Nest-site choice and nest construction in non-avian reptiles: Evolutionary significance and ecological implications

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ABSTRACT

In oviparous animals, nest-site choice is both a critical determinant of an individual’s lifetime fitness, and an important demographic parameter of populations. At the individual level, the location and characteristics of a nest site impact survival of both the nesting female and the nestling or hatchling stage, and can also influence offspring phenotype and the survival of emerging juveniles. At the population level, survival rates of females and offspring, and phenotypes affected by incubation conditions, affect population trends. Reptiles differ from birds in several key life-history traits associated with nesting behaviour in that they have long incubation periods, bury eggs within a substrate, and have minimal parental care. However, studies in reptile systems have also demonstrated several evolutionary drivers of nest-site choice that are also likely to be important in avian systems. These include the role of incubation conditions in affecting offspring phenotype, and the contribution of nest-site choice to survival of the juvenile life stage. Overall, studies on the evolution and ecology of nest-site choice in reptiles and birds have much to offer each other in terms of both theoretical basis and applications to conservation and management. Incorporating knowledge gained from a range of taxa into our research, and testing hypotheses in one system that have demonstrated importance in other systems, will provide a richer understanding of the ecology and evolution of nest-site choice.

Keywords: crocodilian, incubation, life history, lizard, parental care, snake, Tuatara, turtle

1. INTRODUCTION

The decision of where and how to construct a nest is of critical importance in determining an individual’s fitness (Bernardo, 1996; Resetarits, 1996). In addition to influencing the probability of offspring survival, nest-site choice can also affect the survival of the nesting parent (e.g. Ghalambor and Martin, 2001). Therefore, nesting behaviour plays an important role in both population-level demographic parameters and in selective pressures acting on individuals (Refsnider and Janzen, 2010). A large body of literature in oviparous animals, particularly birds, has focused on how nest-site choice affects offspring production and thereby population growth rates (reviewed in Martin, 1993; Chalfoun and Schmidt, 2012). More recently, studies in avian systems have also elucidated how selection pressures on different life stages affect the nest-site choices made by individuals (Sreby et al., 2014a). Together, these studies demonstrate that the ecological outcomes of nest-site choice, at both the individual and population levels, are driven by a variety of selection pressures acting on nest-site choice. Understanding the evolutionary significance of nesting behaviours is critical for predicting the outcome of different nest-site choices, and will better inform conservation and management decisions involving actions that could affect nesting behaviour.

The majority of studies on nest-site choice have been conducted in avian systems (reviewed in Martin, 1992; Chalfoun and Schmidt, 2012; Barber, 2013). More recently, increased attention has been paid to nest-site choice in other oviparous systems, particularly insects (e.g. Pöykkö, 2006), fishes (e.g. Barber, 2013), amphibians (e.g. Doody et al., 2009), and reptiles (e.g. Refsnider and Janzen, 2012). These taxa have several key differences in life-history traits compared to birds, which make them ideal systems for testing additional hypotheses regarding the evolutionary reasons for, and ecological outcomes of, different nest-site choices. Moreover, researchers focused primarily on one taxon, such as birds, could benefit greatly from applying knowledge gained from other taxa, such as fish (e.g. Barber, 2013), when seeking to understand the evolutionary drivers of nest-site choice. By studying nest-site choice across a range of taxa, and in particular by comparing and contrasting reasons for and outcomes of nest-site choice in different taxa, we will gain a more complete understanding of the evolutionary significance of nest-site choice overall.

1.1 Evolutionary drivers of nest-site choice in egg-laying animals

Across oviparous animals, there are several factors driving the evolution of nest-site choice (reviewed in Refsnider
and Janzen, 2010). These include: ensuring the survival of the nesting female; maximising the survival of the offspring produced; enhancing particular offspring phenotypes that are influenced by the nest microhabitat; placing newly-hatched offspring in close proximity to suitable juvenile habitat; promoting natal philopatry of daughters; and ensuring that offspring are sired by a high-quality mate who controls a high-quality nest site. Not all of these drivers of nest-site choice apply to all oviparous species, and the relative importance of each factor may differ dramatically across taxa depending on life history traits (e.g. iteroparity versus semelparity, direct versus indirect embryonic development, or the degree of parental care). Moreover, there are many examples across oviparous taxa in which females experience opposing selection pressures on nest-site choice from one or more of the evolutionary drivers listed above (e.g. Shine et al., 1997a; Spencer and Thompson, 2003; Pöykkö, 2006). Such opposing selection pressures may result in an overall nest-site choice that is a trade-off between two or more evolutionary drivers, and which optimises overall reproductive success while failing to maximise the specific fitness components resulting from a single evolutionary driver (Streby et al., 2014a). Nest-site choices that are the result of balancing two or more evolutionary drivers can appear to be maladaptive if they are considered only in the context of a single evolutionary driver (Streby et al., 2014b). Therefore, to fully appreciate the reasons for nest-site choice in a given species, it is critical to consider species-specific life history traits and the range of evolutionary drivers underlying those traits which may contribute to a female’s decision of where and how to construct her nest.

