**Metabolic consequences of sex-reversal in two lizard species: a test of the like genotype and like phenotype hypotheses**

Kristoffer H. Wild1,2, John H. Roe3, Lisa Schwanz4, Essie Rodgers5, Duminda S. B. Dissanayake2, Arthur Georges2, Stephen D. Sarre2, & Daniel W. A. Noble1

1Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT, AUS

2Centre for Conservation Ecology and Genomics, Institute for Applied Ecology, University of Canberra, Canberra, ACT, AUS

3Department of Biology, University of North Carolina Pembroke, Pembroke, North Carolina, USA

4Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

5 Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, Murdoch, WA, AUS

**\*** Corresponding author: K.H. Wild. kristoffer.wild@anu.edu.au

*Short running title:* Energetic consequences of sex-reversal

**Summary statement:**

*Phenotypic sex drives differences in metabolism in two species that can reverse sex*

**Abstract**

Vertebrate sex is typically determined genetically, but in many ectotherms sex can be determined by genes (Genetic Sex Determination: GSD), temperature (Temperature-dependent Sex Determination: TSD), or interactions between genes and temperature during development. Temperature dependent sex determination may involve GSD systems with either male or female heterogamety (XX/XY or ZZ/ZW) where temperature overrides chromosomal sex determination to cause a mismatch between genetic sex and phenotypic sex (sex-reversal). In these temperature-sensitive lineages, phylogenetic investigations point to recurrent evolutionary shifts between genotypic and temperature-dependent sex determination. These evolutionary transitions in sex determination can occur rapidly if selection favours the reversed sex over their concordant phenotypic sex. To investigate the consequences of sex-reversal on offspring phenotypes, we measured two energy-driven traits (metabolism and growth) and 6-month survival in two species of reptile with different patterns of temperature-induced sex-reversal. Male sex-reversal occurs in *Bassiana duperreyi* when chromosomal females (femaleXX) develop male phenotypes (maleSRXX), while female sex-reversal occurs in *Pogona vitticeps* when chromosomal males (maleZZ) develop female phenotypes (femaleSRZZ). We show metabolism in maleSRXX was like that of maleXY, that is, reflective of phenotypic sex and lower than genotypic sex. In contrast, for *Pogona vitticeps*, femaleSRZZ metabolism was intermediate between maleZZ and femaleZW metabolic rate. For both species, our data indicate differences in metabolism become more apparent as individuals become larger. Our findings provide some evidence for an energetic advantage from sex-reversal in both species but do not exclude energetic processes as a constraint on the distribution of sex-reversal in nature.

**1 | Introduction**

Sex-determination in vertebrates is highly variable, ranging from genotypic sex determination (GSD) where sex is established by sex chromosomes, to environmental sex determination (ESD) where sex is primarily influenced by prevailing environmental conditions (Bull, 1980). For some species, these pathways of reproductive development are not mutually exclusive but can co-occur (Bachtrog et al., 2014; Sarre et al., 2004). In a few well-studied species, GSD systems with either male (XX/XY) or female heterogamety (ZZ/ZW) are influenced by incubation temperature (Temperature-dependent sex determination; TSD) (Holleley et al., 2015; Noble et al., 2018; Quinn et al., 2009). In these GSD species, conditions experienced during critical developmental stages exceed a threshold temperature that overrides genetic sex-determining mechanisms. This temperature override, commonly referred to as sex reversal, causes a discordance between phenotypic and genotypic sex (Holleley et al., 2015; Quinn et al., 2009; Radder et al., 2009). Theoretical models predict that when sex-reversed individuals have a greater fitness advantage, populations can rapidly lose the heterogametic sex chromosome (XY or ZW) and result in pure TSD lineages within a few generations (Grossen et al., 2011; Holleley et al., 2015; Schwanz et al., 2020). Consequently, these TSD lineages should become widely established in free-living populations where environmental conditions favour their emergence. However, sex-reversal in some species is not distributed evenly across ecotypes in natural systems, suggesting free-living animals may experience costs associated with sex-reversal that are not accounted for in theoretical models (Bókony et al., 2021; Castelli et al., 2021; Mikó et al., 2021; Wild et al., 2022). Quantifying costs and benefits of sex-reversal will help clarify patterns of sex-reversal in wild populations and provide insight into the mechanisms that may inhibit or accelerate evolutionary transitions in sex-determining systems (Bachtrog et al., 2014; Sarre et al., 2004).

Of crucial importance for individual growth, reproduction, and survival is energy expenditure which can be estimated by measuring metabolic rates. In both empirical and theoretical studies, estimates for metabolism have been shown to be linked to individual patterns of growth, reproduction and survival (Peterson et al., 1999; Burton et al. 2011; White et al., 2022). Metabolism (and associated energy expenditure) thus provides a crucial link between individual life history traits (somatic growth, developmental rates, and age at maturity) and population processes (population growth, carrying capacity, and rates of competition) in a variety of taxa (Brown et al., 2004; Ernest et al., 2003; Burger et al., 2021; Savage et al., 2004). Importantly, strategies used to secure, allocate and expend energy can vary considerably between phenotypic sexes (Arnqvist et al., 2022; Boratyński et al., 2010; Codding et al., 2011; Geffroy, 2022) and may contribute to energetic differences in sex-reversed individuals and their phenotypic and genotypic counterparts. Exploring how sex-reversal impacts metabolism and other traits that relate to energy use will provide insight into observed patterns of sex-reversal in natural populations.

