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The effect of temperature on sex determination

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CHAPTER 3

Divergent evolution of sex determination in the snow skink *N. ocellatus*: a theoretical analysis

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In preparation for The American Naturalist

Abstract

In most organisms the sex of an individual is determined by its genes. In other organisms, many reptiles for example, sex is determined by environmental factors like temperature. Transitions between the two systems seem to be common, however the evolutionary significance is still unclear. On theoretical grounds several hypotheses have been proposed to explain the evolutionary significance of temperature dependent sex determination, however empirical support is scarce. Here in this study we make use of individual-based simulations to investigate several of these hypotheses by implementing empirical life history as well as environmental data of the snow skink, *N. ocellatus*. The snow skink is especially suitable for this kind of study since genetic as well as temperature dependent sex determination exist within this species in different populations.

Introduction

In most species an individual's sex is uniquely determined by its genetic makeup (genotypic sex determination; GSD), but in some species an individual's sex is determined by properties of its environment (environmental sex determination; ESD) (Bull, 1983; Valenzuela *et al.*, 2003). The most common form of ESD is temperature-dependent sex determination (TSD), where an individual's sex is determined by the temperature experienced during a specific period of the embryonic development (Valenzuela & Lance, 2004). TSD is particularly common in reptiles (Janzen & Paukstis, 1991a), but also occurs in some fish (Conover, 1984) and invertebrates (Korpelainen, 1990). Phylogenetic analyses suggest that in reptiles multiple evolutionary transitions from GSD to TSD and vice versa have occurred (Janzen & Krenz, 2004), but the adaptive significance – if any – of these transitions remains mostly obscure.

Theoretically, whether ESD or GSD is favored by selection, depends on the balance of two opposing forces (Bull, 1983; Shine, 1999; Uller *et al.*, 2007). In favor of ESD is the flexibility it affords in adjusting the sex ratio. There are several hypotheses that specify exactly how a biased sex ratio translates into a benefit (Shine, 1999), but by far the most influential is the Charnov-Bull model (Charnov & Bull, 1977). This model is based on Trivers and Willard's (1973) idea that offspring fitness may co-vary in a sex-specific way with environmental conditions, such as maternal condition or temperature. Thus, ESD is a specific mechanism that facilitates adaptive matching between offspring sex and the environment. In contrast, GSD typically leads to approximately even sex ratio regardless of the environment. This consistency in even sex ratios is precisely the benefit of GSD under conditions that select against ESD, i.e., large between-year variation in environmental conditions that may cause maladaptive large sex ratio fluctuations and even (local) extinctions (Bulmer & Bull, 1982; Bull & Bulmer, 1989; Leimar *et al.*, 2004; Schwanz & Proulx, 2008). Which of the two forces dominates likely depends on the magnitude of the sex-specific fitness differences, the magnitude of environmental fluctuations, life history details and the details of the mechanism of sex determination.

It has proven quite hard to test these ideas, for a number of reasons. First, in species with TSD it's difficult to generate individuals of the "wrong" sex under

temperatures that usually generate the opposite sex. However, using hormonal manipulation to decouple sex and incubation temperature and the appropriate control treatments, Warner and Shine (2008) showed that males (and to a lesser extent females) from their “normal” temperature had higher reproductive success than individuals from incubation temperatures that normally overproduced the other sex. However, this study was carried out in captive colonies and whether the same results will hold in natural populations is unknown. Furthermore, the fitness difference was not related to the proposed selection behind evolution of TSD – matching offspring sex to hatching date (Warner & Shine, 2005; Warner *et al.*, 2009) – and could simply be the result of secondary acquired sex-specific thermal optima for developmental processes. An alternative approach would be to address differences in selection pressures in species or populations that differ in sex determining systems. Several species of lizard and fish show intraspecific variation in sex determining mechanisms. Perhaps the best known is the Atlantic silverside, a fish with a latitudinal cline from GSD to ESD.

