Reptilian Reproduction, Overview

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GLOSSARY

associated reproductive pattern A pattern of reproduction in which the secretion of gonadal sex steroid hormones, the production of gametes, and the display of sexual behavior occur synchronously. Species exhibiting this pattern of reproduction tend to be found in predictable environments with prolonged conditions beneficial to breeding.

constant reproductive pattern A pattern of reproduction in which the secretion of gonadal sex steroid hormones, the production of gametes, and the display of sexual behavior do not occur synchronously. Species exhibiting this pattern of reproduction tend to be found in unpredictable environments with brief periods suitable for breeding.

dissociated reproductive pattern A pattern of reproduction in which the secretion of gonadal sex steroid hormones, the production of gametes, and the display of sexual behavior do not occur synchronously. Species exhibiting this pattern of reproduction tend to be found in predictable environments with restricted breeding opportunities.

parthenogenesis Reproduction by cloning. This form of reproduction is found in some lizards and fish. Parthenogenetic vertebrate species consist entirely of females.

temperature-dependent sex determination A mechanism of sex determination found in many reptiles in which the temperature of the incubating egg during the midtrimester of embryogenesis establishes the gonadal sex of the individual.

Reptiles tend to be restricted to temperate and tropical regions and exhibit a seasonal pattern of reproduction in which birth of offspring occurs during restricted periods of the year. Perhaps most interesting is the variety of ways in which this pattern of reproduction is achieved among reptiles. For example, many species of snakes and freshwater turtles exhibit reproductive patterns in which cycles of gonadal activity and sexual behavior are dissociated and peak at different times of year.

I. COSTS OF REPRODUCTION

Reproduction is the single most costly event in an animal's life and hence patterns of reproduction have evolved to maximize an individual's contribution of genetic information to the next generation. Timing of reproduction in a population is determined by when the most offspring survive and when parents, most often females, are capable of energetically supporting the production of viable young at the least cost to themselves. Furthermore, timing of reproduction not only reflects current conditions but also is influenced by factors regulating the total lifetime production of offspring. Thus, the pattern of reproduction exhibited will be influenced by a variety of factors, including generation time, age to reproduction, life expectancy, and age-specific mortality, as well as by the predictability of the environment, ecological niche, and body size.

The energetic demands of reproduction in reptiles can be considerable. For example, in tropical anolis lizards as much as one-fourth of the female's net metabolizable energy is directed to egg production in a breeding season and some North American iguanid lizard species expend this much energy in the production of a single clutch; thus, the energetic costs of reproduction increase tremendously when more than one clutch is produced per season. In addition to energetic demands there are associated risks of mortality from predation during courtship or mating, complications of pregnancy (in viviparous animals) or gravidity (in oviparous animals), and subsequent parturition and oviposition. Costs to males may also be high, particularly in terms of the aggressive and courtship behaviors associated with reproduction.

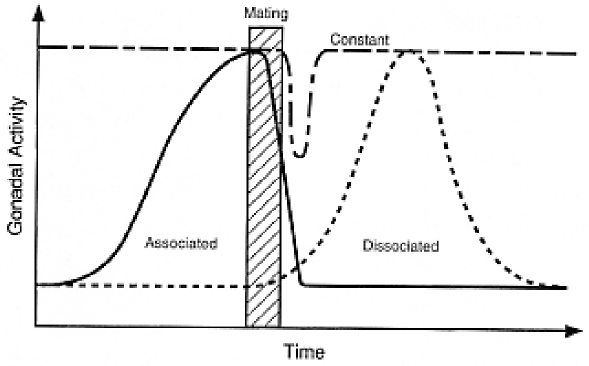

FIGURE 1 Three reproductive patterns exhibited in vertebrates, including reptiles. Gonadal activity is defined in terms of the maturation and shedding of gametes and/or the secretion of sex steroid hormones. In individuals exhibiting the associated reproductive pattern, gonadal activity increases immediately prior to mating. In species-dissociated reproductive pattern, gonadal activity is minimal at mating. In species exhibiting the constant reproductive pattern, the gonads are maintained at or near maximum activity throughout the year.

II. TIMING AND PATTERNS OF REPRODUCTION

Reproduction is considered seasonal when individuals in a population breed at a specific time of year. Usually, all individuals are synchronized in their reproductive activity, but this is not necessarily the case in all species. For example, in sea turtles, males breed each year, but females may breed only every third year such that each year different cohorts of females lay eggs. Thus, seasonal reproductive cycles are not necessarily synonymous with annual reproductive cycles; for example, an individual that breeds in the spring every 2 or 3 years has a seasonal cycle but not an annual one. In aseasonal (or acyclic) reproduction the individuals in a population are not synchronized and breeding may occur continuously or year-round. Aseasonal reproduction may also include reproductive patterns in which individuals of species breed in response to specific but erratic environmental cues. For example, reptiles living in harsh environments such as the deserts of midwestern Australia may breed only when occasional and unpredictable rains inundate an area.

