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Climate change, sex reversal and lability of sex-determining systems

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Abstract

Sex reversal at high temperatures during embryonic development (e.g., *ZZ* females) provides the opportunity for new genotypic crosses (e.g., *ZZ* male × *ZZ* female). This raises the alarming possibility that climatic warming could lead to the loss of an entire chromosome—one member of the sex chromosome pair (the *Y* or *W*)—and the transition of populations to environmental sex determination (ESD). Here we examine the evolutionary dynamics of sex-determining systems exposed to climatic warming using theoretical models. We found that the loss of sex chromosomes is not an inevitable consequence of sex reversal. A large frequency of *ZZ* sex reversal (50% reversal from male to female) typically divides the outcome between loss of the *ZW* genotype and the stable persistence of *ZZ* males, *ZW* females and *ZZ* females. The amount of warming associated with sex chromosome loss depended on several features of wild populations—environmental fluctuation, immigration, heritable variation in temperature sensitivity and differential fecundity of sex-reversed individuals. Chromosome loss was partially or completely buffered when sex-reversed individuals suffered a reproductive fitness cost, when immigration occurred or when heritable variation for temperature sensitivity existed. Thus, under certain circumstances, sex chromosomes may persist cryptically in systems where the environment is the predominant influence on sex.

KEYWORDS

fish, *Pogona*, reptiles, temperature-dependent sex determination

1 | INTRODUCTION

Whereas a dichotomous system of gamete production—anisogamy—is almost ubiquitous among sexually reproducing organisms, sexual systems are quite diverse (Bachtrog et al., 2014; Beukeboom & Perrin, 2014; Otto, 2009). In many species, individuals develop irreversibly into either male or female, and a gene of major effect located on a sex chromosome commits the gonad to ovary or testis during development (genotypic sex determination, GSD). In these species, phenotypic sex assorts with chromosomal complement (male heterogamety, XX/XY, or female heterogamety, ZZ/ZW). In other species, sex chromosomes are not present and environmental conditions during gonadogenesis (e.g., temperature) exert strong influence over sexual development and effectively determine sexual outcome (Environmental Sex Determination, ESD; Bachtrog et al., 2014; Beukeboom & Perrin, 2014).

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There exists also a theoretical continuum of sex-determining systems, with ESD and GSD at opposite extremes and systems with mixed influences of genotype and the environment in the middle (Quinn, Sarre, Ezaz, Marshall Graves, & Georges, 2011; Sarre, Georges, & Quinn, 2004). In particular, it is possible for individuals with sex chromosomes to develop into the phenotypic sex that is discordant with genotypic sex, termed sex reversal. For example, in medaka fish, a copy of the *DMRT1* gene on the *Y* chromosome triggers male development in *XY* individuals; however, high developmental temperatures induce expression of autosomal *DMRT1* genes and lead to male development in *XX* individuals (Hattori et al., 2007; Matsuda et al., 2002; Nanda et al., 2002). Sex reversal owing to extreme temperatures or exposure to exogenous hormones has been demonstrated in captivity in an increasing number of vertebrate species, with many more species likely to be susceptible (Baroiller & D'Cotta, 2016; Devlin & Nagahama, 2002; Flament, 2016; Holleley, Sarre, O'Meally, & Georges, 2016; Senior & Nakagawa, 2013). Moreover, discordant animals have been caught in the wild in a handful of species (Baroiller & D'Cotta, 2016; Holleley et al., 2015, 2016; Perrin, 2009). Sex reversal may therefore be widespread and occur with significant frequency across wild ectothermic vertebrates under changing environmental conditions.

The potential for sex reversal and mixed sex-determining systems in the wild has profound implications for genome evolution. Frequent matings between homogametic males and females (i.e., *ZZ* males × *ZZ* females) could drive the heterogametic genotype and its associated chromosome (i.e., *W*) out of the population. Indeed, sex reversal owing to environmental sensitivity of the sex-determining network may drive the evolutionary lability of sex-determining systems (i.e., GSD vs. ESD) in fishes, amphibians and reptiles (Bachtrog et al., 2014; Gamble et al., 2015; Janzen & Krenz, 2004), with repeated loss and re-establishment of sex chromosomal function under changing environmental conditions (Ezaz, Sarre, O'Meally, Marshall Graves, & Georges, 2009; Georges, Ezaz, Quinn, & Sarre, 2010; Grossen, Neuenschwander, & Perrin, 2011; Perrin, 2009; Sarre, Ezaz, & Georges, 2011). Sex reversal in GSD systems can also be associated with continued recombination between nonhomologous sex chromosomes, thereby facilitating a 'fountain of youth' against chromosomal degradation where deleterious mutations that accumulate on the *Y* are purged through recombination with the *X* in sex-reversed females (Perrin, 2009).

What remains unclear is the outcome of environmentally induced sex reversal in natural populations. Does sex reversal trigger an inexorable turnover in sex-determining systems (GSD to ESD) or can a mixed system of sex determination persist stably across time even in the face of significant environmental change? Theoretical approaches have demonstrated both stability and instability of mixed sex-determining systems, depending on the assumptions. Rapid turnover in sex-determining systems from GSD to ESD occur when there is a selective advantage to having ESD (i.e., there are sex differences in the fitness consequences of incubation temperature; Schwanz, Ezaz, Gruber, & Georges, 2013) or when the environment changes dramatically in one direction such that more than 50% of homogametic individuals are sex-reversed (Grossen et al., 2011; Holleley et al., 2015). Alternatively, mixed systems may persist provided sex reversal occurs in a minority of individuals (Grossen et al., 2011; Holleley et al., 2015). In all cases, frequency-dependent selection on the sex ratio exerts a complex feedback on phenotypic and genotypic frequencies (Grossen et al., 2011; Holleley et al., 2015; Schwanz et al., 2013). Yet, we know nothing about how factors that influence the frequency of genotypes and sexes in natural populations, such as stochasticity, migration and differential fitness, affect the dynamics of sex-determining systems.

Here, we examine the theoretical dynamics of sex-determining systems under realistic, short-term environmental change that causes sex reversal. Our goal is to determine whether such perturbations are likely to lead to the loss of sex chromosomes and trigger turnover to ESD under natural scenarios not previously considered. First, we examine the impact of stochasticity owing to increased interannual temperature variability, because extreme warm years may amplify sex reversal, whereas extreme cool years may buffer the population by augmenting concordant animals. Second, the geographical range of a species may cover a patchy thermal landscape, such that a population with sex reversal may be 'rescued' by immigrants from populations with different frequencies of sex reversal. Third, we examine the extent of buffering provided by genetic variation for the sensitivity of sex reversal to temperature (Holleley et al., 2015), which would create noise in sex ratio biases. Finally, turnover to ESD could be accelerated or buffered through selection if sex-reversed individuals have higher or lower fitness compared to sexually concordant individuals (Holleley et al., 2015; Li, Holleley, Elphick, Georges, & Shine, 2016; Senior, Lim, & Nakagawa, 2012).

