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## Implications of Temperature-Dependent Sex Determination for Population Dynamics

The study of population dynamics involves linking the temporal change in numbers of individuals in a population with different life-history parameters and external environmental forces. External forces can include catastrophic events, but simple physical factors can also drive population dynamics. Temperature is an ecophysical factor that can have a major impact on some species, obviously including reptiles that exhibit temperature-dependent sexual determination (TSD). For turtles, crocodiles, and lizards with TSD, the primary sex ratio is directly dependent on environmental thermal conditions, and it is the direct factor distinguishing between GSD- (genotypic sex determination) and TSD-based population dynamics. Indeed, for many characteristics of population dynamics, the presence of TSD in a population will be neutral. Therefore, the authors integrate in this review only data about specific details of TSD. The majority of data comes from turtle species because TSD in this group has been the best studied, but comparisons with other vertebrate taxa are included whenever possible. The authors also provide the following definitions to simplify the discussion of sex ratio. *Sex ratio* is expressed as male or female frequency. The *primary sex ratio* is defined here as the frequency of male or female at the end of the thermosensitive period (TSP) for sex determination during development (Mrosovsky and Pieau 1991). The *secondary sex ratio* is the sex ratio at hatching. It is generally assumed that secondary and primary sex ratios are equal, although differen-

tial late-stage embryonic mortality can produce differences between the two. Throughout the text the term secondary sex ratio is used only when it differs from the primary sex ratio. *Population sex ratio* is the sex ratio of all individuals in a population that have reached sexual maturity, and *operational sex ratio* is the sex ratio of only those individuals that contribute to reproduction of a population at any given time.

### Basics of Population Dynamics (Adapted from Charlesworth 1980)

Species with TSD are generally long-lived species (Janzen and Paukstis 1991a) and therefore are best described by age-structured population models. Descriptions of population structure are simpler when discrete age classes (or stages) are used (e.g., Heppell 1998). In this case, individuals may survive over many years, but reproduction is limited to one season of the year. Note that this assumption, while largely correct for many temperate species, may be too simplistic for tropical species in which reproduction could occur throughout the year. For example, the Amazonian tortoise *Geochelone denticulata*, can nest nearly year-round (Castaño-Mora and Lugo-Rugeles 1981; Métrailler and Le Gratiet 1996; Moreira 1991; Moskovits 1985). However, as sexual maturity is delayed in these species, age-structured population models can still be used by categorizing individuals into a year-based class.

The number of males and females at the beginning of the breeding season in a given year ( $t$ ) can be described in terms of individuals falling into age classes 1, 2, 3, and so on. These correspond to individuals who were born 1, 2, 3, and so on years previously. The number of females aged  $x$  at the beginning of the breeding season in year  $t$  can be written as  $n(x, t)$  and the number of males as  $n^*(x, t)$ . We describe  $P(x, t)$  and  $P^*(x, t)$  as the probability of survival over one age class (or year in most cases) for females and males, respectively, who are present in age class  $x$  at the start of the breeding season in year  $t$ . Using this notation yields, for age classes other than the first:

$$n(x, t) = n(x - 1, t - 1) P(x - 1, t - 1) \text{ and}$$

$$n^*(x, t) = n^*(x - 1, t - 1) P^*(x - 1, t - 1) \text{ with } (x > 1)$$

Age class 0 requires a specific treatment in order to distinguish between GSD- and TSD-based dynamics.

