5

Cues for Reproduction in Squamate Reptiles

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5.1 INTRODUCTION

To maximize fitness, animals should initiate reproduction based on information from suites of cues that communicate three variables critical to reproductive success: 1) environmental conduciveness for successful reproduction, and survival of offspring and (usually) parents; 2) physiological capability of parents to reproduce; and 3) likelihood of successful mating. Squamates vary widely in reproductive mode (egg-laying, or oviparity vs. live birth, or viviparity), reproductive frequency (including reproducing only once, i.e., semelparity), and output (Tinkle *et al*. 1970; Dunham *et al*. 1988), all of which may alter the phenology of gametogenesis and embryonic development relative to season, physiological state (i.e., body condition), courtship, and mating. These phenomenological differences necessitate divergent reproductive decision-making approaches that may be informed by different suites of cues. In addition, specific components of reproduction, including gametogenesis and mating behavior, may not be stimulated by the same environmental or physiological cues.

The purpose of this review is to discuss the current state of knowledge of the mechanisms squamates use as cues for the decision to reproduce. Here, the decision to reproduce is defined as analogous to a life-history allocation decision (e.g., Dunham *et al*. 1989), rather than as a result of conscious thought processes. The endocrine connections of the

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hypothalamic-pituitary-gonadal axis are briefly reviewed because they are critical to communicating information from reproductive cues to the brain, gonads, and accessory reproductive organs. Associated and dissociated reproduction are also briefly introduced because both strategies might have ramifications for the evolution of reproductive cues in squamates. The bulk of the review then focuses on cues that provide squamates with information regarding season and environmental conditions, resource availability, and the likelihood of mating. In cases where phenomena have been suggested to act as cues for reproduction, but few physiological explanations have been examined in squamates, relevant literature from mammals and birds is discussed in order to suggest possible avenues for future research. Throughout, a heuristic model of hypothetical signaling mechanisms that communicate detected cues to the hypothalamic-pituitary-gonadal axis (Figs. 5.1–5.4) is constructed to clearly identify hypothetical mechanisms linking reproductive cue detection to the hypothalamic-gonadal-pituitary axis. The review concludes with a discussion of how recent advances in
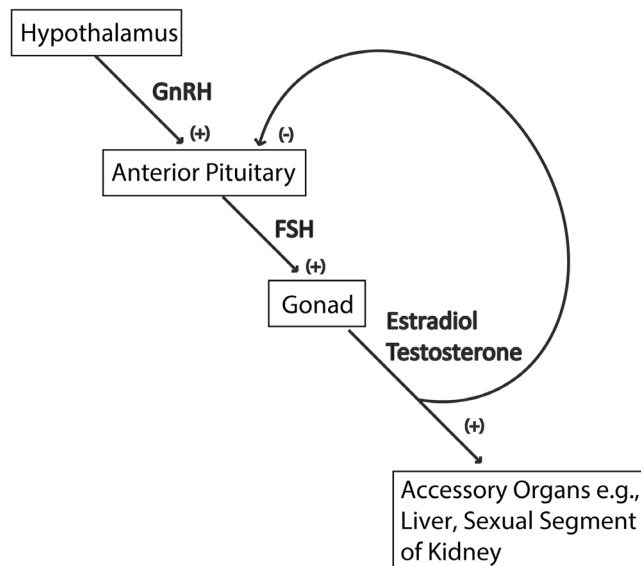

Fig. 5.1 Generalized structure of the vertebrate hypothalamic-pituitary-gonadal axis (HPGA). The HPGA forms the backbone of a heuristic model of the signaling mechanisms that communicate reproductive cues to the brain and result in reproductive decisions. Organs are represented by black boxes, while hormones are blue. Addition signs (+) indicate that a hormone stimulates upregulation of the receiving organ, while subtraction symbols (–) indicate that it stimulates downregulation of the receiving organ. It remains unclear how the HPGA behaves differently in associated or dissociated breeders.

Color image of this figure appears in the color plate section at the end of the book.

next-generation sequencing, candidate-gene approaches, and proteomics might be used to further elucidate the molecular mechanisms underlying reproductive cues. Although this volume focuses on lizards, snakes are included in this review because they are highly specialized lizards (Vidal and Hedges 2005; Pyron *et al*. 2013), and because they have been a major model system for investigations of the effects of resource availability and mating on reproduction, and the roles of the pineal gland and melatonin, in squamates. Where possible, relevant information from tuatara, *Sphenodon punctatus* is also reviewed.

5.2 HYPOTHALAMIC-PITUITARY-GONADAL AXIS

As in other vertebrates, the hypothalamic-pituitary-gonadal axis (HPGA) communicates reproductive cues from the brain to the gonads and accessory reproductive organs in squamate reptiles (Fig. 5.1; Licht 1979; Bona-Gallo *et al*. 1980; Krohmer and Lutterschmidt 2011). Reproduction is initiated by production of gonadotropin-releasing hormones (GnRHs) by the hypothalamus (King and Millar 1980). Secretion of GnRHs is likely pulsatile (Licht and Porter 1987), but the only evidence for pulsatile release in reptiles is from turtles (Tsai and Licht 1993). Gonadotropin-releasing hormones stimulate the production of gonadotropins in the anterior pituitary, which are carried in blood plasma to the gonads (Eyeson 1971; Licht 1979). In response to stimulation by gonadotropins, gonads recruit gametes and synthesize the steroid sex hormones estradiol (in females) and testosterone (in males), which activate accessory reproductive organs (Hahn 1967; Courty and Dufaure 1979; Aldridge 1982; Ho *et al*. 1982).

Estradiol in particular acts to initiate production of yolk (vitellogenesis) in the liver of female squamates (Hahn 1967; Ho *et al*. 1982; Wallace 1985; Ho 1987), while in males of many species testosterone stimulates the hypertrophy of the sexual segment of the kidney and mating behavior, and likely plays a role in spermatogenesis (Prasad and Sanyal 1969; Weil and Aldridge 1981; Weil 1985; Aldridge *et al*. 1990; Aldridge *et al*. 2009; Aldridge *et al*. 2011). Both estradiol and testosterone may also inhibit gonadotropin secretion by the anterior pituitary (reviewed by Licht 1979), producing a negative-feedback loop once reproduction is initiated (Fig. 5.1).

Although the general structure of the HPGA described here is largely conserved across vertebrates, the endocrine components of the squamate HPGA are unique. Most notably, luteinizing hormone (LH), which is an important gonadotropin in many vertebrates, including turtles and crocodilians, does not exist in the squamate HPGA (Licht 1974; Licht *et al*. 1974; Licht and Crews 1975). Instead, follicle-stimulating hormone (FSH) appears to be the only functional gonadotropin in squamates (Licht and

Crews 1975; Licht 1979). Furthermore, the peptide structures of GnRH and FSH (and their receptors) differ across taxa (Licht 1983; Licht *et al*. 1984; Powell *et al*. 1986; Licht and Porter 1987; Borrelli *et al*. 2001). Thus, commercially-available hormone assays, which are designed to target mammal or chicken hormones, are unable to reliably measure titers of GnRH or FSH in squamates. In addition, injections of heterologous GnRH, LH, or FSH into squamates, although seemingly effective (e.g., Jones *et al*. 1973; Sinervo and Licht 1991), may not be reliable indicators of hormone function (Licht 1983). Prolactin may also play a role in the squamate HPGA, but studies examining the effects of prolactin on reproduction have produced contradictory results (reviewed by Mazzi and Vellano 1987). The HPGA of the tuatara, *Sphenodon punctatus* has not been thoroughly examined, but males and females appear to utilize testosterone and estradiol similarly to squamates and other vertebrates (Cree *et al*. 1991; Cree *et al*. 1992).