1.2 Scope of review

Studies of nest-site choice in birds have contributed substantially to our understanding of how nest-site choice can affect population-level parameters. Importantly, though, other oviparous taxa also have much to offer regarding the evolutionary drivers and ecological outcomes of nest-site choice. In particular, the non-avian reptiles (hereafter “reptiles”), the sister clade to birds, encompass a variety of model systems for studying nest-site choice. Despite being closely related to birds, reptiles have several key life-history differences which have resulted in substantial differences in their nesting behaviour in comparison with birds.

In this review, I will discuss the key life-history traits in reptiles that shape nest-site choice in this group, and compare and contrast nest-site choice in reptiles with that in birds. While life-history differences between reptiles and birds mean that the ecological consequences of nest-site choice are quite different between these taxa, the evolutionary drivers behind nest-site choice in both groups share important similarities. I will also discuss aspects of nest construction in reptiles and summarise the functional properties of the incubation environments within reptile nests and their effects on offspring. Finally, I will review the ecological implications of nest-site choice in reptiles at both the individual and population levels. My hope is that this review will provide avian biologists with additional perspective on the evolutionary reasons for nest-site choice, and a greater appreciation for how life-history traits can shape nesting behaviour. By incorporating knowledge gained from a wide range of taxa into our research, and particularly by testing hypotheses in our specific study systems that have demonstrated importance in other systems, we will gain a richer understanding of the process of nest-site choice in general.

2. LIFE-HISTORY TRAITS INFLUENCING NEST-SITE CHOICE IN REPTILES

The reptiles include four orders: Squamata (lizards, snakes, and amphibiaenidae or worm-lizards); Rhynchocephalia (sister clade to Squamata and including only the Tuatara, a species endemic to New Zealand); Chelonia (turtles, tortoises and sea turtles); and Crocodylia (sister clade to Aves and including crocodiles, alligators and the gharial). Turtles, crocodilians, and the Tuatara are entirely oviparous, as are the majority of squamates. However, live birth, or viviparity, has secondarily evolved in some species of lizards and snakes. Most of these viviparous reptiles live in relatively cool climates, such as at high elevations or latitudes, and live bearing is thought to have evolved in these species to allow gravid females increased control over the temperature experienced by developing embryos through maternal basking behaviour (Shine, 2014). The evolution of viviparity in reptiles has been reviewed extensively elsewhere (e.g. Shine, 2002, 2014) and will not be discussed further here. In general, oviparous reptiles share a suite of life-history traits which have uniquely shaped the evolution of nest-site choice in this group, particularly in comparison to their sister clade, the birds. These include long incubation periods, burying eggs within a substrate, and minimal parental care.

2.1 Long incubation periods

Compared with birds (e.g. Martin and Li, 1992), reptiles have lengthy egg incubation periods (Deeming et al., 2006). Incubation periods in small lizards and snakes are typically several weeks at minimum. For example, in the Jacky Dragon (Amphibolurus muricatus), eggs incubate for at least 37 days (Harlow and Taylor, 2000). Eggs of the Bull Snake (Pituophis melanoleucus) incubate for at least 42 days (Gutzke and Packard, 1987). In turtles and crocodilians, eggs may incubate for up to several months, e.g. 46–81 days for the Loggerhead Sea Turtle (Caretta caretta; Matsuzawa et al., 2002) and 69–81 days for the
Broad-snouted Caiman (*Caiman latirostris*; Piña et al., 2003). The Tuatara (*Sphenodon punctatus*; Piña et al., 1987a, 1985b), an adaptation that is particularly of magnitude greater than that of rigid-shelled reptile eggs and two orders of magnitude greater than that of bird eggs (Ackerman et al., 1985a; Ackerman and Lott, 2004; Belinsky et al., 2004). The shells of bird eggs are rigid and calcified, as are the eggs of crocodilians, some turtles, and some lizards (reviewed in Packard et al., 1977). In contrast, snakes and most lizards, some turtles, and the Tuatara produce flexible-shelled, or parchment-shelled eggs (reviewed in Packard et al., 1977).

