

Putting Eggs in One Basket: Ecological and Evolutionary Hypotheses for Variation in Oviposition-Site Choice

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Annu. Rev. Ecol. Evol. Syst. 2010. 41:39–57

First published online as a Review in Advance on August 3, 2010

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-102209-144712

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1543-592X/10/1201-0039\$20.00

Key Words

juvenile habitat, mate choice, maternal survival, natal philopatry, nest-site choice, offspring survival, phenotype

Abstract

Oviposition-site choice is a major maternal effect by which females can affect the survival and phenotype of their offspring. Across oviparous species, the ultimate reasons for females' selection of oviposition sites often differ. We present six hypotheses that have been used to explain nonrandom oviposition-site choice in insects, fish, amphibians, reptiles, and birds: (*a*) maximizing embryo survival, (*b*) maximizing maternal survival, (*c*) modifying offspring phenotype, (*d*) proximity to suitable habitat for offspring, (*e*) maintaining natal philopatry, and (*f*) indirect oviposition-site choice via mate choice. Because these hypotheses differ in their relevance across oviparous taxa, each hypothesis must be tested to ensure accurate understanding of the ultimate reason behind oviposition-site choice in a particular taxon. By presenting the major hypotheses for oviposition-site choice as they relate to diverse oviparous animals, we nonetheless illustrate particular trends across animal taxa, while highlighting avenues for future research into the ecological and evolutionary drivers of oviposition-site choice.

Natal philopatry:
when individuals
return to the location
of their birth to breed
and/or deposit eggs

INTRODUCTION

Females can influence offspring survival and phenotype through both genetic and nongenetic means. In practice, maternal effects are considered to be mechanisms that influence offspring phenotype but which, for the most part, are not transmitted genetically from mother to offspring. One such maternal effect that can have a large impact on offspring survival and phenotype is maternal choice of oviposition site (Bernardo 1996). In oviparous species, oviposition-site choice is a female's assessment of potential nest sites and selection of a particular site. A female's decision about where to lay her eggs can have serious consequences for her own reproductive fitness, as oviposition site affects embryo survival, juvenile performance, and offspring phenotype, as well as potentially the survival of the ovipositing female. Thus, oviposition-site choice is a life-history trait of critical importance (Resetarits 1996).

Scope of Review

In this review, we describe six major ecological and evolutionary hypotheses purported to explain nonrandom oviposition-site choice in oviparous animals: (1) maximizing embryo survival, (2) maximizing maternal survival, (3) modifying offspring phenotype, (4) proximity to suitable habitat for offspring, (5) maintaining natal philopatry, and (6) indirect oviposition-site choice via mate choice. We discuss each hypothesis as it relates to insects, fish, amphibians, nonavian reptiles (hereafter reptiles), and birds. Importantly, we examine ultimate ecological or evolutionary reasons for oviposition-site choice. That is, what is the fitness consequence to an individual that selects an oviposition site based on one of the above hypotheses? We do not discuss proximate reasons for oviposition-site choice, namely, the environmental or social cues that an individual may use as indicators of a site's future incubation conditions.

Because the six hypotheses for oviposition-site choice presented here differ in their relevance across oviparous taxa, one cannot simply generalize the importance of any particular hypothesis from one group to others; instead, the various hypotheses must be tested for the species of interest to ensure accurate understanding of the situational mechanism(s) for oviposition-site choice operating in that species. Moreover, these hypotheses for oviposition-site choice are not mutually exclusive: females may "take into account" more than one hypothesis when making oviposition decisions, and it is likely that females in some taxa "adopt" a hierarchical approach by first choosing a general area for oviposition based on one hypothesis, and then selecting a particular site within that area based on a different hypothesis. By presenting the major hypotheses for oviposition-site choice as they relate to diverse oviparous animals, we nonetheless illustrate particular trends across various animal taxa, while highlighting avenues for future research into mechanisms controlling oviposition-site choice, especially in the current context of rapid environmental change.

Terminology

We use the general term oviposition-site choice or oviposition-site selection in this review to refer to any oviparous animal's selection of a site for deposition of eggs. However, this terminology also encompasses several more specific terms used when referring to certain taxa: Nest-site choice refers to animals that construct a nest in which they oviposit, such as reptiles and birds, and spawning-site choice refers to animals with external fertilization in which pairs copulate and oviposit simultaneously, such as some fishes and anuran amphibians.

Several hypotheses discussed here can be differentiated based on the developmental stage with which they are concerned. Hypothesis 1 deals with embryo survival, which is equivalent

to the egg stage for all taxa discussed in this review. Hypothesis 4, by contrast, discusses the performance and survival of juveniles. In the case of indirect developers such as insects, fish, and most amphibians, the term juvenile is equivalent to the larval stage (that is, caterpillars, fry, or tadpoles, respectively). The juvenile stage of interest for direct developers is simply hatchlings (in reptiles) or nestlings/fledglings (in birds). Finally, Hypothesis 3 discusses offspring phenotype. This hypothesis applies equally to any recently hatched offspring, regardless of whether the taxon of interest undergoes direct or indirect development.

HYPOTHESIS 1: MAXIMIZING EMBRYO SURVIVAL

Maximization of embryo survival has traditionally been considered the most important reason for nonrandom choice of oviposition site in oviparous animals. Females can choose oviposition sites that minimize predation risk, maintain a microclimate suitable for embryo development, or avoid habitats prone to desiccation in aquatic species. However, recent research on insects has shown that females do not necessarily oviposit in the habitat types that result in the greatest embryo survival (see Hypothesis 2), suggesting that alternative selection pressures may override differences in embryo survival among habitat types. Importantly, this result indicates that oviposition-site choice is more complex than simply choosing the location with the highest probability of embryonic survival. Therefore, maximizing embryo survival may not govern oviposition-site choice in some and perhaps many oviparous taxa.