The viviparous snow skink, *Niveoscincus ocellatus*, is a species which appears to have both GSD and TSD (Wapstra *et al.*, 1999; Wapstra & O'Reilly, 2001; Wapstra & Swain, 2001). Females from a coastal population have offspring sex ratios that are temperature-dependent, while females from a mountain population produce an insensitive even sex ratio (Wapstra *et al.*, 2004; Wapstra

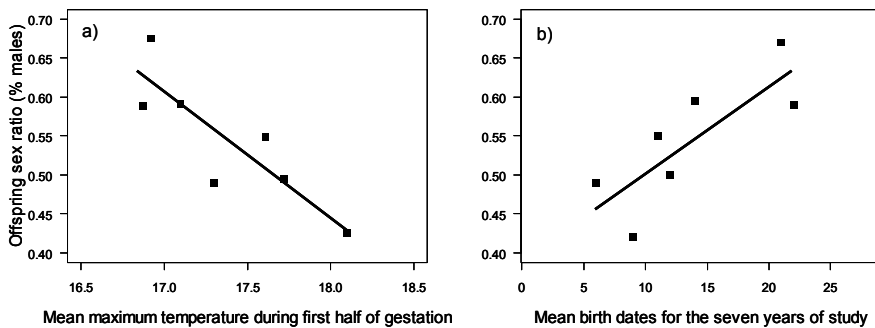


Figure 3.1: Offspring sex ratio in the lowland population dependent on a) the mean maximum temperature during the first half of gestation; b) mean birth dates (January) for the seven years of study. (Adapted from Wapstra *et al.*, 2008.)

et al., 2009; Wapstra *et al.*, unpublished data) (Figure 3.1). Details of the underlying sex determining mechanisms are unknown. In the coastal population, thermal sensitivity results in seasonal sex ratio trends that might be adaptive because females appear to profit more from being born early than males as a result of sex-specific fitness consequences of body size (Wapstra *et al.*, 2004). In the mountain population this advantage appears to be weaker, and there are stronger between year fluctuations in temperature that might select against TSD. Clearly models are needed to investigate whether the advantages outweigh the disadvantages or vice versa.

Here we use an individual-based model approach to address whether models tailored to the life history and climatological differences between the two populations generate differences in sex determination that resemble those found in natural populations. Further, we use different sex determining systems in order to assess to what extent population divergence depends on ancestral sex determination. Our results suggest that observed differences are consistent with an adaptive scenario, in particular as we find temperature dependent sex ratio responses in the lowlands but not in the highlands. Interestingly these results are robust independent of the underlying sex determining system.

The Model

Temperature variation

Temperature data were collected at the lowland and highland field sites on a daily basis from January 1988 – January 2008. These data were used to calculate the long term mean yearly temperature (T_M), between year temperature variation (σ_B) as well as the within year temperature variation (σ_W) (Table 3.1). Temperature sensitivity of sex determination occurs throughout the first half of gestation (Wapstra *et al.*, unpubl data), which corresponds well with the gonadal differentiation in embryos occurs in the first half of gestation (Neaves *et al.*, 2006). We therefore considered a three months range, October-December for the lowlands and November-January for the highlands, to calculate σ_B . To estimate σ_W , we calculated the variation between average temperatures of 10 day intervals within the three months range for both sites separately. To determine the reliability of this estimate, we also determined the

Table 3.1: Overview of standard parameters used in the model.

Parameters	Lowlands	Highlands
Longterm mean yearly temperature (T_M)	17.41	15.43
Between year temperature variation (σ_B)	0.59	1.45
Within year temperature variation (σ_W)	3.22	4.27
Maximum lifespan	8	11
Minimum age of maturation	2	3
Number of offspring per female	2-4	2-6
Number of offspring for females at minimum age maturation	1-2	2-3
Survival probability of early born offspring (S_E)	0.54	0.48
Survival probability of late born offspring (S_L)	0.22	0.35
Survival probability adults (S_A)	0.55	0.45
Probability of early born female offspring to breed with minimum age of maturation (P_E)	0.5	0.9
Probability of late born female offspring to breed the following season (P_L)	0.1	0.7
Probability of being assigned to early/late breeders (P_B)	0.8	0.8
Threshold (gene-product of one Z chromosome = 1)	1.1	1.1
Curve mean (μ_C)	17.41	15.43
Standard deviation of the curve (σ_C)	2.5	2.5
Mutation probability of threshold, curve mean, and curve SD	0.01	0.01
Mutation step size for threshold, curve mean, and curve SD	0.01	0.01

temperature variation for intervals between 5-20 days which resulted in a similar variation and were thus not included in the analysis.

