) and then conducting orientation trials under regular conditions to observe a predicted shift in orientation (Fig. 4) (Schmidt-Koenig et al. 1991). These types of clock-shifting experiments have demonstrated use of a time-compensated sun compass for a number of reptiles, including garter snakes (*Thamnophis sirtalis* and *T. ordinoides*; Lawson 1994), water snakes (*Natrix sipedon* and *Regina septemvittata;* Newcomer et al. 1974), eastern green lizards (*Lacerta viridis*; Fischer 1960), juvenile alligators (Murphy 1981) and both terrestrial and aquatic turtle species (*Terrapene carolina, Trionyx spinifer, Chrysemys picta*; DeRosa and Taylor 1980). Fischer (1964)

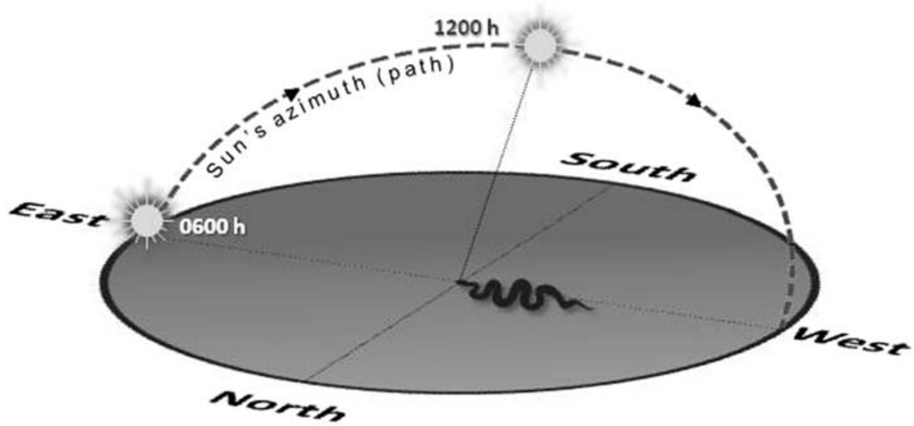

Fig. 4 Schematic representation of the use of clock-shifting to demonstrate sun compass use by a snake in the northern hemisphere. Under normal conditions, the snake will have learned that early in the morning (i.e. 0600 hours), the sun rises in the east; therefore, if it intends to migrate east during that time of day it will need to orient toward the sun. Shifting the snake's photoperiod ahead 6 h will cause it to perceive 1200 hours as being 0600 hours. Under these experimental conditions, if the snake attempts to migrate east by orienting toward the sun as it would normally do at 0600 hours, this will cause it to orient south, 90° from the original direction of orientation

also mentions that clock-shifting post-hatchling green turtles yielded a corresponding shift in orientation under sunny skies; however, supporting data are not provided.

In addition to using the sun itself to obtain compass information, various organisms orient using the pattern of sunlight polarization as a compass cue. The electrical vectors (E-vectors) of rays of sunlight traveling through space oscillate in random directions perpendicular to the axis of the direction of propagation (Sabbah et al. 2005). As sunlight passes through the earth's atmosphere and is scattered by molecules, polarization can occur, where the direction of oscillation occurs predominantly (partial polarization) or completely (full polarization) in one particular direction (Brines and Gould 1982). The pattern of polarization across the entire sky is greatly affected by the extent of overcast and as a result can be quite random, providing little directional information (Brines and Gould 1982). However, the overall degree of skylight polarization is consistent, with sunlight being least polarized closest to the sun and maximally polarized along an axis running perpendicular to the sun's azimuth (i.e. north–south), 90° from the sun's position (Brines and Gould 1982). As is the case for the sun compass, provided that animals are capable of compensating for the movement in the position of the E-vector that occurs throughout the course of the day, this feature can serve as a guidance cue. Polarized light has been found to provide directional information for aquatic as well as terrestrial organisms, as under certain conditions it can penetrate to depths up to 200 m (Sabbah et al. 2005). However, the extent to which light is linearly polarized decreases with depth and therefore this cue might be most suitable for use near the water's surface (Sabbah et al. 2005). Given that the zone of maximum polarization spans the sky, it provides axial (bi-directional) compass information and must therefore be referenced against other cues to ensure that the appropriate direction of orientation is selected (Brines and Gould 1982; Freake 1999). However, a polarized light compass is particularly useful in that it can provide information on the sun's position even in overcast conditions, as long as a partial view of the sky is available (Freake 1999). Interestingly, experiments with migratory birds have suggested that the importance of the polarized light compass is paramount, as it calibrates the magnetic compass, which in turn serves as a reference for sun and star compasses (Muheim et al. 2006).

Unfortunately, few experiments investigating polarized light orientation in reptiles have been conducted to date. During orientation arena experiments in which only celestial cues were available, garter snakes exhibited bimodal orientation (Lawson and Secoy 1991), as did the post-hatchling green turtles in Fischer's (1960) experiments, suggesting movement along the E-vector. Also, during laboratory experiments, fringe-toed (*Uma notata*; Adler and Phillips 1985) and sleepy (*Tiliqua rugosa*; Freake 1999) lizards shifted their orientation when the direction of the perceived E-vector was rotated.

Although detection of polarized light for some vertebrates has been demonstrated to occur by means of photoreceptors in the retina (Novales Flamarique et al. 1998), polarized light detection can also be mediated through extraocular photoreceptors, such as the pineal gland in amphibians (Adler and Taylor 1973). In lizards, the parietal eye (located on the dorsal surface of the head) contains photoreceptors and is involved in transmitting photic cues to the neuroendocrine system, which in turn mediates circadian rhythms and thermoregulatory behavior (Freake 1999). During homing experiments involving lizards (*Sceloporus jarrovi*) previously demonstrated to possess a time-compensated celestial compass, homing ability was disrupted when the parietal eye was painted over (Ellis-Quinn and Simon 1991). The orientation of the photoreceptors in the parietal eye is thought to be well-suited for polarized light detection and as a result, it is possible that covering the eye disrupted the lizards' ability to use this guidance cue (Ellis-Quinn and Simon 1991).

Magnetic cues

As with solar cues, for those organisms that can detect the earth's magnetic field, it has the potential to provide a ubiquitous cue for orientation and navigation (Fig. 5) (Wiltschko and Wiltschko 1995; Rozhok 2008). Although spatial and temporal variations in the magnetic field do occur, overall the field is similar to that of an enormous bar magnet, with field lines emerging from the southern hemisphere and re-entering in the northern hemisphere (Rozhok 2008). Aside from this North–South polarity, the field possesses a number of different features that could provide directional information. Inclination angle is the angle at which the field lines intersect the earth and varies from 0° deg at the equator to 90° at the poles (Wiltschko and Wiltschko 1995). Intensity also increases with latitude, with values of around 30,000 nanoTesla (nT) near the equator and 60,000 nT near the poles (Wiltschko and Wiltschko 1995). Declination, the deviation between magnetic north and true north, also becomes greater at the poles and could potentially inform directional movement (Rozhok 2008). Finally, detection of magnetic anomalies, which are variations in the regular magnetic pattern caused by changes in iron deposition in the earth's crust, might yield spatial information as well (Lohmann et al. 2008a).