Tropical species have traditionally been considered reproductively acyclic. However, the categorization of a species as acyclic implies that each individual of that species is constantly reproductively active. In reality, only a fraction of the population is breeding or in reproductive condition at any one time, and individuals are breeding on a seasonal, cyclic basis but not synchronously.

Not all aspects of reproduction, including gonadal growth, sex steroid hormone secretion, and sexual behavior, are expressed at the same time. In most species that have been studied with respect to the environmental cues and physiological mechanisms influencing reproduction, these three events are functionally associated (Fig. 1). Such species tend to inhabit environments with prolonged and predictable periods suitable for reproduction. However, in environments having brief but predictable benign periods, gonadal activity and sexual behavior are expressed at different times or are dissociated. In particularly harsh environments species may exhibit a constant reproductive pattern in which gonads are maintained in a near ready state and sexual behavior is expressed in response to particular environmental cues. Such differing patterns of reproductive activity indicate that a wide variety of physiological mechanisms have evolved to meet the demands of reproduction in different environments.

III. ENDOGENOUS AND ENVIRONMENTAL REGULATION OF REPRODUCTION

Mechanisms that control seasonal reproduction may be viewed as lying on a continuum between two extremes. At one extreme, in preprogrammed or closed control mechanisms, seasonal reproduction is entirely determined by endogenous cycles and is not influenced by external cues. At the other extreme of this continuum lies labile control, in which seasonal reproduction occurs as a result of responses to exogenous cues. In predictable environments, individuals of a population that rely on preprogrammed control mechanisms may have an advantage because they are ready to reproduce and need not rely on external influences to initiate reproduction. In less predictable environments, preprogrammed control may be disadvantageous if reproductive responses occur under inappropriate conditions. Labile control mechanisms, although they may retard a reproductive response until conditions are favorable, result in fewer risks in unpredictable environments.

Many reptiles exhibit intermediate control mechanisms between these two extremes. For example, preparatory events leading to reproduction, including gonadal growth, can be influenced by endogenous factors, but final stages of maturation as well as reproductive behavior can be controlled by integration of specific cues. Another intermediate stage of control is represented by the "hourglass" mechanism, in which external events initiate but have no further influence on an endogenously controlled cycle.

Different environmental situations provide unique cues that can be exploited to predict the time when reproduction is most likely to succeed. In both benign BS predictably harsh environments, such as found at extreme latitudes and altitudes, photoperiod and temperature are reliable cues associated with the prediction of spring or summer-like conditions. While tropical environments do not undergo seasonal extremes in photoperiod and temperature, often there are regularly recurring wet and dry periods. Some desert environments similarly may have seasonal rainfall. Other environments appear to lack regularly occurring external cues. These would include areas that have favorable conditions year-round, as in some tropical environments. Finally, there are environments in which favorable conditions for reproduction are unpredictable, including some deserts and certain high mountain areas.

The environmental factors affecting reproduction in reptiles have received much study. In general, day length and temperature both serve as proximate cues for gonadal maturation. For example, in the male green anole lizard, temperature is of primary importance in the induction of gonadal recrudescence, whereas photoperiod influences testicular regression. Females are also sensitive to these cues, but there is an additional requirement of sufficient relative humidity if ovarian growth is to occur.

Social cues are also important regulators of reptilian reproductive cycles. Male courtship behavior (in particular, extension of the dewlap) facilitates ovarian development in the green anole lizard. In the Canadian red-sided garter snake the stimulus of mating initiates the neuroendocrine changes that stimulate ovarian growth.

Nutrition, usually in the form of stored fat, has a profound influence on reproduction in reptiles. Many species of northern temperate snakes reproduce facultatively, often every 2 or 3 years rather than on a strictly annual basis. Such facultative reproduction may occur in part as a result of an influence of nutritional reserves on reproduction. For example, in the Canadian red-sided garter snake, females of less than average body weights at a given snout–vent length are less likely to reproduce than heavier individuals. Although low body weight significantly influences ovarian recrudescence in this species, body weight (within normal ranges) does not influence sexual attractivity or receptivity of females. Since female Canadian red-sided garter snakes can store viable sperm for years, as do a number of reptiles, it is not surprising that ovarian responses and sexual behavior can be independently regulated by factors such as body weight. In a related species, the Mexican garter snake, body condition more directly influences the reproductive cycle; nutritional condition of females regulates female attractivity and the incidence of male sexual behavior and testicular cycles.