Difficulties in accurately measuring GnRH and gonadotropin secretion and function have constrained studies of reproductive cues in squamate reptiles. Perhaps as a result, studies of GnRH, gonadotropins, other potential hormonal regulating systems (e.g., inhibins; Licht and Porter 1987), and reproductive cues in squamates have declined in frequency since the early 1990s. In contrast to GnRH and FSH, steroid hormone structures are largely conserved across taxa, and assays targeting mammalian or chicken estradiol, testosterone, and progesterone have been widely used in studies of squamate reproduction (e.g., Naulleau *et al*. 1987; Naulleau and Fleury 1990; Saint Girons *et al*. 1993; Swain and Jones 1994; Schuett *et al*. 1997; Edwards and Jones 2001; Martinez-Torres *et al*. 2003; Zaidan *et al*. 2003; Almeida-Santos *et al*. 2004; Taylor *et al*. 2004; Yamanouye *et al*. 2004; Lind *et al*. 2010; Van Dyke *et al*. 2012).

Elucidating the endocrine components of the HPGA is of paramount importance to understanding the cues for reproduction in squamates. Without this knowledge, we can only determine that a particular event is a cue for reproduction and how it is detected, but we cannot effectively determine how detection of the event is transduced into a reproductive response. We also cannot determine how multiple cues (e.g., temperature, resource availability) are simultaneously transduced in the brain and/or HPGA.

5.3 ASSOCIATED VS. DISSOCIATED REPRODUCTION

Squamate reptiles exhibit remarkable diversity in the timing of gonadal recrudescence, gametogenesis, and mating. In associated reproduction, gonadal recrudescence and gametogenesis occur simultaneously with mating (modified from Crews 1984; Crews 1999; Aldridge *et al*. 2009). In

dissociated reproduction, gametogenesis occurs months prior to mating behavior, and gametes are stored until use (modified from Crews 1984; Crews 1999; Aldridge *et al*. 2009). For the purposes of this review, this distinction is critical because mating and gametogenesis are likely stimulated by the same cues and HPGA hormonal cascade in associated breeders, but may be stimulated by different cues in dissociated breeders. Krohmer and Lutterschmidt (2011) suggest that dissociated reproduction occurs in male snakes when the HPGA stimulates a peak of plasma testosterone concentrations during gametogenesis, and metabolic clearance slowly declines until the mating season. In contrast, gametogenesis and mating may occur at such distant points in time (e.g., late summer vs. the following spring, respectively) that they could even be stimulated by different HPGA hormonal cascades, but this hypothesis has never been tested due to the difficulties of measuring cycles in GnRH and gonadotropin concentrations, and corresponding receptor densities, in reptiles. However, other studies have documented two peaks in plasma testosterone concentration in male snakes with dissociated reproduction, one during spermatogenesis and one during the mating season (Aldridge 1979b; Weil and Aldridge 1981; Aldridge *et al*. 1990). Interestingly, the peak during the mating season is often higher than during spermatogenesis. Weil (1985) suggests that, during spermatogenesis, testicular production of testosterone might not be reflected by plasma concentrations due to capture and metabolic clearance within testicular tissues prior to transport to the bloodstream.

Although many studies consider associated and dissociated reproduction only in males (e.g., Krohmer and Lutterschmidt 2011), I follow Crews (1984) in applying the terms to both males and females. Under this definition, one sex within a species may exhibit associated reproduction, while the other exhibits dissociated reproduction. For example, most male North American colubrids undergo spermatogenesis in the summer, but mate during the following spring (reviewed in Aldridge *et al*. 2009), which is an example of dissociated reproduction. In contrast, all female North American colubrids examined thus far initiate vitellogenesis in the spring, and also mate during the same spring (reviewed in Aldridge *et al*. 2009), which exemplifies associated reproduction. Reproduction in the sympatric North American pit vipers differs greatly from the colubrid condition. Like colubrids, male North American pit vipers all undergo spermatogenesis in the summer, but males of different species mate in the late summer/early autumn immediately after spermatogenesis (associated reproduction), store sperm to mate in the spring long after spermatogenesis (dissociated reproduction), or both (Aldridge and Duvall 2002). In contrast, all female North American pit vipers examined thus far initiate vitellogenesis in the late summer/early autumn, but do not complete vitellogenesis and ovulate until spring (Aldridge and Duvall 2002). Thus, because vitellogenesis may

last from summer to the following spring and mating occurs during either or both seasons, all female North American pit vipers exhibit associated reproduction, regardless of when mating occurs. However, in females that mate in the spring, it is likely that mating behavior and gametogenesis are stimulated by different cues, even though they technically exhibit associated reproduction. While both sexes of most lizards are associated breeders (Aldridge *et al.* 2011), some temperate lizards, including Australian spotted skinks, *Niveoscincus ocellatus* (Jones *et al.* 1997) and tussock skinks, *Pseudemoia entrecasteauxii* (Murphy *et al.* 2006), exhibit a reproductive cycle similar to that of North American pit vipers. The tuatara, *Sphenodon punctatus*, exhibits a unique reproductive cycle: males initiate spermatogenesis just prior to or concurrent with autumn mating, while females initiate vitellogenesis up to three years prior to a given reproductive event (Cree *et al.* 1992; Brown *et al.* 1994). Thus, males appear to be associated breeders, while females are dissociated breeders, but exhibit a reproductive schedule vastly different from dissociated breeding in squamates.

Associated and dissociated reproduction are more thoroughly discussed elsewhere in the primary literature (Crews 1984; Crews 1999; Aldridge and Duvall 2002; Aldridge *et al.* 2009). They are mentioned here to illustrate that cues for reproduction may differ within and among even closely related or sympatric squamate taxa, and may also differ between gametogenesis and mating behavior. In the pit viper example above, the cues for spermatogenesis and vitellogenesis may also stimulate mating behavior in populations that mate in autumn, but gametogenesis and mating behavior may be stimulated by different cues in populations that mate in spring. Similarly, if males of a species initiate spermatogenesis in autumn but females initiate vitellogenesis in spring, then the cues for gonadal recrudescence and gametogenesis, or the physiological processes that detect and transduce those cues, may differ between sexes.

5.4 SEASONAL CUES: PHOTOPERIOD, TEMPERATURE, AND MOISTURE

Reproduction must be coordinated with suitable environmental conditions to maximize developmental success, parental survival, and offspring survival. In squamates, developmental success is directly related to temperature and, especially in oviparous (egg-laying) species, moisture (Packard *et al.* 1982; Gutzke and Packard 1987; Andrews *et al.* 2000; Rock *et al.* 2000; Ji and Du 2001). In temperate and tropical systems, temperature and/or moisture vary seasonally throughout the year. Therefore, squamates can only maximize reproductive success if reproduction is initiated based on cues that provide information on time of year (i.e., season). Seasonal

changes in temperature and rainfall provide direct cues regarding environmental conditions favorable to reproduction, while photoperiod provides an indirect metric of season, and should be correlated, at least partially, with seasonal changes in temperature and moisture. Accordingly, squamates appear to use all three factors as seasonal cues for reproduction (e.g., zeitgebers; Tinkle and Irwin 1965; Licht and Porter 1987; Brown and Shine 2006). Within species, inter-individual variation in the sensitivity of season detecting mechanisms may also play a role in determining how early reproduction occurs (Wapstra *et al*. 1999), which may be critical to maximizing offspring fitness (Olsson and Shine 1997).