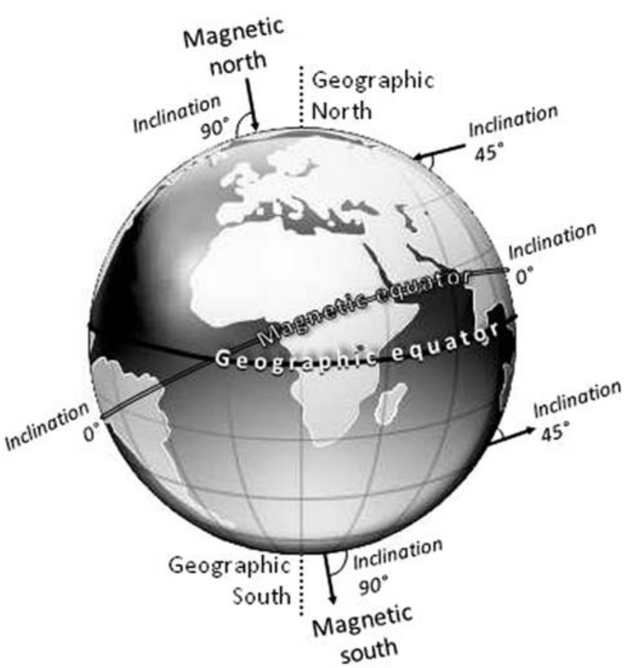

Fig. 5 Schematic diagram of the earth's magnetic field (after Wiltschko and Wiltschko 1995). Magnetic field lines emerge from the southern hemisphere and re-enter in the northern hemisphere. The angle at which the field lines intersect the earth (inclination angle) varies from 0° at the equator to 90° at the poles. The deviation between magnetic north and true north (declination) becomes greater at the poles. Features of the magnetic field may be used in combination to inform directional movement of migrating organisms

To date, studies indicate that the magnetic field can potentially guide animal movement in three different ways. The first is to serve as an external reference for collecting direction and distance information during the outward journey away from a starting point so that this information can later be integrated to determine the bearing back to the original location (Wiltschko and Wiltschko 1982). Magnetic field characteristics may also serve as a compass reference, either through (1) the polarity or northward directionality of magnetic field lines or (2) the inclination or axial direction of the field, which allows discernment of poleward and equatorward directions (Wiltschko and Wiltschko 2006). Finally, magnetic features may function to provide "map" information that can allow organisms to determine their geographic position solely based on cues in their immediate vicinity (Freake et al. 2006). If the gradients of two magnetic parameters occur along axes that are at an angle to one another (preferably perpendicular, as with latitude and longitude), then magnetic information could comprise a "grid" or bicoordinate map (Griffin 1952). If this were the case, each location on the globe would be characterized by a unique combination of the two parameters, allowing precise geographic locations to be determined using this information (Freake et al. 2006). In many locations, isolines (axes along which values are the same) of magnetic inclination and intensity do intersect at angles and studies involving various organisms suggest their use in a magnetic map (Freake et al. 2006). Use of a map sense would require experience, as animals would need to first learn the gradient direction/s within a familiar area prior to attempting to extrapolate outside that familiar range (Rodda 1984; Freake et al. 2006).

A number of reptile orientation studies suggest the use of magnetic information as a guidance cue in some manner. Box turtles exposed to increased magnetic fields during circuitous displacement in darkness away from their capture location were disoriented relative to control turtles that experienced the same treatment, but without the altered magnetic environment (Mathis and Moore 1988). Additionally, the orientation of box turtles trained to move in a particular direction in a laboratory setting was disrupted once magnets were applied to the carapace (Mathis and Moore 1988). Together, the results of this study indicate that the turtles may use the magnetic field not only as an external reference when moving away from their home site, but also as a compass cue.

In other experiments, Rodda (1984) circuitously displaced alligators in all directions from capture locations and then tested their homing orientation ability in an arena that blocked external cues, with the exception of the sky (Rodda 1984). Whereas younger juveniles were unable to compensate for extremely convoluted outward journeys, older juveniles oriented toward the homeward direction regardless of the direction, distance, or complexity of their displacement. Deviations from the homeward direction for older juveniles corresponded strongly with variation in magnetic inclination angle and/or horizontal intensity at the time of release into the experimental arena, suggesting that the animals were using magnetic information in some manner to determine their geographic position relative to the capture location.

Without question, the reptiles for which the role of magnetic information in orientation and navigation has been most extensively studied are the sea turtles. The small size and continuous, frenzied swimming behavior of sea turtle hatchlings subsequent to emergence from the nest combined with incredibly migratory life history of these animals has made them very suitable subjects for such studies (Lohmann et al. 2008b). Hatchling loggerhead and leatherback sea turtles possess an inclination compass sense that is thought to guide their movements offshore to oceanic habitat, where they will spend the first years of their lives (Lohmann et al. 1996). The direction of orientation for hatchlings using the magnetic compass is not inborn, but is flexible (as is appropriate for hatchlings that might be attempting to migrate from beaches facing in any direction) and can be set by crawling or swimming toward light or by swimming into oncoming waves (Lohmann et al. 1996). With respect to specific magnetic parameters that could be used to form a magnetic map, experiments with hatchling loggerhead sea turtles have demonstrated the capability of detecting both inclination angle (Lohmann and Lohmann 1994) and intensity (Lohmann and Lohmann 1996). Loggerhead hatchlings also respond to combinations of those features that simulate geographic positions around the edge of the North Atlantic gyre by orienting to maintain position within the current system, behaviors which would ensure that they do not stray beyond the gyre boundaries and into unfavorable habitat (Lohmann et al. 2001). Although these results suggest that the hatchlings may possess magnetic map capabilities, at this life stage the turtles would not possess the experience thought to be needed to generate a true magnetic map (Freake et al. 2006). As a result, certain characteristics of the magnetic field may simply serve to elicit genetically transmitted responses, which keep the hatchlings from straying too far out of favorable environments (Lohmann et al. 2001), much in the way magnetic features trigger stopovers for migratory birds (Fleissner et al. 2003; Henshaw et al. 2008).

Orientation mechanisms may change as organisms move through ontogenetic stages and therefore it is not possible to assume that the cues used by hatchlings are exactly the same as those used by older turtles (Avens and Lohmann 2003). However, due to the logistical challenges presented by their large size, the number of studies involving older turtles has been limited. Juvenile neritic-stage loggerheads swimming in a water-filled arena were able to set and maintain a direction of orientation when outfitted only with frosted goggles, but their orientation was disrupted when the goggles were applied in conjunction with powerful magnets on the head and at the front of the carapace, suggesting magnetic compass use in older turtles as well as hatchlings (Avens and Lohmann 2003). Juvenile loggerhead and green turtles displaced from their neritic capture locations along circuitous routes exhibited homeward orientation when allowed to swim in an experimental arena that allowed only a view of the sky, eliminating the possible use of chemical, wave, or landmark cues to determine geographic position (Avens and Lohmann 2004). Results of initial field studies indicated that solely disrupting magnetic information did not impact the ability of post-nesting female green turtles from Ascension Island to navigate back to their foraging grounds in Brazil (Papi et al. 2000). However, as with the juvenile loggerheads mentioned above (Avens and Lohmann 2003), it is possible that the turtles were able to compensate for the altered magnetic information through use of other compass cues (Papi et al. 2000). During later experiments, adult female green turtles displaced from their nesting beaches and equipped with oscillating magnets that disrupted the magnetic field surrounding the head during displacement and/or at release did exhibit longer return paths than did controls (Luschi et al. 2007). Interestingly, the finding that the turtles outfitted with magnets only during the outward journey were affected implies that the turtles collect magnetic information during passive displacements (Luschi et al. 2007), much the same as the box turtles mentioned above (Mathis and Moore 1988). Direct evidence for use of a magnetic map in sea turtles past the hatchling stage comes from experiments in which juvenile green turtles were displaced from home foraging areas. When tested in an experimental arena in which they were exposed to combinations of magnetic inclination angle and intensity corresponding with geographic locations north and south of the testing site, the turtles oriented as though they were attempting to return to the capture site from the magnetically simulated locations (Lohmann et al. 2004).