In insects, maximizing the survival of eggs tends to be accomplished by selecting sites that minimize predation or conspecific competition. Both terrestrially (Higashiura 1989) and aquatically ovipositing species (Petranka & Fakhoury 1991) preferred predator-free oviposition sites. Egg survivorship decreased as more eggs were deposited on a host plant (Mitchell 1975), and in some cases, earlier-hatching larvae fed on the eggs of conspecifics on the same plant (Williams & Gilbert 1981). Therefore, females in many species avoid ovipositing on plants that already contain eggs of conspecifics.

Oviposition-site choice in taxa with external fertilization, including many fishes and amphibians, is more complicated. The site must first allow for successful fertilization of the eggs, as well as meet the requirements of spawning adults and developing eggs at the site of oviposition. In fishes, spawning may occur in specific microhabitats that enhance fertilization success (Petersen et al. 1992). The provision of a suitable environment for the developing embryos, however, appears to be the strongest driver of oviposition-site choice in fish.

The wide diversity of habitats occupied by fishes (e.g., salt- and freshwater, fast-flowing rivers and calm pools, and climates ranging from polar to tropical regions) means that the environmental stressors experienced by developing fish eggs are extremely broad. River-spawning salmonids in temperate regions prefer warmer-than-average sites that minimize the likelihood of eggs freezing (Geist et al. 2002), whereas species in more tropical latitudes prefer cooler sites to prevent eggs from overheating (Middaugh et al. 1981). Many stream-dwelling fishes select spawning sites with sufficient water flow to aerate eggs and prevent suffocation (Bilkovic et al. 2002), but occasionally, as in Eurasian perch (*Perca fluviatilis*), spawning sites with higher turbidity may actually be preferred because eggs deposited in such sites will experience reduced UV radiation (Probst et al. 2009). Substrate attributes, such as vegetation and grain size, are important because they provide sites for anchoring eggs, and thereby prevent scouring or washing away of eggs by currents or wave action (Shirotori et al. 2006).

Protection against predation is another important component of how fish maximize offspring survival via oviposition-site choice. Substrate composition, and especially the size of interstitial spaces between particles, is important in protecting fish eggs against predation

Fecundity-survival

hypothesis: parents face a trade-off between responding to the risk of mortality directed toward their offspring versus toward themselves

(Middaugh et al. 1981), cannibalism (Spence et al. 2007), or disturbance by other fish spawning in the same location (Geist et al. 2002). Some galaxiids remove the threat of aquatic predators from their eggs altogether by depositing eggs terrestrially among flooded twigs and leaves (Charteris et al. 2003).

Many fishes exhibit parental care of eggs. In such species, the efficiency of parental care can be increased by selecting a favorable oviposition site. For example, nest-guarding male convict cichlids (*Cichlasoma nigrofasciatum*) that spawn in burrows could more effectively defend eggs against predation when the burrows had one, rather than multiple, entrances (Lavery 1991). Long-finned gobies (*Valenciennae longipinnis*) that spawned in burrows containing underground water flow had a reduced parental burden because the flowing water provided dissolved oxygen and thereby reduced the amount of egg-fanning required by the attending male (Takegaki 2001). Similarly, male three-spine sticklebacks (*Gasterosteus aculeatus*) nesting in concealed locations more efficiently fanned their eggs because they spent less time involved in territorial encounters with other males than did males whose nests were in more exposed locations (Sargent & Gebler 1980).

Selection of oviposition sites in amphibians is strongly driven by pressure to reduce predation on eggs. Many species avoid ovipositing in water bodies containing predators (e.g., Resetaarits & Wilbur 1989, Vredenburg 2004). Similarly, in species with cannibalistic larvae, adults avoid ovipositing in pools already containing conspecific larvae (Matsushima & Kawata 2005). However, some tropical frogs prefer to oviposit at sites containing conspecific eggs or larvae and may use the presence of conspecifics as indicators of predator absence (Rudolf & Rödel 2005).

Unlike fish, amphibians are not necessarily aquatic, and therefore are not obligated to spawn and oviposit in an aquatic environment. But like fish eggs, amphibian eggs lack a protective shell, rendering the eggs extraordinarily sensitive to environmental conditions, particularly moisture levels. Species that oviposit terrestrially, including many salamanders, must select oviposition sites with sufficient water content so that eggs do not desiccate (Figiel & Semlitsch 1995), whereas stream-dwelling species are challenged to select oviposition sites with greater stability to reduce nest displacement during high-flow events (Guy et al. 2004). Conversely, in species that oviposit in temporary pools, hydroperiod length is important because females must assess whether a potential oviposition site will contain water long enough for eggs to develop and larvae to escape before the pool dries (Rudolf & Rödel 2005).

Thermal conditions are also important in maximizing embryo survival in amphibians. Freezing can be problematic for species that breed early or late in the activity season; to compensate, many pool-nesting species select deeper, rather than shallower, oviposition sites (Petranka & Petranka 1981). Interestingly, a few species exhibit plasticity in nesting behavior depending on temperature: Individuals may oviposit in isolation in warm weather but communally in cool weather (Caldwell 1986), which appears to confer a thermal advantage to developing embryos and results in higher embryo survival (reviewed in Doody et al. 2009). Amphibians also maximize embryo survival through oviposition-site choice by avoiding sites containing high salinity (Haramura 2008) and high transparency of water to damaging UV radiation (Palen et al. 2005).