5.4.1 Phenology of Seasonal Cues: Temperate vs. Tropical Taxa

In temperate squamates, seasonal changes in environmental temperature are the primary seasonal cue for initiating reproduction, while seasonal changes in photoperiod appear to be a secondary cue (Saint Girons 1982). Most temperate squamates (but not all; Moore *et al*. 1984) appear to require a period of exposure to cold environmental temperatures during winter, followed by warm temperatures in the spring or summer to initiate gonadal recrudescence, reproductive behavior, or both (Marion 1970; Licht 1972; Botte *et al*. 1978; Marion 1982; Crews 1983; Lutterschmidt 2012). Spermatogenesis in particular appears to be stimulated by warm temperatures in North American colubrids and rattlesnakes, while photoperiod has little effect (Aldridge 1975; Aldridge 1979b; Weil and Aldridge 1979). In captivity, many temperate squamate species only breed after winter exposure to cold temperatures followed by spring warming (Osborne 1982). Delays in seasonal spring warming during spring may delay the initiation of reproduction (e.g., Castilla *et al*. 1992; Smith *et al*. 1995). The seasonal cues for reproduction remain unknown in *Sphenodon*, but males initiate spermatogenesis in late summer/autumn. Females initiate vitellogenesis in the spring following oviposition, yet vitellogenesis may last three years until ovulation occurs, and mating occurs in autumn (Brown *et al*. 1991; Cree *et al*. 1992).

Temperate species that do not require exposure to cold temperatures still exhibit greater reproductive responses to seasonal changes in temperature than to changes in photoperiod. These species exhibit "refractory periods" after reproduction during which changes in neither photoperiod nor temperature stimulate gonadal recrudescence. After the refractory period ends, only increases in temperature, and not day length, can stimulate reproduction (Tinkle and Irwin 1965; Licht *et al*. 1969; Cuellar and Cuellar 1977; Lofts 1978; Cuellar 1984). The animals used in most of these studies (excluding male *Naja naja* in Lofts 1978) were female lizards from species

(*Aspidoscelis uniparens*, *Lacerta* sp., and *Uta stansburiana*) that produce multiple clutches each year. Multi-clutching species do not experience cold temperatures between clutches in a single season, and refractory periods may be necessary to allow females to "recover" in some physiological condition, possibly stored nutrient reserves, prior to subsequent reproductive bouts. Thus, the evolution of post-reproductive refractory periods may be partly associated with the evolution of repeated reproduction in a single season.

Tropical squamates exhibit considerable diversity in the seasonality of reproduction, but relatively few species reproduce continuously throughout the year (reviewed by Brown and Shine 2006). Although tropical squamates do not experience substantial cool periods during winter, slight decreases in temperature, in concert with reduced day length, are sufficient to stimulate reproduction in some species (e.g., tropical anoles; Gorman and Licht 1974). Tropical tropidurine lizards, while potentially capable of reproducing throughout the year, exhibit a peak of reproduction during the wet season (Vitt and Goldberg 1983). In the tropical spiny lizard, *Sceloporus utiformis*, testicular recrudescence is associated with increasing temperature and precipitation, while ovarian recrudescence is associated only with increasing photoperiod (Ramirez-Bautista and Gutierrez-Mayen 2003). In tropical Australian Skinks (*Ctenotus* sp.), reproduction is highly correlated with rainfall (James 1991). Tropical Australian water pythons, *Liasis fuscus*, nest late in the dry season thus maximizing incubation temperatures during development, and coil around their eggs to prevent desiccation, while the sympatric keelback, *Tropidonophis mairii*, nests immediately after the end of the wet season, possibly to reduce egg desiccation (Brown and Shine 2006). In contrast, tropical populations of several Australian skinks (*Carlia pectoralis*, *Cryptoblepharus virgatus*, *Heteronotia binoei*, and *Lampropholis delicata*) do not appear to entrain reproduction with seasonal changes in temperature, photoperiod, or rainfall, and may rely on different environmental factors, such as solar light spectrum (Clerke and Alford 1993). Likewise, monitor lizards (*Varanus* sp.) in the Australian wet tropics exhibit considerable diversity in timing of reproduction relative to wet and dry seasons (James *et al*. 1992). In the absence of natural cues, common boas, *Boa constrictor*, can be induced to reproduce in captivity via reductions in day length, temperature, and feeding for several weeks (De Vosjoli *et al*. 2005). Notably, few of these studies directly investigate the cues that stimulate gonadal recrudescence or reproductive behavior in tropical squamates, but only report when reproductive events occur relative to seasonal environmental conditions. Together, these studies illustrate the potential diversity of seasonal environmental cues that temperate and tropical squamates can use to initiate reproduction. Further study is necessary to determine how environmental cue-detection mechanisms co-evolve with different reproductive cycles in both tropical and temperate ecosystems.

5.4.2 Physiology of Seasonal Cue Detection and Transduction

Reproductive cues derived from photoperiod are transduced by the parietal-pineal complex in squamates and in *Sphenodon* (Fig. 5.2; Firth *et al*. 1989; Underwood 1989; Tosini *et al*. 2001). In many lizards the parietal eye, which is dense in photoreceptors (reviewed by Tosini 1997), appears to be the
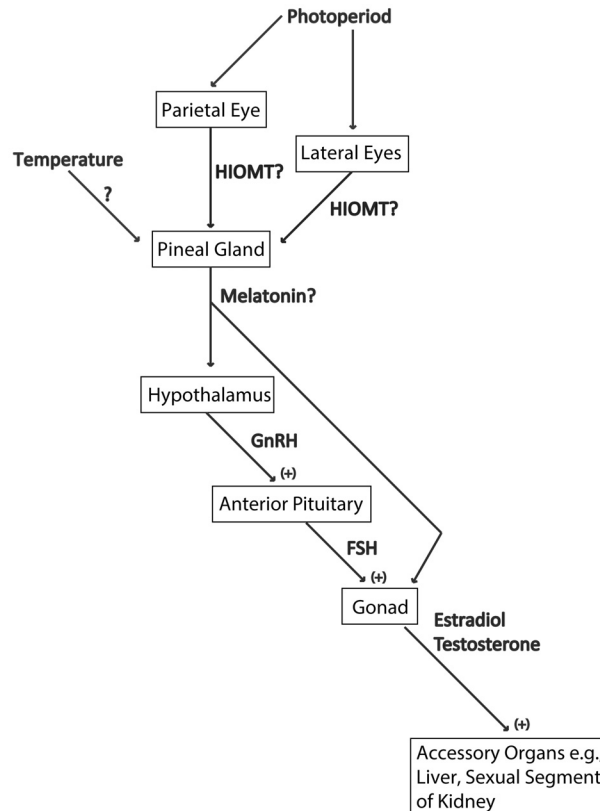

Fig. 5.2 Hypothetical mechanisms squamates might use to detect environmental conduciveness for reproduction are added to the generalized HPGA. Question marks indicate that detection or signaling mechanisms are unknown (temperature), are hypothetical (HIOMT), or are not fully understood (melatonin). Temperature is likely to be more important than photoperiod in stimulating reproduction, but the mechanisms for detecting and communicating temperature to the pineal gland are unknown. HIOMT represents hydroxyindole-O-methyltransferase, but serotonin or norepinephrine could also act as signaling factors between both the parietal and lateral eyes, and the pineal gland. The pineal also directly innervates the pretectal and tegmental areas of the brain, which could provide a mechanism for neuronal signaling to the HPGA. The estradiol/testosterone negative feedback loop to the anterior pituitary is removed for clarity. Organs are represented by black boxes, hormones are blue, and cues are green.