Evidence has therefore accumulated to support the ability of sea turtles to use a magnetic map sense, potentially to imprint to the natal beach and subsequently guide return breeding migrations. One criticism of this model is based on the phenomenon of secular variation, whereby the angle at which the inclination and intensity isolines intersect changes over time, as does isoline location (Courtillot et al. 1997). Recent estimates of age at maturation for the larger hard-shelled Cheloniid sea turtle species range from 30 to 50 years (reviewed by Avens et al. 2009) and secular variation over such a time frame has the potential to be quite significant. However, genetic studies indicate that after completing the oceanic juvenile stage (1–10 years or possibly more, depending on the species; reviewed by Avens et al. 2009), neritic juveniles tend to preferentially inhabit foraging areas in the general region of their natal beach (Bowen and Karl 2007). This differential recruitment could allow them to recalibrate their map information far in advance of attempting to home for breeding purposes (Lohmann et al. 2008b). In addition, analyses of changes in magnetic inclination and intensity over the past centuries suggest that magnetic imprinting may suffice to guide adult sea turtles to the general vicinity of their natal beach, despite the occurrence of secular variation (Putnam and Lohmann 2008).

Despite decades of research, the sensory mechanisms underlying magnetic field detection remain elusive, due in part to the fact that biological tissue is permeable to magnetic field lines and therefore receptors could theoretically be located anywhere within the body (Johnsen and Lohmann 2005). However, mainly through studies on avian systems, evidence has accumulated to support two possible transduction mechanisms that might also be used by reptiles. The first of these is based on chemical reactions and involves excitation of singlet-state radical pairs that results in electron transfer and the formation of spin correlated singlet and triplet states for these pairs (reviewed in Rozhok 2008). The triplet decay rate (rate of electron back-transfer) is influenced by the ambient magnetic field and therefore the final proportion of triplet states relative to singlet states could provide information about field characteristics, such as inclination (Rozhok 2008) and intensity (Ritz et al. 2000). Retinal photoreceptors are thought to be a probable location for radical pair reactions, as they occur in ordered arrays that would maintain the fixed orientation and compartmentalization needed for the components of this type of molecular detection system to function (Rozhok 2008). In addition, this location would facilitate exposure of radical pairs within the arrays to light energy, which could facilitate the initial excitation and electron transfer (Johnsen and Lohmann 2005). Transduction of magnetic information in this manner is thought to form the basis for the inclination compass, as bird orientation shifts under different wavelengths of light and is disrupted in complete darkness (Stapput et al. 2008). Although the magnetic inclination compass of sea turtles functions in the absence of light, suggesting alternative means of magnetoreception (Lohmann et al. 1996), other light-independent sources of excitation energy that could induce electron transfer have been suggested (Rozhok 2008).

The second possible category of magnetoreception mechanisms is based on biogenic ferromagnetic materials, such as single-domain (SD) or superparamagnetic magnetite and maghemite (Kirschvink et al. 1985). SD particles retain their own magnetic moment, which would cause the particles to rotate to align with the ambient magnetic field (Kirschvink et al. 1985). In contrast, the moment of superparamagnetic particles reflects the surrounding magnetic field, which would cause adjacent particles to interact with one another in different ways, depending on ambient field characteristics (Freake et al. 2006). Transduction models for all types of magnetic particles propose that their movement relative to the magnetic field modulates ion flow across nerve membranes, resulting in conversion of magnetic information into neural information (Johnsen and Lohmann 2005). Researchers attempting to demonstrate the involvement of magnetite in magnetoreception have typically done so by means of pulse-remagnetization experiments, which disrupt the moment of SD particles, but would have no effect on chemical magnetoreception (Rozhok 2008). Such treatment has been found to disrupt the magnetic compass orientation of loggerhead sea turtle hatchlings (Irwin and Lohmann 2005) and magnetite has been isolated from the heads of adult green turtles (Perry et al. 1985), findings concordant with SD magnetite-based transduction.

Concluding remarks and future directions

Great progress has been made in elucidating the behaviors and mechanisms associated with migration in reptiles, but there is still much to learn. We have highlighted potential areas for future research throughout this text, and encourage investigators to use a comparative approach to assess common mechanisms of migration found in reptile migrants and migrants from other taxa, as well as behaviors and physiological adjustments unique to reptiles. The most detailed and extensive data on migratory behaviors in reptiles come from studies with sea turtles, as their large size and accessibility on nesting beaches make them good subjects for remote monitoring instrumentation. Advances in miniaturized data logging and tracking technology may permit more in depth studies of behavioral patterns of smaller terrestrial and semi-aquatic reptiles as well. Aspects of the physiology of migration in reptiles may best be addressed using a combination of field and laboratory approaches with smaller species or size classes.

Research on the behaviors and physiology associated with migration in reptiles has important implications for conservation efforts. Although the distances travelled are short compared with migrants in other taxa, reptiles are vulnerable to predation and anthropogenic sources of mortality when they undertake seasonal movements. This problem is highlighted by the number of snake and turtle mortalities due to roadkill during periods of reproductive migrations or movements to foraging areas (Bonnet et al. 1999; Steen et al. 2006; Row et al. 2007). Differential mortality for males and females due to differences in their movement patterns may lead to altered sex ratios and shifts in population demography (Steen et al. 2006). Roads may also act as barriers that interfere with seasonal movement patterns and reduce gene flow within a population (Shepard et al. 2008). For sea turtles, seasonal migrations may increase the likelihood of interactions with and mortality from coastal or offshore fishing operations (Polovina et al. 2000; Lewison et al. 2004; James et al. 2005). Data on migratory routes, timing and duration of movements, and energetic requirements to successfully complete migration are necessary in order to devise effective management strategies to prevent human-related sources of mortality and facilitate movements of reptiles between critical habitats.

Decisions regarding habitat management, particularly with regards to wetland buffer zones and protected corridors, may also benefit from improved knowledge of reptile migration. Radiotracking studies of freshwater turtles (*Kinosternum subrubrum, Pseudemys floridana, Trachemys scripta*) within a protected wetland site in South Carolina demonstrated that the majority of nesting and overwintering sites for turtles lay outside the federally mandated buffer zone encircling the wetlands (Burke and Gibbons 1995). Inadequate protection of terrestrial nesting habitat adjacent to wetlands has also been noted for *Chrysemeys picta* (Baldwin et al. 2004) and *Emys marmorata*, a species of conservation concern (Spinks et al. 2003). Information regarding critical nesting and overwintering habitats and the timing of movements between habitats is necessary in order to enact effective habitat preservation efforts for wetland species.

Alterations in abiotic and biotic environmental conditions associated with climate change may impact migratory behavior, physiology, and energetics of reptiles. Changes in distribution and reproductive phenology in response to shifts in environmental temperature regimes have been documented for a wide variety of species (Hughes 2000; Hawkes et al. 2009), including marine and semi-aquatic turtles (Weishampel et al. 2004; McMahon and Hays 2006; Chaloupka et al. 2008; Schwanz and Janzen 2008). The potential impacts of climate change on endangered sea turtles were reviewed recently by Hawkes et al. (2009). Alterations in oceanic currents and sea surface temperatures may affect distribution and movement patterns of sea turtles, as well as energetics of migration via impacts on primary productivity and resource availability (Saba et al. 2008; Hawkes et al. 2009). The degree to which sea turtles and other species of reptiles will be able to adapt to climate change remains to be seen. Efforts to assess the resiliency and adaptability of organisms to predicted impacts of climate change will be critical for mitigation efforts and conservation strategies (Williams et al. 2008).