Our theoretical formulation is broad enough to maintain applicability across taxa; however, we base our formulation on the bearded dragon of arid Australia (*Pogona vitticeps*), one of the few species known to exhibit sex reversal in wild populations (Holleley et al., 2015). This sex reversal has been shown in the laboratory to be caused by high temperatures experienced by the egg during incubation such that genotypic (*ZZ*) males become viable phenotypic females (Holleley et al., 2015; Quinn et al., 2007). The species demonstrates within-population variation in sensitivity to sex reversal and a fecundity advantage in sex-reversed females (Holleley et al., 2015), provoking critical questions on how these features impact the stability of the sex-determining system. This species has emerged as a testing ground for the ecological and evolutionary dynamics of mixed sex-determining systems and as a poster child for unanticipated impacts of climatic warming.

2 | MATHEMATICAL MODEL

We first consider a simple, structured model of a *ZZ*/*ZW* population to project the number of *ZZ* males (concordant males, n_{ZZm}), *ZZ* females (sex-reversed females, n_{ZZf}) and *ZW* females (concordant females, n_{ZWf}) over time (t). We assume that all phenotypic males are *ZZ* and that female fecundity does not depend on the number of males in the population. In addition, we assume that concordant and sex-reversed females do not differ in fecundity (b) or in the frequency of sex reversal in *ZZ* offspring (ν). A discrete time model may be represented as:

$$n_{ZWf}(t+1) = \frac{1}{2} n_{ZWf}(t) b.$$

$$n_{ZZm}(t+1) = \left[n_{ZZf}(t) + \frac{1}{2} n_{ZWf}(t) \right] b(1-\nu).$$

$$n_{ZZf}(t+1) = \left[n_{ZZf}(t) + \frac{1}{2} n_{ZWf}(t) \right] b\nu.$$

The population projection matrix can be used to track the frequency of males (n_{ZZm}/N), the frequency of phenotypic females that are sex-reversed ($n_{ZZf}/(n_{ZZf} + n_{ZWf})$) and the frequency of the *ZW* genotype (n_{ZWf}/N) in the population, where N is the total population size. In addition, the eigenvector associated with the dominant eigenvalue of the 3 × 3 matrix provides the frequency of each type at stable state for a given level of sex reversal.

Under this formulation, sex reversal of less than 50% leads to a stable and intermediate frequency of sex-reversed females (Figure 1). Thus, populations can persist with mixed influences of environmental and genotypic sex determination, where some individuals have phenotypes concordant with chromosomal complement, whereas others are discordant. High levels of sex reversal (ν = 0.5) are required before *ZZ*f replaces *ZW*f in the population, and the *W* chromosome disappears. When sex reversal is greater than 50%, the *ZZ* genotype becomes fixed in the population. The sex ratio becomes increasingly female-biased as the proportion of sex reversal increases, under the absence of novel sex-determining alleles.

3 | SIMULATION MODEL

We used an individual-based simulation model to address four questions related to the stability of genotypic sex determination under conditions more realistic for wild populations:

1. How are sex reversal and sex chromosome stability impacted by an increase in mean or variance of annual nest temperatures?
2. How are these outcomes counteracted by immigration of *ZW* individuals?
3. How are these outcomes influenced by genetic and heritable variation in sensitivity of sex reversal to temperature?
4. How are these outcomes influenced by sex-reversed females (*ZZ*f) having differential fecundity compared to concordant females (*ZW*f)?

To address each of these questions, the model was parameterized as in Table 1, with replicate simulations differing according to (a) the global mean of the annual mean nest temperatures, quantified as a departure in degrees Celsius from an arbitrary baseline (i.e., historical) level, as well as standard deviation of annual mean nest temperatures (i.e., interannual climatic variability); (b) the immigration of *ZZ* and *ZW* individuals drawn from an identically parameterized background population breeding at the global mean temperature; (c) the existence of heritable variation among individuals in the temperature at which sex reversal occurs in *ZZ* genotypes ('temperature sensitivity'); and (d) differential fecundity of *ZZ* females (*ZZ*f have 20%, 80%, 100%, 120% and 180% fecundity compared to *ZW*f). Each of these parameters was drawn randomly for each of 2,000 replicate simulations, as described below and in Table 1.

3.1 | Sex-determination system

We formulated sex determination following a dosage mechanism proposed by Quinn et al. (2011) and used previously in evolutionary simulations (Figure 2a; Schwanz et al., 2013). The formulation is a conceptual hypothesis that can be applied to all vertebrate taxa, with modest modification for taxa with male heterogamety (*XX*/*XY*) or ESD (Quinn et al., 2011). Individuals have a diploid, major sex-determining locus with two alleles with incomplete dominance (additive); here, these alleles are *Z* and *W* to encapsulate a system of female heterogamety. Both alleles express a signal to generate a male sexual outcome. At peak expression, the *W* allele produces a reduced male signal (here 25%) compared to the *Z* allele (100%). Thus, a *ZW* genotype produces a weaker male signal (62.5%) than a *ZZ* genotype (100%). Expression of the male signal peaks at an intermediate incubation temperature and declines at colder and hotter temperatures, described here by a normal curve, in contrast to the linear reaction norm presented in Grossen et al. (2011). We parameterized the temperature of peak signal (μ_{signal}; mean at arbitrary 0) and fixed the standard deviation of the signal curve (σ_{signal}; Table 1).

Crucially, there is a threshold level of male signal required to commit an individual to developing as a male (τ). We fixed this threshold to a level such that *ZW* individuals never exceeded the threshold and thus were always female (*ZW*f). At many incubation temperatures, the male signal of *ZZ* individuals exceed the threshold, and *ZZ* develop as male (*ZZ*m). However, at cold and hot temperatures, *ZZ* individuals have low male signal expression and become sex-reversed, developing as females (*ZZ*f). This formulation, therefore, accommodates empirical findings that *ZZ*, but not *ZW*, bearded dragons may be sex-reversed (*ZZ*f) at hot temperatures (Quinn et al., 2007). The arbitrary parameter values we assigned for the signal curve and threshold (mean μ_{signal}, σ_{signal}, and τ) led to sex reversal of the *ZZ* genotype at temperatures warmer than 3.7°C above the mean. Generality is maintained by focusing on the occurrence and consequences of sex reversal rather than the precise temperatures at which sex reversal occurs.

