12

Sex and Gender

TURK RHEN

DAVID CREWS

In this chapter, sex will refer to the central process of meiosis and syngamy[1] in eukaryotic organisms. Although some form of sexuality characterizes the life cycle of many eukaryotic organisms (i.e., virtually all fungi, plants, and animals), not all eukaryotes are sexual (e.g., many protists) (Margulis 1970, 1996; Bell 1982). Certain asexual protists, for example, only undergo mitosis and never alternate between haploid and diploid stages by way of meiosis and syngamy. Consequently, one of the most fundamental questions in biology is: Why do certain organisms go through meiosis and syngamy while others do not? Despite the apparent simplicity of this query, evolutionary biologists have not provided an entirely satisfactory explanation for the evolution of sex. Much of the difficulty arises because there appears to be no single answer. Moreover, sex is often confused with other associated phenomenon. For instance, one completely subordinate, but intimately related, occurrence is the evolution of gender in organisms that go through meiosis and syngamy.

In his essay on the evolution of sex, Ghiselin (1988) aptly wrote, "Gender means the differentiation into males, females, and such alternatives as hermaphrodites. It also includes the differences between sperm and eggs. Such differences are important because they create the circumstances that make sex a puzzle" (p. 9). Yet he dismisses this subject in the next sentence: "Otherwise we are not much concerned about gender either." Here we clarify the relationship between the evolution of sex and the evolution of gender. This is a critical concept to comprehend because gender differences are nearly universal in sexual organisms. We also discuss some of the major hypotheses proposed to explain why sex exists and recent empirical work that sheds light on the factors that may favor meiosis and syngamy regardless of gender differences. In the remainder of the chapter, we present a more thorough analysis of the evolution of gender, including a discussion of what the fundamental gender difference is and why there are so many different mechanisms that produce more derived gender differences.

The latter question has been hard to address because gender differences have usually been framed in terms of such contrasting alternatives as simultaneous versus sequential hermaphroditism,[2] hermaphroditism versus gonochorism,[3] and environmental sex determination versus genotypic sex determination. Sex allocation theory (Orzack, this volume) indicates that these phenomena are simply life history adaptations that maximize individual fitness through male and/or female function in light of various constraints. To illustrate how natural and sexual selection act to mold gender differences within specific genetic, developmental, and ecological constraints, we review some of our own work on the evolution of temperature-dependent sex determination in reptiles.

The Evolution of Eukaryotes, Mitosis, and Sex

Although the exact historical events that led to the evolution of eukaryotes are not clear, Margulis (1970, 1996) has proposed that eukaryotes arose as the result of a series of endosymbiotic relationships among various archaebacterial and eubacterial cells. In this scenario, an initial symbiosis or symbioses produced the first eukaryotic (i.e., nucleated) cells. These primordial eukaryotes then acquired other symbionts, which gave rise to organelles like mitochondria and chloroplasts. The serial endosymbiotic theory is supported by phylogenetic evidence that mitochondrial DNA and chloroplast DNA are related to the genomes of various prokaryotes (e.g., Williamson 1993; Turmel et al. 1999). In other words, eukaryotes are composite organisms made up of heterospecific cells and their genomes. The concomitant evolution of a regular pattern of inheritance of these genomes (i.e., mitosis and sex) represented a major evolutionary innovation in the history of life.

In addition, Margulis proposed that the evolution of mitosis involved a symbiotic association between early eukaryotes and motile prokaryotes that contained an actinlike protein. This symbiotic relationship was presumably the progenitor to the eukaryotic flagellum and its basal body. The protoflagellum, in turn, differentiated via gradual evolutionary steps into the mitotic apparatus that we recognize today (see chapter 8 in Margulis 1970 for a series of hypothetical transitions based on putative intermediate forms of mitosis in extant protists). Whatever the evolutionary history of the mitotic and meiotic apparatus, it is generally accepted that mitosis evolved first as a means to efficiently distribute chromosomes to daughter cells and that meiosis and syngamy followed.

Although there are a number of potential costs to sex that make its evolutionary origin and subsequent maintenance paradoxical (see Ghiselin 1988; Shields 1988), the only inescapable consequence of meiosis and syngamy is the alternation of ploidy. In unicellular and small multicellular eukaryotes, this process bears a significant and direct "cellular-mechanical cost" in terms of additional time required for meiosis, gametic union, and nuclear fusion when compared to mitosis (Lewis 1983). It was estimated, for example, that the production of two daughter cells via sex takes at least twice (and

up to 10 times) as long as the production of two daughter cells via mitosis. Accordingly, and in the absence of other mitigating factors, asexual forms should easily supplant sexual forms when they are placed in direct competition with each other.