The above-ground nests of birds allow for sufficient aerial exchange of respiratory gases and water vapour across the rigid eggshell via diffusion (Ar and Rahn, 1978). The incubation environment within enclosed reptile nests, however, is characterised by high concentrations of carbon dioxide, low levels of oxygen, and very high humidity (Seymour and Ackerman, 1980; Ackerman and Lott, 2004). Moreover, soil is much more resistant to diffusion than is air; therefore, the increased conductance of reptile eggshells compared to bird eggshells likely evolved to compensate for soil’s resistance to diffusion (Seymour and Ackerman, 1980). Parchment-shelled eggs are more sensitive to the hydric environment within the nest than are rigid-shelled reptile eggs (Packard et al., 1982), which means that soil moisture is an important parameter for females to assess when selecting a nest site (e.g. Miller, 1993; Brown and Shine, 2004; Socci et al., 2005).

Many reptile eggs increase in mass throughout incubation by absorbing water from the nest environment (Packard et al., 1977; Deeming and Birchard, 2007). The water vapour conductance of parchment-shelled eggs is particularly large, approximately one order of magnitude greater than that of rigid-shelled reptile eggs and two orders of magnitude greater than that of bird eggs (Ackerman et al., 1985a; Ackerman and Lott, 2004; Belinsky et al., 2004). Water vapour transport and heat transport are coupled in parchment-shelled eggs such that when eggs lose water to the environment, sufficient heat is also transferred to cool eggs below the ambient temperature (Ackerman et al., 1985a, 1985b), an adaptation that is particularly important in hot climates. Oxygen consumption by reptile eggs also increases continuously throughout incubation, and is often highest just before hatching (Seymour and Ackerman, 1980). Despite the resistance of subterranean environments to diffusion, reptile eggs buried within a substrate depend on the exchange of energy, water vapour and respiratory gases with the environment. Therefore,
the substrate type, soil composition, particle size and humidity level of a female's nest site can have profound effects on the incubation conditions experienced by developing embryos (e.g. Kolbe and Janzen, 2002; Hughes and Brooks, 2006; Somaweera and Shine, 2013; Bodensteiner et al., 2015).

2.3 Little parental care

In birds, contact incubation of eggs and rearing of the young by one or both parents is nearly universal (Lack, 1968). In reptiles, however, parental care of either eggs or hatchlings is relatively rare (reviewed in Shine, 1988, 2005). Where parental care is present in reptiles, it is often associated with nest defence. Crocodilians are the reptiles best known for their parental care, particularly defence of the juvenile life stage (reviewed in Lang, 1987). Many species of crocodilians construct large nest mounds of decaying vegetation, which release heat during decomposition and thereby warm the eggs within the nest mound (e.g. Magnusson, 1979). Females remain with the nest mound throughout the incubation period to guard the eggs, and they guard their hatchlings in a crèche once they have reached wetland habitat (Webb and Manolis, 2002; Platt et al., 2008). In some crocodilians, hatchlings vocalise upon emerging from the egg, and in response the female opens the nest mound and carries the hatchlings from the nest to water (Platt et al., 2008). Short periods of nest guarding also occur in Tuatara (Refsnider et al., 2009) and lizards such as Green Iguanas (Iguana iguana; Bock and Rand, 1989) and Galápagos lava lizards (Tropidurus spp.; Burger, 1993), and in these species its function is to protect nests against conspecific females seeking to usurp the nest site for themselves.

In some cases, parental care in reptiles serves to maintain the thermal environment of the nest, as in birds that incubate their eggs (reviewed in Shine, 2005). For example, some snakes, such as Ball Pythons (Python regius), brood their eggs within the coils of their bodies and use rhythmic muscle contractions to keep the eggs warm (Aubret et al., 2003). Some crocodilians also apparently adjust the thermal environment of their nest mounds by periodically reshaping or covering the nest during incubation (Lang, 1987).

In the majority of reptiles, once the nest has been constructed and the eggs have been deposited, the female provides no further care for the developing embryos (reviewed in Shine, 2005). The consequences of this lack of parental care in reptiles are twofold. First, because the vast majority of reptiles are not present at the end of the lengthy incubation period, they are unable to observe whether their offspring successfully hatched. Therefore, there is no opportunity for most reptiles to adjust subsequent nest-site choices by learning from the results of previous choices. Second, hatchlings are left to make their own way from nest sites to suitable habitat without being led by a parent. For this reason, placing a nest in close proximity to suitable juvenile habitat is an important consideration in the nest-site choice of reptiles (Refsnider and Janzen, 2010). For example, aquatic turtles nest on land, but their hatchlings must then travel terrestrially from the nest to reach aquatic habitat, making them vulnerable to predation, desiccation, physiological stress and disorientation (e.g. Mitchell et al., 2013a). In Painted Turtles, nest location influenced the amount of mass lost by hatchlings as they travelled from the nest to wetland habitat (Mitchell et al., 2013a). Sea turtles increase their hatchlings' chances of successfully reaching the water by avoiding nesting far from the water where misorientation of hatchlings is likely (Kamel and Mrosovsky, 2004, 2005). At a landscape scale, Kemp's Ridley Sea Turtles (Lepidochelys kempii) concentrate nesting on beaches that most effectively facilitate the migration of hatchlings to ocean currents that will carry them to suitable habitat for the juvenile life stage (Putnam et al., 2010).