In addition to environmental cues, some species utilize endogenous cues to regulate timing of reproduction. Endogenous circannual cycles are defined by the occurrence of complete reproductive cycles on a near annual basis under constant conditions (e.g., constant darkness or a nonvarying 10-hr light : 14-hr dark photoregimen and constant temperature). Interactions between endogenous cycles in sensitivity to environmental stimuli and the regular progressions of changes in the environment regulate the period (length) of the cycles. Few long-term studies have investigated endogenous circannual cycles in reptiles, although evidence with parthenogenetic whiptail lizards indicates such cycles may occur. Several species of reptiles do exhibit seasonal variation in sensitivity to exogenous cues. This is primarily manifested by a refractory period following the breeding season and extending to midwinter. This has been documented most extensively in the green anole lizard. Females of this species become unresponsive to long photoperiods and warm temperatures after the breeding season. The lack of response may be due, at least in part, to the presence of large atretic follicles. Male anoles also exhibit refractoriness to exogenous cues during late summer. Again, circadian rhythmicity to exogenous cues has been implicated as mediating the response.

Finally, there often are interactions between endogenous events and seasonal cues. Thus, different environmental factors can alter reproduction during particular gonadal phases. Such considerations complicate experimental approaches to environmental influences on reproduction.

IV. NEUROENDOCRINE CONTROL OF REPRODUCTION

The specific cues utilized for regulating reproduction, be they internal or external, must be integrated in such a way so that gonadal products are produced and sexual behavior is expressed at the appropriate time(s). The neuroendocrine system has evolved to perform this function in a precise, and often complex, way. Redundancy often is found in neuroendocrinological controlling mechanisms so that removal or addition of particular substances may not always result in a single predictable result. In other words, the notion that one mechanism regulates all reproductive events or even a single reproductive event is overly simplistic.

Reptiles possess similar neuroendocrinological regulating mechanisms as other vertebrates that have been studied. Sensory systems and specific brain areas serve to integrate external and internal events to bring about changes in the reproductive system. The eyes and the pineal appear to be involved in the influence of photoperiod on the reproductive system, and in snakes and turtles the pineal appears to be involved in the transduction of temperature. Chemical signals are detected by the vomeronasal system in lizards and snakes and probably other reptiles as well. The integration of these cues is not well understood, but, as in other vertebrates, specific nuclei in the limbic system receive input from these sensory systems. Many of these brain areas also concentrate steroid hormones, and areas such as the preoptic area, anterior hypothalamus, and ventromedial hypothalamus are involved in the regulation of social and sexual behaviors. Specific areas of the hypothalamus secrete gonadotropin-releasing hormone (GnRH) that influences release of gonadotropin from the anterior pituitary. Gonadotropins in turn stimulate gonadal maturation and steroid hormone production. Steroid hormones feed back on the hypothalamus and the pituitary to modulate subsequent function of these structures. Administration of exogenous GnRH stimulates release of gonadotropin and repeated pulses of GnRH administered to females increase the frequency of aggressive and reproductive behaviors of conspecific males and induce receptive behavior in females. Finally, both steroid hormones and behavioral context regulate the expression of genes coding for sex hormone receptors in limbic nuclei.

In contrast to species with an associated reproductive pattern, in the Canadian red-sided garter snake, which exhibits a dissociated pattern of reproductive cycle (Fig. 1), neither hypophysectomy nor administration of exogenous GnRH or a number of other neuroendocrine substances affect male sexual behavior. In fact, in this species a prolonged period of cold temperature followed by warming, thereby simulating the natural course of events of hibernation and spring emergence, initiates courtship behavior of males. Pituitary and gonadal hormones are not involved in the activation of mating behavior, although melatonin from the pineal and the eyes appear to be essential.

Although there is a large amount of information available on neuroendocrinological control of reproduction in reptiles, little is known of the interactions responsible for normal seasonal changes. For example, female green anole lizards undergo a seasonal cycle in which their ovaries recrudesce in the spring, produce eggs for approximately 12 weeks, and then regress in late summer. Sexual behavior is linked to the ovarian cycle and can be stimulated by the administration of the ovarian hormones estrogen and progesterone. There is seasonal change in sensitivity of the brain of ovariectomized female green anoles to the stimulatory effects of estrogen and progesterone on sexual receptivity. Paralleling this is the seasonal refractoriness of ovarian responses to exogenous follicle-stimulating hormone. Thus, in the green anole lizard, although there is a suggestion of seasonal changes at the brain and gonad, potential interactions between these events over an entire reproductive season are not understood.

V. TEMPERATURE-DEPENDENT SEX DETERMINATION

Reptiles exhibit two basic forms of sex determination. All snakes and apparently all viviparous lizards exhibit genotypic sex determination, having either male or female heterogamety. However, many, but by no means all, egg-laying reptiles lack sex chromosomes. Instead, all crocodilians, most turtles, and many lizards, including the tuatara, depend on the temperature experienced by the embryo during the middle third of incubation to determine the sex of the offspring. This process is termed temperature-dependent sex determination (TSD). Interestingly, no snakes and no viviparous lizards appear to exhibit TSD, relying instead on genotypic sex determination.