In an elegant study of sex in yeast, Birdsell and Wills (1996) eliminated this "cellular-mechanical cost of sex," as well as most of the other potential costs of sex. They found that one round of meiosis and syngamy bestowed a significant competitive advantage in all of their replicate competitions between sexual and asexual strains; strains that had gone through one sexual bout replaced asexual strains in as few as 100 generations. Birdsell and Wills were able to ascribe the payoff of sex to a number of factors (i.e., overdominance at the mating type locus, meiotic recombination). However, it is unclear from this study whether the demonstrated benefits of sex would be enough to outweigh the intrinsic "cellular-mechanical cost of sex" or any of its various other costs. Nevertheless, this experiment provides a classic model for the careful dissection and evaluation of the theoretical costs and benefits of meiosis and syngamy. In a general sense, this work also simulates the presumed circumstances during the origin of sex: the first sexual organisms were almost certainly simple eukaryotes in which reproduction was normally via mitosis and the costs of sex were relatively low.

Another frequent, though not inescapable, consequence of sex is mixis, or the rearrangement of genetic material into new combinations. Mixis occurs during meiosis through intrachromosomal recombination and/or independent assortment of different chromosomes. Effective mixis, however, ultimately depends on syngamy between gametes that were produced by different individuals (i.e., outcrossing). This union of gametes from genetically unrelated individuals has been simultaneously touted as the "two-fold genetic cost of sex" and as the adaptive explanation for the evolution of sex. Organisms that reproduce by outcrossing contribute only half of their offspring's genes. It has been argued on these grounds that, to obtain an equal genetic representation in the next generation, a sexually reproducing organism would need to contribute twice as many surviving progeny as would an asexually reproducing organism. In short, sexual reproduction is an inefficient way to pass on one's genes. On the other hand, outcrossing organisms produce offspring with the maximal

Some species, for instance, have major genotypic factors that determine gonadal phenotype and that dictate an inflexible sex ratio of 50% males and 50% females (i.e., the X-Y sex determining mechanism of mammals or the Z-W mechanism of birds). Despite this constraint on sex ratio evolution, other mechanisms have evolved to produce gender differences. For example, it is thought that genetic differences between males and females evolve when alleles with antagonistic effects on the two genders are linked to a new sex-determining gene. This pattern of selection favors suppressed recombination between the loci which, in turn, allows genetic differentiation of new sex chromosomes (Rice 1996). Close examination of nucleotide sequences of gene homologs on the X and Y chromosomes in humans supports this scenario for the evolution of mammalian sex chromosomes (Lahn and Page 1999). While an initial event (i.e., mutation) conferred the primary sex determining role on SRY in early mammals, subsequent evolutionary events, presumably Y chromosome inversions, suppressed recombination between the nascent sex chromosomes. Once recombination was suppressed, alleles on the X and Y chromosomes were then able to fully differentiate into gene homologs with distinct functions. Some Y-linked genes have roles in male-specific processes like spermatogenesis, and certain X-linked genes function during the female-specific process of X chromosome inactivation. In contrast, alleles at other loci on the Y chromosome degenerated into pseudogenes, and their counterparts on the X chromosome were left as intact, functional genes.

Notwithstanding the evolution of genotypic sex determination and sex chromosomes, many genes that produce gender differences are autosomal. At its most fundamental level, sex-limited expression of autosomal genes involves the activation or repression of different genes in males and females. Sex-limited expression of such loci can result from interactions with genes located on the sex chromosomes, as in *Drosophila melanogaster*, or hormone-dependent mechanisms, as found in many vertebrates. For example, androgenic steroids, like testosterone, are produced in different amounts in male and female vertebrates. Androgens at the high levels typically found in males then act via androgen-specific receptors to initiate (or inhibit) gene transcription. A recent theoretical model for the evolution of sex limitation at such loci indicates that, much like models for sex allocation, se-

lection acts to maximize the product of the fitness gain through males times the fitness gain through females (Rhen 2000). These models suggest that various mechanisms of gender differentiation evolve according to this unifying principle.

To illustrate this theorem in more detail, let us examine some examples of optimal life history strategies for hermaphrodites. The following model for sequential hermaphroditism has been dubbed size-dependent sex reversal. Consider a hermaphroditic fish in which fitness through male function does not vary with body size but fitness through female function increases with size (i.e., because larger individuals can produce more eggs). In this simple case, sequential hermaphroditism is favored over simultaneous hermaphroditism because an individual can maximize its lifetime fitness by reproducing first as a male (i.e., at a small body size) and then switching to female function later in life (i.e., at a larger body size) rather than reproducing as both genders throughout its life (figure 12.2). In other words, selection acts to maximize $W_M \times W_F$ in light of the developmental constraint that the fish increases in size during its lifetime. Other hermaphroditic fish appear to maximize their fitness by reversing this sequence of gender change. In some populations of the blue-headed wrasse, for example, ecological conditions permit the largest male to dominate smaller males and monopolize matings with all resident females. If the male dies or is removed, the next largest individual (a female) changes gender to become the sole reproducing male. This example can be referred to as behavior-dependent sex reversal because it is the conduct of the dominant fish that suppresses sex change in the other resident fish. Selection again acts on the pattern of sex allocation to maximize the product of $W_M \times W_F$, but this time it does so under both developmental (i.e., growth) and ecological (i.e., mating system) constraints.