In the model “yearly temperature” (T_Y) is calculated each time-step by drawing a value from a normal distribution with mean T_M and with standard deviation σ_B . T_Y is further used to calculate the female specific temperature (T_F) which resembles within year temperature fluctuations by drawing a value from a normal distribution with mean T_Y and with standard deviation σ_W .

Underlying sex determining systems

As the sex determining system in *N. ocellatus* is unknown we implement several different system in order to test the robustness of our results. First, we used a gene dosage system based on the system described for the dragon lizard, *Pogona vitticeps* (Quinn *et al.*, 2007). In this system intermediate temperatures lead to a 1:1 sex ratio, warm temperatures lead to female bias while cold temperatures lead to unviable offspring. The sum of gene-product produced by two Z chromosomes reaches the threshold level leading to male development (Figure 3.2). In females, which are ZW and thus only possess one Z chromosome but also under extreme temperature conditions the amount of gene-product is too small to reach the threshold and thus female development is induced.

In our model each individual has four loci which are necessary for sex determination. (1) The ZW-locus determines whether an individual contains ZW or ZZ chromosomes. (2) The curveMean-locus determines the mean of the curve (μ_C) which is the point along the temperature axis with maximum amount of gene product produced. μ_C equals the longterm mean yearly temperature (T_M) at the start of the simulations (Figure 3.1). (3) The curveSD-locus determines the curve standard deviation (σ_C) with μ_C as mean. (4) The threshold-locus determines the threshold (θ_C), thus the amount of gene-product that has to be produced as minimum to result in male development. To allow for new genetic variation, each curve trait locus has a probability of 0.01 to mutate and the mutation step size is drawn from a normal distribution with mean 0 and standard deviation of 0.1.

An offspring will become male if the amount of gene product produced reaches θ_C , and otherwise become female. The amount of gene product depends on the number of Z chromosomes, the curve traits of an offspring, determined by the curve trait loci, as well as on the developmental temperature, thus T_F (Figure 3.2).

In addition to the above mentioned system we also implement an XX/XY system in a similar manner. In the first scenario X is producing the gene product, where only two X chromosomes can produce enough product to reach the threshold and lead to female development, but dependent on temperature. In the second scenario Y was producing the gene product, thus the presence or

absence of Y determined whether an individual would develop as male or female, with the amount of gene product dependent on temperature.

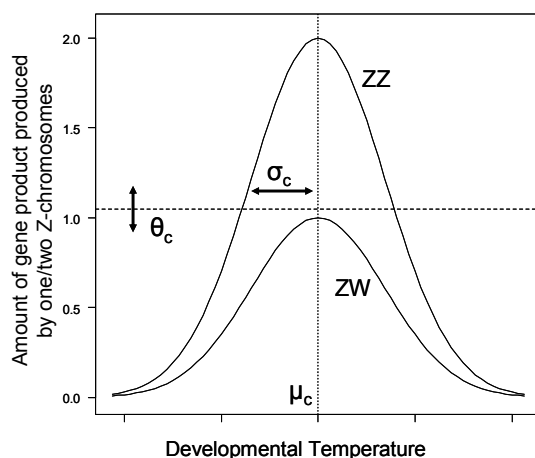


Figure 3.2: Amount of gene product produced as a function of developmental temperature. μ_c = curve mean; σ_c = curve standard deviation; θ_c = threshold that has to be reached for male development.