3. NEST CONSTRUCTION IN REPTILES

Nest construction in birds and reptiles is driven, in large part, by the degree of parental care provided to nests and juveniles. Bird nests may be constructed by females, males, or both sexes (Deeming and Mainwaring, 2015), and generally one or both parents then incubate the eggs and care for the young until they reach independence (Lack, 1968). Because birds usually provide thermal benefits to their eggs and offspring through contact incubation and brooding, parental presence can buffer environmental variability experienced within the nest. As discussed above, the life-history traits of reptiles differ substantially from those of birds, with important consequences for the evolution of nest-site choice and nest construction. To ensure reproductive success and thereby individual fitness, nesting reptiles must choose nest sites with incubation conditions that will ensure offspring survival, enhance particular offspring phenotypes, and be in close proximity to juvenile habitat (Refsnider and Janzen, 2010). Furthermore, nest sites must provide incubation conditions that are suitable over a lengthy incubation period, allow energy exchange between the egg and the surrounding substrate at the appropriate times, optimise multiple offspring phenotypes and accomplish all of this with little or no parental care. As in birds, reptiles are iteroparous and have multiple opportunities to reproduce over their lifetimes; therefore, choosing nest sites that ensure the survival of the nesting female is also important (e.g. Spencer, 2002). Importantly, because almost no reptiles incubate their eggs, safety of the incubating parent throughout embryonic development is less of a consideration in the nest-site choice of reptiles than in birds (but see Madsen and Shine, 1999).
3.1 Types of nests constructed by reptiles

Once an appropriate nest site has been chosen, a female must construct her nest. Birds construct a variety of nest types, including open-cup nests, enclosed nests, and cavity nests. Reptile nests are quite different and fall into four general categories: no site preparation, digging a simple hole, constructing a burrow, or piling up material to form a mound. Nests constructed by many small lizards are often quite simple, with eggs simply oviposited in a crevice between rocks, e.g. lava lizards (Vitt, 1993), under a cover object, or within the leaf litter, e.g. anoles (Socci et al., 2005; Figure 1A). Larger lizards, turtles, and Tuatara dig cavities or burrows in which to lay their eggs, e.g. sea turtles (Bustard, 1972); iguanas (Mora, 1989); Tuatara (Nelson et al., 2004b; Figure 1B, Figure 1C). More complex burrow systems, or warrens, are constructed by the Yellow-spotted Monitor Lizard (Varanus panoptes) and may be used by multiple females for oviposition (Doody et al., 2014). In reptiles, the most complex nests are the large nest mounds constructed by many crocodilians (Figure 1D). These nest mounds, which are similar in function to those of the mound-building megapodes (Frith, 1962), are made up of decaying vegetation piled together by the female (Webb and Manolis, 2002). Crocodilians usually place their nest mounds along the edge of a water body, where the female can shelter while guarding the developing eggs and which provides easy access to aquatic habitat necessary for the vulnerable hatchlings (reviewed in Lang, 1987).

Most birds spend several days constructing nests. Similarly, in reptiles such as Tuatara (Cree and Daugherty, 1990) and Green Iguanas (Bock and Rand, 1989), females may return to their nest burrow over several consecutive nights to continue nest excavation and construction. However, turtles generally complete the entire nesting process (including excavation of the nest cavity, oviposition, and refilling the nest cavity) in a few hours. For example, female Blanding’s Turtles (Emydoidea blandingii) typically take 2.5 hours to dig a hole and subsequently complete the nest the same night (Congdon et al., 1983), and Painted Turtles often complete the entire nesting process within 2 hours (Refsnider, J.M., personal observation).

3.2 Environmental cues used in reptilian nest-site choice

To achieve the incubation conditions within their nests that optimise offspring survival, phenotype, and ability to reach suitable juvenile habitat, reptiles base their nest-site choices on a variety of specific environmental factors. For