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References

Able KP (1991) Common themes and variations in animal orientation systems. Am Zool 31:157–167

Able KP (1996) The debate over olfactory navigation by homing pigeons. J Exp Biol 199:121–124

Able KP (2001) The concepts and terminology of bird navigation. J Avian Biol 32:174–183

Adler K, Phillips JB (1985) Orientation in a desert lizard (*Uma notate*): time-compensated compass movement and polarotaxis. J Comp Physiol A 156:547–552

Adler K, Taylor DH (1973) Extraocular perception of polarized light by orienting salamanders. J Comp Physiol 87:203–212

Åkesson S, Hedenström A (2007) How migrants get there: migratory performance and orientation. Bioscience 57:123–133

Åkesson S, Wehner R (2002) Visual navigation in desert ants *Cataglyphis fortis*: are snapshots coupled to a celestial system of reference? J Exp Biol 205:1971–1978

Aldridge RD, Bufalino AP, Reeves A (2005) Pheromone communication in the watersnake, *Nerodia sipedon*: a mechanistic difference between semi-aquatic and terrestrial species. Am Midl Nat 154:412–422

Andrews RM, Pough FH (1985) Metabolism of squamate reptiles: allometric and ecological relationships. Physiol Zool 58:214–231

Aubret F, Bonnet X, Shine R, Lourdais O (2002) Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). Horm Behav 42:135–147

Avens L, Lohmann KJ (2003) Use of multiple orientation cues by juvenile loggerhead sea turtles (*Caretta caretta*). J Exp Biol 206:4317–4325

Avens L, Lohmann KJ (2004) Navigation and seasonal migratory orientation in juvenile sea turtles. J Exp Biol 207:1771–1778

Avens L, Wang JH, Johnsen S, Dukes P, Lohmann KJ (2003) Responses of hatchling sea turtles to rotational displacements. J Exp Mar Biol Ecol 288:111–124

Avens L, Taylor JC, Goshe LR, Jones TT, Hastings M (2009) Age estimation for leatherback sea turtles (*Dermochelys coriacea*) in the western North Atlantic using skeletochronological analysis. End Spec Res 8:165–177

Baldwin EA, Marchand MN, Litvaitis JA (2004) Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. Northeast Nat 11(1):41–48

Bartol SM, Musick JA (2003) Sensory biology of sea turtles. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, vol II. CRC Press, Boca Raton, pp 79–102

Baudinette RV, Miller AM, Sarre MP (2000) Aquatic and terrestrial locomotory energetics in a toad and a turtle: a search for generalizations among ectotherms. Physiol Biochem Zool 73(6):672–682

Bennett AF (1978) Activity metabolism of the lower vertebrates. Ann Rev Physiol 40:447–469

Bennett AF (1982) The energetics of reptilian activity. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 13. Academic Press, New York, pp 155–199

Bennett AF (1985) Energetics and locomotion. In: Hildebrand M, Bramble DM, Liem KF, Wake DB (eds) Functional vertebrate morphology. Harvard University Press, Cambridge

Bennett AF (1991) The evolution of activity capacity. J Exp Biol 160:1–23

Bennett AF, Dawson WR (1976) Metabolism. In: Gans C, Dawson WR (eds) The biology of Reptilia, vol 5. Academic Press, New York, pp 127–223

Berger J (2004) The last mile: how to sustain long-distance migration in mammals. Conserv Biol 18(2):320–331

Berkson H (1967) Physiological adjustments to deep diving in the Pacific green turtle (*Chelonia mydas agassizii*). Comp Biochem Physiol 21:507–524

Berner NJ (1999) Oxygen consumption by mitochondria from an endotherm and an ectotherm. Com Biochem Physiol B 124:25–31

Bickler PE, Anderson RA (1986) Ventilation, gas exchange, and aerobic scope in a small monitor lizard, *Varanus gilleni*. Physiol Zool 59:76–83

Blem CR (1980) The energetics of migration. In: Gauthreaux SA Jr (ed) Animal migration, orientation, and navigation. Academic Press, New York, pp 175–224

Bock BC (1989) Nesting season movements of female green iguanas (*Iguana iguana*) in Panama. Copeia 1989(1):214–216

Bock BC, Rand AS, Burghardt GM (1985) Seasonal migration and nesting fidelity in the green iguana. In: Rankin MA (ed) Migration: mechanisms and adaptive significance. Contrib Mar Sci 27(Suppl):435–443

Bodie JR, Semlitsch RD (2000) Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. Oecologia 122:138–146

Bonnet X, Bradshaw D, Shine R (1998) Capital versus income breeding: an ectothermic perspective. Oikos 83(2):333–342

Bonnet X, Naulleau G, Shine R (1999) The dangers of leaving home: dispersal and mortality in snakes. Biol Conserv 89:39–50

Bonnet X, Naulleau G, Shine R, Lourdais O (2001) Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*. Oikos 92:297–308

Booth DT (2009) Swimming for your life: locomotor effort and oxygen consumption during the green turtle (*Chelonia mydas*) hatchling frenzy. J Exp Biol 212:50–55

Bowen BW, Karl SA (2007) Population genetics and phylogeography of sea turtles. Molec Ecol 16:4886–4907

Brand MD, Couture P, Else PL, Withers KW, Hulbert AJ (1991) Evolution of energy metabolism: proton permeability of the inner membrane of liver mitochondria is greater in a mammal than in a reptile. Biochem J 275:81–86

Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Bd Can 21:1183–1226

Brines ML, Gould JL (1982) Skylight polarization paterns and animal orientation. J Exp Biol 96:69–91

Brown GP, Brooks RJ (1993) Sexual and seasonal differences in activity in a northern population of snapping turtles, *Chelydra serpentina*. Herpetologica 49(3):311–318

Brown GP, Brooks RJ (1994) Characteristics of and fidelity to hibernacula in a northern population of snapping turtles, *Chelydra serpentina*. Copeia 1994(1):222–226

Brown WS, MacLean FM (1983) Conspecific scent-trailing by newborn timber rattlesnakes, *Crotalus horridus*. Herpetologica 39:430–436

Brown GP, Shine R, Madsen T (2005) Spatial ecology of slatey-grey snakes (*Stegonotus cucullatus*, Colubridae) on a tropical Australian floodplain. J Trop Ecol 21:605–612

Burger J (1976) Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) in the field. Copeia 1976(4):742–748

Burger J (1989) Following of conspecific and avoidance of predator chemical cues by pine snakes. J Chem Ecol 15(3):799–806

Burke VJ, Gibbons JW (1995) Terrestrial buffer zones and wetland conservation: a case of freshwater turtles in a Carolina Bay. Conserv Biol 9(6):1365–1369

Burns G, Heatwole H (1998) Home range and habitat use of the olive sea snake, *Aipysurus laevis*, on the Great Barrier Reef, Australia. J Herpetol 32(3):350–358

Butler PJ, Milsom WK, Woakes AJ (1984) Respiratory, cardiovascular and metabolic adjustments during steady state swimming in the green turtle, *Chelonia mydas*. J Comp Physiol B 154:167–174

Carr A, Goodman D (1970) Ecological implications of size and growth in Chelonia. Copeia 1970(4):783–786

Carrier DR (1987) The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. Paleobiology 13:326–341

Cash WB, Holberton RL (1999) Effects of exogenous corticosterone on locomotor activity in the red-eared slider turtle, *Trachemys scripta elagans*. J Exp Zool 284:637–644

Cash WB, Holberton RL (2005) Endocrine and behavioral response to a decline in habitat quality: effects of pond drying on the slider turtle, *Trachemys scripta elagans*. J Exp Zool 303A:872–879

Cease AJ, Lutterschmidt DI, Mason RT (2007) Corticosterone and the transition from courtship behavior to dispersal in male red-sided garter snakes (*Thamnophis sirtalis parietalis*). Gen Comp Endocrin 150:124–131

Chaloupka M, Kamezaki N, Limpus C (2008) Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? J Exp Mar Biol Ecol 356:136–143

Chelazzi G, Delfino G (1986) A field test on the use of olfaction in homing by *Testudo hermanni* (Reptilia: Testudinidae). J Herp 20(3):451–455

Cheng K, Shettleworth SJ, Huttenlocher J, Rieser JJ (2007) Bayesian integration of spatial information. Psych Bull 133(4):625–637

Chodrow RE, Taylor CR (1973) Energetic cost of limbless locomotion in snakes. Proc Fedn Am Soc Exp Biol 32:422

Claessens LPAM (2009) Archosaurian respiration and the pelvic girdle aspiration breathing of crocodyliforms. Proc R Soc Lond B 271:1461–1465