In contrast to hermaphrodites, gonochorists are developmentally committed to reproduce as only one gender. Nevertheless, they can still maximize gender-specific fitness by altering their sex ratio (the proportions of males and females in a population) to prevailing ecological conditions (Charnov 1982). Sex ratios can vary in an adaptive manner in spatially structured populations. Under these conditions, strong local mate competition is thought to favor female-biased sex ratios because only a few males are necessary to fertilize all the females within a local population. The most convincing ex-
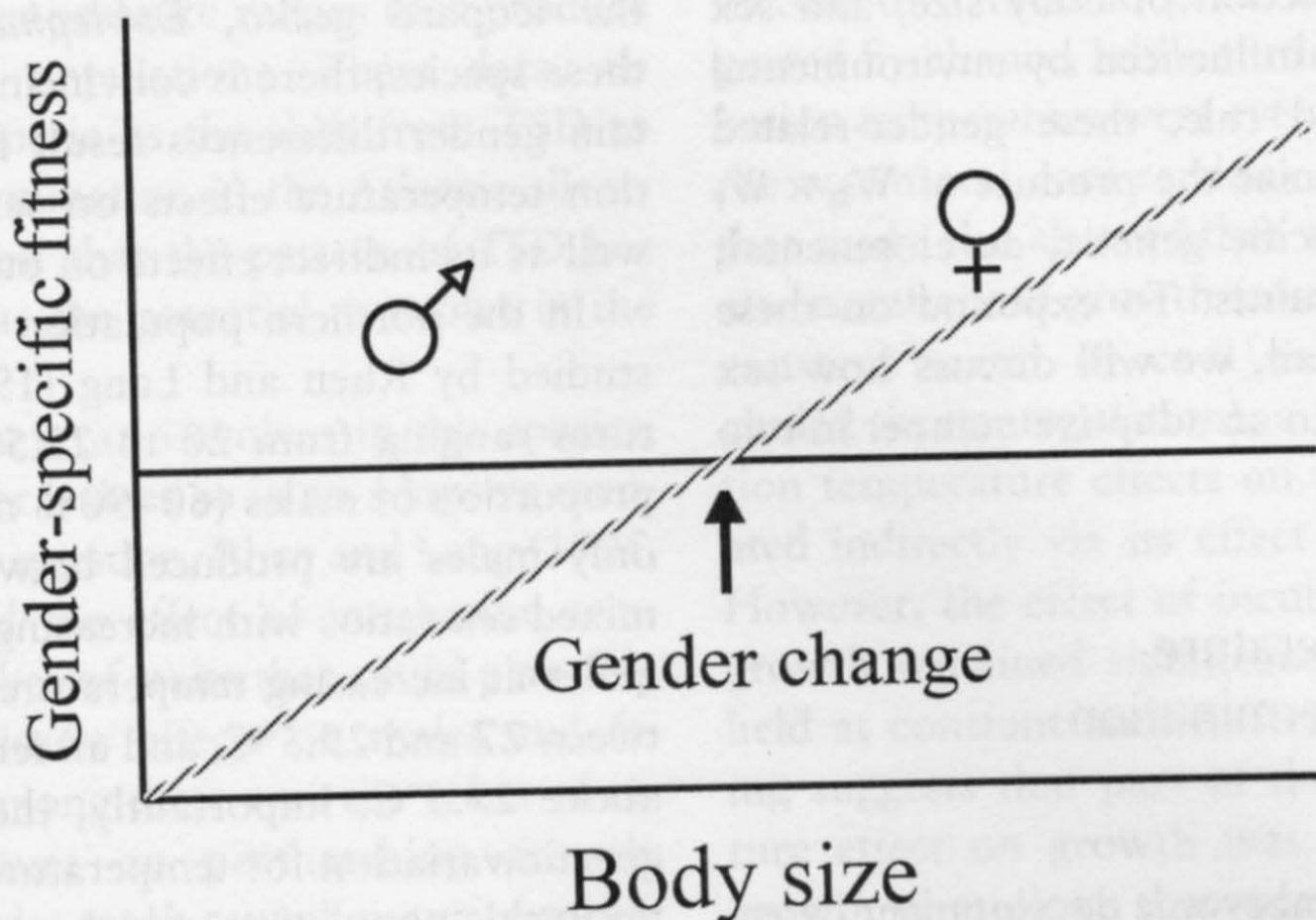
Figure 12.2 Gender-specific fitness as a function of body size in a hypothetical sex-changing fish. The optimal size for gender reversal is indicated by the arrow.

idence for this model comes from haplodiploid hymenoptera, in which females can control the sex of their offspring by allowing or not allowing fertilization of their eggs (males are haploid and females are diploid).