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primary detector of photoperiod. For example, circadian melatonin cycles are eliminated after parietalectomy in shingleback skinks, *Tiliqua rugosa* (Firth and Kennaway 1980). In contrast, snakes and geckos have secondarily lost the parietal eye (Quay 1979). Perception of day length may primarily occur in the lateral eyes in these taxa, but it is notable that even blinding does not prevent circadian entrainment in geckos (Underwood and Groos 1982); similar studies have not been performed on snakes.

Regardless of whether photoperiod is detected by the lateral eyes, parietal eye, or both (Tosini *et al*. 2001), perception of day length is communicated to the body via secretion of melatonin by the pineal organ (Underwood 1989; Mendonça *et al*. 1995; Mendonça *et al*. 1996b). The pineal organ also directly innervates the pretectal and tegmental areas of the brain (Tosini 1997), which may allow direct neuronal communication between the pineal gland and the HPGA. How light cues from the parietal eye and lateral eyes are communicated to the pineal gland is not well understood, but could occur via secretion of serotonin, norepinephrine, or hydroxyindole-O-methyltransferase (HIOMT; Tosini 1997).

The pineal organ is also responsible for transducing seasonal information from body temperature. It is not known whether the pineal organ itself detects body temperature, or only transduces thermal signals from other detecting mechanisms (Underwood 1989). Regardless, the pineal organ appears to be responsible for simultaneously transducing seasonal information based on both photoperiod and body temperature via secretion of melatonin. Daily melatonin secretions in squamates cycle between maxima synchronized by cool temperatures during scotophase, and minima synchronized by warm temperatures during photophase (Firth *et al*. 1979; Underwood and Calaban 1987; Firth *et al*. 1989; Tilden and Hutchinson 1993). Together, seasonal increases in day length and temperature are accompanied by overall diel decreases in plasma melatonin concentration, and vice-versa (Firth *et al*. 1979; Mendonça *et al*. 1995). Interestingly, photic suppression of melatonin secretion during long photoperiods is less pronounced in *Anolis* lizards than in other vertebrates (Moore and Menaker 2011). It remains unclear whether circadian cycles in circulating melatonin in *Sphenodon* are entrained primarily by temperature or photoperiod, but the presence of a well-developed parietal eye and thermal effects on melatonin secretion suggest both mechanisms are possible (Dendy 1911; Firth *et al*. 1989). After secretion, circulating melatonin is bound by receptors throughout the brain (Wiechmann and Wirsig-Wiechmann 1994), and possibly in the gonads (Mayer *et al*. 1997). In mammals, high-affinity melatonin receptors in the hypothalamus may play a role in activating the HPGA (Reppert *et al*. 1994), but the existence of melatonin receptors in the squamate hypothalamus has not been tested.

High serum melatonin concentrations generally suppress reproduction in male squamates. Pinealectomy, which eliminates most melatonin secretion, induces testicular recrudescence in male green anoles, *Anolis carolinensis*, in autumn, but not in summer (Underwood 1981). Injected melatonin does not inhibit testicular recrudescence in pinealectomized males, but does so in intact males (Underwood 1981). Similarly, summer injections of melatonin in male oriental garden lizards, *Calotes versicolor*, inhibit testicular recrudescence (Haldar and Thapliyal 1981), while pinealectomy induces testicular recrudescence during both summer and winter (Thapliyal and Haldar 1979). Fall pinealectomy inhibits spring reproductive behavior in male *Thamnophis sirtalis* (Mendonça *et al.* 1996b), while spring pinealectomy does not (Mendonça *et al.* 1996a). This suggests that pineal transduction of thermal and photoperiod cues for reproduction occurs during or prior to hibernation in male *Thamnophis sirtalis* (Mendonça *et al.* 1996a). Seasonal differences in the effect of pinealectomy and melatonin injection may indicate physiological mechanisms that explain refractory periods, or why exposure to cold temperatures during winter is critical to successful reproduction in many temperate squamates.

Studies of melatonin effects on reproduction in female squamates have been less frequent. Pinealectomy induces ovarian recrudescence in female *Anolis carolinensis*, while subsequent melatonin injections inhibit it outside of the reproductive season; however, the effects of pinealectomy decrease during the reproductive season (Levey 1973). Parietalectomy accelerates gonadal recrudescence in female *Sceloporus* lizards, but not males, indicating that the role of the parietal eye (and presumably, the pineal gland and melatonin) in regulating reproduction might differ between sexes (Stebbins and Cohen 1973).

The mechanisms squamates use to detect seasonal changes in moisture or rainfall remain unknown. Rainfall and soil moisture levels may not act as cues for the initiation of gametogenesis, but may act as cues for specific reproductive behaviors, especially oviposition (Stamps 1976; Brown and Shine 2006). In captive reptiles, availability of moist nesting environments is critical to successful oviposition, and, in dry conditions, females may retain eggs for so long that they develop dystocia (e.g., egg binding; DeNardo 2006). Nest moisture is especially important for successful development in many oviparous squamates because many taxa produce leathery eggshells with relatively high water permeability (Packard *et al.* 1982). In contrast, female pythons, many of which actively incubate their eggs via encirclement with their bodies, can limit egg desiccation even in dry nest environments (Lourdais *et al.* 2007).

Reproduction might also be correlated with rainfall if increased rainfall is associated with increased food abundance, which could maximize resources available for reproduction, or could maximize offspring growth

and survival rates (but there is limited evidence for this pattern in squamates; James and Shine 1985; Brown and Shine 2006; Shine and Brown 2008). Therefore, food availability, rather than rainfall *per se*, might be the primary cue for reproduction (Wikelski *et al*. 2000). If food availability is limiting to offspring survival after reproduction, females might over-allocate nutrients to yolk in order to provide offspring with energy reserves to sustain them until they can successfully forage (e.g., residual yolk; Troyer 1983; Van Dyke *et al*. 2011).

Most studies of reproductive cues and phenology in response to environmental conditions have been conducted on iteroparous squamates with no embryonic diapause. Environmental cues for reproduction might vary among squamate taxa depending on whether they are semelparous (reproduce only once in their lifetime) or iteroparous (reproduce multiple times throughout life), produce single or multiple litters/clutches per year, or exhibit embryonic diapause. Indeed, the selection pressure to tightly coordinate reproduction with suitable environmental conditions should be strongest in semelparous and single-litter/clutch species because the risks of total reproductive failure are higher than in iteroparous and multi-clutching species.