The authors also describe  $M(x, t)$  as the expected number of fertile eggs produced in year  $t$  by a female aged  $x$  at the start of the breeding season. The proportion of females among the offspring resulting from these eggs is  $a(t)$  (note that primary sex ratio is supposed to be independent of the age of the mother), and the survival of these offspring is  $P(0, t)$  for females or  $P^*(0, t)$  for males (note that survival in the first year is also supposed to be independent of the age of the mother). For species with TSD, the parameters  $P(0, t)$  and  $P^*(0, t)$  can be calculated at three separate time periods: (1) before sex determination, when no sex-specific function is needed, survival is described as  $P_u(0, t)$ ; (2) during and after sex determination but before hatching, survival of females is  $P_d(0, t)$  and that of males is  $P_d^*(0, t)$ ; and (3) during the first age class (or year) after hatching, survival of females is  $P_h(0, t)$  and that of males is  $P_h^*(0, t)$ . From this,

$$P(0, t) = P_u(0, t) P_d(0, t) P_h(0, t)$$

for females and

$$P^*(0, t) = P_u(0, t) P_d^*(0, t) P_h^*(0, t)$$

for males.

Note that the secondary sex ratio is simply  $a(t) / \{a(t) + [1 - a(t)] y\}$ , with  $y$  being  $P_d^*(0, t) / P_d(0, t)$ . Thus secondary sex ratio depends on primary sex ratio [ $a(t)$ , female frequency] but also on differential survivorship of males and females during development ( $y$  parameter).

The net expected contribution from a female aged  $x$  in year  $t$  to the population aged 1 in year  $t + 1$  is thus:

$$f(x, t) = M(x, t) a(t) P(0, t)$$

for the female offspring and

$$f^*(x, t) = M(x, t) [1 - a(t)] P^*(0, t)$$

for the male offspring.

The earliest possible age of reproduction of females (sexual maturity) is defined as  $b$  for females and  $b^*$  for males. Reproductive senescence has not been demonstrated in any reptile species with TSD and therefore no upper limit is set.

Then, from the above definitions, one obtains the following relations:

$$n(1, t) = \sum_{x=b}^{\infty} n(x, t - 1) f(x, t - 1)$$

for females and

$$n^*(1, t) = \sum_{x=b^*}^{\infty} n^*(x, t - 1) f^*(x, t - 1)$$

for males.

Note that the number of males  $n^*(x, t)$  is relatively unimportant in this model, a phenomenon called "female dominance." An alternative birth function can be used to introduce some limitation due to male number (e.g., dependent on harmonic mean of the population sex ratio; see Caswell and Weeks 1986). From these equations, the primary sex ratio  $a(t)$  must be defined independently each year, which introduces a temporal stochasticity.

A previous study has attempted to make a direct description of the process of population dynamics for a species with TSD (Woodward and Murray 1993), but in that study,  $a(t)$ ,  $P(x, t)$ , and  $P^*(x, t)$  were assumed to be constant across years, which is likely incorrect. In another study, a simplified model was used to check for the relative influence of sex-specific differences in survival rates or sex-specific differences in age at maturity to account for an overall bias in the population sex ratio (Girondot and Picaud 1993). In that particular case, neither time ( $t$ ) nor age dependency ( $x$ ) was taken into account in any of the parameters, making description of sex-specific frequencies quite simple:  $f = M \cdot P_u \cdot a$  for numbers of females and  $m = M \cdot P_u \cdot (1 - a)$  for number of males at the time of sex determination.

Then, the number of females of age 1 (second year) was assumed to be the fraction  $P$  of the  $f$  females that survived to age 1 (described as  $f \cdot P$ , and  $m \cdot P^*$  for males). For the second year (note that no temporal variability was taken into account),  $f$  newborn females and  $m$  newborn males entered in the population. The same process was assumed to continue across all years, and therefore at any given year, the population was composed of  $f + f \cdot P + f \cdot P^2 + f \cdot P^3 + \dots + f \cdot P^a$  females and similarly for males. Only sexually mature individuals account for the population sex ratio, and therefore the following equations were used to determine the number of sexually mature individuals:

$$\sum_{i=b}^{\infty} f P^i = \frac{f P^b}{1 - P}$$

for females and

$$\sum_{i=b^*}^{\infty} m P^{*i} = \frac{m P^{*b^*}}{1 - P^*}$$

for males.