In many reptiles, oviposition sites are selected to minimize predation on the developing eggs (e.g., Rand & Dugan 1983). In some cases, however, females must choose between minimizing predation on their nests or on themselves, known as the fecundity-survival hypothesis. For example, females in a population of tropical pythons (*Liasis fuscus*) chose between two types of nest locations: cool sites, which carry a lower risk of egg predation but require costly brooding by the female; and warm sites, which do not require maternal brooding but have a higher risk of egg predation (Madsen & Shine 1999). Females that nested in cool sites were emaciated following the nesting season, and many later died of starvation. The high costs to females associated with selecting cool

nest sites suggest that they favored survival of their offspring over their own survival (Madsen & Shine 1999).

Although reptile eggs are more protected from environmental conditions than are eggs of species lacking calcified egg shells, such as amphibians and fish, selecting an oviposition site that will experience conditions suitable for embryonic development is nonetheless important. Incubation temperature has a profound effect on embryo survival (e.g., Schwarzkopf & Brooks 1987), which is thought to be more important in nest-site choice than sex ratio adjustment in species with temperature-dependent sex determination (TSD) (see Hypothesis 3 below; Ewert et al. 2005). In species from temperate regions where neonates overwinter in the nest, offspring survival is further influenced by the winter conditions they experience within the nest (Weisrock & Janzen 1999). Crocodilians have a particularly restricted range of suitable incubation temperatures, and offspring survival is low in areas that lack sufficient open, sunny sites for nest mound construction (Leslie & Spotila 2001). Soil moisture also strongly affects embryo survival in reptiles, and respiratory gas concentrations may be important as well, but few data are available on their impact on reptilian embryos in nests (Packard & Packard 1988). Eggs can desiccate in soil that is too dry (Socci et al. 2005); moreover, reptiles with flexible-shelled eggs must absorb some moisture from the environment to successfully complete development (Packard & Packard 1988). However, eggs in nests that are too moist are susceptible to fungal infection (Socci et al. 2005) or drowning. The risks to nests of many beach-nesting reptiles, such as sea turtles, commonly differ depending on a nest's location: Nests closer to water are at highest risk of inundation or egg loss due to erosion, whereas eggs farther from water are at highest risk of desiccation (Kamel & Mrosovsky 2004).

Predation is the greatest source of nest mortality in passerine birds (Martin 1992), and the selection of nest sites that reduce the risk of predation is thought to be the predominant driver of nest-site choice in birds in general (Martin 1993). Many birds minimize nest predation by selecting nest sites that are concealed by vegetative or other cover and are therefore less detectable to predators than are random sites (e.g., Liebezeit & George 2002). However, many studies found no relationship between nest concealment and likelihood of predation (reviewed in Martin 1993). In these cases, birds may reduce predation through parental presence at the nest, either during incubation or the period of parental care in species with altricial nestlings (the parental compensation hypothesis; Remeš 2005). Nest predation can be further reduced in colonially nesting species, where each individual benefits from the increased vigilance of numerous adults. Some species, particularly shorebirds, take advantage of the vigilance and predator-mobbing behavior of colonially nesting species and place their nests within a colony of another species, thereby increasing their own nesting success (Pius & Leberg 1998).

However, parental presence at the nest can be costly in birds, as incubating adults are vulnerable to predation and unfavorable environmental conditions. Evidence supporting the fecundity-survival hypothesis in birds is mixed (Miller et al. 2007), but a review of North American bird species suggested that, in general, adults of the reviewed species acted to reduce predation risk to their offspring over reducing their own predation risk (Ghalambor & Martin 2001). In particular, a trade-off exists between concealing the nest from the view of predators and maintaining the incubating parent's view of the surroundings (Götmark et al. 1995), which may explain why increased nest concealment does not always result in decreased nest predation in birds (e.g., Holway 1991).

Because most bird nests are constructed in the open (that is, they are not buffered by water or soil), the developing eggs and nestlings are particularly vulnerable to environmental stressors such as extreme heat or cold. Birds whose nests are exposed to particularly high temperatures, such as grassland- or beach-nesting species, must select nest sites that minimize heat stress to eggs and nestlings. Nesting among patches of vegetation (Davis 2005) or orienting the nest opening away from the sun during the hottest part of the day can reduce direct solar radiation on eggs and

Temperature-dependent sex determination (TSD): the sex of individuals is irreversibly determined by the temperature experienced by the developing embryo during a thermosensitive period

Parental compensation hypothesis: when nest concealment alone is insufficient to mitigate against predation pressure, parents compensate for remaining risk by their presence at the nest via plumage camouflage, antipredator behavior, etc.

Preference-performance hypothesis:

female insects prefer to oviposit on host species having the highest nutritional quality for their larvae to feed upon after hatching

Time versus egg limitation:

a female insect's realized lifetime reproduction may be constrained by either the time available for locating suitable oviposition sites (time limitation) or by her supply of mature eggs (egg limitation)

nestlings (Facemire et al. 1990). However, species from cold climates may select sites that increase solar radiation (Marzluff 1988) or have a decreased risk of being covered by snowdrift (Stonehouse 1970). Megapodes construct nest mounds from which the young emerge fully independent of adults, and these birds select mound sites with thick vegetative cover to prevent desiccation of the incubating eggs (Jones 1988).

Studies on a few passerine birds have documented a generalist strategy, wherein no specific nest-site variables were predictive of nest success or failure (e.g., Filliater et al. 1994). Instead, a rich guild of nest predators may eliminate predictably safe nest sites and thereby select for generality over specificity in nest-site choice. Alternatively, such species may not select nest sites to maximize embryo survival, but instead for one of the reasons discussed below.