Maturation and clutch size determination

To facilitate model building, we divided the breeding and birth season into two categories, early and late. To determine whether a female and later her offspring are classified as early/late breeding or born respectively, T_F is compared to T_M . If T_F is higher than T_M , the female and her offspring are assigned to early breeders/born with a certain probability P_B , and otherwise to late breeders/born and vice versa. Offspring that are born early in the season have more time to develop and grow till winter compared to individuals that were born late in the season. Therefore early born females have a higher chance to breed when reaching minimum age of maturation than the late born females which will give early born females a fitness advantage compared to late born females. Female clutch sizes varied according to estimates from natural populations (Table 3.2). Females with minimum age of maturation generally have smaller clutches compared to older females. For males the probability to mature early, independent on whether they were born early or late in the season, is 90% in both populations, thus males fitness is not affected differentially by being born early or late in the season.

Table 3.2: Probabilities of clutch sizes for young and adult females in the two populations.

Age of female	Lowland population		Highland population	
	clutch size	probability	clutch size	probability
Minimum age maturity	1	0.7	2	0.8
	2	0.3	3	0.2
Adult	2	0.5	2	0.1
	3	0.3	3	0.2
	4	0.2	4	0.4
			5	0.2
		6	0.1	

Life cycle

Each simulation started with 1000 male (ZZ) and 1000 female (ZW) individuals, with equal curve trait values and the age set to minimum age of maturation. Each simulation was run for 50 000 time steps (= generations), for lowland and highland population separately, i.e. we did not consider gene-flow between the populations. Since all our parameters are of course estimates we performed a sensitivity analysis to get insights in the dependency of our results on the chosen estimates. For the parameters of interest we therefore ran simulations with the according standard value +/- 25% and +/- 50% (Table 3.1).

Females mate with a randomly assigned male and produce offspring. For each of the four loci the offspring is randomly assigned one allele of the mother and one of the father, the alleles can mutate. The sex of the offspring is determined dependent on the number of Z chromosomes, its curve traits, the threshold and the T_F . Early born offspring, late born offspring and adults have a certain probability S_E , S_L , S_A to survive to the next generation respectively until they reach maximum lifespan and will die. Offspring that have reached minimum age of maturation, have a certain probability ($P_{E/L}$) to be moved to the reproductives pool, older offspring are directly moved to the reproductives pool. From there, individuals are randomly assigned to the empty breeding spots, up to the maximum number of 1000 males and females respectively. At the end of each time step all individuals in the population age by one year and the cycle is re-started.

Throughout the simulations allele values and frequencies for all loci are monitored and the correlation between yearly temperature and sex ratio of the offspring is calculated.

Statistical analyses

For each of the 20 replica-runs with standard parameter settings we calculated the correlation coefficient between sex ratio and temperature for the early and late born offspring of the last 300 generations. A student's t-test was performed to test whether the strength of the correlation between the early and late born offspring for both the lowland and the highland population differed significantly. To test whether sex ratios were dependent on the population, date of birth, or a combination of both we performed an ANOVA. Both statistical analyses were performed in R (R Development Core Team).

Results

All three implemented sex determination scenarios resulted principally in the same outcome. The differences between the lowland and highland populations were little less pronounced under the two XY scenarios compared to the ZW scenario. Since the differences in outcome between the systems were very small we focus mainly on the results of the ZW system.

As can be seen clearly in Figure 3.3, the simulations with the standard parameters (Table 3.1) result in different sex ratio responses comparing the lowland and the highland population. In the lowland population the sex ratio of early born offspring is female biased whereas the sex ratio of late born offspring is male biased (Figure 3.3). In the highland population an even sex ratio is observed in the early as well as late born offspring. When plotting sex ratios against temperature a clear negative correlation with more females being produced at warm temperatures is observed for the lowland population, whereas no correlation is found for the highlands. The correlation between sex ratio and temperature between the 20 replica runs is significantly higher in the lowland compared to the highland population (t-test: $df = 36$; $t = 3.29$; $p = 0.002$). An Anova revealed that sex ratio variation is significantly dependent on population, date of birth, as well as the combination of population and birth date (Table 3.3).

Table 3.3: Results of an Anova testing the effect of birth date and population on sex ratio. Both factors as well as the interaction of population and birth data have a significant effect on the sex ratio.