Sex ratios also vary in an adaptive manner when sex determination occurs after fertilization and is under the control of the embryo. Competition for host resources or, more precisely, variation in nutritional content of hosts favors one form of environmental sex determination in parasitic nematodes in the family Mermithidae (Charnov 1982). In this group, sex ratios are female-biased on large hosts or at low rates of infection when food is relatively abundant. Individual worms under these environmental conditions are able to grow to a larger size, which presumably benefits females more than males. In contrast, sex ratios are male-biased on small hosts or at higher rates of infection when food is more restricted. Feeding the host, while holding the number of parasites constant, alters the sex ratio of the parasites (increases the proportion of females produced). Overall, these results strongly support the idea that nutritional content of the host, rather than some other factor like local mate competition, influences sex determination in these parasites.

Abiotic factors can also influence sex determination. Conover and Heins (1987), for instance, clearly demonstrated adaptive variation in environmental versus genotypic sex determination in the Atlantic silverside, *Menidia menidia*. In southern populations of this species, water temperature acts as a reliable cue that indicates the length of the growing season and therefore adult body size. Temperature also has a strong effect on sex ratios, with female-biased ratios produced below approximately 18°C and male-biased ratios above this temperature. This phenomenon is called *temperature-dependent sex determination*, or TSD. Since larger size differentially benefits females (larger females produce more eggs than smaller females), it pays for larvae to develop as females when water temperatures are relatively cool early in the season. Males, whose fitness is not size-dependent, develop later, when temperatures are warmer. In contrast, sex ratios in northern populations are insensitive to the effect of temperature (gender is determined by genetic factors) because the breeding and growing seasons are too short for substantial differences in growth to occur between offspring produced early and late in the season. In other words, there is an ecological constraint on the evolution of TSD in circumstances where fitness does not vary with environmental temperature.

In sum, various mechanisms have evolved to produce gender differences. These include genetic differences between males and females (i.e., sex chromosomes), autosomal loci that are expressed in a sex-limited manner, gender change in her-

maphrodites as a function of body size, and sex determination that is influenced by environmental factors. As a general rule, these gender-related traits evolve to maximize the product of $W_M \times W_F$ in the context of specific genetic, developmental, and ecological constraints. To expound on these concepts in more detail, we will discuss how sex ratio appears to vary in an adaptive manner in two reptiles with TSD.

Case Studies: Temperature-Dependent Sex Determination in Reptiles

Temperature during embryonic development determines gonadal sex in all crocodilians, many turtles, and some lizards (figure 12.3). Although the adaptive significance of TSD in reptiles has been debated, there is growing evidence that temperature may have gender-specific fitness effects in this group, much as it does in the Atlantic silverside. Some important discoveries have been made in the common snapping turtle, *Chelydra serpentina*, and

the leopard gecko, *Eublepharis macularius*. these species, there is convincing evidence that ce tain gender differences result from direct incub tion temperature effects on sex determination a well as its indirect effects on other traits.