![Figure 1. Types of nests most commonly constructed by reptiles: (A) female deposits eggs in a simple shelter such as a rock crevice or tree stump (egg of Norops spp. of the Iguanidae); (B) female digs a cavity in the ground (painted turtle, Chrysemys picta); (C) female constructs a burrow (Tuatara, Sphenodon punctatus); (D) female constructs a nest mound (nest of a saltwater crocodile, Crocodylus porosus). Photos A–C by J. Refsnider, D by A. Odum.](image-url)
example, the amount of shade cover over nest sites exerts significant influence over the temperature within nests across all orders of reptiles. Shade cover can influence whether a site achieves suitable incubation temperatures for embryonic development, as has been demonstrated in Tuatara (Thompson et al., 1996), Nile Crocodiles (Crocodylus niloticus; Leslie and Spotila, 2001) and Bull Snakes (Burger and Zappalorti, 1986). In addition, shade can allow females to exert control over the sex ratio of their offspring, as in the case of the Painted Turtle (Janzen and Morjan, 2001; Mitchell et al., 2013b). Differences in shade cover over nest sites may also compensate for climatic differences across a species’ geographic range, as demonstrated in the Australian Water Dragon (Physignathus lesueurii; Doody et al., 2006), the Snapping Turtle (Chelydra serpentina; Ewert et al., 2005); and the Painted Turtle (Refsnider et al., 2014). Moreover, a female can change the amount of shade cover under which she chooses to nest, which can match incubation temperature within the nest to prevailing environmental conditions and thereby compensate for anthropogenically-driven climate change, as observed in Painted Turtles (Refsnider and Janzen, 2012).

The distance from water at which nests are constructed is also important in many reptiles. For example, sea turtles must balance the risk of nest inundation close to water with the higher likelihood of hatching misorientation at sites farther from water (Wood and Bjorndal, 2000; Kamel and Mrosovsky, 2004). Murray River Turtles (Emydura macquarii) must also balance nesting close to the water’s edge, which carries a high risk of nest predation but a low risk to themselves, with nesting farther from water, where they face a higher risk of predation but nest predation is less likely (Spencer, 2002; Spencer and Thompson, 2003).

Substrate properties, such as soil type and moisture content, strongly affect hydric conditions within nests and specific conditions are sought out in some reptiles (Ackerman and Lott, 2004). For example, Painted Turtles selected sites with low organic content for nesting, as such sites were associated with high hatching survival (Hughes and Brooks, 2006); in Snapping Turtles, nests with a high proportion of sand had the highest hatching survival (Kolbe and Janzen, 2002). In small iguanid lizards (Norops spp.), females select moist nest sites, which provide optimal incubation conditions for offspring survival: eggs laid in drier soil desiccated, while those laid in saturated soil became infected with fungus (Socci et al., 2005).

Finally, some reptiles bypass the process of assessing potential nest sites altogether and simply “copy” the nest-site choice of other females. Nest-site copying may simply function to save a female the time and energy of choosing and constructing her own nest (Plummer, 1981; Rand and Dugan, 1983). However, theory suggests that females should actively seek out sites with recently-laid or recently-hatched eggs, which likely indicate the site’s effectiveness at producing offspring (Freedberg and Wade, 2001). Indeed, female selection of nest sites with evidence of previous use by conspecifics has been observed in the Common Keelback Snake (Tropidonophis mairii; Brown and Shine, 2005) and Tuatara (Refsnider et al., 2010). Basing nest-site choice on social cues is also hypothesised to be important in songbirds (Chalfoun and Schmidt, 2012). For example, in Collared Flycatchers (Ficedula albicollis) parental feeding rate is a reliable predictor of reproductive productivity, and therefore individuals select breeding habitat patches by cueing in on sites with high parental activity (Pärtil and Doligez, 2003).

3.3 Altering nest construction

The most important mechanism by which reptiles can affect the incubation conditions within their nest is through their choice of where to place their nest, as discussed above. Importantly, however, aspects of nest construction can also be altered to achieve specific incubation conditions. Burrow-nesting species may adjust the depth of their nest, such as constructing a deeper and thereby cooler nest under warmer environmental conditions. For example, Australian Water Dragons nesting at low elevations constructed deeper nests than their counterparts nesting at cooler, high-elevation sites (Doody, 2009). Similarly, as environmental temperatures during the incubation period have increased, Eastern Three-lined Skinks (Bassiana duperreyi) in Australia constructed deeper nests (Telemeoco et al., 2009). However, adjustment of nest depth to control incubation temperature is not always possible. In Tuatara nesting on a very small and ecologically homogenous island, a shallow layer of soil over bedrock prevents females from digging deeper nesting burrows (Mitchell et al., 2008). Morphological characteristics may also constrain nest depth. Turtles construct nesting cavities using their rear limbs, which means that nest cavities can only be as deep as the limbs are long. In Painted Turtles, the depth of nest required to affect incubation temperature is deeper than females are able to dig without a concomitant increase in female body size (Refsnider et al., 2013a).