Clemente CJ, Withers PC, Thompson GG (2009) Metabolic rate and endurance capacity in Australian varanid lizards (Squamata: Varanidae: *Varanus*). Biol J Linnean Soc 97:664–676

Cobb VA, Green JJ, Worrall T, Pruett J, Glorioso B (2005) Initial den location behavior in a litter of neonate *Crotalus horridus* (Timber rattlesnakes). Southeast Nat 4(4):723–730

Collett TS (1996) Insect navigation *en route* to the goal: multiple strategies for use of landmarks. J Exp Biol 199:227–235

Costanzo JP (1989) Conspecific scent trailing by garter snakes (*Thamnophis sirtalis*) during autumn. J Chem Ecol 15(11):2531–2538

Courtillot V, Gauthier H, Alexandrescu M, le Mouël J-L, Kirschvink JL (1997) Sensitivity and evolution of sea-turtle magnetoreception: observations, modeling and constraints from geomagnetic secular variation. Terra Nova 9:203–207

Davenport J, Munks SA, Oxford PJ (1984) A comparison of the swimming of marine and freshwater turtles. Proc R Soc Lond B 220:447–475

DeBose JL, Nevitt GA (2009) The use of odors at different spatial scales: comparing birds with fish. J Chem Ecol. doi:10.1007/s10886-008-9493-4

Derickson WK (1976) Lipid storage and utilization in reptiles. Am Zool 16:711–723

DeRosa CT, Taylor DH (1980) Homeward orientation mechanisms in three species of turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene carolina*). Behav Ecol Sociobiol 7:15–23

Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, New York

Ehrenfeld DW, Koch AL (1967) Visual accommodation in the green turtle. Science 155(3764):827–828

Ellis-Quinn BA, Simon CA (1991) Lizard homing behavior: the role of the parietal yee during displacement and radio-tracking, and time-compensated celestial orientation in the lizard *Sceloporus jarrovi*. Behav Ecol Sociobiol 28:397–407

Else PL, Hulbert JA (1981) Comparison of the "mammal machine" and the "reptile machine": energy production. Am J Physiol 240:R3–R9

Epperly SP, Braun J, Veishlow A (1995a) Sea turtles in North Carolina waters. Conserv Biol 9:384–394

Epperly SP, Braun J, Chester AJ, Cross FA, Merriner JV, Tester PA (1995b) Winter distributions of sea turtles in the vicinity of Cape Hatteras and their interactions with the summer flounder trawl fishery. Bull Mar Sci 56:547–568

Etienne AS, Maurer R, Seguinot V (1996) Path integration in mammals and its interaction with visual landmarks. J Exp Biol 199:201–209

Fachin-Teran A, Vogt RC, Thorbjarnarson JB (2006) Seasonal movements of Podocnemis sextuberculata (Testudines: Podocnemididae) in the Mamiraua Sustainable Development Reserve, Amazonas, Brazil. Chel Conserv Biol 5(1):18–24

Farmer CG, Carrier DR (2000) Ventilation and gas exchange during treadmill locomotion in the American alligator (*Alligator mississippiensis*). J Exp Biol 203:1671–1678

Fischer K (1960) Experimentelle Beeinflussung der inneren Uhr bei der Sonnenkompassorientierund und der Laufaktivität von *Lacerta viridis* (Laur.). Naturwissenschaften 47:287–288

Fischer K (1964) Spontanes Richtungsfinden nach dem Sonnenstand bei *Chelonia mydas* L. (Suppenschildkrote). Naturwissenschaften 51:203

Fleissner G, Holtkamp-Rötzler E, Hanzlik M, Winklhofer M, Fleissner G, Petersen N, Wiltschko W (2003) Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. J Comp Neurol 458:350–360

Ford N (1986) The role of pheromone trails in the sociobiology of snakes. In: Duvall D, Muller-Schwarze D, Silverstein R (eds) Chemical signals in vertebrates, vol IV. Plenum Press, New York, pp 261–278

Fossette S, Gaspar P, Handrich Y, LeMaho Y, Georges JY (2008) Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during internesting intervals in French Guiana. J Anim Ecol 77:236–246

Frappell PB, Schultz TJ, Christian KA (2002) The respiratory system in varanid lizards: determinants of O_2 transfer. Comp Biochem Physiol A 133:239–258

Freake MJ (1999) Evidence for orientation using the e-vector direction of polarized light in the sleepy lizard *Tiliqua rugosa*. J Exp Biol 202:1159–1166

Freake MJ, Muheim R, Phillips JB (2006) Magnetic maps in animals: a theory comes of age? Q Rev Biol 81(4):327–347

Fry FEJ (1947) Effects of the environment on animal activity. Pub Ont Fish Res Lab 68:1–62

Full RJ (1991) The concepts of efficiency and economy in land locomotion. In: Blake RW (ed) Efficiency and economy in animal physiology. Cambridge University Press, Cambridge

Galois P, Leveille M, Bouthillier L, Daigle C, Parren S (2002) Movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain, Quebec, Vermont. J Herpetol 36(3):402–411

Garland T Jr (1982) Scaling maximal running speed and maximal aerobic speed to body mass in mammals and lizards. Physiologist 25:338

Gibbons JW, Semlitsch RD (1987) Activity patterns. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Macmillan, New York

Girard C, Sudre J, Benhamou S, Roos D, Luschi P (2006) Homing in green turtles *Chelonia mydas*: oceanic currents act as a constraint rather than as an information source. Mar Ecol Prog Ser 322:281–289

Glaudas X, Andrews KM, Willson JD, Gibbons JW (2007) Migration patterns in a population of cottonmouths (*Agkistrodon piscivorous*) inhabiting an isolated wetland. J Zool 271:119–124

Gleeson TT (1979) Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiol Zool 52:549–557

Gleeson TT, Mitchell GS, Bennett AF (1980) Cardiovascular responses to graded activity in the lizards *Varanus* and *Iguana*. Am J Physiol 239:R174–R179

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: where have we been and where do we go next? End Species Res 4:3–22

Goodwin TM, Marion WR (1979) Seasonal activity ranges and habitat preferences of adult alligators in a north-central Florida lake. J Herpetol 13:157–164

Gould E (1957) Orientation in box turtles, *Terrapene c.* Carolina (Linnaeus). Biol Bull 112:336–348

Graham TE, Graham AA (1997) Ecology of the eastern spiny softshell turtle, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. Chel Conserv Biol 2:363–369

Graham JB, Lowell WR, Rubinoff I, Motta J (1987) Surface and subsurface swimming of the sea snake *Pelamis platurus*. J Exp Biol 127:27–44

Graham T, Georges A, McElhinney N (1996) Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis*, from Australia. J Herp 30(4):467–477

Grassman MA, Owens DW (1986) Chemosensory imprinting in juvenile green sea turtles, *Chelonia mydas*. Anim Behav 35(3):929–931

Grassman MA, Owens DW, McVey JP, Marquez R (1984) Olfactory-based orientation in artificially imprinted sea turtles. Science 224:83–84

Gregory PT (1982) Reptilian hibernation. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 13. Academic Press, New York, pp 53–154

Gregory PT, Stewart KW (1975) Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. Can J Zool 53:238–245

Gregory PT, Macartney JM, Larsen KW (1987) Spatial patterns and movements. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Macmillan, New York

Griffin DR (1952) Bird navigation. Biol Rev 27:359–400

Hamann M, Limpus CJ, Whittier JM (2002) Patterns of lipid storage and mobilization in the female green sea turtle (*Chelonia mydas*). J Comp Physiol B 172:485–493

Hamann M, Jessop TS, Schauble CS (2007) Fuel use and corticosterone dynamics in hatchling green sea turtles (*Chelonia mydas*) during natal dispersal. J Exp Mar Biol Ecol 353:13–21

Hasler AD, Scholz AT (1983) Olfactory Imprinting and Homing in Salmon. Springer, New York