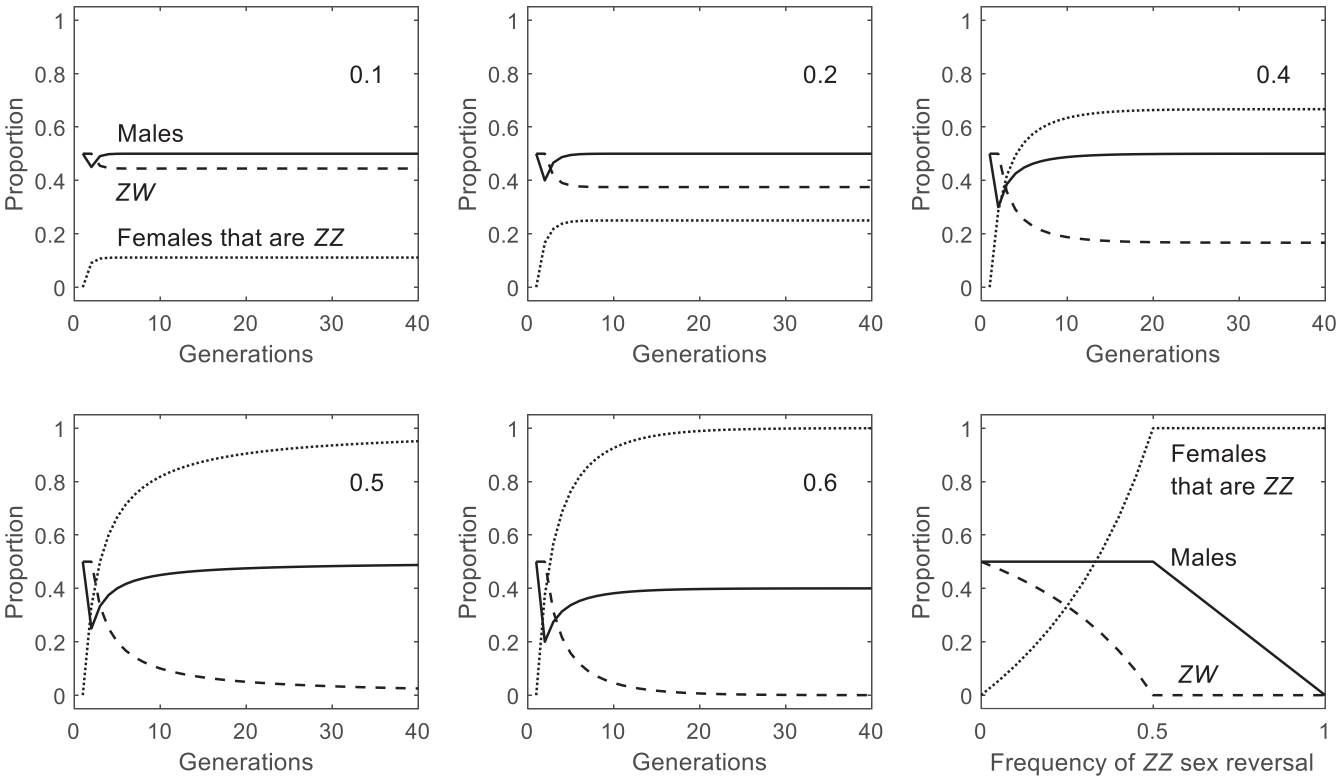

FIGURE 1 Projections and stable states of the proportion of males in the population (solid), the proportion of individuals of *ZW* genotype (dashed) and the proportion of females in the population that are sex-reversed *ZZ* (dotted; vs. *ZW*). Projections are plotted for 40 generations under 5 levels of frequency of *ZZ* sex reversal (frequency of *ZZ* that develop into females rather than males = 0.1, 0.2, 0.4, 0.5, 0.6), as shown in the number inset. Proportions of each stage at stable state are presented across all levels of sex reversal

3.2 | Defining climatic perturbation

In wild, oviparous populations, the temperature of a nest during incubation varies among nests each year owing to nest depth, moisture and cover (intra-annual variation), as well as among years according to changes in local climate (interannual variation). Both within-year and among-year variation in nest temperatures vary greatly across natural reptile populations (Tables S1 and S2; historical nest temperatures for bearded dragons are unknown). To capture intra-annual variation in our model, nest temperatures for each reproductive female were drawn from a normal distribution with a mean T_{ann} and standard deviation σ_{ann}. Intra-annual variation (σ_{ann}) was fixed in our model at 1.2, based on empirical data from several reptile species (Table S1). This value is expected to influence how step-like the response of the population is to climate change but not the fundamental features (Grossen et al., 2011). To capture mean population ('global') climate and interannual variation in climate as it relates to nest temperatures during incubation, T_{ann} was drawn each iteration of the simulation from a normal distribution with mean T_{glob} and standard deviation σ_{glob}. Our model established a set of baseline climatic conditions where the mean of annual nest temperatures (T_{glob}) was arbitrarily set to zero, thus being matched to the sex-determining signal peak. The baseline standard deviation of annual nest temperatures (σ_{glob}) was set equal to 0.5 (Figure 2b), which is a low level based on empirical data of among-year variance in reptile populations (Table S2). Under these baseline conditions, we observed no occurrence of *ZZ*f.

All simulations were initiated then iterated for 100 years at baseline climatic conditions to stabilize population demographics. At year 101, a climatic perturbation scenario was initiated. To determine this scenario—how much warmer and more variable among years the climate becomes—new T_{glob} and σ_{glob} were chosen randomly for each replicate simulation from a uniform distribution between a parameterized range of values (Figure 2c; Table 1).

3.3 | Life cycle, population dynamics and demography

In addition to defining the climatic perturbation scenario, each simulation was randomly assigned a *ZZ*f fitness differential $b_{ZZ\text{f,diff}}$, fixed or varying temperature sensitivity (μ_{signal}) and immigration rate (u) of 0 or 0.01 (as a proportion of the resident population; see Table 1), as described in the life cycle below. The fixed life history parameters for survival and fecundity approximate those of the bearded dragon, describing an iteroparous, polytocous animal with substantial overlap in generations (Table 1).

A population of 100 individuals was established upon initiation of each simulation. All individuals were randomly assigned a genotype (*ZZ* or *ZW*) at the major sex-determining locus. They

TABLE 1 Parameter values in the individual-based simulation

Parameter	Description	Values
Variable		
T_{glob}	Global mean of annual temperature	[0:6] Baseline value = 0
σ_{glob}	Standard deviation in mean annual temperature	[0.5:2] Baseline value = 0.5
$b_{ZZf,diff}$	Sex-reversed (*ZZ*f) fecundity differential, parameterized as a proportion of concordant (*ZW*f) fecundity	[0.2, 0.8, 1, 1.2, 1.8]
μ_{signal}	Temperature of peak of male signal, inherited at diploid locus: 1. invariant 2. variable among individuals, providing variation in sensitivity to sex reversal at a given temperature	[0, 0 ± 1 (normal distribution, mean ± *SD*)]
u	Annual immigration rate to the population, parameterized as a fixed proportion of current resident population size	[0, 0.01]
T_{ann}	Annual mean nest temperature of incubation	Drawn each iteration of simulation from a normal distribution with mean of T_{glob}, and *SD* of σ_{glob}
Fixed		
σ_{ann}	Within-year standard deviation in nest temperatures	1.2
q	Annual mortality rate after age 1	0.1
c	Density-dependent parameter for hatchling survival	0.01
α	Age at sexual maturity	3
b_{ZWf}	Annual clutch size of a ZW female	25
Z_{signal}	Peak signal expression of the Z allele	1
W_{signal}	Peak signal expression of the W allele	0.25
σ_{signal}	Standard deviation used to describe the male signal curve as a function of temperature	4
τ	Threshold level of male signal required to produce a male outcome	0.65