HYPOTHESIS 2: MAXIMIZING MATERNAL SURVIVAL

Maximizing maternal survival is important in any oviparous animal, but it is of particular importance in iteroparous species, where the lifetime reproductive success of a female depends on her survival across periodic breeding events. In species where some form of parental care occurs (e.g., nest attendance in salamanders, egg incubation in birds), the period of maternal vulnerability while at the oviposition site extends beyond oviposition itself and lasts throughout the period of parental care. This observation has given rise to the fecundity-survival hypothesis, where females must choose between increasing their fecundity despite the concurrent increase in mortality risk to themselves and reducing their own mortality risk at a cost to their offspring.

The preference-performance hypothesis for insects states that females should prefer to oviposit on hosts with the highest nutritional quality for offspring, which would promote short development time, higher adult biomass, and increased maternal fecundity (see Hypothesis 4 below; Pöykkö 2006). However, oviposition-site choice in many phytophagous insects fails to support this hypothesis: In the pierid butterfly *Anthocharis cardamines*, females oviposited on a host plant that provided poor nutrition for the larvae and did not oviposit on the plant on which larvae had the highest performance (Courtney 1981); similarly, a grass miner (*Chromatomyia nigra*) optimized the number of eggs laid per host plant rather than optimizing the quality of the host plant selected for the larvae (Scheirs et al. 2000). Rather than optimizing habitat quality for the offspring, such species were instead optimizing maternal fitness and/or survival. Female *A. cardamines* fed extensively on the nectar of the plant they selected for oviposition (Courtney 1981), and the grass miners optimized their own fecundity over the performance of their offspring (Scheirs et al. 2000). Selection of oviposition sites that are suboptimal for offspring may also result from time limitation, rather than egg limitation, in many insects. That is, time-limited females should be less choosy about where they oviposit than egg-limited females, because the former want simply to lay all of their eggs before they die (Rosenheim et al. 2008). Therefore, suitable host plants may be chosen for oviposition simply to maximize maternal fecundity, even though those host plants are not ideal for offspring performance.

In fish and amphibians, where external fertilization requires that both parents be present at the time of oviposition, minimizing predation on vulnerable mating pairs is an important consideration in choice of oviposition site. In many species of wrasse (*Thalassoma* spp.), females require information about the safety of a potential spawning site before they mate with the resident male (Warner & Dill 2000). Similarly, both the habitat patches used for spawning by river herring (*Alosa* spp.; O'Connell & Angermeier 1997) and the rapid upward dashes characteristic of many spawning tropical coastal fish (Johannes 1978) minimize predation on spawning adults. In amphibians, the unique posture adopted by a mating pair of anurans (that is, amplexus) has metabolic and locomotor costs (Bowcock et al. 2009), and this posture is also likely to increase the pair's

vulnerability to predation, which may influence where a pair chooses to oviposit. Female salamanders that brood egg masses incur metabolic costs and probably a higher direct risk of mortality as well (e.g., Forester 1981).

Because nesting reptiles generally provide little, if any, parental care, and mating is spatially and temporally separated from nesting due to internal fertilization, the mortality risk to nesting females is usually restricted to traveling to a nesting area and constructing the nest. For example, *Sceloporus* lizards selected warm nest sites in open areas that accelerated embryonic growth and development, but females nested at night to minimize risk of overheating at the nest site (Angilletta et al. 2009). Other species select nest sites that protect the nesting female from predation (e.g., Burger 1993). Nests of the turtle *Emydura macquarii* experienced lower predation rates when located farther from, rather than nearer to, the shoreline. However, when direct predation risk to females increased, the turtles favored their own survival by nesting closer to the shoreline at the expense of increased predation risk to the nest, supporting the fecundity-survival hypothesis (Spencer 2002). Females may also minimize energy expended on selecting and constructing nest sites by nesting communally (reviewed by Doody et al. 2009) or copying the nest-site choice of conspecifics (Refsnider et al. 2010).

The prolonged stage of parental care in birds, particularly during incubation, means that adults are vulnerable to the same risks as their developing offspring, namely predation and environmental stressors. According to the microclimate selection hypothesis, nest sites are chosen to minimize physiological stress on the incubating adult (With & Webb 1993). Studies of nest-site choice of individuals differing in body condition provide support for this hypothesis: In Kentish plovers (*Charadrius alexandrinus*), females in poor body condition chose nest sites that were thermally less stressful for the female but had a higher risk of nest predation, whereas females in better body condition chose thermally more stressful nest sites with a lower risk of nest predation (Amat & Masero 2004). In several grassland passerines, whose nests are exposed to high temperatures and prolonged periods of direct sunlight, nest sites were chosen such that the degree of radiative cover provided shade and convective cooling to incubating adults, which is particularly important in dark-colored species (With & Webb 1993). A review of South American passerine species supported the fecundity-survival hypothesis, whereby parents acted to reduce predation risk to themselves over that of their offspring (in contrast to the behavior of North American passerines; see Hypothesis 1); moreover, this response increased as clutch size decreased (Ghalambor & Martin 2001).

Although many birds select nest sites to minimize detection by predators, a cost of selecting a concealed nest site is that heavy cover obstructs the incubating parent's view of the surroundings (Götmark et al. 1995). In Canada geese (*Branta canadensis*), female survival, rather than nest survival, was more dependent on the incubating female's early detection of predators, and therefore a negative correlation existed between nest concealment and adult survival (Miller et al. 2007).

HYPOTHESIS 3: MODIFYING OFFSPRING PHENOTYPE

In reptiles and, to a lesser extent, fish and amphibians, the microhabitat in which a female oviposits can dramatically affect the phenotype of her offspring. Incubation regime influences numerous fundamental characteristics, such as duration of embryonic development, offspring size, posthatching growth rate, locomotor performance, and behavior. In addition, in species with TSD, thermal characteristics of the nest site determine offspring sex ratio. Therefore, choice of oviposition site directly affects not only the survival of a female's developing embryos, but also the quality of her offspring.