The population sex ratio is consequently:

$$\frac{(f P^b)(1 - P^*)}{(f P^b)(1 - P^*) + (m P^{*b^*})(1 - P)}$$

In instances when  $P$  and  $P^*$  are large (near 1), a small difference between  $P$  and  $P^*$  will make the overall sex ratio value to tend toward 1 (all females) or 0 (all males). In other words, when survival is high, a small difference in the mean annual survival of males and females produces a strong bias in the population sex ratio. Differences in the values of  $b$  and  $b^*$  will alter the population sex ratio mostly for populations with low survival rates.

### Primary and Secondary Sex Ratios in Natural Populations

Biases observed in the primary sex ratio in offspring of the squamate *Agama agama* facilitated the original discovery of TSD (Charnier 1966) in lizards and later in turtles (Pieau 1971, 1972). Sex ratio biases in clutches incubated in natural conditions have also been demonstrated in many reptile species, mainly turtles (Pieau 1974; Bull 1985; Mrosovsky et al. 1984b) and crocodilian species (Webb and Smith 1984; Lance et al. 2000). Recently, Freedberg and Wade (2001) reviewed the published literature and suggested that different populations of sea turtle species (all exhibit TSD) tend to

produce female-biased primary sex ratios. Furthermore, these same authors suggested that there is an "ubiquity of biased sex ratios" in reptile populations (Freedberg and Wade 2001, 1053). Regardless of whether this accurately reflects all published accounts of reptilian sex ratios, this proposition assumes that published results represent a random subset of all TSD populations. This is probably not true (see also Valenzuela, Chapter 14). Indeed, it is likely that results of sex ratio studies will have a greater chance of being published if the results are different from equality (Festa-Bianchet 1996). Therefore, at the current time, any review of the published literature on primary sex ratios of TSD species should not be used as an indication of general trends in primary sex ratio production in nature.

Given that TSD species tend to be long-lived and that environmental conditions vary from year to year, the best estimates of mean primary sex ratio production in TSD populations must be based on multiyear data sets. But it is logistically difficult to directly estimate primary sex ratios, principally because for many reptile species, there is no sexual dimorphism before maturity. Distinguishing the sex of immature individuals usually requires invasive methods (e.g., histological preparation of the gonads or laparoscopy in larger individuals). These methods are limited in that they can only give current time information; they cannot be used to go back and reconstruct primary sex ratios over a number of years. For these reasons, long-term data sets on primary sex ratio production in TSD species are often based on indirect estimates, using environmental correlates (temperatures, rainfall, vegetational cover) or clutch characteristics (incubation duration with some direct sexing of dead or laboratory-incubated hatchlings) to predict hatchling sex. Note that few studies using indirect predictors of sex ratio have subsequently validated the methods used to estimate the sex ratios, which makes it difficult to assess the validity of the results (cf. Mrosovsky et al. 1999).

It is beyond the purview of this chapter to provide an exhaustive review of sex ratio studies in reptilian TSD species. Rather, several studies with (1) large numbers of sampling localities or analysis of entire reproductive localities and (2) long-term data sets will be presented, and they will be used to highlight several consistent properties of sex ratios by TSD populations.

### Extensive Spatial Analysis

For crocodilian species, several authors have suggested that female-biased sex ratios are the norm (Deeming and Ferguson 1989b; Woodward and Murray 1993). Thorbjarnarson

(1997) provided an extensive review of available information on primary, secondary, and operational sex ratios of different crocodile populations and reported that there are more male-biased sex ratios reported in the literature than female-biased sex ratios. More importantly, it was noted that a wide range of different sex ratios have been observed at the intraspecific level, and thus caution must be used when making statements about the significance of sex ratios at the species level. An extensive study on the sex ratios of the American alligator (*Alligator mississippiensis*) based on six years of data over 11 different sites in southern Louisiana reported that overall there was a slight male bias (58% male sex ratio) in juvenile sex ratios, but that local sex ratios varied in time and location (Lance et al. 2000). Thus, some sites produced a strong female bias (29% male sex ratio), others a strong male bias (83% male sex ratio), and some very close to equality (50% male sex ratio). Interestingly, these authors also report a five-year female-biased sex ratio for hatchlings produced by nests in Louisiana, although not in the same time period as the juvenile sex ratio results (Lance et al. 2000). Thus, there are cases where the juvenile and operational sex ratios in TSD populations are not the same as the primary sex ratios.