were assigned a quantitative trait value for the temperature of peak male signal (μ_{signal}), specified via two alleles with incomplete dominance. μ_{signal} was either fixed or variable among individuals, depending on the simulation scenario. If fixed, the peak of all individuals matched the long-term mean nest temperature (0; Table 1). If variable, we initiated simulated populations with genetic variants in the temperature of peak male signal, μ_{signal}. This produces variation among individuals in the temperature at which the male signal of *ZZ* genotypes falls below the threshold for male outcome, thus producing variation in the temperature at which *ZZ* individuals experience sex reversal to female. For these scenarios, alleles were chosen randomly for each individual from a normal distribution with mean = 0 and standard deviation = 1. These values are based on data from bearded dragons (Holleley et al., 2015), where the majority of variation in temperature of sex reversal (*ZZ* and *ZW* maternal genotypes) lies within a 4°C range (between 32 and 36°C) and that the accumulation of variation in the threshold of sex reversal is sigmoidal.

Each individual in the starting population was assigned a developmental temperature from a baseline normal distribution (T_{glob}, σ_{glob}), sex was determined based on genetic attributes and temperature, and all individuals were given an age of α, the age of sexual maturity (Table 1).

Each iteration of the simulation included the following steps: selection of mean nest temperatures for the year, immigration (if occurring), mating and production of clutches, assigning genetic and nongenetic attributes to embryos and survival to the next year. As described above, mean annual nest temperature T_{ann} was selected each iteration based on T_{glob} and σ_{glob}. If immigration occurred ($u = 0.01$), an integer number of immigrants was introduced into the population, where the integer is approximately 1% of the focal population size. All immigrants were at the age of first maturity. They were randomly assigned *ZZ* or *ZW*, and were fixed or varying in μ_{signal} to match the scenario of the resident population. These immigrants were drawn from a population at the mean global temperature (T_{glob}); thus, *ZZ* individuals may have been sex-reversed.

Each female of age equal or greater than age at maturity (α) produced a clutch. Male mates were assigned randomly from the pool of mature males. A nest temperature was assigned to all embryos in a clutch by drawing from a normal distribution with mean T_{ann} and standard deviation σ_{ann}. Clutch size was parameterized for *ZW*f (b_{ZWf}), whereas clutch size for *ZZ*f was calculated based on the fecundity differential scenario ($b_{ZZf,diff}$; Table 1). All embryos were randomly assigned one allele from their mother and one allele from their father at two loci: the major sex-determining locus and μ_{signal}. Sex was assigned based on temperature and genetics, and age was set at 0.

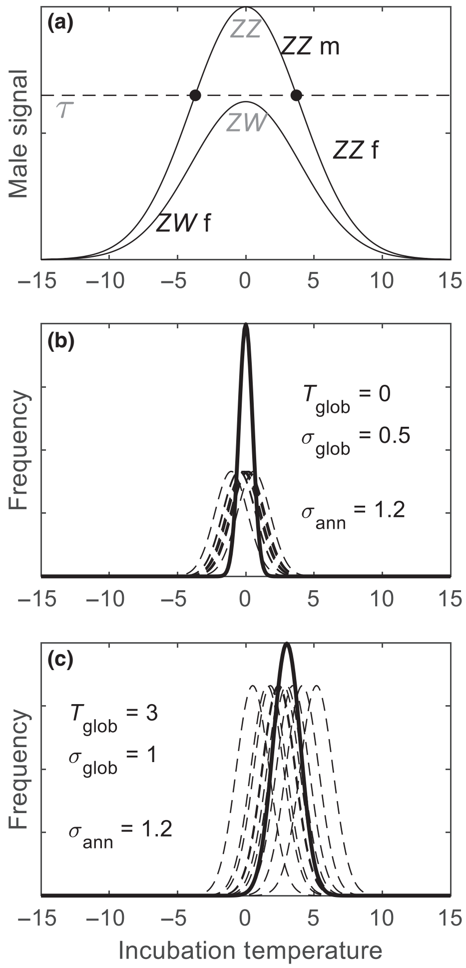

FIGURE 2 Sex determination system and climatic scenarios in the simulation model, centred around an arbitrary value of zero. (a) The high expression of male signal by the *ZZ* genotype (upper solid line) typically exceeds the threshold for developing as a male (τ, dashed line), whereas the lower expression of the *ZW* genotype (lower solid line) never exceeds the threshold. The points represent the temperatures at which the *ZZ* genotype becomes sex-reversed. This model is based on Quinn et al. (2011). Under baseline climatic conditions (b), *ZZ* individuals develop as male whereas *ZW* individuals develop as female. However, under climatic warming (c), some *ZZ* individuals develop at incubation temperatures above the hot temperature for sex reversal (+3.7°C) and are sex-reversed (*ZZ*f). For illustrative purposes, one scenario is depicted with greater mean annual temperature and greater interannual climatic variability. In (b) and (c), the solid line presents the 'global', or interannual, distribution of annual mean nest temperatures, whereas the dashed lines depict 10 annual nest temperature distributions drawn from the interannual distribution

For simplicity, viability of embryos was not dependent on nest temperature. Mortality of embryos in their first year was density-dependent and described by $1-e^{-cN}$, where c is a constant and N is the population size. Survival after the first year was based on a fixed mortality rate (q) applied uniformly regardless of age, sex or genotype. At the completion of each iteration, the age of all surviving individuals was incremented by 1 year.

The simulation was iterated for an additional 200 years of climatic perturbation to record sex reversal, population size and stability in sex-determining systems. This time frame was chosen as a relevant ecological time scale. Results from the final iteration of each simulation were used to generate contour plots.

4 | SIMULATION RESULTS

4.1 | Simple scenario

We first considered the simplest simulation scenario—no immigration, no genetic variation for temperature sensitivity and no fecundity difference between concordant and sex-reversed females. These scenarios varied according to how much temperature increased overall (T_{glob}) and how much their interannual temperature variability increased (σ_{glob}). Trajectories of selected simulations demonstrated that the demographic and genotypic features change quickly following the climatic shift. With less than 50% *ZZ* sex reversal (Figure 3 top row, red), the sex ratio (black) remained even and the *ZW* genotype (blue) persisted below 50% of the population. When *ZZ* sex reversal exceeded 50% (Figure 3 top row, red), the frequency of *ZW* declined in the population over 200 years, as the proportion of females that were *ZZ* increased (green). As the proportion of *ZW* declined, the adult sex ratio became unstable and female-biased (Figure 3 top row).