Hatase H, Tsukamoto K (2008) Smaller longer, larger shorter: energy budget calculations explain interpopulation variation in remigration intervals for loggerhead sea turtles (*Caretta caretta*). Can J Zool 86:595–600

Hatase H, Matsuzawa Y, Sato K, Bando T, Goto K (2004) Remigration and growth of loggerhead turtles (*Caretta caretta*) nesting on Senri Beach in Minabe, Japan: life-history polymorphism in a sea turtle population. Mar Biol 144:807–811

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtle. Diversity Distrib 13:447–457

Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. End Spec Res 7:137–154

Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Luschi P (2003) Island-finding ability of marine turtles. Proc R Soc Lond B (Suppl) 270:S5–S7

Hays GC, Marshall GJ, Seminoff JA (2007) Flipper beat frequency and amplitude changes in diving green turtles, *Chelonia mydas*. Mar Biol 150:1003–1009

Heard GW, Black D, Robertson P (2004) Habitat use by the inland carpet python (*Morelia spilota metcalfi*: Pythonidae): Seasonal relationships with habitat structure and prey distribution in a rural landscape. Aus Ecol 29:446–460

Hemmingsen AM (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. Report Steno Mem Hosp Nord Insulinlab 9:1–110

Henshaw I, Fransson T, Jakobsson S, Lind J, Vallin A, Kullberg C (2008) Food intake and fuel deposition in a migratory bird is affected by multiple as well as single-step changes in the magnetic field. J Exp Biol 211:649–653

Hill RW, Wyse GA, Anderson M (2008) Animal physiolgy, 2nd edn. Sinauer Associates, Sunderland

Hirth HF, Pendleton RC, King AC, Downard TR (1969) Dispersal of snakes from a hibernaculum in northwestern Utah. Ecology 50:332–339

Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. Mar Ecol Prog Ser 185:101–112

Holzmann DA, Harris TW, Aranguren G, Bostocks E (1999) Spatial learning of an escape task by young corn snakes (*Elaphe guttata guttata*). Anim Behav 57:51–60

Hughes L (2000) Biological consequences of global warming: is the signal already. TREE 15:56–61

Hulbert AJ, Else PL (1981) Comparison of the “mammal machine” and the “reptile machine”: energy use and thyroid activity. Am J Physiol 241:R350–R356

Hurd LE, Smedes G, Dean TA (1979) An ecological study of a natural population of diamondback terrapins (*Malaclemys t. terrapin*) in a Delaware salt marsh. Estuaries 2:28–33

Irwin WP, Lohmann KJ (2005) Disruption of magnetic orientation behavior in hatchling loggerhead sea turtles by magnetic pulse. J Comp Physiol A 191:475–480

Jackson DC, Prange HD (1979) Ventilation and gas exchange during rest and exercise in adult green sea turtles. J Comp Physiol B 134:315–319

James MC, Ottensmeyer CA, Myers RA (2005) Identification of high-use habitat and threats to leatherback sea turtles in northern water: new directions for conservation. Ecol Lett 8:195–201

Jessop TS, Hamann M, Limpus CJ (2004) Body condition and physiological changes in male green turtles during breeding. Mar Ecol Prog Ser 276:281–288

John-Alder HB (1983) Effects of thyroxine supplementation on metabolic rate and aerobic capacity in a lizard. Am J Physiol 244:R659–R666

John-Alder HB (1984) Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. J Comp Physiol 154:409–419

John-Alder HB (1990a) Effects of thyroxine on standard metabolic rate and selected intermediary metabolic enzymes in field-active lizards *Sceloporus undulatus*. Physiol Zool 63:600–614

John-Alder HB (1990b) Thyroid regulation of a resting metabolic rate and intermediary metabolic enzymes in a lizard (*Sceloporus occidentalis*). Gen Comp Endocrin 77:52–62

John-Alder HB, Garland T Jr, Bennett AF (1986) Locomotor capacities, oxygen consumption, and the cost of locomotion of the shingleback lizard (*Trachydosaurus rugosus*). Physiol Zool 59(5):523–531

Johnsen S, Lohmann KL (2005) The physics and neurobiology of magnetoreception. Neuroscience 6:703–712

Jones TT, Reina RD, Darveau CA, Lutz PL (2007) Ontogeny of energetics in leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) sea turtle hatchlings. Comp Biochem Physiol A 147:313–322

Kay WR (2004) Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. Wild Res 31:495–508

Kennedy JS (1985) Migration, behavioral and ecological. In: Rankin MA (ed) Migration: mechanisms and adaptive significance. Contrib Mar Sci 27(Suppl):5–26

Kirschvink JL, Jones DS, McFadden BJ (1985) Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism. Plenum Press, New York

Koch AL, Carr A, Ehrenfeld DW (1969) The problem of open-sea navigation: the migration of green turtles to Ascension Island. J Theor Biol 22:163–179

Kohel KA, MacKenzie DS, Rostal DC, Grumbles JS, Lance VA (2001) Seasonality in plasma thyroxine in the desert tortoise, *Gopherus agassizii*. Gen Comp Endocrin 121:214–222

Kwan D (1994) Fat reserves and reproduction in the green turtle, *Chelonia mydas*. Wildlife Res 21:257–266

Landreth HF (1973) Orientation and behavior of the rattlesnake, *Crotalus atrox*. Copeia 1973(1):26–31

Lawson PA (1994) Orientation abilities and mechanisms in nonmigratory populations of garter snakes (*Thamnophis sirtalis* and *T. ordinoides*). Copeia 1994(2):263–274

Lawson PA, Secoy DM (1991) The use of solar cues as migratory orientation guides by the plains garter snake, *Thamnophis radix*. Can J Zool 69:2700–2702

LeMaster MP, Moore IT, Mason RT (2001) Conspecific trailing behavior of red-sided garter snakes, *Thamnophis sirtalis parietalis*, in the natural environment. Anim Behav 61:827–833

Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecol Lett 7:221–231

Limpus CJ, Nicholls N (1988) The Southern Oscillation regulates the annual number of green turtles (*Chelonia mydas*) breeding around Northern Australia. Aust J Wild Res 15:157–161

Lohmann KJ, Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. J Exp Biol 194:23–32

Lohmann KJ, Lohmann CMF (1996) Detection of magnetic field intensity by sea turtles. Nature 380:59–61

Lohmann KJ, Witherington BE, Lohmann CMF, Salmon M (1996) Orientation, navigation, and natal beach homing in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, pp 107–136

Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. Science 294:364–366

Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing T (2004) Geomagnetic map used in sea-turtle navigation: these migratory animals have their own equivalent of a global positioning system. Nature 428:909–910

Lohmann KJ, Lohmann CMF, Endres CS (2008a) The sensory ecology of ocean navigation. J Exp Biol 211:1719–1728

Lohmann KJ, Luschi P, Hays GC (2008b) Goal navigation and island-finding in sea turtles. J Exp Mar Biol Ecol 356:83–95

López JC, Gómez Y, Rodríguez F, Broglio C, Vargas JP, Salas C (2001) Spatial learning in turtles. Anim Cogn 4:49–59

Lukoschek V, Heatwole H, Grech A, Burns G, Marsh H (2007) Distribution of two species of sea snakes, *Aipysurus laevis* and *Emydocephalus annulatus*, in the southern Great Barrier Reef: metapopulation dynamics, marine protected areas and conservation. Coral Reefs 26:291–307

Luschi P, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Hays GC (2001) Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). Behav Ecol Sociobiol 50:528–534

Luschi P, Hays GC, Papi F (2003) A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103:293–302

Luschi P, Benhamou S, Girard C, Ciccione S, Roos D, Sudre J, Benvenuti S (2007) Marine turtles use geomagnetic cues during open-sea homing. Curr Biol 17:126–133

Lutcavage ME, Lutz PL (1997) Diving physiology. In: Lutz PL, Musick JA (eds) The biology of sea turtles, vol 1. CRC Press, Boca Raton, pp 277–296