Because eggs of fish and amphibians are generally unattended after oviposition, the incubation conditions they experience during development are solely those of the oviposition site. Warmer

Microclimate selection hypothesis: nest placement in birds functions to ameliorate adverse microclimatic effects on eggs, nestlings, and/or incubating adults

conditions accelerate embryonic development in fish (Bermudes & Ritar 1999), amphibians (Pearl et al. 2007), and reptiles (Shine et al. 1997). This relationship is especially important in species where early hatching is favored, such as frogs whose larvae must escape from drying ephemeral pools or temperate-zone reptiles with limited time in which to acquire sufficient reserves before entering hibernation.

Moisture level and thermal conditions (including both means and variances) also affect numerous other offspring characteristics in reptiles. Moisture level and incubation temperature affected offspring size in snakes (e.g., Brown & Shine 2004), and the effects of incubation temperature on growth rate in snapping turtles (*Chelydra serpentina*) persisted for at least seven months after hatching (Brooks et al. 1991). Incubation conditions affect several measures of offspring performance including metabolic efficiency in lizards (Van Damme et al. 1992), swimming speed in turtles (Miller 1993), and sprint speed in lizards (Shine et al. 1997). Offspring behaviors such as basking (Shine & Harlow 1996), retreating from predators (Burger 1989), and sociosexual behaviors (Flores et al. 1994) also vary significantly along a gradient of incubation conditions.

Many reptiles, and a few species of fishes, have TSD, whereby offspring sex is irreversibly determined by the incubation temperature within the nest cavity (Bull & Vogt 1979). Therefore, TSD potentially affords reptiles control over the offspring sex ratio via nest-site choice (Janzen & Morjan 2001). By choosing a nest site to produce a specific sex, a female theoretically could increase her fitness by producing the rarer, and therefore more valuable, sex (Girondot et al. 1998); the sex that will benefit more from a higher quality nest site (Reinhold 1998); or the sex whose fitness is maximized by the incubation regime that produces that sex (Conover 1984, Warner & Shine 2008). Therefore, though nest-site choice in TSD reptiles may be driven predominantly by selecting a site that maximizes nest success (as offspring phenotype is meaningless if the eggs fail to hatch; Escalona et al. 2009), optimizing offspring phenotype is likely the next most important reason for selecting a particular site (Ewert et al. 2005).

HYPOTHESIS 4: PROXIMITY TO SUITABLE HABITAT FOR OFFSPRING

Larval and juvenile animals are often especially vulnerable to predation, desiccation, and/or starvation. It is therefore critical that, immediately following hatching, juveniles locate suitable habitat in which to hide from predators and obtain sufficient nutrients for growth and development. In insects, females that oviposit on ideal host plants decrease the length of time their offspring spend in the vulnerable larval stage. Similarly, salamanders that oviposit in deeper temporary ponds increase the chances that their offspring will complete larval development and escape from their ponds before they dry up. In species that oviposit in a different habitat from that required by juveniles immediately after nest emergence, offspring survival may be enhanced if females oviposit in close proximity to the habitat required by juveniles. Examples include hatchling turtles moving from their terrestrial nest site to appropriate aquatic habitat or fledgling birds that must quickly find suitable foraging habitat or risk starvation.

The preference-performance hypothesis for phytophagous insects states that females should prefer to oviposit on the host plants that confer the highest nutritional benefits to their larvae (Pöykkö 2006). Studies on many insect species support this hypothesis, which indicates that such species likely select oviposition sites to provide suitable habitat for their larvae. For example, larvae whose eggs were laid on hosts preferred by females grew larger (Rausher 1983), had shorter development time (Vacek et al. 1985), and had higher digestive efficiency (Sadeghi & Gilbert 1999) than did larvae that hatched on hosts not preferred by ovipositing females. Nutritional quality is not the only benefit that larval insects may receive from their host plant, however. Female insects can also affect larval performance by ovipositing on host plants that allow larvae to

sequester defensive chemicals (Thompson & Pellmyr 1991); support ant species that protect larvae from predators and parasitoids (Pierce & Elgar 1985); allow larvae to move easily among several host species and, thus, achieve a mixed diet (Ballabeni et al. 2001); give larvae sufficient time to complete development before the host plant dehisces (Wiklund & Friberg 2009); and minimize intraspecific competition on the host plant (Rausher 1983). Females of carnivorous species, such as pitcher plant mosquitoes (*Wyeomyia smithii*), preferred to oviposit in larger pitchers, which contained more prey for their larvae and therefore facilitated decreased larval development time and increased size of larvae (Heard 1994).

Insect larvae that develop in temporary pools are at risk of predation, interspecific competition, and desiccation from pool drying. Mosquitoes (*Culiseta longiareolata*) avoided ovipositing in pools that contained predators of their larvae (Spencer et al. 2002), thus ensuring safer habitat for their offspring. Similarly, where larval mosquitoes (*Anopheles punctipennis*) compete with species such as anuran tadpoles for food resources, female mosquitoes avoided ovipositing in pools containing the competitor species (Petranka & Fakhoury 1991). A pool that lacks predators or interspecific competitors is often temporary; therefore, larvae must complete development and escape before the pool dries (Blaustein & Margalit 1996), which favors maternal ability to assess a pool's hydroperiod.

The spawning site can affect the transport of eggs and/or larvae in many fishes. Temperate, stream-dwelling species may spawn in upstream reaches, which contain both suitable conditions for embryonic development and fast currents that transport larvae to downstream environments rich in food resources (Bilkovic et al. 2002, Charteris et al. 2003). Many coral reef fishes spawn at times and locations that favor transport of pelagic larvae offshore, where predation is drastically reduced (Johannes 1978). Conversely, tropical pelagic species spawn at sites such that tides or currents transport eggs reefward, where larvae can develop in protected, food-rich sites (Leis 1991). Increasingly, however, we recognize that the larvae of many coral reef fishes are behaviorally sophisticated rather than passive plankters (Leis 1991), which suggests that these larvae play an active role in arriving at suitable habitat rather than relying on currents in the vicinity of spawning grounds to transport them passively.