	DF	Sum Sq	Mean Sq	F	P
Population	1	0.020	0.020	7.76	0.007
Birth date	1	0.196	0.196	75.14	<0.001
Population x Birth date	1	0.088	0.088	33.74	<0.001
Residual	76	0.199	0.003		

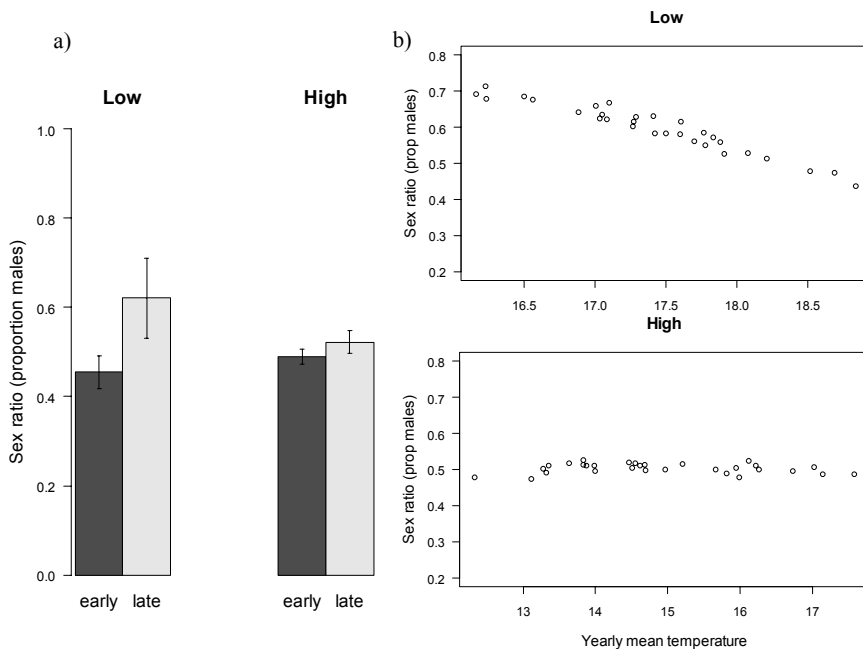


Figure 3.3: Comparison of sex ratios between the highland and lowland populations. a) Mean sex ratios of the lowland and highland population as well as between early and late born offspring of 20 replicate runs. Error bars indicate the standard deviations between the runs. Sex ratios are significantly dependent on the population, birth date as well as the interaction of both (Table 3); b) Sex ratio – temperature correlation over 30 generations in the lowland and highland population depicted for one example run. The correlation between sex ratio and temperature of the last 30 generations, calculated over 20 replica runs, is significantly higher in the lowland population compared to the highland population (t-test: $df=36$; $t=3.29$; $p=0.002$).