4. FUNCTIONAL PROPERTIES OF REPTILE NEST INCUBATION ENVIRONMENTS AND EFFECTS ON OFFSPRING

While there is mounting evidence that incubation conditions affect offspring phenotype in birds (reviewed in DuRant et al., 2013; Hepp et al., 2015), this phenomenon is much more extensively demonstrated in ectotherms. In reptiles, thermal and hydric conditions within the nest during egg incubation influence a variety of offspring phenotypes (reviewed in Deeming, 2004a; Booth, 2006). These include: length of embryonic development (Shine et al., 1997b); offspring size (Shine et al., 1997a; Brown
and Shine, 2004) and pigmentation (Deeming, 2004a); post-hatching growth rate (Brooks et al., 1991); locomotor performance (Miller, 1993; Refsnider, 2013); metabolic rate (Van Damme et al., 1992); immune function (Les et al., 2009); basking behaviour (Shine and Harlow, 1996); and predator escape behaviour (Burger, 1989). For example, hatchlings of Eastern Three-lined Skinks incubated in warmer nests were longer, exhibited slower sprint speeds, spent less time basking, and were less active overall than hatchlings incubated from cooler nests (Shine and Harlow, 1996). Similarly, Snapping Turtle hatchlings incubated in moist nests swim and ran faster than those incubated in drier nests, even relative to body size (Miller et al., 1987; Miller, 1993).

In many reptiles, an additional phenotype determined by incubation conditions within the nest is offspring sex. Turtles, crocodilians, Tuatara, and some lizards have temperature-dependent sex determination (TSD), in which offspring sex is irreversibly determined by the temperature experienced by the developing embryo, usually during the middle third of development. There are several different patterns of TSD: most turtles exhibit Type 1a TSD, where females are produced at high incubation temperatures and males are produced at low temperatures (e.g. Ewert et al., 1994). The opposite pattern, where males are produced at high incubation temperatures and females are produced at low temperatures, is found in Type 1b species such as the Tuatara (Cree et al., 1995). A few species including the Snapping Turtle (Ewert et al., 1994), Jacky Dragon (Harlow and Taylor, 2000), and all crocodilians (Lang and Andrews, 1994; Deeming 2004b), have Type 2 TSD, where males are produced at intermediate incubation temperatures and either females or a mixed sex ratio are produced at extreme (either high or low) temperatures. In all three patterns of TSD, the range of incubation temperatures within which a mixed sex ratio is produced is narrow (often only 1–2 °C; Hulin et al., 2009), which generally results in unisexual nests. However, in reptiles with relatively deep nests such as crocodilians and Diamondback Terrapins (Malaclemys terrapin), incubation conditions can differ sufficiently between the upper and lower portions of the nest cavity that nests may produce hatchlings of both sexes (Ferguson and Joanen, 1983; Roosenburg, 1996). While birds possess genetic sex determination, and therefore incubation temperature does not directly affect offspring sex ratio, the sex ratio of offspring can be mediated by incubation temperature via temperature-dependent embryo mortality in the brush-turkey Alectura lathami (Göth and Booth, 2005).

Recent studies have demonstrated that offspring phenotypes in reptiles are also affected by the variation in thermal conditions during incubation, both in terms of total magnitude of fluctuation (Les et al., 2009; Refsnider, 2013) and whether such fluctuation occurs primarily around the upper or lower thermal limit (Neuwald and Valenzuela, 2011). Incubation temperatures near the thermal extremes can be lethally warm and lead to embryo mortality, or be too cool to support embryonic development and lead to developmental diapause or embryo mortality. Recently, in Painted Turtles, incubation temperatures near the thermal extremes reversed the sex ratio expected at high and low temperatures based on the pattern of TSD exhibited by that species, suggesting that thermal fluctuations help to shape biological responses to climate change (Neuwald and Valenzuela, 2011).

As a consequence of the extreme sensitivity of offspring phenotype to incubation conditions in reptiles, females can exert significant control over the “quality” of their offspring through their choice of nest site. Female Common Keelback Snakes actively select moist nest sites, which produce larger hatchlings with enhanced survival, thereby demonstrating a direct link between a female’s nest-site choice and her reproductive success (Brown and Shine, 2004). Painted Turtles use shade cover as a cue in selecting nest sites with particular thermal conditions in order to influence the sex ratio of their offspring (Janzen and Morjan, 2001; Mitchell et al., 2013b). There is also mounting evidence that reptiles can, to some extent, compensate for increasing environmental temperatures by adjusting their choice of nest site, thereby mitigating some negative impacts that climate change might otherwise have on offspring phenotypes, such as skewed sex ratios (Doody et al., 2006; Telemeco et al., 2009; Refsnider and Janzen, 2012; Urban et al., 2014). Importantly, however, reptiles’ capacity to adjust their nest-site choice can be constrained if alternative, suitable nesting habitat is unavailable (Mitchell et al., 2008; Refsnider et al., 2013b).