Due to the larval stage of taxa with indirect development, amphibian tadpoles face many of the same pressures as larval fish. Selecting pools that minimize predation (e.g., Resetarits & Wilbur 1989), cannibalism (Halloy & Fiano 2000), and intraspecific competition (e.g., Matsushima & Kawata 2005) among tadpoles is of primary importance in oviposition-site choice in many anurans. Male Madagascan poison frogs (*Mantella laevis*) select oviposition sites and then call to attract females to those sites; however, males actively discriminated against potential oviposition sites already containing competing frog species (Heying 2004). Similarly, gray treefrogs (*Hyla versicolor*) avoided ovipositing in pools containing high densities of parasitic snails (Kiesecker & Skelly 2000).

Like larvae of insects that oviposit in temporary pools, amphibian larvae developing in an ephemeral water body must metamorphose and escape before a pool dries (Blaustein & Margalit 1996). Females may therefore prefer to oviposit in pools with longer hydroperiods to increase the likelihood that tadpoles can develop and metamorphose before drying occurs (Resetarits & Wilbur 1989). Stream-dwelling species, such as *Desmognathus* salamanders, nested in headwater habitats that passively transported larvae into optimal juvenile habitat in moderate-sized streams, thus minimizing transport to suboptimal habitats in large rivers (Snodgrass et al. 2007). This is a strategy similar to the larval transport mechanisms observed in many fishes.

Choice of nest sites in areas that reduce predation on newly hatched offspring is known in some reptiles. Nests laid by green iguanas (*Iguana iguana*) and slider turtles (*Trachemys ornata*) on an island were subject to much less predation on the resulting hatchlings compared to nests laid in nearby mainland habitat (Drummond 1983), and hatchling snapping turtles (*C. serpentina*)

Active-return model:

nest site selection is based on characteristics that influence offspring survival, and a site remains the primary site of choice for subsequent reproductive bouts as long as it remains suitable

were more likely to survive the journey from nest to wetland if the nest site was characterized by sparse vegetation and little slope and was in close proximity to water (Kolbe & Janzen 2001). Upon emergence from the nest, sea turtle hatchlings must orient correctly in order to reach the ocean. Female leatherback (*Dermochelys coriacea*) sea turtles selected nest sites at an intermediate distance from the high tide line, where hatchling disorientation was less likely than at sites farther from the water (Kamel & Mrosovsky 2004). On a larger spatial scale, female sea turtles may select nesting beaches that are in close proximity to ocean currents that will transport hatchlings to suitable developmental habitats (Lohmann et al. 2008).

Upon fledging, young birds lose the protection provided by their nest against predation and environmental stressors. Parents of many species, therefore, often lead newly fledged offspring away from the vicinity of the nest and into different habitat that provides food (Vega Rivera et al. 1998) and concealment from predators (Anders et al. 1998). Habitat that provides food and protection is important for both altricial species where fledglings continue to be fed by the parents, as well as precocial species in which young are completely independent upon hatching (Göth and Vogel 2002). The necessity to quickly lead vulnerable young from the nest site to suitable fledgling habitat favors parental selection of nest sites that are close to fledgling habitat (H.M. Streby and D.E. Andersen, unpublished data). Indeed, in cases with no correlation between nest-site variables and nest survival (e.g., Misenhelter & Rotenberry 2000), nest sites may be selected on the basis of proximity to suitable fledgling habitat rather than for the nest microhabitat. Because an individual's lifetime fitness is based on reproductive success (which in birds includes both nest success and survival of fledglings until independence), rather than nest success per se, it would not be surprising if proximity to suitable fledgling habitat was as important in driving nest-site choice in birds as maximizing nest success. Research on the fledgling stage of birds is necessary to test this idea. Other taxa that move their offspring, such as some dendrobatid frogs that transport tadpoles (Aichinger 1991), may also choose their initial oviposition site on the basis of proximity to suitable habitat to which adults can transport juveniles.

HYPOTHESIS 5: MAINTAINING NATAL PHILOPATRY

In some taxa, oviposition-site choice may be an artifact of natal philopatry, with females returning to nest at the same location where they themselves hatched. If oviposition-site choice is heritable, females that oviposit at sites that produce high-quality offspring would pass on this oviposition-site choice to their daughters, thereby maintaining a lineage that produces high-quality offspring resulting from oviposition-site choice. Although maintaining natal philopatry is probably less important in driving oviposition-site choice than the hypotheses described above, it nevertheless affects where females of some species choose to oviposit.

Selection favors philopatry when dispersal from natal habitat entails high costs. For example, in damselflies (*Enallagma* spp.) that are unable to determine if a potential oviposition site contains predators, females are strongly philopatric and, thus, maintain within their lineage daughters that continue to oviposit in the habitat in which they themselves hatched (McPeck 1989).

In contrast, dispersing species may display natal philopatry to ensure that daughters return to, and oviposit at, successful nest sites. Such philopatry may be passive, as in the case of many tropical fishes that spawn near gyre currents that periodically return larvae to the vicinity of origin (Johannes 1978); or daughters may actively return to the site of their own hatching, as noted in northern spectacled salamanders (*Salamandrina perspicillata*; Romano et al. 2008) and sea turtles (e.g., Meylan et al. 1990). Under this active-return model, a dispersing female initially selects a nest site based on characteristics that influence offspring survivorship, and then returns to that site on subsequent nesting forays as long as the site retains the features for which it was selected;

the natal nest area may be the first site chosen under this model (Lindeman 1992). Particularly in unpredictable environments, nesting success in the previous generation may be the best predictor of future success, so inheritance of oviposition-site preference would provide a mechanism by which a female could identify a suitable oviposition site and then transmit that information to her female descendents (Freedberg & Wade 2001). Moreover, imperfect natal homing could result in occasional colonization of a new oviposition habitat, thereby fostering gene flow and providing an alternative oviposition site if previously used sites become unsuitable (Bowen et al. 1989).