In the northern population of snapping turtle studied by Rhen and Lang (1998), low temperatures ranging from 20 to 22.5°C produce a high proportion of males (60–90% males, respectively) only males are produced between 23 and 27°C, mixed sex ratios with increasing proportions of females at increasing temperatures are produced between 27 and 29.5°C, and all females are produced above 29.5°C. Importantly, there is evidence for genetic variation for temperature effects on sex ratio in this population, which suggests that the pattern of TSD may be relatively free to evolve. In support of this inference, there is substantial geographic variation in the sex-ratio reaction norm (Ewert et al. 1994). For example, low temperatures produce fewer males (< 10% males) in southern populations. The upper transition from male- to female-biased sex ratios is also shifted, but to a lower temperature range. Consequently, there is a
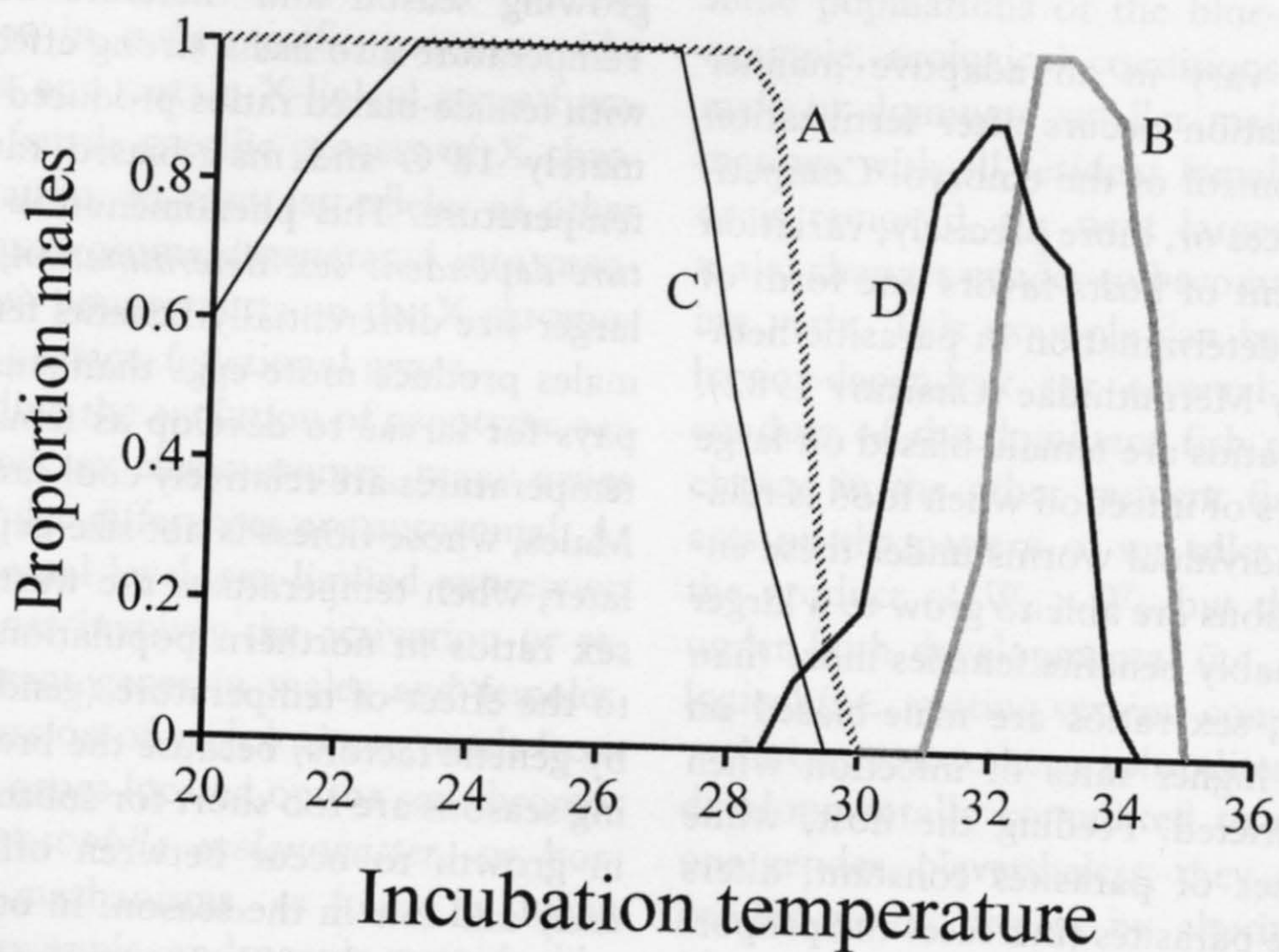

Figure 12.3 Representative effects of embryonic incubation temperature on sex ratio in various reptiles. (Redrawn from Rhen and Lang 1998) and Viets et al. 1993.) (A) Painted turtle. (B) American alligator. (C) Common snapping turtle. (D) Leopard gecko. Many reptiles with TSD have rather abrupt transitions (i.e., approximately 1°C) from temperatures that produce only males to temperatures that produce only females (or vice versa).

narrowing of the temperature ranges that produce males in southern populations. These data, although not as dramatic as the shift from TSD to genotypic sex determination in the Atlantic silverside, strongly suggest that the pattern of TSD has evolved and still has the potential to evolve in the snapping turtle.

Assuming that sex ratio evolves in this species, one can ask whether it does so in an adaptive manner. To address this question, Rhen and Lang (1995, 1999a,b) examined the effect of incubation temperature on a number of traits that could plausibly have differential fitness effects on males and females. Foremost among these was the effect of incubation temperature on posthatching growth. Snapping-turtle males reach sexual maturity earlier and at a larger size than females, which indicates that males grow faster than females. Consequently, if growth influences fitness in a gender-dependent manner, sex allocation theory predicts that there should be covariance for growth and for sex ratio as a function of incubation temperature. Yet any effort to associate a growth advantage with a particular incubation temperature would be confounded by potential sex effects on growth.