5. IMPLICATIONS OF NEST-SITE CHOICE IN REPTILES

Nest-site choice influences both the reproductive fitness of individuals and the recruitment of juveniles into populations because of its profound effect on offspring survival. Understanding the drivers of nest-site choice and how individuals alter nesting behaviour is therefore of importance in both evolutionary and ecological contexts, and can have important implications in management and conservation of wildlife populations.

5.1 Selective pressures acting on individuals

A female’s choice of nest site can impact her fitness in several key ways. First, the act of nesting itself can increase a female reptile’s vulnerability to predation or other sources of mortality. For example, in Australia, introduced red foxes are the primary predators of turtle nests, but they also destroy nesting females (Spencer, 2002). In general, gravid females may be less able to escape from predators due to reduced mobility, and may be at increased risk of predation while traveling to nest sites, constructing nests, or guarding nests (e.g. Shine, 1980; Rand and Dugan, 1983; Refsnider et al., 2009).
Selection may therefore favour females that nest in areas that minimise predation risk. Indeed, risk of predation by introduced foxes limits female Murray River Turtles from nesting in preferred areas away from shore, where nest predation is reduced (Spencer, 2002). Similarly, in many South American passerine birds, parents nest in locations that reduce predation risk to themselves, often at the expense of higher predation risk to their offspring (Ghalambor and Martin, 2001). But unlike birds, which typically nest within a home territory, many reptiles must migrate away from home ranges to specific areas with suitable nesting habitat, and traveling to such nesting areas may entail movement through inhospitable habitat (e.g. Angilletta et al., 2009). For example, many freshwater turtle species experience high road mortality of females during the nesting season (Haxton, 2000; Steen and Gibbs, 2004). Reptiles are iteroparous, so females that survive a given nesting season will have future reproductive opportunities. Moreover, in reptiles, such as Blanding’s Turtle, contrary to the pattern seen in animals that display reproductive senescence, reproductive output actually seems to increase with age (Congdon et al., 2001). Therefore, minimising mortality risk during a given nesting season can dramatically increase a female’s overall lifetime fitness.

Second, as discussed previously, the microhabitat of the nest site can strongly influence the survival of the incubating offspring. Nests that are too extreme in temperature or humidity can lead to embryo mortality (e.g. Van Damme et al., 1992), and those that are too exposed are more likely to be detected by predators (e.g. Rand and Dugan, 1983). Nests constructed too far from suitable juvenile habitat may produce hatchlings that subsequently die while attempting to reach suitable habitat (e.g. Kamel and Mrosovsky, 2004). Birds face the added challenge of choosing nest sites that minimise physiological stress on the incubating adult (With and Webb, 1993). Not only must female reptiles balance these complex requirements when choosing a nest site, but they must be able to predict the future incubation conditions their eggs will experience from the conditions present at the time of nest construction (e.g. Shine, 2002). Environmental cues that accurately predict future incubation conditions are particularly important in species with prolonged incubation periods, and selection is likely to favour females that can most accurately assess future incubation conditions based on such cues (Janzen and Morjan, 2001). In species where conspecific nest destruction is a common cause of nest failure, selection may also favour females who remain to guard their eggs after oviposition (Refsnider et al., 2009).

Third, the incubation conditions within a nest influence phenotypes, and therefore quality, of offspring. Females can therefore exert some control over offspring phenotypes through nest-site choice. For example, in reptiles with TSD, females can choose nest sites that will produce a specific sex (Mitchell et al., 2013b), which can be favourable in situations where one sex is rarer and therefore more valuable in the population (e.g. Girondot et al., 1998). In fact, TSD is thought to have evolved as a mechanism by which offspring phenotypes produced at particular incubation temperatures are coupled with production of the sex in which those traits are most favourable (Warner and Shine, 2008). While refinement of offspring phenotype through female nest-site choice likely experiences weaker selective pressure than does production of surviving offspring, it is nonetheless an important target of selection in reptiles, and is likely an under-appreciated driver of nest-site choice in birds as well (DuRant et al., 2013; Hepp et al., 2015).

One final consequence of nest-site choice involving individual fitness is that, in most reptiles, adults are not present when hatchlings emerge from the nest, and therefore they do not have the opportunity to learn about the success of their nest-site choice. This lack of opportunity for learning means that females cannot adjust their future nest-site choices in response to the outcome of previous choices. When females exhibit strong nest-site fidelity in combination with a preference for nest sites in risky areas such as along road edges, repetition of “poor” nest-site choice may increase their susceptibility to anthropogenically-created ecological traps (e.g. Kolbe and Janzen, 2002). Birds may be unique in having the opportunity to learn from their nest-site choices because they can directly observe the outcome on their nestlings and, subsequently, fledglings.