Across all replicates in this scenario (Figure 4, top row), an increase in the mean incubation temperature of a few degrees from baseline had little impact on the population, as sex reversal of *ZZ* genotypes was still only 10% (at 2-degree increase in global mean temperature). That is, a modest increase in the overall mean temperature largely produced nest temperatures that did not exceed the temperature of sex reversal (3.7°C above baseline). However, for higher mean temperatures, the incidence of sex reversal among *ZZ* individuals increased linearly with mean temperature. As *ZZ* sex reversal shifted from 10% to 50%–60% (corresponding to a temperature rise to 4°C above baseline), the populations experienced very different outcomes. Over this range of sex reversal, the proportion of *ZW* genotypes in the population dropped rapidly to close to zero, and accordingly, the proportion of females that were *ZZ* rose to nearly 1. Thus, in agreement with our mathematical model, sex reversal of approximately 50% or higher led to loss of the heterogametic (*W*) chromosome and transition to ESD (Figure 4).

High interannual variance in temperature (σ_{glob}) led to a modest increase in *ZZ* sex reversal at low levels of warming (<2°C warming; Figure 4, top row), as we would expect from extremely hot years producing a pulse of hot nest temperatures and sex reversal. This caused a reduction in *ZW* genotypes in the population at lower mean temperatures than was seen under less-variable climates. Similarly, there was a modest decrease in sex reversal at high levels of warming (>4°C warming) due to occasional extremely cold years producing unusually low numbers of sex-reversed animals. However, the buffering of sex reversal at high mean temperatures did not translate to a buffering of sex-determining system, as sex reversal was already greater than 50%.

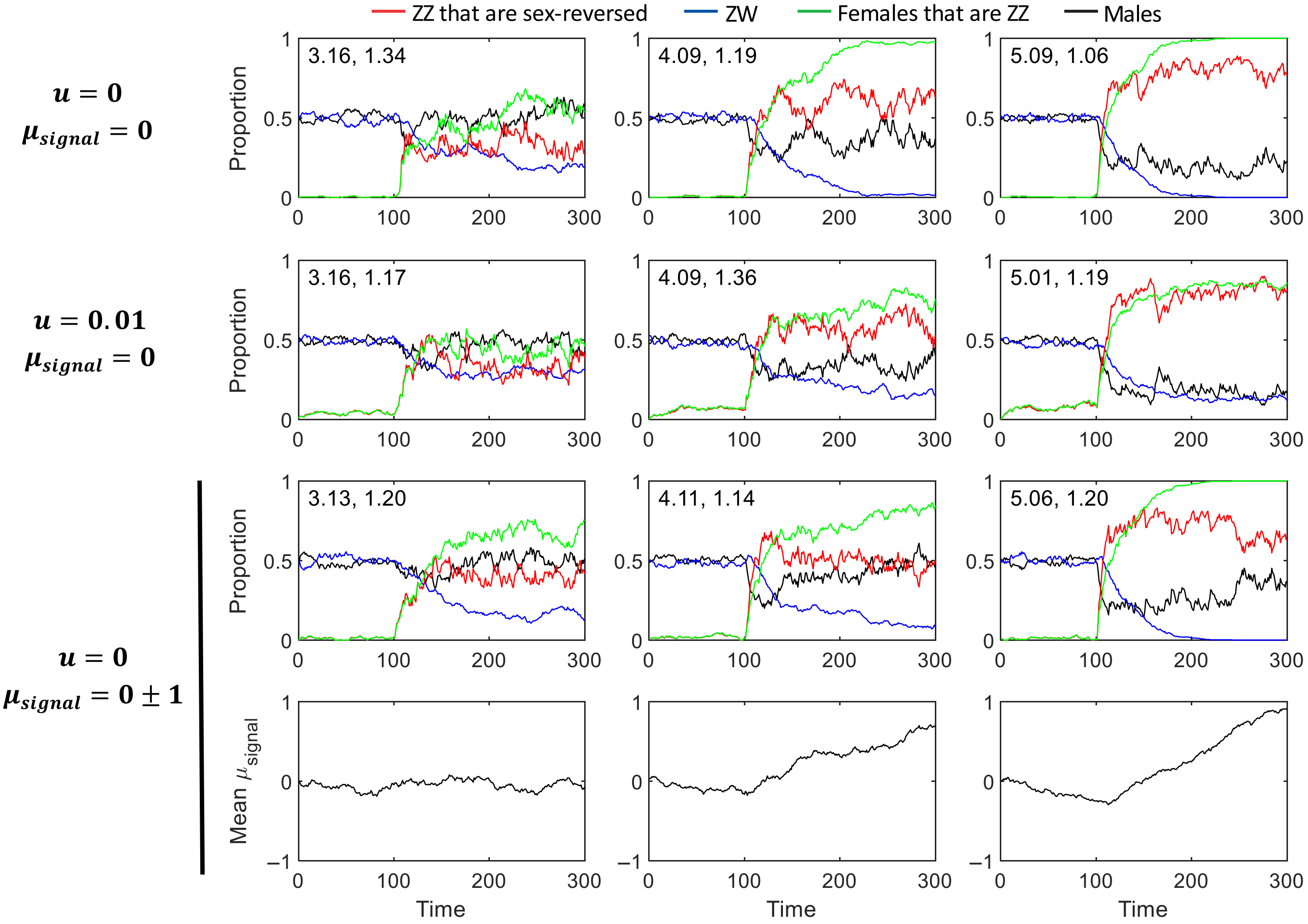

FIGURE 3 Example simulation trajectories for three levels of climatic warming where population outcomes differ (columns, inset T_{glob}, σ_{glob}; values within a column are not exactly the same due to random selection within each simulation replicate). Panel rows are from different simulation scenarios that vary according to the occurrence of immigration of sexually concordant individuals and the presence of genetic variation for temperature sensitivity of sex reversal. For all, fecundity of *ZZ*f matched that of *ZW*f. Trajectories show the first 100 iterations at baseline climate conditions, followed by 200 years of climatic perturbation. The top three rows show the proportion of *ZZ* individuals that are sex-reversed (red; *ZZ*f/[*ZZ*f + *ZZ*m]), the proportion of individuals in the population that are *ZW* (blue; *ZW*/[*ZW* + *ZZ*]), the proportion of females that are *ZZ* (green; *ZZ*f/[*ZZ*f + *ZW*]) and the proportion of males in the population (black; *ZZ*m/[*ZZ*m + *ZZ*f +*ZW*]). Bottom row shows the evolution of the population mean μ_{signal} over time for the run directly above

4.2 | Immigration

Allowing 1% annual immigration (approx. 50% *ZW*) led to a decline in *ZW* genotypes at modest warming that was similar to the scenario without immigration (approx. 2°C warming; Figure 4, middle row). However, it greatly buffered populations from the complete loss of *ZW*. Even the warmest populations maintained approximately 10% of individuals as *ZW* (Figures 3 and 4 middle rows), indicating that the infusion of the *W* allele went beyond the numerical representation of immigrants.