To resolve this dilemma, Rhen and Lang (1994) altered the gender (i.e., gonadal phenotype) of snapping-turtle embryos via hormonal manipulations at three representative incubation temperatures. The experimental manipulations produced females at two male-producing temperatures (i.e., 24 and 26.5°C) and males at a temperature that usually produces mostly females (i.e., 29°C). Thus, the normally confounded effects of incubation temperature and gonadal sex were separated. In short, embryonic incubation temperature had a strong effect on subsequent growth of hatchlings, whereas gonadal sex did not: Temperatures that normally yield males produced faster growth than the temperature that produces mostly females (Rhen and Lang 1995). These results imply that the gender differences in growth observed in nature are due to the matching of gonadal phenotype to particular incubation conditions during embryonic development (figure 12.4).

Further experiments were designed to determine how embryonic temperature regulates subsequent growth. Those studies revealed that behavioral thermoregulation of juvenile turtles was also influenced by incubation temperature (Rhen and Lang 1999a). Turtles from the low and intermediate incubation temperatures were found in the warm section of a thermal gradient more than was expected by chance, while turtles from the high incubation temperature were evenly distributed between the warm and cool sections of the gradient. Since that study also showed that warm ambient temperatures enhanced growth (some turtles were held in constant warm or cool environments that precluded thermoregulation), a portion of the incubation temperature effects on growth may be mediated indirectly via its effect on thermoregulation. However, the effect of incubation temperature on growth remained significant even in those turtles held at constant ambient temperatures. This finding suggests that part of the incubation temperature effect on growth was due to differences in growth physiology that were not mediated by behavioral thermoregulation. Similar results in other studies of the snapping turtle support the notion that embryonic temperature has both direct and indirect (i.e., through temperature choice) effects on posthatching growth (see discussion in Rhen and Lang 1999a).

A final study demonstrated incubation temperature and gender effects on total body mass and energy reserves in snapping turtles shortly after hatching (Rhen and Lang 1999b). Since hatchling snapping turtles struggle, often for a considerable period of time, to emerge from their subterranean nest and then must traverse large distances to reach water, all without access to food, incubation temperature and gender effects on the initial levels of energy reserves or how those reserves are utilized prior to feeding may have implications for survival. More important, perhaps, incubation temperature effects on posthatching growth could influence male and female fitness differently. In some populations of snapping turtles, female fecundity increases with body size so that larger females generally lay more eggs than smaller females. Bigger male snapping turtles also presumably have a fitness advantage because males have been observed fighting during the breeding season: It is a virtual axiom in behavioral ecology that larger individuals win aggressive encounters. Thus, if larger and dominant males are able to monopolize or obtain a greater share of matings than smaller males, the relative gain in fitness with body size may be greater for males than for females. In sum, embryonic temperature has numerous phenotypic effects on snapping turtles that may be related to fitness.

Relative to snapping turtles, which take 4 to 5 years to mature in populations with the fastest
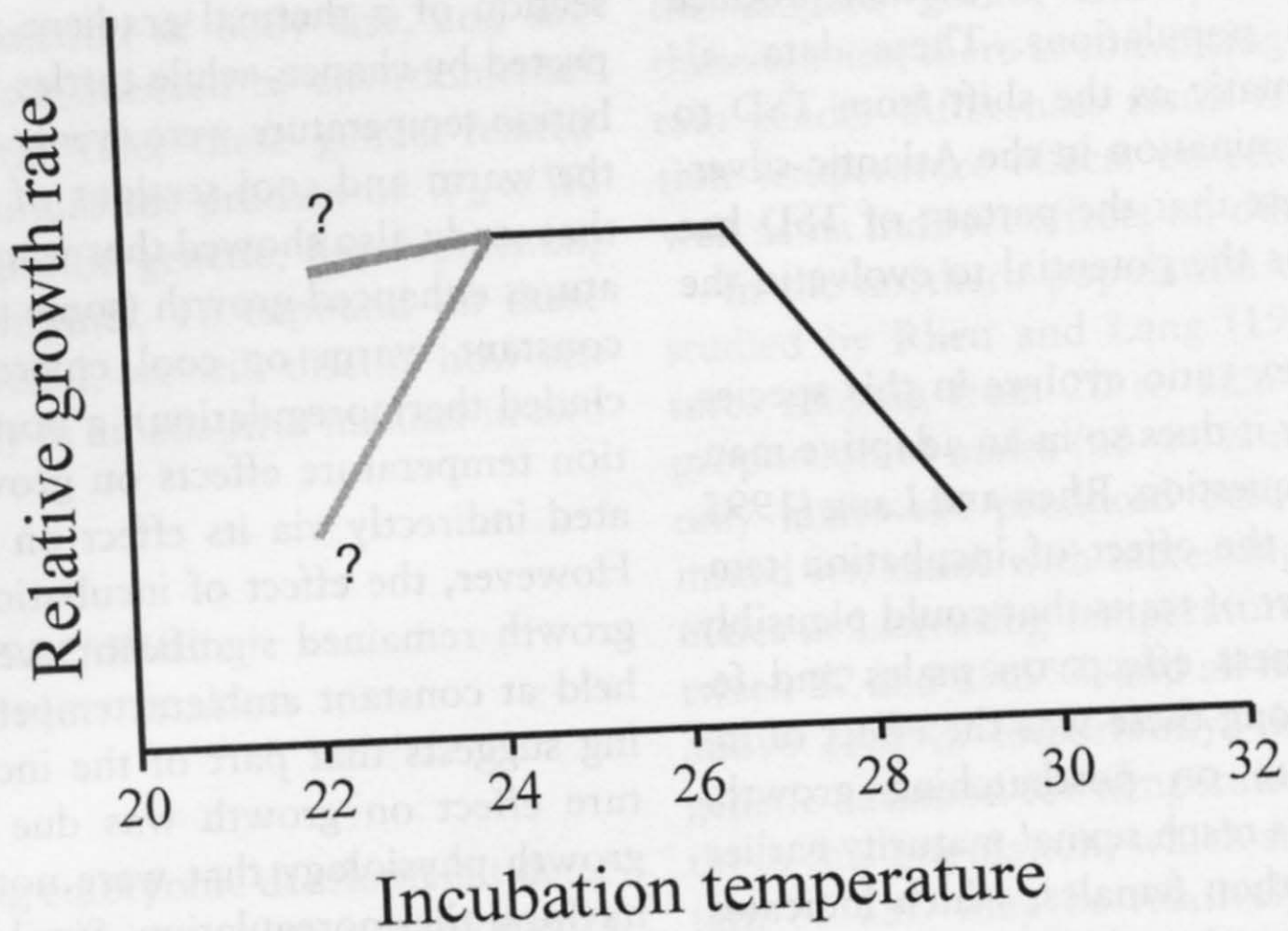
Figure 12.4 Composite effect of embryonic incubation temperature on growth rate after hatching in the common snapping turtle. (Solid line redrawn from Rhen and Lang 1995, 1999a.) Dashed line represents possible patterns of growth at low temperatures that may vary geographically with sex ratio.