At this time, information on the sex ratios of hatchlings produced by the entire reproductive population of sea turtles is available for only two locations. Broderick et al. (2000) reported an extreme female bias (4–14% male) in green turtle hatchlings produced over a five-year period in Northern Cyprus, based on data from incubation durations. The larger breeding population of green turtles in the Mediterranean is largely restricted to nesting on beaches in Cyprus, Turkey, and more rarely, in Lebanon, Israel, and Egypt (Kasperek et al. 2001). Data from incubation durations in the other nesting areas also suggested that the majority of hatchlings produced over an extended time period were female (Broderick et al. 2000). Hence, it is likely that the overall estimate of a female-biased hatchling sex ratio for green turtles in the Mediterranean can be applied to the entire reproductive population. Godfrey et al. (1999) reported an extreme sex ratio bias (<10% male) of hatchlings produced by hawksbills in Bahia, Brazil, over a six-year period, with indications of similar extremes going back almost 20 years. Given that there are no other regular nesting areas for this species along the Atlantic coast of South America, and no reported nests on any islands off of Brazil, it is likely that these sex ratio estimates are representative of the entire reproductive population. Interestingly, both breeding populations are considered small (< 500 reproductively active females). Note, however, that *Eretmochelys*

*imbricata* also nests in West Africa coast and that the relationships with the Brazilian population are unknown.

#### Long-Term Data Sets

One of the longest data sets available for primary sex ratio under TSD comes from Janzen (1994a), who reconstructed the annual hatchling sex ratio for a population of freshwater painted turtles (*Chrysemys picta*) over 49 years, using mean air temperatures. The overall mean for this period was 47.8% males, although individual years were highly variable, ranging from 0–100% males. This study highlights the necessity of integrating sex ratio data over time, to account for interannual variation in sex ratios that is inherently linked to variability in the environment. Similarly, using rainfall data, long-term data sets on hatchling sex ratios have been generated for leatherback (*Dermochelys coriacea*) and green turtle (*Chelonia mydas*) hatchlings produced on a major nesting beach in Suriname (Godfrey et al. 1996). Again, variation was observed in the annual mean sex ratio of hatchlings produced by the two species, ranging from extremely male-biased to extremely female-biased sex ratios, but the overall (based on all years) sex ratios was 54.6% male for leatherbacks and 31.7% male for green turtles. However, these estimates of hatchling sex ratio production represent only one nesting beach in the larger breeding range of these two populations. Female turtles from the larger reproductive populations use other nesting areas in Suriname and French Guiana (Schulz 1975), and information is lacking on the sex ratios of hatchlings produced over the entire range of beaches. Some studies of sea turtle hatchling sex ratios have reported extreme female biases, including loggerheads (*Caretta caretta*) nesting in the southeastern United States (Mrosovsky and Provancha 1992; Hanson et al. 1998), loggerheads nesting in Brazil (Marcovaldi et al. 1997), loggerheads nesting in the Mediterranean (Godley et al. 2001), green turtles nesting on Ascension Island (Godley et al. 2002), leatherbacks nesting on the Pacific coast of Costa Rica (Binckley et al. 1998), and hawksbills (*Eretmochelys imbricata*) nesting in Brazil (Godfrey et al. 1999).