4.3 | Genetic variation for thermal sensitivity

Initiating a population with variation in the threshold of sensitivity expanded the temperature range at which *ZZ* sex reversal occurred (Figure 4, bottom row). Across the temperature range studied, there were no populations that experienced reversal of all *ZZ* genotypes. The incidence of sex reversal at modest temperature rises was increased compared to populations with invariant threshold of temperature sensitivity (because some genotypes had very low thresholds for sex reversal), and much warmer mean temperatures were required to see more than 50% sex reversal (some genotypes had very high thresholds for sex reversal). In many of these simulations, the temperature of sex reversal evolved to higher thresholds in the population (Figure 3 bottom rows), presumably through frequency-dependent selection on sex. Despite these changes in frequency of sex reversal, there was only a modest buffering of *ZW* loss as a result of rising nest temperatures (Figures 3 and 4).

4.4 | Fecundity differential for sex-reversed females

Altered *ZZ*f fecundity (*ZZ*f fecundity as 20%, 80%, 120% or 180% of *ZW*f fecundity) had a large impact on population response to a given

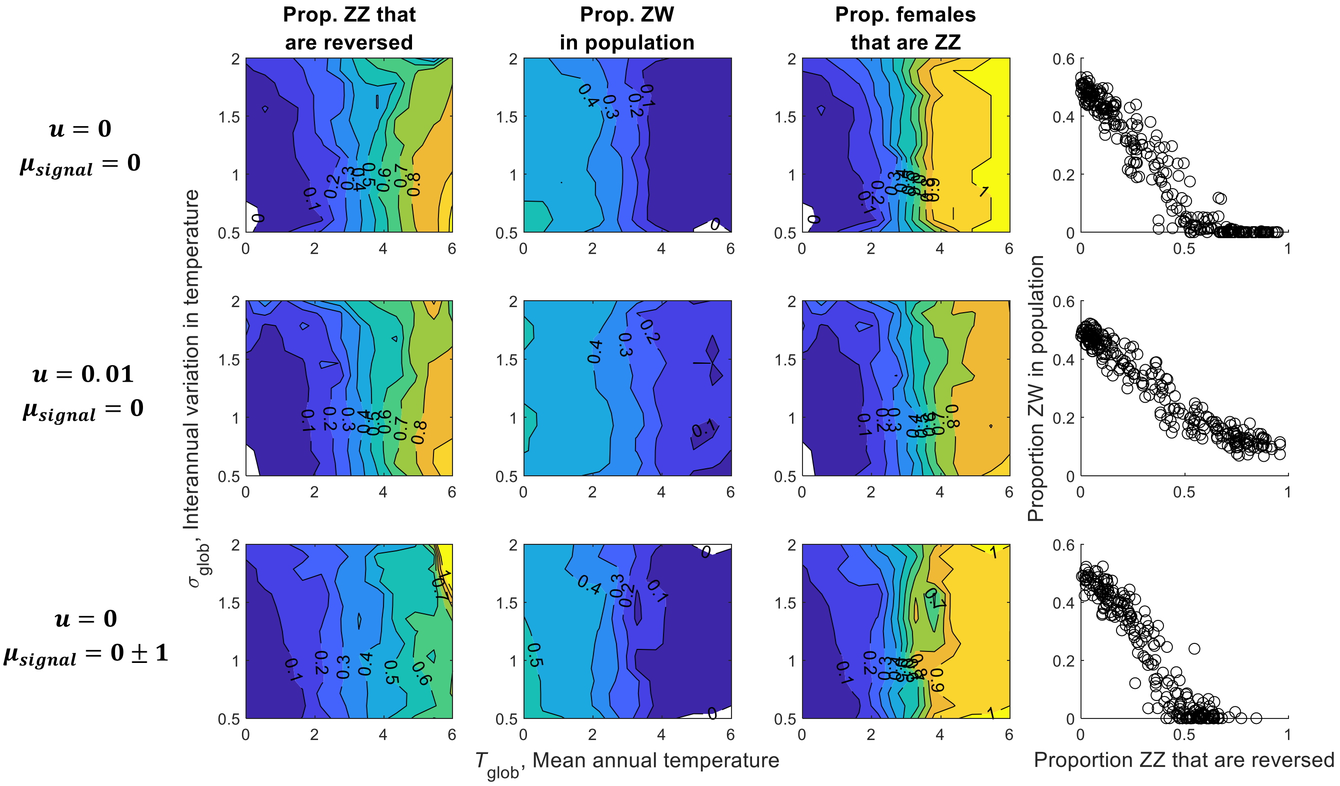

FIGURE 4 Simulation results of sex-determining system across rising global mean temperature and rising interannual variation in temperature, shown for three scenarios—simple (top row, *N* = 271), with immigration (middle row, *N* = 246) or with genetic variation in temperature sensitivity (bottom row, *N* = 228). Contour plots show the proportion of *ZZ* individuals that are sex-reversed (*ZZ*f/[*ZZ*f + *ZZ*m]), the proportion of *ZW* individuals in the population (*ZW*/[*ZW* + *ZZ*]) and the proportion of females in the population that are *ZZ* (*ZZ*f/[*ZZ*f + *ZW*]). The scatter plots present the maintenance of the *ZW* genotype as a function of *ZZ* sex reversal. Data represent the 200th year following the initiation of temperature change

climatic change when the fecundity differential was large (Figure 5). When *ZZ*f had 20% fecundity compared to *ZW*f (top row), the population was nearly completely buffered from the loss of *ZW* genotype across the range of sex reversal possible; all populations in the scenario maintained *ZW* at ≥40% of the population. *ZZ*f fecundity of 180% that of concordant females advanced the likelihood of losing the *ZW* genotype, with populations losing *ZW* at 30%–40% reversal of *ZZ* rather than 50% (bottom row). When *ZZ*f had smaller fecundity differentials (80% or 120% the fecundity of *ZW*f), more modest changes to *ZW* genotype loss were observed (2nd and 4th rows).

Considering the combined effects of the natural factors considered here, we found that the strongest fecundity advantage to *ZZ* females led to a rapid decline in the *ZW* genotype at low levels of sex reversal across all scenarios (Figure S1). However, immigration prevented the complete loss of *ZW* even under this strong *ZZ*f fitness advantage. In addition, initial variation in temperature sensitivity led to an increase in the levels of sex-reversed required for *ZW* to be lost.

5 | DISCUSSION

Temperature-dependent sex reversal does not inevitably lead to the loss of sex chromosomes and conversion to ESD. Indeed, our mathematical and simulation analyses show that, in the simplest populations, an astonishingly high level of sex reversal in the homogametic sex (50%) is required to lose the *W* or *Y* chromosome. This level of sex reversal occurs when mean nest temperatures in the population equal the temperature at which sex reversal occurs (consistent with Grossen et al., 2011). When sex reversal occurs in fewer than 50% of homogametic individuals, sex determination persists in a mixed, stable form. That is, *ZW*f, *ZZ*m and *ZZ*f all persist in the population at stable frequencies.