growth, leopard geckos mature at a young (~45–50 weeks) age. Thus, it is feasible to directly determine if incubation temperature has any phenotypic effects that persist into adulthood and whether such phenotypes influence fitness differently in males and females. Female leopard geckos are normally produced across the entire range of viable incubation temperatures, while males are also produced across a fairly broad range of temperatures, although in varying proportions. An incubation temperature of 26°C produces all females, 30°C produces a female-biased sex ratio (~20% males), 32.5°C produces a male-biased sex ratio (~70% males), and 34°C again produces a female-biased sex ratio (5% males) (Viets et al. 1993). This pattern of TSD facilitates the investigation of incubation temperature effects in both sexes without experimental manipulations of sex ratio.

Incubation temperature has been shown to influence various traits in adult female and male leopard geckos (Gutzke and Crews 1988; Flores et al. 1994; reviewed in Crews et al. 1998). For example, females from the intermediate temperature that produces a male-biased sex ratio are less attractive (i.e., elicit less male courtship behavior) than females from temperatures that produce fe-

male-biased sex ratios. Conversely, those unat[t]ive females are more aggressive toward males [of?] their attractive counterparts from other tem[pera]tures. Hormone levels also vary in accord with bryonic temperature, so that less attractive, aggressive females have higher androgen levels more attractive, less aggressive females (Gutzk[e and] Crews 1988). Moreover, females from the biased temperature are larger than females other temperatures (Tousignant and Crews 1 Thus, incubation temperature has effects on f behavior, endocrine physiology, and body siz are correlated with its effects on sex ratio.

It was originally hypothesized that the m linized females from male-biased temperature compromised reproductive success (Gutzk Crews 1988). Further study, however, in[d] that temperature does not have any major ence on female fitness. For instance, there incubation temperature effects on fecundity, sexual maturity, or other measures of repro success (Tousignant and Crews 1995; Tou et al. 1995). Likewise, recent analyses of a larger set of cumulative data on hundreds mals from our colony at the University o[f] indicates that important measures of femal[e]

are not influenced by incubation temperature (J. Sakata, T. Rhen, and D. Crews, unpublished data). Fecundity does not vary with temperature because females have a determinate clutch size of just two eggs (females occasionally lay one egg in a clutch). Moreover, females from the entire range of temperatures produce approximately the same number of eggs during their lifetime. A slight incubation temperature effect on the fertility of eggs shows that, if anything, females from the high temperature lay a higher proportion of infertile eggs than females from the three other temperatures. This finding suggests that female attractivity and aggressiveness are not indicators of actual mating success: Relatively unattractive and aggressive females from the male-biased temperature still copulate with males and produce as many fertile eggs as females from temperatures that produce mostly or all females. Finally, the viability of embryos does not vary with maternal incubation temperature.