Lutcavage ME, Lutz PL, Baier H (1987) Gas exchange in the loggerhead sea turtle *Caretta caretta*. J Exp Biol 131:365–372

Lynch TP (2000) The behavioural ecology of the olive sea snake, *Aipysurus laevis*. PhD thesis, James Cook University, Townsville, Australia

Macartney JM, Gregory PT, Larsen KW (1988) A tabular survey of data on movements and home ranges of snakes. J Herp 22(1):61–73

Madsen T (1984) Movements, home range size and habitat use of radio-tracked grass snakes (Natrix natrix) in southern Sweden. Copeia 1984(3):707–713

Madsen T, Shine R (1996) Seasonal migration of predators and prey—a study of pythons and rats in tropical Australia. Ecology 77(1):149–156

Madsen T, Shine R (1999) The adjustment of reproductive threshold to prey abundance in a capital breeder. J Anim Ecol 68:571–580

Manning EL, Cate HS, Lohmann KJ (1997) Discrimination of ocean wave features by hatchling loggerhead sea turtles, *Caretta caretta*. Mar Biol 127:539–544

Manton M, Karr A, Ehrenfeld DW (1972) Chemoreception in the migratory sea turtle, *Chelonia mydas*. Biol Bull 143:184–195

Marshall JC Jr, Manning JV, Kingsbury BA (2006) Movement and macrohabitat selection of the eastern massasauga in a fen habitat. Herpetologica 62(2):141–150

Mathis A, Moore FR (1988) Geomagnetism and the homeward orientation of the box turtle, *Terrapene Carolina*. Ethology 78:265–274

McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. Biol Lett 3:592–594

McMahon CR, Hays GC (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. Glo Change Biol 12:1330–1338

Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, vol 1. CRC Press, Boca Raton, pp 137–163

Moberly WR (1968) The metabolic responses of the common iguana, *Iguana iguana*, to walking and diving. Comp Biochem Physiol 27:21–32

Modha ML (1967) The ecology of the Nile crocodile (*Crocodylus niloticus laurenti*) on Central Island, Lake Rudolf. Afr J Ecol 5(1):74–95

Montgomery GG (1973) Post-nesting movements of iguanas from a nesting aggregation. Copeia 1973(3):620–622

Montgomery J, Carton G, Voigt R, Baker C, Diebel C (2000) Sensory processing of water currents by fishes. Phil Trans R Soc Lond B 355(1401):1325–1327

Mrosovsky N, Boycott BB (1965) Intra- and interspecific differences in phototactic behavior of freshwater turtles. Behaviour 26(3/4):215–227

Muheim R, Phillips JB, Åkesson S (2006) Polarized light cues underlie compass calibration in migratory songbirds. Science 313:837–839

Murphy PA (1981) Celestial compass orientation in juvenile American alligators (*Alligator mississippiensis*). Copeia 1981:638–645

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, vol 1. CRC Press, Boca Raton, pp 137–163

Myers AE, Hays GC (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. Mar Ecol Prog Ser 322:259–267

Nalleau G, Bonnet X (1996) Body condition threshold for breeding in a viviparous snake. Oecologia 107:301–306

Newcomer RT, Taylor DH, Guttman SI (1974) Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). Herpetologica 30:194–200

Novales Flamarique I, Hawryshyn CW, Hárosi FI (1998) Double-cone internal reflection as a basis for polarization detection in fish. J Opt Soc Am A 15(2):349–358

Obbard ME, Brooks RJ (1980) Nesting migrations of the snapping turtle (*Chelydra serpentina*). Herpetologica 36(2):158–162

Orr RT (1970) Animals in migration. Macmillan, London

Ortleb EP, Sexton OJ (1964) Orientation of the painted turtle, *Chrysemys picta*. Am Midl Nat 71(2):320–334

Paladino FV, O'Connor P, Spotila JR (1990) Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. Nature 344:858–860

Papi F (1992) General aspects. In: Papi F (ed) Animal homing. Chapman and Hall, London, pp 263–314

Papi F, Luschi P, Åkesson S, Capogrossi S, Hays GC (2000) Open-sea migration of magnetically disturbed sea turtles. J Exp Biol 203:3435–3443

Papi F, Gagliardo A, Meschini E (2007) Moon orientation in sandhoppers: effects of lighting treatments on the persistence of orientation ability. Mar Biol 150(5):953–965

Perry SF (1983) Reptilian lungs: functional anatomy and evolution. Adv Anat Embryol Cell Biol 79:1–81

Perry A, Bauer GB, Dizon AE (1985) Magnetoreception and biomineralization of magnetite in amphibians and reptiles. In: Kirschvink JL, Jones DS, McFadden BJ (eds) Magnetite biomineralization and magnetoreception in organisms: a new biomagnetism. Plenum Press, New York, pp 439–454

Plotkin P (2003) Adult migrations and habitat use. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, vol 2. CRC Press, Boca Raton, pp 225–242

Plummer MV (1983) Annual variation in stored lipids and reproduction in green snakes (*Opheodrys aestivus*). Copeia 1983(3):741–745

Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH (2000) Turtles on the edge: movement of loggerhead turtles (Caretta caretta) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. Fish Oceanog 9:71–82

Pough FH, Andrews RM, Cadle JE, Crump ML, Savitzky AH, Wells KD (2004) Herpetology, 3rd edn. Pearson, Upper Saddle River

Prange HD (1976) Energetics of swimming of a sea turtle. J Exp Biol 64:1–12

Prange HD, Jackson DC (1976) Ventilation, gas exchange and metabolic scaling of a sea turtle. Resp Physiol 27:369–377

Putnam NF, Lohmann KJ (2008) Compatibility of magnetic imprinting and secular variation. Curr Biol 18(14):R596–R597

Rand AS (1968) A nesting aggregation of iguanas. Copeia 1968(3): 552–561

Reina RD, Spotila JR, Paladino FV, Dunham AE (2009) Changed reproductive schedule of eastern Pacific leatherback turtles Dermochelys coriacea following the 1997–98 El Nino to La Nina transition. End Spec Res 7:155–161

Reinert HK (1993) Habitat selection in snakes. In: Seigel RA, Collins JT (eds) Snakes: ecology and behavior. The Blackburn Press, Caldwell

Ritz T, Adem S, Schulten K (2000) A model of photoreceptor-based magnetoreception in birds. Biophys J 78:707–718

Rodda GH (1984) The orientation and navigation of juvenile alligators: evidence of magnetic sensitivity. J Comp Physiol A 154:649–658

Rodhouse P, Barling RWA, Clark WIC, Kinmonth AL, Mark EM, Armitage LE, Austin PR, Baldwin SP, Bellairs ADA, Nightingale PJ (1975) Feeding and ranging behavior of Galapagos giant tortoises (Geochelone elephantopus)—Cambridge and London University Galapagos expeditions, 1972 and 1973. J Zool 176:297–310

Rootes WL, Chabreck RH (1993) Reproductive status and movement of adult female alligators. J Herpetol 27(2):121–126

Row JR, Blouin-Demers G, Weatherhead PJ (2007) Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biol Conserv 137:117–124

Rozhok A (2008) Orientation and navigation in vertebrates. Springer, Berlin

Ruben JA (1976) Aerobic and anaerobic metabolism during activity in snakes. J Comp Physiol 109:147–157

Rubinoff I, Graham JB, Motta J (1988) Diving of the sea snake Pelamis platurus in the Gulf of Panama II. Horizontal movements. Mar Biol 97:157–163

Russell AP, Bauer AM, Johnson MK (2005) Migration in amphibians and reptiles: an overview of patterns and orientation mechanisms in relation to life history strategies. In: Elewa MAT (ed) Migration of organisms. Springer, Berlin, pp 151–203

Saba VS, Santidrian-Tomillo P, Reina RD, Spotila JR, Musick JA, Evans DA, Paladino FV (2007) The effect of the El Nino Southern Oscillation on the reproductive frequency of eastern Pacific leatherback turtles. J Appl Ecol 44:395–404