In nearly all cases, the estimates represent only a portion of the hatchlings produced in the larger breeding range of each population. Thus, these observed extreme female biases (sometimes < 10% male) in hatchling sex ratio may be countered by different sex ratios of hatchlings produced on unmonitored nesting beaches elsewhere, which are nevertheless part of the larger population. For instance, the green turtles nesting at Ascension Island migrate to feeding areas off of northeastern Brazil (Carr 1964). These feeding grounds

are also frequented by turtles from nesting areas in Suriname, French Guiana (Pritchard 1976), and perhaps other nesting areas in Brazil (e.g., Trindade Island, Atol das Rocas), which all likely contribute to the larger interbreeding green turtle population in the midwestern Atlantic (Karl et al. 1992). Without information on hatchling sex ratios from the entire range of the breeding population, it is not possible to estimate the primary sex ratio for the total reproductive population.

Studies conducted on immature loggerhead turtles found in the waters off the southeastern shore of the United States report that these individuals exhibit in general a female-biased (33% male) sex ratio (Wibbels et al. 1991d; Shoop et al. 1998). This is significantly different from the extreme female bias (< 20% male) reported for loggerhead hatchlings produced on nearby nesting beaches (Mrosovsky and Provancha 1992; Hanson et al. 1998). Potential explanations include sex-biased differences in the likelihood of capture and sampling, sex-biased differential mortality following hatching, and differential population origin of the individuals sampled. Some sampled turtles could have been produced at distant nesting beaches and have arrived in the study area during foraging migrations (e.g., Bolten et al. 1998). For these reasons, it is extremely difficult to interpret the results of sex ratio studies of immature sea turtles.

In reviewing the currently available data, there are certain generalities that can be made concerning the primary and secondary sex ratios of reptiles in natural populations. First, although some populations do produce extreme female biases, this is far from being the norm for all species. Indeed, in the case of the Crocodylia, more populations have been observed to be male biased than female biased. Second, when long-term data sets exist, there is often interannual variation in overall primary and secondary sex ratios produced, with extremes in both directions, which when averaged may or may not result in biased sex ratios. Third, many sex ratio studies have focused on only a portion of the entire nesting range of the breeding population. Given that there are often thermal differences across different nesting areas, it is nearly impossible to extrapolate observed sex ratios to the overall output of the larger population.

#### Primary Sex Ratio versus Operational Sex Ratio and Population Dynamics

For the study of population dynamics, the number of juveniles produced in a population is a key factor (see Basics of Population Dynamics, above). For many species with TSD, the number of juveniles produced is directly related to the number of sexually mature females (female dominance

phenomenon; see Basics of Population Dynamics, above). Moreover, no conclusive data exist concerning the minimum number of males necessary to successfully fertilize all females in reproductive condition in a population, although it is thought that small numbers of males may be a limiting factor of population dynamics for reproduction, based on observations of green turtles made in artificial conditions where the operational sex ratio was strongly biased (Wood and Wood 1980).

One major difficulty has been to find a direct relationship between primary and operational sex ratio. The operational sex ratio is dependent on the population sex ratio, which in turn is influenced not only by primary sex ratio, but also by sex-specific differences in first age at maturity, survivorship, and emigration or immigration (Gibbons 1990). An example of the differences between observed primary and juvenile sex ratios concerns the loggerhead sea turtle (see previous section, Long-Term Data Sets).

For long-lived TSD species, the principal factor that is responsible for the decoupling of primary sex ratio and population sex ratio is thought to be differential survivorship between males and females (Girondot and Pieau 1993; Janzen and Paukstis 1991b). In this case, the population sex ratio is composed of the primary sex ratios of several cohorts of offspring. In general, the population sex ratio is by definition less variable statistically than the primary sex ratio. In addition, the population sex ratio itself can be different from the operational sex ratio due to either behavioral factors such as male-male competition for mates in *Alligator mississippiensis* (Woodward and Murray 1993) or environmental pressures such as the variable availability of minimal nutritional resources that are required for entering into the reproductive state (Limpus and Nicholls 1988; Broderick et al. 2001).