Support for the benefits of natal philopatry in birds is somewhat mixed and depends mainly on the quality of territory in which an individual hatches (Stacey & Ligon 1991). On the one hand, a female breeding for the first time benefits from searching a familiar, high-quality area for a suitable nest site (Emlen 1994), and the fact that a nest site has already been successful indicates that nesting as close as possible to her natal site is a safe strategy (Ruusila et al. 2001). On the other hand, in areas lacking a necessary resource, females benefit by remaining in their natal territory, helping relatives to breed, and waiting to inherit the parental territory (Emlen 1994). Natal philopatry is also beneficial in species such as waterfowl, in which intraspecific brood parasitism and/or postfledging brood amalgamation occur, as the costs of these behaviors decrease when performed among relatives (Weatherhead 1998).

The degree to which natal philopatry occurs may vary between individuals and between populations of the same species. For example, about 70% of California tiger salamanders returned to breed at the pond in which they had metamorphosed, whereas about 30% dispersed and bred at a different pond (Trenham et al. 2001). Is such variation (*a*) a population strategy to maintain gene flow among habitat patches, (*b*) a behavioral syndrome wherein some individuals are always dispersers while others always show natal philopatry, (*c*) a result of within-individual behavioral plasticity based on environmental conditions, or (*d*) the result of dispersing individuals simply showing imperfect natal homing? Determining the mechanism(s) driving natal philopatry will give us insight into both its adaptive significance in general and its role in oviposition-site choice specifically.

HYPOTHESIS 6: INDIRECT OVIPOSITION-SITE CHOICE VIA MATE CHOICE

In some cases, females may be able to affect the phenotype of their offspring indirectly through mate choice. For example, in fish where males construct nests and/or tend eggs, the quality of the spawning site may be correlated with the quality of the male tending that site. Therefore, if offspring from eggs deposited in high-quality oviposition sites are more likely to be sired by males with high-quality phenotypes, the genetic quality of a female's offspring is within the female's control via her selection of an oviposition site. Indeed, in a review of resource quality and male reproductive success, males with higher resource-holding potential controlled better territories in insects, amphibians, and birds (Kelly 2008).

In several fishes displaying paternal care of eggs, characteristics such as size are reliable indicators of a male's quality. For example, larger males are less likely to abandon the nest, experience less egg loss to predation or cannibalism, and control larger nests that accommodate more eggs (e.g., Nelson 1995). Females that mate with these higher quality males therefore not only achieve better genes for their offspring via mate choice (Jones 1981), but also increase their offspring's likelihood of survival. Similarly, in bullfrogs (*Rana catesbeiana*), larger males controlled territories with lower predation risk than did smaller males, so females increased survival of their tadpoles by mating with larger males and ovipositing in their territory (Howard 1978).

Males of many bird species set up nesting territories to which they attempt to attract females. Most studies attempting to disentangle mate choice from nest-site choice in birds have concluded

Intraspecific brood parasitism: a female lays eggs in the nest of another female of the same species without subsequently caring for the eggs or young

Postfledging brood amalgamation: upon fledging from the nest, multiple broods converge to form temporary or permanent associations, and parents defend a common brood-rearing area

that females choose a male based on the quality of his territory rather than the reverse (e.g., Alatalo et al. 1986). However, as males controlling better territories tend to be higher quality males, females that select higher quality mates on the basis of territory quality are nevertheless passing on better genes to their offspring than females mating with lower quality males.

CONCLUSIONS

The ultimate reasons for an individual's choice of oviposition site vary widely both among and within oviparous taxa. Such variation, particularly that occurring within one of the taxonomic groups discussed above, emphasizes the importance of hypothesis testing in studies of oviposition-site choice rather than generalizing based on results from other taxa. Research on several taxonomic groups has traditionally focused on a specific hypothesis for oviposition-site choice within that group, to the exclusion of other possible explanations. For example, a plethora of studies has examined oviposition-site choice in insects in the context of testing the preference-performance hypothesis, while in fact the oviposition-site choices of many insects do not support this hypothesis. Similarly, numerous studies of nest-site choice in birds fail to find relationships between nest-site characteristics and nest success. Although such studies effectively eliminate the tested hypothesis as an explanation for oviposition-site choice in the species of interest, the next logical step is to test other hypotheses, one of which will likely explain the observed oviposition-site choice. For example, many insects select oviposition sites that maximize maternal, rather than offspring, survival and/or performance, and recent research on the postfledging period in birds suggests that suitability of habitat for fledglings is as important as nest success in determining a parent's reproductive success. The hypotheses discussed herein are not mutually exclusive, and it is likely that females in some taxa select oviposition sites hierarchically, based first on one hypothesis (such as maximizing female survival) and secondarily on another hypothesis (such as maximizing embryo survival) within the context of the first. The relative importance of each hypothesis is likely to differ among taxa, however, so even hierarchies of oviposition decisions should not necessarily be extrapolated across taxa.