Species that exhibit embryonic diapause (e.g., Chameleons; Andrews 2004) might be able to reproduce in spite of poor environmental conditions. In chameleons, embryonic diapause may also allow delayed hatching until seasonal environmental conditions maximize offspring survival (Andrews and Donoghue 2004). In addition, some viviparous lizards that inhabit cold climates, including the Australian southern snow skink, *Niveoscincus microlepidotus*, and the New Zealand common gecko, *Hoplodactylus maculatus*, carry fully-developed offspring over winter and give birth in the following spring (Olsson and Shine 1999; Girling *et al*. 2002; Rock 2006). In these taxa, delaying birth via embryonic diapause has been suggested to maximize potential offspring foraging and growth during the summer prior to the subsequent winter (Olsson and Shine 1998). Thus, embryonic diapause might allow the dissociation of environmental constraints on offspring survival from parents' decisions to reproduce. Taken together, the diversity of reproductive strategies exhibited among squamates could promote the utilization of different environmental cues for reproduction, and phylogenetic analyses are needed to understand how divergent mechanisms of cue detection and transduction have evolved as a response.

5.5 RESOURCE AVAILABILITY CUES: INCOME AND CAPITAL

Reproduction requires a significant investment of energy and nutrients. Gametes, especially eggs, are rich in energy and nutrients and expensive to produce (Olsson *et al*. 1997; Van Dyke and Beaupre 2011), and females may

incur additional metabolic costs of gravidity or pregnancy (Birchard *et al*. 1984; DeMarco and Guillette 1992; Angilletta and Sears 2000; Robert and Thompson 2000; Schultz *et al*. 2008). In addition, reproductive behaviors, including mate-searching, courtship, mating, and nest brooding, may be energetically expensive (Harlow and Grigg 1984; Olsson *et al*. 1997; Friesen *et al*. 2009). As a result, the availability of resources, including both food and stored reserves, is an important constraint on reproduction, and detection of resource availability may function as a cue for the decision to reproduce.

5.5.1 Phenology of Resource Availability Cues

Individuals of many squamate species do not reproduce annually (Bull and Shine 1979), and multi-year gaps between reproductive events have been suggested to be the result of adults requiring multiple years to accumulate the resources necessary for reproduction (Hahn and Tinkle 1966; Aldridge 1979a; Slip and Shine 1988; Gloyd and Conant 1990; Brown 1991; Van Wyk 1991; Naulleau *et al*. 1999; Olsson and Shine 1999; Diller and Wallace 2002; Ernst and Ernst 2003; Ibargüengoytía 2004). Even within a given active season, low resource availability can delay the initiation of reproduction until sufficient resources are accumulated (Vitt *et al*. 1978; Bauwens and Verheyen 1985; Abell 1999), which may reduce offspring fitness (Olsson and Shine 1997). The capital-income dichotomy predicts that animals base the decision to reproduce on either the magnitude of stored reserves (capital) or the rate of nutrient assimilation from diet (income; Drent and Daan 1980). In squamates, this prediction has been frequently tested in studies that compare body condition indices between reproductive and non-reproductive individuals in tropical spiny lizards, *Sceloporus mucronatus* (de la Cruz *et al*. 1988), viviparous lizards, *Zootaca vivipara* (Bleu *et al*. 2013), smooth snakes, *Coronella austriaca* (Reading 2004), garter snakes, *Thamnophis sirtalis* (Gregory 2006), and Aspic vipers, *Vipera aspis* (Naulleau and Bonnet 1996; Aubret *et al*. 2002). Other studies have correlated body condition indices with total reproductive output in collared lizards, *Crotaphytus collaris* (Telemeco and Baird 2011), and water skinks, *Eulamprus tympanum* (Doughty and Shine 1998). In these comparisons, body condition is usually (but not always; Doughty and Shine 1997) defined either as the ratio of body mass to body length, or via a regression of body mass and body length. Regardless, reproductive individuals often exhibit higher body conditions than do non-reproductive individuals, which is frequently interpreted as evidence for body-condition thresholds for reproduction (e.g., capital breeding; Bonnet *et al*. 1998).

Unfortunately, most studies of the effects of body condition on reproduction in squamates are correlative, and do not directly distinguish

between contributions made by fat mass and muscle mass to total body condition. Whereas fat mass is often described as the primary cause of fluctuations in body condition (e.g., Bonnet *et al*. 1998; Aubret *et al*. 2002), changes in muscle mass may also drive fluctuations in body condition (Lourdais *et al*. 2004). In addition, other studies report that reproductive allocation decisions, particularly clutch or litter size, are at least partially dependent upon food availability during reproduction (income) rather than capital, in marine iguanas, *Amblyrhynchus cristatus* (Rubenstein and Wikelski 2003), Asian northern grass lizards, *Takydromus septentrionalis* (Du 2006), swamp snakes, *Seminatrix pygaea* (Winne *et al*. 2006), and Aesculapian snakes, *Zamensis longissimus* (Naulleau and Bonnet 1995), as well as in so-called capital breeders like *Vipera aspis* (Madsen and Shine 1999; Bonnet *et al*. 2001). In *Sphenodon*, gravidity rates do not differ across populations in correlation with population differences in body condition (Tyrrell *et al*. 2000), so magnitude of capital may not be a cue for reproduction. Notably, most studies of capital and income effects on reproduction in squamates have focused on females, and male reproductive decisions may be made using different cues (Aubret *et al*. 2002).

5.5.2 Physiology of Resource Availability Detection and Transduction

The possibility that reproductive decisions depend on magnitude of capital or rate of income assimilation raises the implicit hypothesis that squamates have physiological mechanisms for detecting the magnitude of their stored reserves (capital) of lipid, protein, total energy, and/or specific limiting nutrients, or the rate of assimilation (income) of at least one of those resources. To date, few experiments have tested this hypothesis, but ghrelin (Unniappan 2010) and leptin (Niewiarowski *et al*. 2000), or similar hormones, might play roles in communicating income and capital resource abundance to the brain. As a regulator of serum glucose, insulin might also play a role in communicating nutritional status to the brain, but insulin has not been investigated in reptiles aside from structural comparisons with other taxa (Conlon and Hicks 1990). In addition, it is not clear how the HPGA functions when opportunities for reproduction are skipped. Females of some species (e.g., *Vipera aspis*) appear to skip opportunities for reproduction by not initiating vitellogenesis at all (Aubret *et al*. 2002), which suggests that hormonal cascades in the HPGA either do not occur or are arrested prior to reaching the ovary. Females of other species (e.g., *Nerodia sipedon* and *Tantilla coronata*) appear to initiate vitellogenesis, presumably via activation of the HPGA, but do not ovulate and instead undergo follicular atresia (Aldridge 1982; Aldridge and Semlitsch 1992). It is not clear whether atresia occurs

because available resources become limiting after vitellogenesis is initiated. Other factors, such as courtship or mating, could play a role in ensuring that vitellogenesis is completed (discussed in the next section).