Gibbons (1990) provided a review of population sex ratios for 52 species or subspecies of turtles. To this list, the authors add data from the European pond turtle, *Emys orbicularis* (Girondot et al. 1994), *Testudo hermanni* (Hailey and Willemsen 2000), and *Chelonoidis denticulata* (Josseaume 2002), but they exclude data from the only marine turtle species due to the difficulties in obtaining reliable data for this species. GSD or TSD patterns of sex determination are not known for all these species. The authors used phylogenetic analysis to infer the most probable pattern for the unknown species as follows (Girondot et al., unpubl. data). A composite phylogeny of turtles (Caccone et al. 1999; Dutton et al. 1996; Georges and Adams 1992; Georges et al. 1999; Krenz and Janzen 2000; Noonan 2000; Shaffer et al. 1997) has been used to infer the mode of sex determination (two states, TSD or GSD) in these 52 species or subspecies

based on parsimony criteria. Among all 153 populations, nine originated from species with GSD, 143 from species with TSD, and one (*Clemmys marmorata*) was ambiguous based on parsimony criteria and has thus been removed from the analysis. For the GSD populations, three of nine (30%) exhibited significant biases of population sex ratio, whereas for TSD populations, 52 of 143 (37%) show significant biases in population sex ratio. No significant difference was detected in the proportion of population with or without significant bias between the groups with TSD or GSD (Fisher exact test,  $p > 0.99$ ). Therefore, whereas biased primary sex ratios are often observed in TSD species and 0.5 is the rule for GSD species, mode of sex determination seems less important than other demographic factors, such as survivorship (Girondot and Pieau 1993) or sex-specific differences in capture likelihood (Gibbons 1990), in determining the observed population sex ratio. Nevertheless, there is no reason to think that species with GSD are more prone to sampling bias than species with TSD, but species-specific and sex-specific differences in behavior may increase the potential for sampling bias. The end result is that available data show there is no clear difference in mean population sex ratios between TSD and GSD species.

The lack of overall differences in population sex ratios between TSD and GSD groups of species appears surprising, although several key points should be kept in mind. First, as already noted, the primary sex ratio is less influential than differential survivorship between the sexes on the overall population sex ratio for long-lived species (Girondot and Pieau 1993). Second, primary sex ratios fluctuate from year to year around an average sex ratio (Janzen 1994a; Godfrey et al. 1996), and the standard deviation of population sex ratio is inversely proportional to the number of years of cohorts contributing to reproduction, and therefore to longevity. When longevity is very high, population sex ratio is dependent on the weighted average of primary sex ratio of many different cohorts. Thus longevity induces a buffer effect on population sex ratio that could be identically variable in TSD or GSD populations. The same argument can be used when short-lived span lizards lay several clutches during the year; the annual cohort concept should be changed to cohorts of eggs deposited the same month, for example. However, while the character of GSD or TSD may not definitely result in clear differences in population sex ratio and therefore population dynamics, it is likely that for specific situations, for example, during extended periods of rapid climate change, population sex ratios in TSD species would be vastly different from those of GSD species.

Recently, several models linking dispersal patterns and TSD have been proposed (Reinhold 1998; Julliard 2000;

Freedberg and Wade 2001). These models and some tests are discussed in Valenzuela (Chapter 14).

#### TSD as a Factor of Decline

It is evident that if during sufficiently extended period of time only one sex were produced, the population would disappear. Temperature extremes in the environment can produce extreme biases in offspring sex ratios in species with TSD. For this reason, some authors have hypothesized that the occurrence of TSD in a species increases the probability of extinction in the face of a catastrophic environmental event. For instance, there have been suggestions that the large extinction event of many dinosaur species at the Cretaceous/Tertiary (K/T) boundary was likely due to large climatic changes coupled with the presence of TSD in these species (Bull 1983; Ferguson and Joanen 1982; Harvey and Partridge 1984; Janzen and Paukstis 1991a; Standora and Spotila 1985). However, several points relevant to this hypothesis must be kept in mind. First, the extinction events involved around 90% of all species existing during this period, and probably many species had GSD. Second, the sex-determining mechanism in dinosaurs remains entirely unknown; indeed the current phylogeny suggests that dinosaurs could have had TSD or GSD, because the only remaining within group (Aves) possesses GSD, and the remaining sister group (Crocodylia) possesses TSD (Janzen and Krenz, Chapter 13). Therefore, the hypothesis that Cretaceous dinosaurs had TSD is equally parsimonious with the hypothesis that they had GSD. Moreover, many groups for which TSD can be inferred by parsimony survived beyond the great extinction events of the K/T boundary (e.g., Carettochelyidae, Chelydridae, Sphenodontidae) (Rage 1998). Third, many groups with TSD have continued to exist since the late Eocene, when another severe climatic cooling event was observed (Pomeroy and Premoli Silva 1986). Therefore, it seems implausible that TSD and a general cooling trend could have been the single major reason for the extinction of dinosaurs.