Although 50% sex reversal is very high, we found that this threshold level of sex reversal could be reached quite suddenly as a function of warming nest temperatures, with only a small change in temperature (2°C) separating populations experiencing a small incidence of sex reversal (~10%) and those experiencing 50% sex reversal. Thus, once sex reversal begins occurring in wild populations, it is likely that only modest climatic warming will further push the populations towards sex chromosome loss (Holleley et al., 2015). The stepwise fashion of this response, however, would depend on variability in nest temperatures within a year (Grossen et al., 2011), a parameter that we fixed at a single value.

This study provides novel predictions for how several biological factors associated with wild populations affect the likelihood of transition from GSD to ESD. These factors can be categorized into

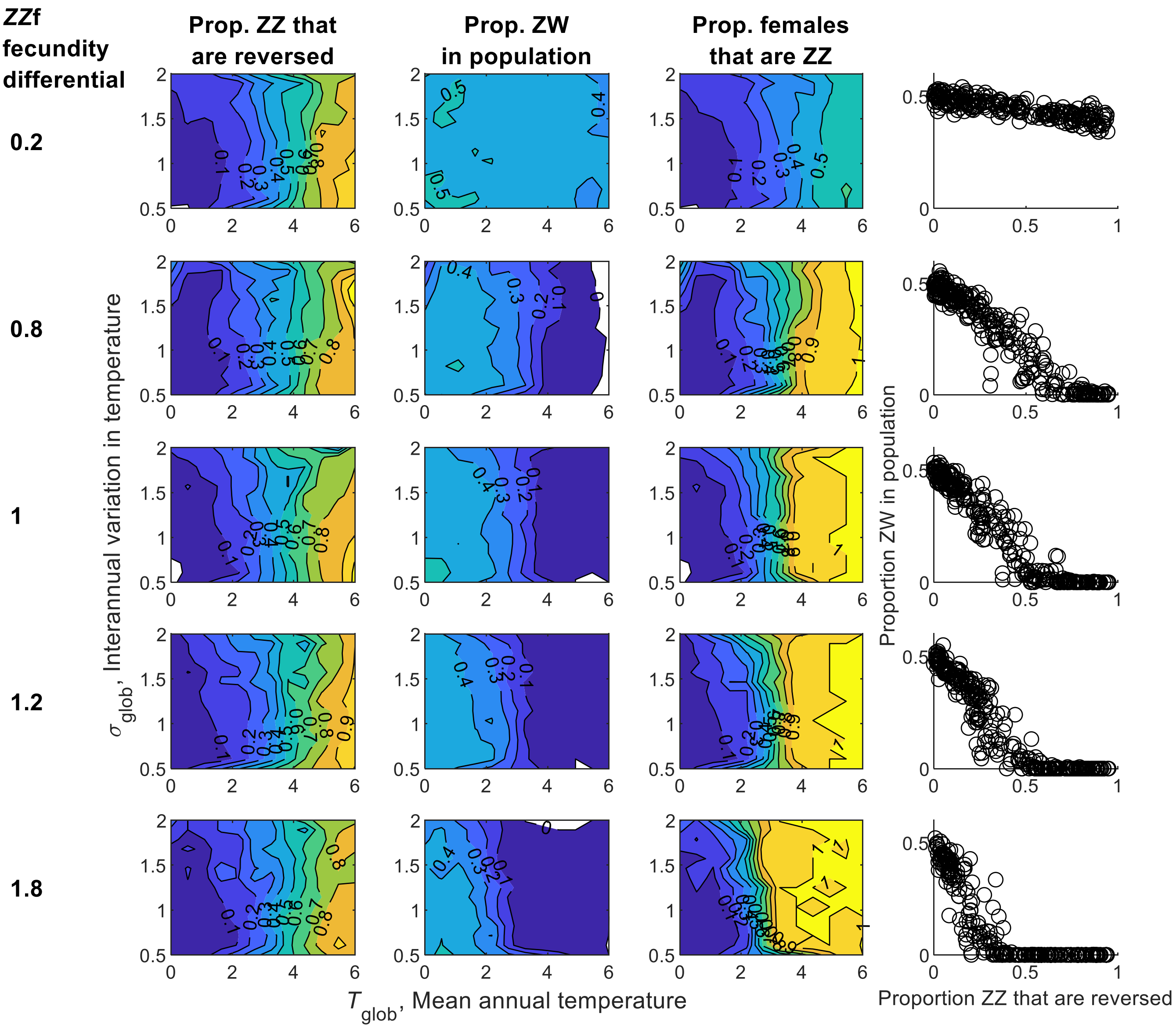

FIGURE 5 Simulation results of sex-determining system across rising global mean temperature and rising interannual variation in temperature, shown for five scenarios of fecundity differential for *ZZf* compared to *ZWf* (*ZZf*/*ZWf*)—0.2 (top row, *N* = 234), 0.8 (second row, *N* = 258), 1 (middle row, *N* = 271), 1.2 (fourth row, *N* = 258) or 1.8 (bottom row, *N* = 216). Contour plots show the proportion of *ZZ* individuals that are sex-reversed (*ZZf*/[*ZZf* + *ZZm*]), the proportion of *ZW* individuals in the population (*ZW*/[*ZW* + *ZZ*]) and the proportion of females in the population that are *ZZ* (*ZZf*/[*ZZf* + *ZW*]). The scatter plots present the maintenance of the *ZW* genotype as a function of *ZZ* sex reversal. Data represent the 200th year following the initiation of temperature change

forces that affect the incidence of sex reversal and forces that impact adult demography and life history.

First, we explored two natural features that impact the frequency or stochasticity of sex reversal in developing animals—increased interannual variability in nest temperatures and genetic variation in the temperature of sex reversal. Under both of these scenarios, we found that the nest temperature range associated with 0%–100% sex reversal expanded when compared to a scenario with less-variable climate or no genetic variation—such that sex reversal increased under modest warming and decreased at extreme warming. Interannual variability in mean nest temperatures is pervasive and unavoidable in wild populations, as maternal nesting behaviour does not appear to compensate for among-year variation in air temperature (Hawkes, Broderick, Godfrey, & Godley, 2007; Schwanz & Janzen, 2008; Telemeco, Elphick, & Shine, 2009). This adds stochasticity to the frequency of sex reversal across years and, in a long-lived animal, will moderate the influence of extremes in sex reversal in any one year. Genetic variation in temperature sensitivity led to a striking result that 100% sex reversal of the *ZZ* genotype was not observed in even the warmest climates we explored.