In mammals, ghrelin is a multifunctional peptide hormone that is primarily secreted by the stomach in response to stomach emptying and filling (Murakami *et al.* 2002). Ghrelin regulates appetite across vertebrate taxa, but is also linked to gonadotropin production in fish (Kaiya *et al.* 2008). Ghrelin has been identified in the slider turtle, *Trachemys scripta*, in which it shares most of its tertiary structure with other vertebrates (Kaiya *et al.* 2004). Ghrelin has not been identified in squamates and its functions in reptiles remain untested. Regardless, the role of ghrelin in regulating appetite, as well as its secretion in response to changes in stomach filling, suggests that it could communicate the rate of income (i.e., food) acquisition in squamate reptiles. If squamate ghrelin also stimulates gonadotropin production, as in fish, then ghrelin might be an important mechanistic link between the rate of food acquisition and the decision to reproduce. Stomach fullness and ghrelin secretion may therefore be a physiological mechanism by which food availability acts as a cue for reproduction in some squamate taxa. The apparent conservation of the tertiary structure of ghrelin across vertebrate taxa also suggests that the role that ghrelin plays in reproduction could be easily tested using standard immunoassays.

In mammals, leptin is a peptide hormone secreted by adipose tissue in proportion to adipose tissue mass (Havel 2000). In the Italian wall lizard, *Podarcis sicula*, serum leptin concentrations are highest in spring immediately prior to vitellogenesis, when adipose tissue mass is greatest, and fall as adipose tissue mass decreases during vitellogenesis (Paolucci *et al.* 2001). Serum leptin concentrations are also usually correlated with adipose tissue mass in the fence lizard, *Sceloporus undulatus,* but are notably lowest in autumn, when adipose tissue mass is greatest (Spanovich *et al.* 2006).

In mammals, serum leptin concentrations are directly correlated with the release of GnRH, gonadotropin, and estradiol (Caprio *et al.* 2001), and maternal allocations to offspring increase with increasing serum leptin (French *et al.* 2009). In addition, birds can be induced to lay additional clutches as a result of artificially increased serum leptin concentrations (Lõhmus and Björklund 2009). Thus, leptin may be a mechanism for communicating adipose tissue mass (i.e., fat/capital storage) to the brain, and may allow fat mass to serve as a cue for reproduction in apparent capital breeders, but this hypothesis has not been tested in squamates. Importantly, the temporal disconnect between adipose tissue mass and serum leptin concentration that occurs in autumn in *Scleropus undulatus* (and in some mammals; Kronfeld-Schor *et al.* 2000), if conserved across taxa, would compromise studies of direct relationships between leptin and reproduction in species that initiate reproduction in autumn. In bats, leptin

production declines in autumn, regardless of fat mass, to maximize pre-hibernatory fattening (Kronfeld-Schor *et al*. 2000), and could follow a similar trend in temperate squamates. Thus, in temperate squamates that initiate reproduction in the autumn, any "signal" for reproduction transduced from fat mass could be received by the brain prior to the autumn down-regulation of leptin production. Alternatively, reception or interpretation of the leptin "signal" in the brain could be modified by transduction of photoperiod or temperature. Indeed, leptin sensitivity, presumably modulated by receptor density in target tissue, is regulated by photoperiod in both hamsters and voles (Klingenspor *et al*. 2000; Krol *et al*. 2006). If similar mechanisms occur in squamate reptiles, then leptin might not promote reproduction on its own. Instead, reproduction might be promoted by a decrease in serum leptin simultaneous with increased melatonin production. Possible interactions between cues for time-of-year and resource availability illustrate that reproduction is promoted by multifaceted regulatory systems (Fig. 5.3), possibly tuned by natural selection to initiate reproduction only when multiple cues indicate that reproductive success is likely to be maximized.

As noted in the prior section, even when reproduction is initiated, female squamates appear to adjust clutch and litter sizes depending on resource availability. Clutch/litter size may be determined at two points during the reproductive cycle: first, females recruit a given number of ovarian follicles for primary vitellogenesis at the start of a reproductive cycle; secondly, females selectively allocate yolk to, and ovulate, a fraction of the "committed" follicles, while the rest undergo atresia (Aldridge 1982; Aldridge and Semlitsch 1992). Selective atresia of follicles, in particular, appears to be widespread in squamate reptiles (Shine 1977; Jones *et al*. 1978; Trauth 1978; Etches and Petitte 1990; Mendez-De La Cruz *et al*. 1993).

Whether clutch/litter size is ultimately determined at the initiation of vitellogenesis or by selective ovulation/atresia remains unknown, but exogenous FSH has been shown to increase clutch size in several species (Sinervo and Licht 1991; Jones and Swain 2000). The correlations between body condition (or fat body mass) and clutch/size, along with the observation that artificial increases in FSH stimulate increases in clutch size, suggest that hormones that signal resource abundance to the brain, if they exist, act in a dose-dependent manner. This could provide a mechanism for females to adjust clutch/litter size to abundance based on resource availability. Selection could be expected to act strongly on this ability, because overcommitting resources to reproduction could lead to starvation prior to parturition, while undercommitting could prevent females from realizing their actual reproductive value (e.g., Fisher 1930; Lack 1954).
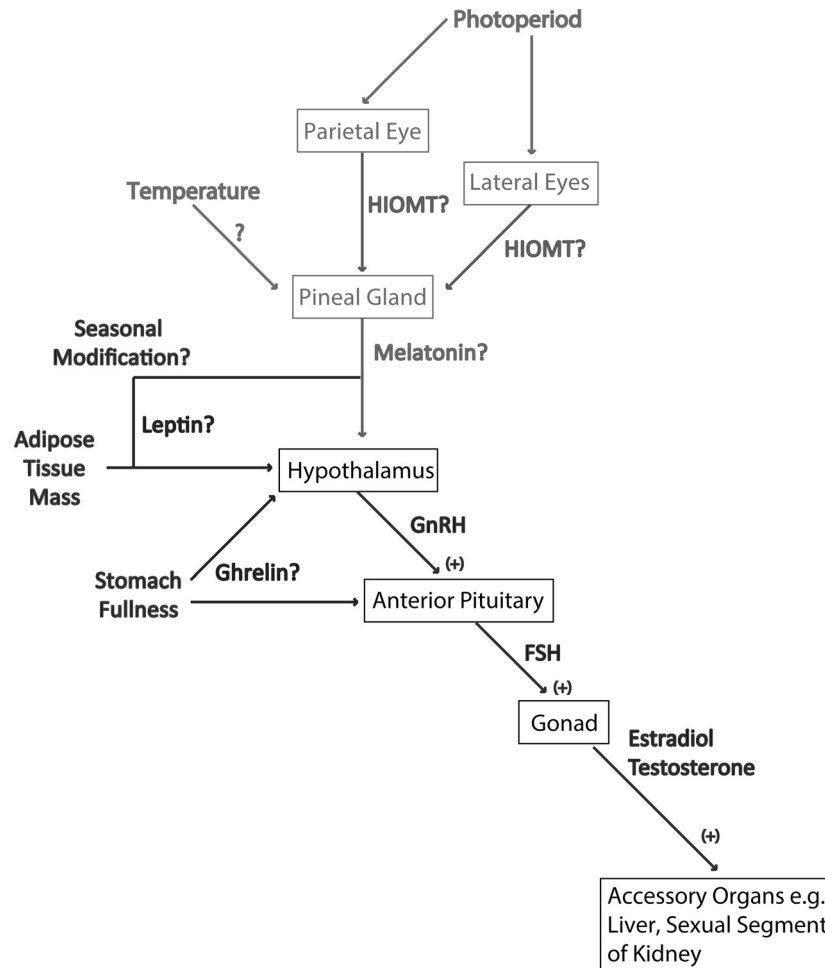
Fig. 5.3 Mechanisms squamates might use to detect resource availability are added to the generalized HPGA. Question marks indicate that leptin and ghrelin signaling mechanisms are hypothetical indicators of resource availability to the HPGA, and that melatonin may seasonally modify the action of leptin. Organs are represented by black boxes, hormones are blue, and cues are green. Mechanisms of detecting environmental conduciveness, introduced in Fig. 2, are obscured to enhance clarity yet emphasize that multiple detection systems might interact to inform the decision to reproduce. The pathway linking melatonin directly to the gonad has been removed for clarity.