In some species low temperatures produce males and high temperatures produce females, whereas in other species the opposite pattern occurs; in still other species extreme incubation temperatures produce females and intermediate temperatures produce males (Fig. 2). For example, in the red-eared slider turtle the spectrum of temperature is slight, extending over no more than 5–7°C, with the transitional temperature range (those temperatures yielding a mixed sex ratio rather than all males or all females) <1°C. Furthermore, the effect of temperature during this window of sensitivity is quantitative, having a cumulative effect on sex determination.

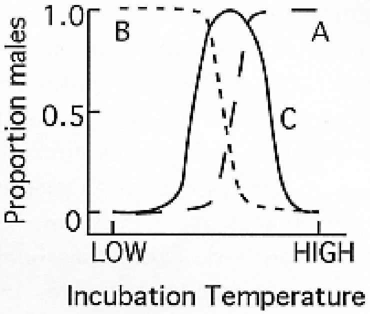

FIGURE 2 Response of hatchling sex ratio to incubation temperature in various egg-laying reptiles. These graphs represent only the approximate pattern of the response and are not drawn according to any single species. The following are the three patterns recognized: (A) only females produced from low incubation temperatures, with males at high temperatures; (B) only males produced from low incubation temperatures, with females at high temperatures; and (C) only females produced at the temperature extremes, with male production at the intermediate incubation temperatures. Genotypic sex determination also occurs in reptiles with the result that the hatchling sex ratio is fixed at 1:1 despite incubation conditions.

Incubation temperature is transduced in the urogenital system and perhaps the brain of the developing embryo and acts by modifying the activity as well as the temporal and spatial sequence of enzymes and sex hormone receptors. The temperature-typical hormone milieus that are created in the urogenital system in turn determine the type of gonad formed. Because the genetic machinery necessary for the formation of both ovaries and testes are present in the embryo, this means that temperature must activate one gonad-determining cascade while inhibiting the complementary gonad-determining cascade.

The temperature experienced by the embryo not only determines gonadal sex but also influences sexual differentiation. Indeed, it appears that much of the variation observed within the sexes of TSD reptiles can be traced back to the incubation temperature of the eggs, much like intrasexual variation in polytocous mammals can be traced to the position of the fetus relative to the sex of its neighbors *in utero*.

This is demonstrated particularly well in the leopard gecko, in which adult variations in morphology, endocrine physiology, behavior, and brain chemistry both between and within a sex are affected profoundly by the temperature experienced as an egg. For example, in the leopard gecko the male is the larger sex. However, females from a male-biased incubation temperature grow faster and larger than do females from a female-biased incubation temperature, growing as rapidly and as large as males from lower, female-biased incubation temperatures. When the effects of gonadal sex and incubation temperature are experimentally dissociated using estrogen to sex-reverse eggs incubating at a male-biased temperature, estrogen-determined females grow according to the incubation temperature rather than their gonadal sex.

VI. PARTHENOGENESIS

Reptiles are the only amniote vertebrates (mammals, birds, and reptiles) that exhibit obligate parthenogenesis. Such species consist only of female individuals that do not need to mate (and hence do not require sperm to activate embryogenesis) in order to reproduce. In such cloning species only female offspring are produced that are genetically identical to the mother. In obligate parthenogenesis there is no reduction in ploidy (indeed, usually there is an increase) prior to meiosis. Parthenoforms can arise by mutation through hybridization between sexual species; indeed, in many instances we actually know which species hybridized to create the parthenogen. Obligate parthenogenesis appears to be restricted to the lizards; the Brahminy blind snake may also be unisexual, although this has not been confirmed. There are about 40 species of lizards, including the Australian geckos, eurasian rock lizards, and southwestern whiptail lizards, that reproduce in this manner.

The evolution of a cloning reproductive pattern does not mean that the genes for maleness were lost. Administration of aromatase inhibitor during a specific time in embryonic development will result in the complete suppression of the ovary-determining cascade and the activation of the testis-determining cascade, resulting in individuals having testes, producing motile sperm as adults, and mating as males. This effect is not simply the result of sex steroid hormones determining gonad type directly, because administration of steroid hormones or their antagonists does not alter the normal (ovary) development or primary sex structure. This suggests that the key to parthenogenetic reproduction may lie in the dual process of activation of the ovary-determining cascade and the concomitant suppression of the testis-determining cascade.

See Also the Following Articles

Amphibian Reproduction, Overview; Female Reproductive System, Reptiles; Fish, Modes of Reproduction in; Male Reproductive System, Reptiles

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