Despite the apparent buffering of the population from sex reversal at hot climates under these two scenarios, there was little change in how nest temperatures caused the loss of the heterogametic genotype. This is because the buffering of sex reversal occurred at levels so high (>50%) that conversion to ESD was unavoidable. Under high temperature fluctuations, the mean temperature at which 50% sex reversal occurred was unchanged; thus, the temperature at which *ZW* was lost was unchanged. When the population was seeded with initial variation in temperature sensitivity, there was a modest increase in the nest temperatures required to reach 50% sex reversal and induce loss of *ZW*. In these scenarios, the average sensitivity to sex reversal declined with time (μ_{signal} increased). Because *ZZ* individuals with higher μ_{signal} are more likely to be males than those with lower μ_{signal}, they would have a rare-sex fitness advantage in female-biased populations (i.e., there would be frequency-dependent selection favouring nonreversed males). Although the buffering against *ZW* loss by evolution of temperature sensitivity was modest in our simulations, we did not allow mutation in either of the signal traits or the threshold (e.g., Schwanz et al., 2013). The importance of evolution in a wild population will depend on the standing variation in temperature sensitivity and the generation of new variation relative to the rate of climatic change. New variation may arise faster than mutation rates if there is plasticity in temperature sensitivity due to nongenetic mechanisms (e.g., Deveson et al., 2017; Ge et al., 2018; Piferrer, 2013; Schwanz, Janzen, & Proulx, 2010).

Second, we examined the influence of two important forces of evolution that drive adult demography—immigration and fecundity selection. Here, we found that the relationship between sex reversal and conversion to ESD was dramatically altered. Even under 100% sex reversal of natally hatched *ZZ* offspring, 1% immigration of mixed-genotype individuals (*ZZ* or *ZW*) maintained *ZW* at approximately 10% of the population. Thus, immigration provided a major buffering effect and should be a priority for research exploring the impact of sex reversal in a given population. In particular, different levels of migration, sex-specific migration or different life history traits that influence dispersal, and hence gene flow, were not considered in this study. It is also unclear how likely it is that a population experiencing high sex reversal would receive *ZW* migrants. Natural nest temperatures are known to vary considerably on a spatial scale relevant for animal meta-populations owing to variation in nesting substrate and use of human-modified habitats (Hall & Warner, 2018; Huang & Pike, 2011; Kolbe & Janzen, 2002; Tiatragul, Hall, Pavlik, & Warner, 2019; Weber et al., 2011). Green sea turtles nesting on Ascension Island experience nest temperatures 2.2°C higher in a dark sand beach compared to a pale sand beach, despite the beaches being only 6 km apart (Weber et al., 2011). In Taiwan, nests for long-tailed skinks in a man-made structure are hotter and are heating more rapidly with climate change, compared to nests in natural habitats 150 m away (Huang & Pike, 2011). The results presented here highlight the need for future theoretical work exploring the meta-population context of sex reversal and sex chromosome maintenance across landscapes (e.g., Harts, Schwanz, & Kokko, 2014).

In addition, we found that differential fecundity between concordant (*ZW*f) and sex-reversed (*ZZ*f) females had a large impact on the level of warming and sex reversal necessary to lose *ZW* from the population. Large fecundity advantages of *ZZ*f led to loss of the *ZW* genotype with only 35%–40% sex reversal. Interestingly, 1% immigration counteracted the influence of the strongest *ZZ*f fecundity advantage. Conversely, a fecundity disadvantage to *ZZ*f individuals had a large buffering effect that allowed *ZW* to persist over 200 years with 100% sex reversal (population feminization).

Our simulations occurred over a short timescale and without extensive evolutionary potential because we were interested in understanding the response of populations over ecological time. Based on the trajectories, most populations reached an apparent equilibrium over this timescale (Figure 3). Over a longer timescale, it is likely that evolution of the sex-determining system would complicate the predictions. Even over the short time of 200 years (approx. 30 generations), we observed evolution of average temperature sensitivity. However, in the absence of rapid evolution under directional climate change, loss of *ZW* genotypes (at approximately 50% *ZZ* reversal) would be followed rapidly by female-biased sex ratios. Without evolutionary potential in the temperature sensitivity of sex reversal or for de novo sex-determining alleles (Grossen et al., 2011), populations with only *ZZ* genotypes and high sex reversal would eventually experience limitations in the number of males and possibly population decline (Boyle, Hone, Schwanz, & Georges, 2014). Moreover, female-biased populations can greatly impact the evolution and demography of other populations connected through gene flow (Harts et al., 2014).

The consequences for wild populations can be highlighted by considering the bearded dragon of Australia. In this species, sex reversal in most individuals occurs by 34–35°C, though some individuals reverse at temperatures as low as ~ 32°C (Holleley et al., 2015; Quinn et al., 2007). Thus, mean nest temperatures near 34–35°C will be necessary to induce a transition to ESD (see also Holleley et al., 2015). Embryo survivorship at these temperatures (~75%; Holleley et al., 2015; Quinn et al., 2007) is sufficient to permit hatching of sex-reversed offspring. No information is available on historical nest temperatures in bearded dragons. However, in the eastern part of the species' range, where mean daily air temperatures have been rising, nest temperatures have averaged 35–36°C (late summer nests; P. Pearson, pers. comm.). In this region, the recorded proportion of phenotypic females that are genotypically male (*ZZ*) has been on the rise between 2003 and 2011, exceeding 20% in 2011 (Holleley et al., 2015). Our results suggest that only a small amount of additional warming would induce 50% sex reversal and raise the risk of sex chromosome loss. The possibility that ZZ females have close to twice the fecundity of *ZW* females (Holleley et al., 2015) and other behavioural attributes differentially affecting fitness (Li et al., 2016) further suggests that the transition to ESD for these populations could occur closer to 33°C average nest temperatures (1–2°C lower, with *ZZ* sex reversal near 35%–40%). If nest temperatures stabilize at current levels, or if migration of *ZW* females occurs, our models predict stable systems of mixed sex determination.

Climate change can cause the loss of a sex chromosome and a transition to ESD. An increasing number of vertebrate species with sex chromosomes display sex reversal in response to high incubation temperatures, and this susceptibility may be a widespread trait in ectothermic, gonochoristic vertebrates (Baroiller & D'Cotta, 2016; Flament, 2016; Holleley et al., 2016). The conclusions apply analogously to polygenic taxa (multiple loci contributing quantitatively to sex; Beukeboom & Perrin, 2014) if there are some genetic combinations that are susceptible to sex reversal and others which are not (e.g., male signal curves that show continuous variation in height among individuals). In this case, we would predict that sufficient sex reversal would cause the fixation of alleles contributing to temperature-sensitive sexual development, analogous to fixation of the *Z* allele. Thus, our findings may inform our understanding of climate change response across vertebrates. Moreover, climate change is only one environmental stressor that organisms face. Environmental exposure to exogenous hormones or endocrine-disrupting chemicals induces sex reversal in many fish species (Devlin & Nagahama, 2002; Senior & Nakagawa, 2013) and may become an increasing feature of the human-impacted landscape. Overall, our study highlights the evolutionary lability and dynamics of sex-determining systems under environmental perturbation and reveals how integral features of wild populations can lead to the co-occurrence of sex chromosomes and sex reversal, thus increasing the opportunity for long-term sex chromosome persistence.

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AUTHOR CONTRIBUTION

LES, AG, CEH and SS conceptualized the research, acquired grant funding and contributed to results interpretation and manuscript revision. LES developed and implemented the theoretical models and wrote the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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