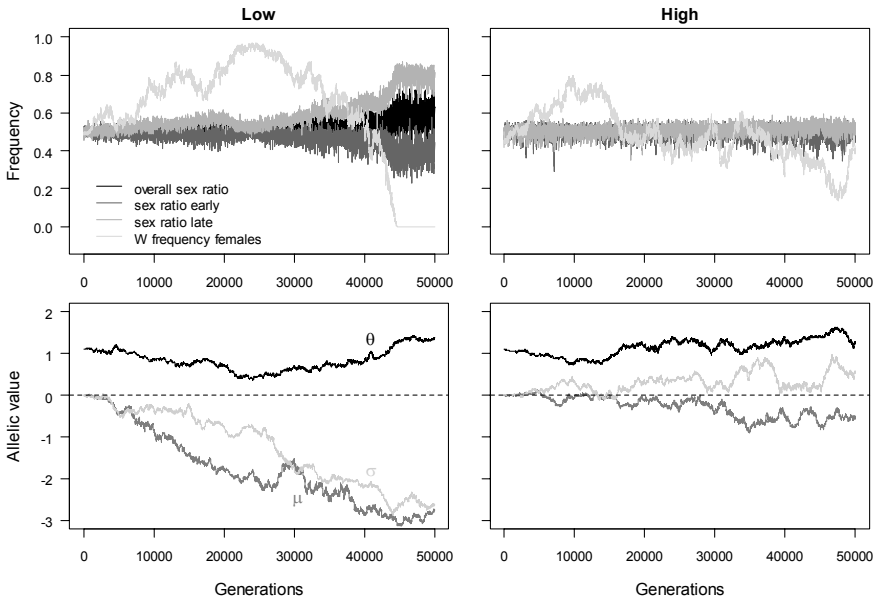


Figure 3.4: Typical simulation runs for the canonical lowland and highland parameter sets. Upper panels depict dynamics of sex ratios and frequencies of the W chromosome. Lower panels show dynamics of average threshold values (θ) as well as the deviation from the mean at the curve mean (μ_C) and curve SD (σ_C) locus. For the lowland population the σ_C and μ_C become smaller, which leads to shift of the curve to the left, resulting in differential sex ratios for early and late born offspring, determined by temperature. In the highland population allele values fluctuate, however a balanced sex ratio independent of the birth timing, is given throughout the simulation.

When looking at the dynamics of the simulations (example of one run with standard parameters Figure 3.4) one can also see clear differences between the lowland and the highland population. In the lowland population the curve mean (μ_C) and the standard deviation of the curve (σ_C) decrease constantly (Figure 3.4). The more the curve shifts to the left, the less females are produced at low temperatures until at some point mostly males are produced at low and mostly females at high temperatures. As the effect of temperature on sex determination becomes stronger the role of W becomes weaker and it goes extinct. The reason why sex ratios are not biased up to 100% male and 100% female at extreme temperatures is that additional variation to the yearly mean temperature is added by introducing within year temperature variation. This translates into between

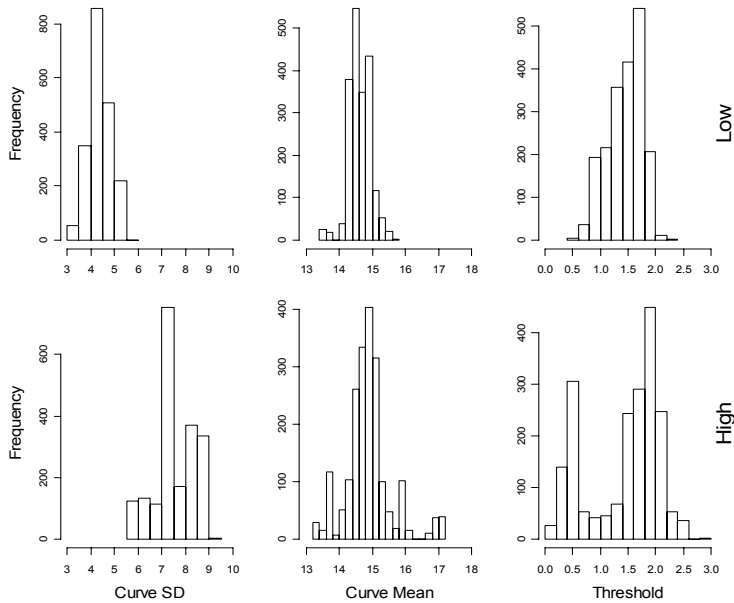


Figure 3.5: Allele distribution in the last generation at the curve SD, curve mean and threshold locus. Examples result from one simulation with standard parameters for the low- and highland populations.

female temperature variation, which means that in years with cold temperatures that would normally result in male offspring only, some females still produce female offspring and vice versa.

In the highland population several allele values fluctuate over time, however the overall sex ratio as well as sex ratio in the early and late born offspring stays balanced (Figure 3.4). The allele distribution in the lowland and highland population of the last adult generation are depicted in Figure 3.5. Here again, as mentioned above, it can be seen that in the lowland population σ_C and μ_C have become smaller and shifted from a previous mean of 7.0 and 17.41 to approximately 4.2 and 14.6 respectively. The threshold on the other hand increased from 1.1 to approximately 1.5. For the highland population the mean at the three loci changed only slightly over the 50 000 generations. However, the allele distributions at the θ_C locus seems to follow a bimodal distribution which might indicate that the alleles are branching, and the population evolves towards allelic minima and maxima. The negative effect on the evolution of