Color image of this figure appears in the color plate section at the end of the book.

5.6 SOCIAL CUES: MATING AND COURTSHIP

Cues that communicate likelihood of successful mating are likely to be important in the decision to reproduce in species that experience high fitness and/or energy costs of reproduction. Cues communicating likelihood of successful mating may be especially important in females, who may incur both high energetic costs of gametogenesis and gestation (Robert and Thompson 2000; Schultz *et al*. 2008; Van Dyke and Beaupre 2011), and high fitness and energetic costs of transport while gravid or pregnant (Shine 1980; Webb and Lannoo 2004). As a result, females may be under strong selective pressure to avoid potential costs of reproduction unless mating and fertilization are likely.

5.6.1 Phenology of Mating and Courtship Cues

Induced ovulation, in which mating physically or chemically stimulates ovulation in the female (Taymor 1978), is the most likely cue for communicating the likelihood of successful mating. Induced ovulation is widespread among eutherian mammals (Lariviere and Ferguson 2003), but among reptiles has only been reported in sea turtles (Manire *et al*. 2008). Although induced ovulation has not been reported in squamates, females of some species, especially *Thamnophis sirtalis*, appear to initiate ovarian recrudescence and/or vitellogenesis only after mating (Bona-Gallo and Licht 1983; Whittier and Crews 1986b; Mendonça and Crews 1990; Mathies *et al*. 2004). If the disparity between mating-induced ovulation and ovarian recrudescence represents a taxonomic difference between mammals and squamates, it could be because vitellogenesis is more energetically expensive than pregnancy or gravidity in squamates (Van Dyke and Beaupre 2011), while pregnancy and lactation are more energetically expensive than vitellogenesis in mammals (Gittleman and Thompson 1988). Thus, squamates may be more likely to avoid initiating vitellogenesis unless mating has occurred, whereas mammals are more likely to avoid ovulation unless mating has occurred. Long-term oviducal sperm storage is also common in squamates (Sever and Hamlett 2002), and allows females to store sperm from matings that occur prior to vitellogenesis.

In addition to mating, courtship and/or the presence of males alone may be sufficient to induce reproduction in females of some squamate species, possibly because it confers a reasonable expectation of successful mating. Captive female blood pythons, *Python curtus*, are more likely to initiate vitellogenesis when housed with males (DeNardo and Autumn 2001) and male courtship plays a role in environmentally-induced ovarian recrudescence during vitellogenesis in green anoles, *Anolis*

carolinensis (Crews 1975). Similarly, male courtship is linked to ovulation in sexual whiptail lizards (*Aspidoscelis* sp.; Crews *et al*. 1986). Interestingly, parthenogenetic whiptails like *Aspidoscelis uniparens* retain this response, and ovulation can be stimulated by courtship and pseudocopulation by male-like females (Moore *et al*. 1985; Crews *et al*. 1986).

Despite the preceding examples, mating and/or courtship may not be important cues for reproduction in all female squamates. Female viviparous lizards, *Zootoca vivipara*, ovulate eggs regardless of whether they have mated or experienced courtship, and may produce unfertilized eggs as a result (Bleu *et al*. 2011). Likewise, female leopard geckos, *Eublepharis macularius*, initiate vitellogenesis regardless of exposure to males (LaDage and Ferkin 2008). Female tuataras, *Sphenodon punctatus*, initiate vitellogenesis years prior to mating (Brown *et al*. 1991; Cree *et al*. 1992), but it is not clear whether mating affects the decision to ovulate. Furthermore, observed relationships between mating and/or courtship and vitellogenesis or ovulation in squamates are, with some exceptions (e.g., Mendonça and Crews 1990), largely correlative. In female *Thamnophis sirtalis*, both vitellogenesis and pheromone production are stimulated by elevated serum estradiol concentrations (Parker and Mason 2012). Therefore, vitellogenesis may not be stimulated by courtship; instead, vitellogenesis and attractiveness (and subsequent courtship) may be simultaneous consequences of females initiating reproduction as a result of courtship-independent cues.

5.6.2 Physiology of Mating and Courtship Cue Detection and Transduction

Nearly all studies of the physiology underlying the effects of mating and courtship on ovarian recrudescence and vitellogenesis in squamates have focused on *Thamnophis sirtalis*. Female *T. sirtalis* exhibit a pronounced surge in serum estradiol and prostaglandin (PG-F2α) in response to mating (Whittier *et al*. 1987; Mendonça and Crews 2001), which is probably the result of a neuroendocrine cascade initiated by physical stimulation of stretch receptors in the cloaca during intromission (Whittier and Crews 1986b). Spinal transection and injection of both lidocaine and tetracaine near the cloaca inhibit the mating-induced estradiol surge, but only tetracaine inhibits post-mating ovarian recrudescence in *T. sirtalis* (Mendonça and Crews 1990). Similar phenomena have been observed in cats, which induce ovulation after physical stimulation of the vagina during mating (Greulich 1934), as a result of direct neuronal communication with the brain (Rose 1978).

Mendonça and Crews (1990, 2001) suggested that tactile stimulation of the skin during both mating and courtship could also contribute to the

ovarian response to mating in *Thamnophis sirtalis*, but it is not clear whether estradiol or PG-F2α mediate this response. Many male squamates bite females during intromission (Stamps 1975; Carpenter 1977; Gillingham 1979; Pandav *et al*. 2007), and male boas and pythons are well-known for using their pelvic spurs to "stimulate" females during courtship (Gillingham and Chambers 1982). These tactile behaviors could provide alternative means of physical neuronal stimulation in addition to intromission. A relationship between tactile stimulation of the skin and ovarian recrudescence could also provide a mechanism for explaining why male presence and/or courtship alone can stimulate vitellogenesis and/or ovulation in other squamate taxa.

Most research on mating-induced ovarian recrudescence and ovulation in squamates has focused on physical stimulation during intromission, but other mechanisms have been investigated in mammals and could exist in squamates. Ovulation-inducing factors (OIF), which stimulate LH surges in females after mating, have been identified in the seminal fluid of camels (Adams *et al*. 2005), and similar mechanisms may also exist in rabbits, mice, pigs, and horses (Bogle *et al*. 2011; Silva *et al*. 2011). In pigs, seminal prostaglandins may play a role in ovulation induction (Ratto *et al*. 2011). In squamates, unmated female *Thamnophis sirtalis*, whose cloacae were smeared with male seminal fluid, exhibited reduced attractiveness to other males (Shine *et al*. 2000). Female attractiveness in snakes is primarily mediated by pheromone production, which is stimulated by estradiol (Parker and Mason 2012), so these data suggest that male seminal fluid might alter estradiol production in females that have mated. If that is the case, then the possibility remains that male seminal fluid contains factors that could also interact with female HPGA to initiate or regulate vitellogenesis, possibly in an interaction with physical stimuli during intromission and/or courtship (Fig. 5.4). Prostaglandins are abundant in snake seminal fluid (Whittier and Crews 1986a), and may be a useful candidate mechanism for investigating the possibility of chemical induction of vitellogenesis in female squamates (Friesen 2012). Finally, females of many species store sperm in oviducal crypts after mating (Sever and Hamlett 2002). These crypts could produce a neuronal or hormonal signal that notifies the brain and/or HPGA whether healthy sperm are present at the appropriate time for reproduction to be initiated.