Another commonly cited threat to TSD species is rapid global warming due to the greenhouse effect (Deeming and Ferguson 1989b; Janzen 1994a; Mrosovsky et al. 1984b). Again, the idea is that increased incubation temperatures will result in extreme biases of sex ratios, leading to the inability of populations to reproduce. However, it should be noted that nest incubation temperatures usually vary across temporal or geographic ranges, so nesting females could potentially adjust their behavior (in space and/or time) to achieve certain offspring sex ratios. Indeed, a change in the nesting period or nest location can be a response of an in-

dividual (Morjan 2002). Therefore, even if mean temperatures rapidly increase, individuals still may be able to nest earlier or later in the season and therefore achieve incubation temperatures similar to those experienced before global warming. Behavioral changes as a means to achieve or maintain certain primary sex ratios may explain the difficulties to date in finding a significant relationship between latitude and pivotal temperature (the constant incubation temperature that produces a 50% offspring sex ratio) (Bull et al. 1982b; Ewert et al. 1994). Note that the fluctuation of primary sex ratio can be high for both small-sized populations (Girondot et al. 1994) and short-lived species (Janzen and Paukstis 1991b). At the same time, wide interannual fluctuation of the primary sex ratio is more likely to lead to extinction for a smaller population than for a larger one (Girondot et al. 1994).

TSD also has been linked with the decline of small populations by the way of the Allee effect (Berec et al. 2001). The Allee effect describes the general situation in which the growth rate of a population becomes negative when the population size falls below a certain threshold (the Allee limit; Courchamp et al. 1999). According to Berec et al. (2001), a population with TSD is more susceptible to the Allee effect due to its biased sex ratio, because the probability of finding a mate is reduced relative to a population with GSD and a balanced sex ratio. This hypothesis assumes that TSD results in a biased operational sex ratio as a direct result of biased primary sex ratios, but as discussed previously, the former does not necessarily follow from the latter. Additionally, the model of sex determination given by Berec et al. (2001), which uses directly the sex ratio versus constant incubation temperatures curve as a model of sex determination in natural conditions, is too simplistic to give realistic outputs (see also Valenzuela, Chapter 14). Nevertheless, it is an interesting avenue of approach to the study of the implications of TSD on population dynamics, and future studies along these lines should prove to be enlightening.

Another way by which a biased sex ratio can drive the decline of a population is by reduction of the effective population size, which in turn increases genetic drift. The effective size of the population ( $N_e$ ) is the size of a hypothetical population that would have the same rate of change in homozygosity as the observed population (Crow and Kimura 1970). If  $N_m$  males and  $N_f$  females are present in the population, then  $N_e = (4 N_m N_f) / (N_m + N_f)$ . If  $N_m = N_f$ , then  $N_e = 2 N_m$ , but is lower if  $N_m \neq N_f$ . Therefore, populations with biased operational sex ratio are more susceptible to genetic drift and thus to accumulation of deleterious mutations (Charlesworth and Charlesworth 1998). How-

ever, the impact of this effect will be significant only for small population sizes over long periods of time. Rapid increases in population size due to female-biased sex ratio can overcome this problem (Wedekind 2002). However, in this particular case, there will be selection for masculinizing alleles (Girondot et al. 1994; Mrosovsky 1994) due to frequency-dependent selection for unbiased primary sex ratios (Shaw and Mohler 1953). Depending on the variability of sensitivity of sex ratios to temperature for a population, this effect can be neutral or deleterious due to an increase of males following limited resource availability (Girondot et al. 1994).