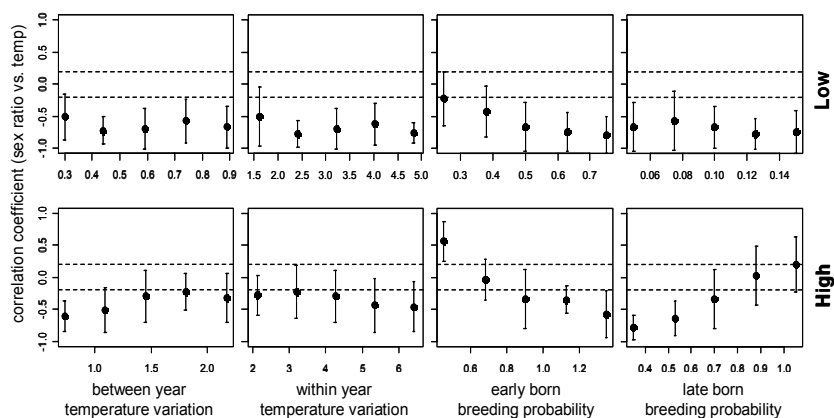


Figure 3.6: Results of the sensitivity analysis to test the influence of various parameters on the probability of TSD to evolve and the strength of the correlation between sex ratio and temperature. The mean correlation coefficient of the last 300 generations of 20 replicate runs was used to calculate the overall mean and standard deviation. The intermediate data point represents the results for the standard parameter value with the others being $\pm 25\%$, $\pm 50\%$ of the standard value. The dotted line indicates the significant level of the correlation coefficient for $N = 100$.

TSD of between year temperature variation can be seen in the results of the sensitivity analysis for the highland population (Figure 3.6). We expect the same to hold true for the lowlands however the investigated temperature range is smaller in the lowlands compared to the highlands. A certain amount of within year temperature variation promotes TSD in the highlands, leading to a higher sex ratio variation between females within the population, thus preventing extremely biased sex ratios. The fitness difference in the probability of female offspring breeding in advance influences the probability of TSD evolution and also the strength of the sex ratio – temperature correlation (Figure 3.6). To test whether indeed the difference in breeding probability in early and late born offspring is the driving force behind TSD evolution simulations were run with similar parameter settings as before, except early and late born offspring had the same breeding probability and the same number of offspring. None of the parameter combinations resulted in a significant correlation between sex ratio and temperature, thus strongly suggesting that the fitness advantage of early born females leads to the evolution of TSD (data not shown). To test whether GSD would evolve from a TSD system, additional simulations

were run starting with a TSD system (curve mean moved to the lower limit of the mean within year temperature variation). For all parameter combination these runs resulted in very high correlation coefficients in both populations with lower standard deviation compared to the results with the standard mean (data not shown).

Discussion

As outlined above the evolution of GSD or TSD seems to depend on the interaction and strength of various factors, like sex-specific fitness differences, environmental fluctuations, life history details and possibly also the underlying sex determining mechanism. Warner & Shine (2008) recently investigated the effect of sex-specific fitness differences in the Jacky dragon, *Amphibolurus muricatus*. By hormonally manipulating the sex of the offspring it was shown that individuals from their “normal” temperature had a higher reproductive success than individuals incubated at the opposite temperature. However, in that study it can not be ruled out that e.g. secondarily acquired sex-specific thermal optima play a role instead of the formerly proposed matching offspring sex to hatching data (Warner & Shine, 2005). With the snow skink, *N. ocellatus*, this problem can be circumvented as both TSD and GSD exist within one species. By making use of individual-based simulations we investigated the effect of sex-specific fitness differences, environmental fluctuations and life history details.