### 5.2 Population-level demographic parameters

The most obvious consequence of nest-site choice at the population level is its effect on juvenile recruitment, and thereby on population growth rate. Whilst population growth rate is not a target of selection, it is a parameter of interest to managers, particularly in the case of rare or declining species. Therefore, as long recognised by avian ecologists, nest-site choice has important consequences for managing populations (Mainwaring et al., 2015).

If nest sites are poorly chosen, or fail to produce offspring for some other reason, recruitment will decline and population growth will slow. Extreme weather events can easily destroy vulnerable nests in both birds and reptiles (Jergenson et al., 2014; Newell et al., 2015). Reptiles, however, may be more vulnerable to such events than birds for several reasons. Due to their lengthy incubation periods, reptile nests are vulnerable to environmental conditions over a much longer period than birds, potentially providing more “opportunities” for destruction by extreme events. Many birds can renest following a failed nesting attempt, but reptiles do not observe the outcome of a nesting attempt and therefore are unable compensate for a failed attempt by renesting. Therefore, extreme weather conditions are more likely...
to destroy an entire cohort in reptiles than in birds, which can have substantial consequences for reptile populations that already demonstrate very slow growth rates (e.g., Ernst, 1974; Janzen, 1994).

The extraordinary sensitivity of developing reptile embryos to environmental conditions means that environmental variation in general, and climate change specifically, can strongly affect offspring phenotypes. In particular, species with TSD may experience sex ratio skews as a result of climate change producing predominantly the “warmer” sex (e.g., Janzen 1994; Chu et al.; 2008; Mitchell et al. 2008). Although among-individual response to incubation temperature may be adaptive over the course of normal inter-annual variation because there will always be some “warm-adapted” individuals (Deeming and Ferguson, 1989), the current magnitude of warming driven by anthropogenic effects may swamp populations’ natural ability to adapt to minor fluctuations in inter-annual temperatures. If sex ratio skews induced by climate warming persist for more than a few generations, and particularly if such skews are in the male direction, we may start to see extinctions of reptile populations (Mitchell and Janzen, 2010). Already, a small population of Tuatara living in areas without appreciable variation in available nesting habitat is strongly male biased (Nelson et al., 2002). The ability to compensate for a warming climate, and thereby continue to produce offspring of both sexes, may become increasingly important in populations of reptiles with TSD (e.g., Doody et al., 2006; Refsnider and Janzen, 2012; Telemeco et al., 2013).

6. CONCLUSIONS

To date, research on nest-site choice in birds has focused almost exclusively on the roles of nestling and female survival in driving nest-site choice, and how these factors may impact population growth trends. Studies on other oviparous taxa, however, have demonstrated that nest-site choice is often driven by additional factors. Moreover, because nest-site choice directly impacts an individual’s lifetime fitness, studying nest-site choice also presents an excellent opportunity for measuring the selection pressures acting on individuals and thereby driving evolution within a population. Reptiles differ from birds in several key life-history traits associated with nesting (i.e. long incubation periods, burying eggs within a substrate, and minimal parental care), and which have different ecological implications for the two groups. For example, the lengthy incubation periods and general lack of parental care in reptiles mean that reptiles must be able to predict future incubation conditions from cues present at the time of oviposition, cannot affect egg incubation conditions following oviposition (such as by contact incubation, as in birds), and do not have the opportunity to adjust future nest-site choices based on the success of past choices. Nevertheless, studies in reptiles have contributed substantially to our understanding of the evolutionary drivers and ecological implications of nest-site choice.

First, incubation environment has a profound effect on a variety of offspring phenotypes in reptiles, and enhancement of particular phenotypes is a major driver of nest-site choice in many reptiles. Selection operates on nest-site choice when a particular phenotype is favoured in a given environment, and the effect of nest-site choice on offspring phenotype can also impact population parameters, such as sex ratio in the case of reptiles with TSD. That incubation conditions can also affect offspring phenotype in birds is becoming increasingly recognised. Second, studies in reptiles have demonstrated that survival of the juvenile stage (as opposed to the egg or adult stage) can also be a critical driver of nest-site choice. In such cases, nest sites may be chosen such that emerging hatchlings are placed in close proximity to suitable juvenile habitat. Birds, too, have recently been demonstrated to choose nest sites based on proximity to suitable juvenile (i.e. fledgling) habitat, and such selection pressure may explain the incongruence between nest-site choice and nest success common across avian studies.

Although life-history traits differ substantially between reptiles and birds, the evolutionary drivers underlying nest-site choice in these taxa share several similarities and have similar consequences for selection on individuals and effects on populations. Studies on the evolution and ecology of nest-site choice in these taxa have much to offer each other in terms of both theoretical basis and applications to conservation and management. Incorporating knowledge gained from a range of taxa into our research, and testing hypotheses in one system that have demonstrated importance in other systems, will provide a deeper understanding of the ecology and evolution of nest-site choice.

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