Saba VS, Shillinger GL, Swithenbank AM, Block BA, Spotila JR, Musick JA, Paladino FV (2008) An oceanographic context for the foraging ecology of eastern Pacific leatherback turtles: consequences of ENSO? Deep-Sea Res I 55:646–660

Sabbah S, Lerner A, Erlick C, Shashar N (2005) Under water polarization vision—a physical examination. Recent Res Devel Exper Theor Biol 1:123–176

Samu D, Erős P, Ujfalussy B, Kiss T (2009) Robust path integration in the entorhinal grid cell system with hippocampal feed-back. Biol Cybern. doi:10.1007/s00422-009-311-z

Sand O, Karlsen HE (2000) Detection of infrasound and linear acceleration in fishes. Phil Trans R Soc Lond B 355(1401):1295–1298

Schmidt-Koenig K, Ganzhorm JU, Ranvaud R (1991) The sun compass. In: Berthold P (ed) Orientation in birds. Birkhäuser Verlag, Basel, pp 1–15

Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying, and running. Science 177:222–228

Schwanz LE, Janzen FJ (2008) Climate change and temperature-dependent sex determination: can individual plasticity in nesting phenology prevent extreme sex ratios? Physiol Biochem Zool 81:826–834

Scott DE, Fischer RU, Congdon JD, Busa SA (1995) Whole body lipid dynamics and reproduction in the eastern cottonmouth, *Agkistrodon piscivorous*. Herpetologica 51(4):472–487

Secor SM, Nagy KA (1994) Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophus flagellum*. Ecology 75:1600–1614

Secor SM, Jayne BC, Bennett AF (1992) Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes*. J Exp Biol 163:1–14

Seigel RA, Ford NB (1987) Reproductive ecology. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Macmillan, New York

Seymour RS (1982) Physiological adaptations to aquatic life. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 13. Academic Press, New York, pp 1–51

Shelton G, Jones DR (1991) The physiology of the alligator heart: the cardiac cycle. J Exp Biol 158:539–564

Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA (2008) Roads as barriers to animal movement in fragmented landscapes. Anim Conserv 11:288–296

Shine R (2009) Reproductive strategies in snakes. Proc R Soc Lond B 270:995–1004

Shine R, Lambeck R (1985) A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes: Achrochordidae). Herpetologica 41(3):351–361

Shine R, Cogger HG, Reed RR, Shetty S, Bonnett X (2003) Aquatic and terrestrial locomotor speeds of amphibious sea snakes (Serpentes, Laticaudidae). J Zool Lond 259:261–268

Shine R, Webb JK, Lane A, Mason RT (2005) Mate location tactics in garter snakes: effects of rival males, interrupted trails and non-pheromonal cues. Functional Ecol 19:1017–1024

Spinks PQ, Pauly GB, Crayon JJ, Shaffer HB (2003) Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. Biol Conserv 113:257–267

Stapput K, Thalau P, Wiltschko R, Wiltschko W (2008) Orientation of birds in total darkness. Curr Biol 18:602–606

Steen DA, Aresco MJ, Beilke SG, Compton BW, Condon EP, Dodd CK Jr, Forrester H, Gibbons JW, Greene JL, Johnson G, Langen TA, Oldham MJ, Oxier DN, Saumure RA, Schueler FW, Sleeman JM, Smith LL, Tucker JK, Gibbs JP (2006) Relative vulnerability of female turtles to road mortality. An Conserv 9:269–273

Swingland IR, North PM, Dennis A, Parker MJ (1989) Movement patterns and morphometrics in giant tortoises. J Anim Ecol 58:971–985

Taylor CR, Heglund NC, Maloiy GMO (1982) Energetics and mechanics of terrestrial locomotion. J Exp Biol 97:1–21

Tenney SM, Bartlett D, Farber JP, Remmers JE (1974) Mechanics of the respiratory cycle in the green turtle (*Chelonia mydas*). Resp Physiol 22:361–368

Thompson GG, Withers PC (1997) Standard and maximal metabolic rates of goannas (Squamata: Varanidae). Physiol Zool 70:307–323

Tucker VA (1967) The role of the cardiovascular system in oxygen transport and thermoregulation in lizards. In: Milstead WW (ed) Lizard ecology: a symposium. University of Missouri Press, Columbia, pp 258–269

Tucker VA (1970) Energetic cost of locomotion in animals. Comp Biochem Physiol 34:841–846

Tucker VA (1975) The energetic cost of moving about. Am Sci 63:413–419

Tuttle SE, Carroll DM (2005) Movements and behavior of hatchling wood turtles (*Glyptemys insculpta*). Northeast Nat 12(3):331–348

Wallace BP, Kilham SS, Paladino FV, Spotila JR (2006) Energy budget calculations indicate resource limitation in Eastern Pacific leatherback turtles. Mar Ecol Prog Ser 318:263–270

Walton M, Jayne BC, Bennett AF (1990) The energetic cost of limbless locomotion. Science 249:524–527

Wang JH, Jackson JK, Lohmann KJ (1998) Perception of wave surge motion by hatchling sea turtles. J Exp Mar Biol Ecol 229:177–186

Weber JM (2009) The physiology of long-distance migration: extending the limits of endurance metabolism. J Exp Biol 212:593–597

Wehner R (2001) Polarization vision—a uniform sensory capacity? J Exp Biol 204:2589–2596

Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. J Exp Biol 199:129–140

Weishampel JF, Bagley DA, Ehrhart LE (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. Glob Change Biol 10:1424–1427

Werner DI (1983) Reproduction in the iguana *Conolophus subcristatus* on Fernandina Island, Galapagos: clutch size and migration costs. Am Nat 121(6):757–775

West NH, Butler PJ, Bevan RM (1992) Pulmonary blood flow at rest and during swimming in the green turtle, *Chelonia mydas*. Physiol Zool 65:287–310

Williams SE, Shoo LP, Isaac JL, Hoffman AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 6(12):2621–2626

Wilkinson A, Coward S, Hall G (2009) Visual and response-based navigation in the tortoise (*Geochelone carbonaria*). Anim Cogn. doi:10.1007/s10071-009-0237-9

Wiltschko W, Wiltschko R (1982) The role of outward journey information in the orientation of homing pigeons. In: Papi F, Wallraff HG (eds) Avian navigation. Springer, Berlin, pp 239–252

Wiltschko R, Wiltschko W (1995) Magnetic orientation in animals. Springer, Berlin

Wiltschko R, Wiltschko W (2003) Avian navigation: from historical to modern concepts. Anim Behav 65:257–272

Wiltschko R, Wiltschko W (2006) Magnetoreception. Bioessays 28:157–168

Wiltschko W, Weindler P, Wiltschko R (1998) Interaction of magnetic and celestial cues in the migratory orientation of passerines. J Avian Biol 29:606–617

Wingfield JC, Schwabl H, Mattocks PW Jr (1990) Endocrine mechanisms of migration. In: Gwinner E (ed) Bird migration: physiology and ecophysiology. Springer, Berlin, pp 232–256

Woledge RC (1968) The energetics of tortoise muscle. J Physiol 197:685–707

Wood SC, Johansen K, Glass ML, Maloiy GMO (1978) Aerobic metabolism of the lizard *Varanus exanthematicus*: effects of activity, temperature, and size. J Comp Physiol 127:331–336

Wyneken J (1997) Sea turtle locomotion: mechanisms, behavior, and energetics. In: Lutz PL, Musick JA (eds) The biology of sea turtles, vol 1. CRC Press, Boca Raton, pp 165–198

Yeomans RS (1995) Water-finding in adult turtles: random search or oriented behavior. Anim Behav 49(4):977–987

Zani PA, Kram R (2008) Low metabolic cost of locomotion in ornate box turtles, *Terrapene ornata*. J Exp Biol 211:3671–3676