Our results show that by implementing empirical information on life history data and data on environmental conditions, we were able to simulate the evolution of the two different sex ratio response patterns observed in the two snow skink populations. Our results also show that the outcome with TSD in the lowland and GSD in the highland population, is robust independent of the underlying sex determining system. In addition we show that the driving force leading to the evolution of TSD in the lowland population is temperature dependent sex specific fitness differences. In the lowland population female offspring that are born early in the population have a higher chance of breeding the following season and have a higher survival probability compared to late born offspring (Table 3.1), which under standard settings leads to the evolution of TSD, a correlation between sex ratio and temperature respectively. Simulations in which early and late born offspring had the same chance of

breeding the following season as well as the same survival probability, did not lead to a correlation between sex ratio and temperature whatsoever (data not shown). The potential of differential fitness to promote the evolution of TSD is additionally shown by the sensitivity analysis (Figure 3.6), where in both populations higher differences between early and late born females in breeding probability, lead to higher sex ratio-temperature correlation, thus higher probability of TSD evolution. In the highland population early born female offspring also have a higher chance of breeding sooner than late born female offspring and also a higher chance of survival, however the differences are less pronounced and also the temperature sex ratio correlations are lower compared to the lowland population. The sensitivity analysis also shows that these subtle differences might already be enough to select for TSD, however strong between year temperature fluctuations in the highlands lead to selection for GSD (Figure 3.6). This brings us to the next point. Besides showing the potential of differential fitness to promote the evolution of TSD, the results of the sensitivity analyses also seem to match previous hypotheses that strong environmental fluctuations leading to strong sex ratio fluctuations select for GSD (Bulmer & Bull, 1982; Leimar *et al.*, 2004). Within year temperature variation on the other hand, which can also be considered as temperature variation between females, has only a marginal effect on the strength of the sex ratio-temperature correlation. However, when looking at the average yearly sex ratio within year temperature variation plays an important role, and might explain the absence of 100% female and male sex ratios, at least for the simulation results. This is because within year temperature fluctuations add additional variation to the temperature range. Therefore in years with extreme mean temperatures, which by itself would lead to the development of single sexed offspring, some females experience less extreme temperatures and produce offspring of the opposite sex, preventing single sexed average sex ratios. Whether between female temperature variations prevent the occurrence of extreme average sex ratios in nature is unknown, but could be investigated by measuring body temperatures of single females during the gestation period, determining the temperature variation and also the sex ratio of the offspring.

A very interesting finding of our results is the bimodal allele distribution at the threshold locus in the highland population, which suggests that the alleles at this locus are branching (Figure 3.5). The implications of extreme alleles at the

threshold locus are that in this population a mixture of two GSD systems is evolving. For heterozygous individuals, thus with a low and high threshold allele, sex determination would function as depicted in Figure 3.2. In *ZW* individuals only one *Z* produces gene product, which is not enough to reach the threshold and therefore the individual becomes female. In *ZZ* individuals intermediate temperatures result in enough gene produce of the two *Z* chromosomes that the individual will become male. At extreme temperatures however, not enough gene product is produced and even *ZZ* individuals become females. Homozygous individuals for the low threshold alleles will become exclusively males as the gene product of one *Z* chromosome is enough to reach the threshold. On the other hand individuals homozygous for the high threshold alleles will become female as even two *ZZ* chromosomes will not be able to produce enough gene product to reach the threshold. Overall the mixture of these two systems still results in an even sex ratio independent of temperature. In another, more general model of ours, we recently investigated the probability of transitions from GSD to TSD and also encountered several parameter combinations in which mixed systems, such as this or mixtures of TSD and GSD evolved (Feldmeyer *et al.*, in prep). To detect such a system in nature will be very challenging as the second mechanism (the branched threshold locus in our example) is hard to detect and easily overlooked compared to differentiated sex chromosomes. In species without differentiated sex chromosomes one might be able to find sex determination linked to two loci.

In summary, our results show that it seems possible to model the occurrence of two sex determining systems in the snow skink by implementing empirically obtained life history as well as temperature data. Furthermore our results match the differential fitness hypothesis proposed by Charnov & Bull (1977) as well as hypotheses that temperature fluctuations negatively affect the evolution of TSD (Bulmer & Bull, 1982; Leimar *et al.*, 2004). Our approach might prove useful in other species with uncertain temperature effect on sex determination of which life history parameters as well as environmental conditions are studied, to investigate the probabilities of certain sex determining systems to evolve and possibly be presence in the focal species. We additionally could show that it is of minor relevance which underlying sex determining system is chosen to start the simulations, as our results are robust independent of the starting GSD system.

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Part II: Empirical Approach