Research on oviposition-site choice increasingly focuses on its relationship with anthropogenic changes to the environment, such as climate change, habitat loss, and the widespread introduction of invasive species. Habitat destruction and fragmentation are likely to eliminate habitats required by certain species for oviposition and thereby reduce successful recruitment. Invasive species may compete with native species for oviposition sites, replace native host species of some insects, or alter the microclimate of oviposition sites. Finally, climate change not only will exacerbate habitat loss and the establishment of invasive species, but also has the potential to directly alter the phenotypic composition of populations, such as skewing sex ratios in species with TSD. It is therefore important to understand both the ultimate reasons for an individual's selection of an oviposition site and the proximate cues used to select a site from a range of potential sites.

Perhaps most importantly in the face of global environmental change, it is also critical to understand the adaptive potential of oviposition-site choice—that is, how likely is it that a given species can shift its oviposition-site choice to compensate for changes in the environment? Important insight into this question can be gained by examining oviposition-site choice across the geographic range of widespread species. By examining patterns in oviposition-site choice across space, we gain power to predict the capacity for temporal response to environmental change (Doody 2009). Species could potentially shift oviposition-site choices to adapt to environmental change via a shift in allele frequencies (which would require genetic variation for oviposition-site choice) and/or via behavioral plasticity (which would require possessing a range of potential responses to environmental cues). Determining the mechanism(s) by which geographic variation in oviposition-site choice is maintained would aid in predicting adaptive potential in response to

environmental change and, thus, in determining vulnerability to threats such as climate change, habitat loss, and invasive species.

FUTURE ISSUES

1. Many studies have examined oviposition-site choice to determine whether specific sites are chosen nonrandomly. Such studies should also attempt to link oviposition decisions to fitness. That is, do chosen sites differ from random sites in parameters such as maternal survival, embryo survival, or offspring phenotype? Extending studies on oviposition-site choice to examine effects on fitness would give us insight into the adaptive significance of particular oviposition decisions.
2. Studies integrating both laboratory experiments and field observations, though not feasible in all circumstances, will go a long way toward illuminating the importance of specific variables in oviposition decisions and the subsequent effect on individual fitness. Experimentally manipulating specific variables will help identify the features of greatest importance in a female's selection of an oviposition site, which may be difficult to elucidate solely via observational study. However, careful observation of oviposition-site choice and its impact on fitness is crucial to pinpoint which variables are likely to be important in a female's selection of an oviposition site, and therefore which are worthy of more detailed experimental study.
3. Variation in oviposition-site choice in geographically widespread species can inform us about the adaptive significance and mechanistic basis of this trait. Such species are likely to experience different environmental conditions across their range and may exhibit variation in oviposition-site choice behavior to match local conditions. Whether geographic differences in oviposition-site choice are primarily genetically based due to local adaptation or more behaviorally plastic across the range has important implications for a species' capacity to compensate for rapid environmental changes such as climate change, shifting community structure, and the introduction of invasive species.
4. Future research should focus on testing Hypothesis 4 (proximity to suitable habitat for offspring). Many studies that find no effect of oviposition-site characteristics on survival of the eggs or nest may find an effect when those same characteristics are examined in relation to juvenile survival. Thus, proximity to suitable habitat for offspring is likely to be an underappreciated driver of oviposition-site choice. Studies testing this hypothesis are particularly lacking in birds, but additional research on insects, amphibians (such as dendrobatid frogs that transport tadpoles), and reptiles (especially sea turtles and model species such as *Anolis* lizards) would also be very illuminating.
5. Technical advances in molecular biology and radioisotope analysis have drastically improved our ability to study individual movements and population relatedness over wide geographic scales. In many systems, we are only just beginning to understand the extent to which individuals show natal philopatry and the mechanisms used in navigation and homing. Studies on reproductive ecology in any taxon should also include research on whether natal philopatry occurs in the study species. In systems where natal philopatry is found, it would be very useful to examine the costs and benefits of philopatry and to determine whether philopatry is a behavioral syndrome, an adoptable strategy, or individuals making homing mistakes. Answering these questions could give particular

insight into systems where not all individuals are philopatric and a comparative approach could be taken. This situation would provide valuable insight into the evolution of natal philopatry and its role in driving oviposition-site choice.

6. In taxa where mate choice and oviposition-site choice are interrelated, particularly in fish, amphibians, and birds, researchers should attempt to disentangle whether females select oviposition sites directly and mates indirectly, or vice versa. In some taxa, separating mate choice from oviposition-site choice may be accomplished through a simple factorial design in which females are presented with combinations of high- and low-quality males and oviposition sites. This problem has particular implications for sexual selection research in groups such as birds, where females could select a social mate based on the quality of his territory, but could also acquire the genes of a higher quality mate through extrapair fertilizations.
7. Very little research has been conducted on the costs of spawning in amphibians, aside from potential costs to females of multiple matings. Specifically, research on the costs of amplexus in anurans is necessary to assess the importance of maximizing maternal survival in the oviposition-site choice of amphibians.
8. Although research on reproduction in fish is particularly difficult to conduct compared to the other taxa discussed in this review, substantial advances have been made in understanding the habitat requirements of juvenile and spawning adults of many game species. Comparable studies should be conducted on nongame species as well. Research is also needed on the habitat use and movement patterns of larval fishes, and particularly the role of oceanic currents in transporting juvenile fishes among different habitat types.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The literature examining oviposition-site choice in animals is vast, and due to space constraints we are able to cite only a small fraction of the relevant papers on this topic. Many thanks to the following people for enlightening discussion of the topic and comments on earlier versions of the manuscript: A. Bronikowski, C. Chandler, G. Cordero, P. Dixon, C. Kelly, T. Mitchell, A. Sethuraman, H. Streby, E. Takle, R. Telemeco, and D. Warner. Funding was provided by the Iowa Academy of Science and the Department of Ecology, Evolution & Organismal Biology at Iowa State University (to J.M.R.) and NSF DEB-0640932 (to F.J.J.).

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