5.7 FUTURE DIRECTIONS

Squamates are excellent model organisms for studying the function and evolution of reproductive cue-detecting mechanisms, but studies have been limited by difficulty in accurately measuring the secretion and function of peptide hormones, especially GnRH and gonadotropins. As a result, we still
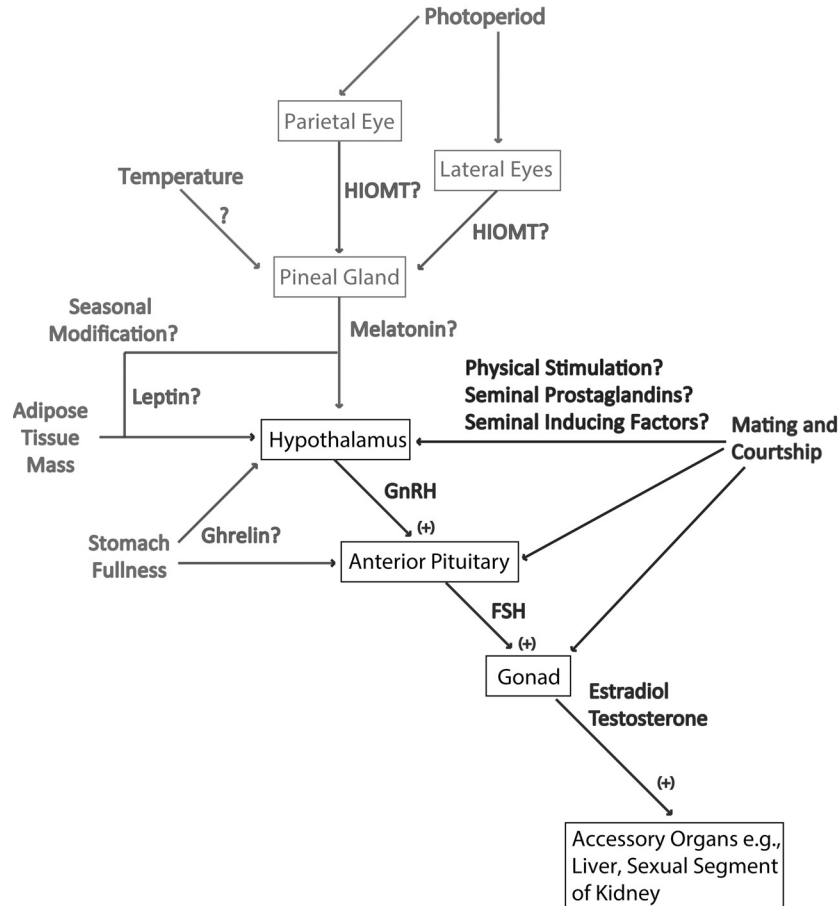
Fig. 5.4 Mechanisms female squamates might use to determine whether fertilization is likely are added to the generalized HPGA. Question marks indicate that all signaling mechanisms that might communicate mating and/or courtship to the HPGA are hypothetical. It is also unclear whether any of these hypothetical mechanisms act directly on the hypothalamus, anterior pituitary, or gonads. Organs are represented by black boxes, hormones and neural signaling are blue, and cues are green. Previously introduced cue detection mechanisms are obscured to enhance clarity yet emphasize that multiple detection systems might interact to inform the decision to reproduce.

Color image of this figure appears in the color plate section at the end of the book.

lack a comprehensive understanding of the phenomena squamates use as cues for reproduction, and how those cues are detected and communicated to the HPGA. Indeed, the mechanisms summarized in this review are largely untested in reptiles, and it is possible that alternative mechanisms remain to be discovered. The advent of low-cost next-generation transcriptome

sequencing (e.g., Mardis 2008; Ekblom and Galindo 2011; Brandley *et al*. 2012), along with the growing availability of genomes for non-model organisms, including squamates (Castoe *et al*. 2013; Vonk *et al*. 2013), is poised to significantly advance our ability to identify both hypothetical and novel hormonal pathways, as well as other molecular mechanisms involved in cue detection and transduction. In particular, a transcriptome sequencing approach examining total gene expression in the organs involved in both the HPGA and reproductive cue detection could determine 1) what hormones are involved in communication of reproductive cues to and within the HPGA; 2) where those hormones are produced; 3) what organs produce receptors for those hormones and might be important in transduction of reproductive cues; and 4) whether dissociated breeders initiate gametogenesis and mating using separate cues, or even separate HPGA hormonal cascades.

Both nucleotide and peptide sequences can be identified from transcriptome sequencing, thereby allowing researchers to design functional experiments using standard molecular methods, including both gene expression (e.g., quantitative PCR or *in situ* hybridization) and immunological approaches (e.g., western blot, immunohistochemistry) if suitable antibodies are readily available. Furthermore, the combination of transcriptome sequencing and proteomics allows simultaneous examination of gene expression and protein translation (e.g., Wong *et al*. 2012; Margres *et al*. 2014), which would be a powerful method for examining hormonal cascades throughout cue detection, stimulation of the HPGA, and upregulation of reproductive physiology. Similar approaches are already being used to study multiple aspects of the biology of non-model organisms, including the evolution of extreme digestive physiology, venom, and viviparity in squamates (Murphy and Thompson 2011; Brandley *et al*. 2012; Margres *et al*. 2014; Castoe *et al*. 2013), thus they represent powerful tools for an area of research that has been historically constrained by the limitations of traditional methods.

Elucidating how reproductive cue-detection mechanisms function in concert with diverse reproductive strategies and environmental conditions is a critical component to understanding how species respond to environmental change. Indeed, mismatches between reproductive cues and optimal reproductive conditions, caused by global climate change, have already been reported in migratory birds (Visser *et al*. 2004). As environmental temperatures have warmed, vegetation and insect production has advanced earlier in the year, while reproduction, which is cued by photoperiod in some birds, has not (Visser *et al*. 1998). The potential for similar mismatches in squamate reptiles is unclear because they potentially utilize multiple simultaneous cues for reproduction, including both photoperiod and temperature. Nevertheless, some squamate

species may be highly vulnerable to global climate change (Huey *et al*. 2010; Sinervo *et al*. 2010), and assessing the role of mismatches between reproductive cue detection and changes in environmental conditions is currently not possible in most taxa. As a result, integrated investigations of reproductive cue detection mechanisms, utilizing genomic, molecular, and ecological methods, may hold great promise for improving the conservation of these species. More broadly, these investigations are needed to advance understanding of how animals make reproductive decisions (e.g., when to reproduce, reproductive frequency, clutch size), which are critical components of life-history evolution.

5.8 ACKNOWLEDGMENTS

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