### Interaction of TSD and Population Dynamics

Some interesting cases have been described in species with TSD in which the characteristics of population dynamics can modify the sex ratio at hatching, and therefore the consequences of TSD. One example is the sex ratio bias in offspring production due to nest destruction by the leatherback sea turtle *Dermochelys coriacea* nesting on Awala-Yalimapo beach in French Guiana (Girondot et al. 2002). There, the nesting season encompasses both the rainy and dry seasons. Therefore, nests laid earlier, during the rainy season, tend to produce a male-biased sex ratio, while nests laid later, during the dry season, tend to produce a female-biased sex ratio (Rimblot-Baly et al. 1986). However, nests laid earlier in the season are more likely to be accidentally destroyed during the nesting process by laying females, as nest destruction by subsequent nesting females is common on this high-density nesting beach (4 km long), where as many as 60,000 nests have been deposited during a single nesting season. Therefore, earlier male-producing nests produce fewer offspring than later female-producing nests, resulting in a feminizing bias in the overall sex ratio of hatchlings produced on the beach. Indeed, there is a positive relationship between the number of total nests laid and the female bias of the secondary sex ratio due to nest destruction. However, because of the higher nest destruction associated with higher nest density, there is no associated increase in female offspring with increased nesting effort.

Another example of direct interaction between TSD (and therefore sex ratio) and population density has been described for the alligator *Alligator mississippiensis* (Woodward and Murray 1993). Females of this species compete for and strongly defend their nests and nesting areas. Therefore, not all females are able to secure preferred nesting habitat, which is the wet marsh where cooler incubation temperatures produced nearly exclusively female hatchlings. Nesting females that are unable to find a location in the pre-



ferred areas will then attempt to nest in dry marsh or dry levees, where warmer incubation temperatures produce more males. A smaller reproductive population usually results in the possibility that all reproductive females are able to successfully secure locations in the preferred habitat, and thus the primary sex ratio will be female biased. Conversely, a larger reproductive population usually results in more nests being laid in dry warmer areas, thus leading to a more male-biased primary sex ratio. This mechanism facilitates the regulation of population size by altering the primary sex ratio: smaller populations produce relatively more females until the population grows sufficiently large and begins to produce relatively more males, which should slow population growth. However, given these hypotheses, the prevalence of observed female-biased primary sex ratios in populations is not an evolutionarily stable strategy because masculinizing alleles invade the population (Girondot and Pieau 1996; see also Valenzuela, Chapter 14).

### Conclusions

Much emphasis has been given to the theoretical consequences of TSD for population dynamics (e.g., Head et al. 1987), but few experimental or observational data exist to

test the strength of these hypotheses. Given that there is commonly much spatial and temporal variability in the thermal environment of nesting sites of TSD species and that many TSD species have relatively extended reproductive longevity, there is usually variation in mean primary sex ratios over a large time scale in TSD species. This observed variation is at odds with hypothetical models that often assume that TSD species have dramatic and unidirectional sex ratio biases (e.g., Freedberg and Wade 2001). Furthermore, the dynamics of a population are greatly affected by the operational sex ratio, which appears to be as variable in GSD species as it is in TSD species. Nevertheless, for small populations, the presence of TSD is likely associated with a higher risk of extinction than for small populations with GSD. Overall, there is little difference in the adaptive benefits of GSD and TSD for large populations with extended adult longevity and variable primary sex ratios across reproductive seasons (see Valenzuela, Chapter 14). In all other cases, TSD should be selected against, although its continued existence in smaller populations has necessitated the construction of alternative selection hypotheses (Charnov and Bull 1977).

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