Hence, if TSD has any adaptive significance in the leopard gecko, temperature effects on fitness must be present in males. In the following discussion, we focus on males from the lower female-biased temperature (i.e., 30°C) and males from the male-biased temperature (i.e., 32.5°C). These incubation temperatures produce sufficient numbers of males for robust statistical comparisons of intra- and intersexual behavioral interactions.

In general, intermale aggression is extreme in the leopard gecko. In an encounter with a conspecific of either gender, male leopard geckos will often raise their body off the ground, standing on all four limbs in a high-posture display. The next step in a typical interaction depends on whether the conspecific is perceived as a male or a female (high postures may convey the signaler's gender because females do not display this behavior nearly as much as males do). Consequently, when two males are placed together they usually exhibit the high-posture display in unison. The males then slowly approach and lick each other. Pheromonal cues then elicit almost instantaneous aggression that entails reciprocal episodes of biting. Fights regularly include rapid body rolls that are reminiscent of crocodilians tearing flesh from their prey. Such agonistic encounters, if not stopped, can lead to severe skin lacerations, loss of limbs, or even the loss of a tail. Considering that combat is so costly and that high-posture displays might serve as a way to evaluate ones' opponent without fighting, the effects of relative body size on agonistic encounters were investigated (J. Sakata and D. Crews, unpublished data).

Most staged interactions between males resulted in fights regardless of the animals' relative body size. Males with a 10% weight advantage always won contests; the loser fled and rapidly waved his tail in defeat. Clearly, relative body size plays a critical role in determining dominance relationships in male leopard geckos. And since males from a male-biased temperature are on average larger than males from a female-biased temperature (Tousignant and Crews 1995), we hypothesize that it may be advantageous for males to develop at the temperature that produces more males. This scenario is plausible if large size and dominance enable individual males to control or gain access to multiple females. For example, male leopard geckos could establish territories that encompass the home ranges of multiple females. In fact, males from a male-biased temperature scent-mark significantly more than males from a female-biased temperature (Rhen and Crews 1999), a finding suggesting that male leopard geckos may be territorial. However, males from the female-biased temperature are more sexually active than males from the male-biased temperature (Rhen and Crews 1999). Thus, an interesting possibility is that males from different temperatures have different reproductive tactics, some males adopting an aggressive, territorial strategy (i.e., those males from the male-biased temperature) and others a satellite strategy (i.e., those males from the female-biased temperature). Although polygyny arising from territoriality is typical of many animals and is plausible for the leopard gecko, this explanation for the adaptive significance of TSD in the leopard gecko is speculative. There is currently nothing known about the mating system of leopard geckos in nature.

Future Directions

Persuasive evidence indicates that some gender differences in the snapping turtle and the leopard gecko result from the influence of incubation temperature directly on gonadal sex and indirectly on the individual's subsequent physiology, growth, and behavior. Although it is plausible that the observed correlations between sex ratio and such

traits are adaptive, it remains to be clearly demonstrated that temperature-induced phenotypes actually have differential fitness effects on males and females. Future studies of the phenomenon of TSD in reptiles should focus on this critical link between phenotype and lifetime fitness. Studies of TSD in reptiles, including those described above, have been conducted in the laboratory under constant incubation temperatures, but temperatures in nature fluctuate on multiple spatial and temporal scales. Consequently, another critical point that needs to be addressed is whether temperature effects are observed under natural conditions and whether such effects are related to the outcomes that have already been detected in the laboratory. To date, a few studies have shown that the process of TSD is operable in the field and that it is correlated with laboratory results, but none have shown that temperature influences the development of traits other than gonadal sex in nature.

In conclusion, various developmental mechanisms have evolved to produce gender differences. Sex allocation in hermaphrodites and mechanisms of sex determination in gonochorists evolve to maximize the product of fitness gain through male function (gametes that do not contain organelles) times fitness gain through female function (gametes that contain organelles). Interestingly, this principle also governs the evolution of sex-limited

expression of autosomal loci. A major quest whether this principle also applies to the evol of other gender differences like gamete d phism, sex chromosomes, and genomic impri (*imprinting* refers to alleles at a given locus are expressed differently when inherited vi mother vs. the father). Perhaps this principl be generalized. In any event, the fact that g differences are theoretically uneccessary fo evoluton of meiosis and syngamy but are n ubiquitous in sexual organisms is an evolutio puzzle that needs explanation. Finally, addit empirical studies on the adaptive significan sex are clearly needed.

Notes

1. The fusion of two gametes in fertilizatio
2. Possessing both male and female reprod tive organs.
3. Separation of the sexes into separate indi uals; in plants, this is referred to as dioecy; see kai and Westneat (this volume).