Here, we test whether and to what degree sex-reversed individuals differ in metabolism, growth, and survival compared to their phenotypic and genotypic counterparts using two species of lizard, *Pogona vitticeps* and *Bassiana duperreyi*, that undergo sex-reversal in the wild (Dissanayake et al., 2021a; Holleley et al., 2015; Wild et al., 2022). Sex-reversal in *B. duperreyi* occurs when chromosomal females (female XX) develop male phenotypes [maleSR XX] (Dissanayake et al., 2021a; Quinn et al., 2009), whereas sex-reversal in *P. vitticeps* occurs when chromosomal males (maleZZ) develop female phenotypes [femaleSR ZZ] (Holleley et al., 2015; Quinn et al., 2007). Three plausible phenotypic/genetic patterns may manifest that can influence the evolution of sex-reversal in nature (Fig. 1 – e.g., metabolism):

1. there is no difference in metabolism, growth, or survival among different genotype-phenotype combinations such that males, females, and sex-reversed individuals are indistinguishable (Null);
2. sexes are phenotypically similar with discordant sex-reversed individuals (e.g. femaleSR ZZ or maleSR XX) and concordant individuals of the same *phenotypic* sex (e.g. female ZW, maleSR XY) exhibiting similar metabolic rate, growth, and/or survival (Like Phenotype); or
3. sexes are phenotypically different with discordant sex-reversed individuals (e.g. femaleSR ZZ or maleSR XX) and concordant individuals of the same *chromosomal* sex (e.g. male ZZ, female XX) exhibiting similar metabolic rate, growth, and/or survival (Like Genotype).

Evidence for the Like Phenotype hypothesis would suggest that metabolic differences between phenotypic sexes (i.e., male vs. female) may be driven by hormonal mechanisms or sexually-antagonistic selection that leads to sexual dimorphism in traits such as morphology or physiology (Cox et al., 2017; Eyer et al., 2019; Lipinska et al., 2015; van Doorn and Kirkpatrick, 2010). Support for the Like Genotype hypothesis would imply that sex-linked genes may be involved in the expression of traits associated with metabolism, energy use, and potentially other fitness-related endpoints(Charlesworth and Charlesworth, 1980; Fisher, 1931; Harrison et al., 2015). To date, no studies have explored how energetic components (i.e. metabolism, growth, maintenance) are affected by sex-reversal, even though sex-specific strategies of energy allocation have been documented between phenotypic males and phenotypic females (Geffroy, 2022; Somjee et al., 2022).

**2 | Materials and methods**

**2.1| Lizard collection and husbandry**

*Bassiana duperreyi* –Twenty-five *B. duperreyi* nests with a total of 40 eggs (1-4 eggs per nest) were opportunistically located in November 2020 by flipping rocks, logs, and other cover objects at two field locations within the Brindabella Range (Mount Ginini – 1640 m a.s.l., 35°31’29.6“S 148°46’58.7”E; Piccadilly Circus – 1240 m a.s.l., 35°21’42.0“S 148°48’12.5”E). These sites were selected because of high frequencies of sex-reversal previously documented within these populations (Dissanayake et al., 2021a). The number of eggs per nest was recorded, and temperature dataloggers (iButton® model DS1921G; accuracy°C) were placed at the core of each nest to monitor nest temperatures. Each nest was maintained in natural conditions for 9-10 weeks at each location, and the mean nest temperatures (Mount Ginini – 18.94°C 0.98 & Piccadilly Circus – 20.42°C 0.84; Fig. S1) were monitored to ensure approximately 90% of the development period passed in natural conditions (Shine et al., 2002). Therefore, sex-reversal in *B. duperreyi* occurred in natural nest sites due to exposure to sex-reversing low temperatures (<20°C) *in situ*. The eggs were then collected, placed in moist vermiculite, and transported back to the University of Canberra. Eggs were placed in incubators (LabWit, ZXSDR1090) that maintained 23°C, which produces a balanced sex ratio(Shine et al., 2002). For the study site description and further detail regarding general egg collection methods see (Dissanayake et al., 2021b).

Phenotypic sex was determined by squeezing the tail base to evert the hemipenes (Harolow, 1996) for 3-to-7-day old hatchlings and was checked again by hemipene transilluminationafter 5 weeks (Dissanayake et al., 2021b). Blood from the tail of each individual was collected on Whatman FTATM Elute Micro Card (CAT No. WB120410). Lizards were housed individually in plastic containers (0.35x0.25x0.15m). Each tub contained cardboard tubes and paper egg carton pieces for hides. Full-spectrum UV bulbs and heat bulbs were placed alternating between tubs to create a thermal gradient in each tub (heat from one side, UV from the other). Hatchlings were fed live, gut-loaded crickets once per day *ad libitum* and twice per week the crickets were dusted with calcium powder. Hatchlings were provided with shallow water dishes that were replenished daily, and they were misted twice per day with water.

*Pogona vitticeps* – The University of Canberra (UC) maintains a breeding colony of adult *P. vitticeps*, where breeding enclosures are comprised of one male (maleZZ) to either three sex-reversed females (femaleSR ZZ) or three concordant females (female ZW). During the summer of 2020–2021, females were allowed to lay eggs, which were collected within 2h of deposition. Eggs (n= 96) from 15 clutches were randomly allocated to either 28°C (n= 43; no sex-reversal expected) or 34°C (n = 53; reversal of 50% of ZZ genotypes expected) in temperature-controlled incubators (LabWit, ZXSDR1090) on moist vermiculite. Thus, sex-reversal in *P. vitticeps* occurred because of exposure to sex-reversing high temperatures (> 32°C) during incubation. Once hatchlings emerged, the determination of phenotypic sex and blood sampling followed the same protocols as for *B. duperreyi*. Hatchlings were housed in plastic tubs (0.8x0.5x0.35m; 5 individuals per tub), and in addition to crickets, finely grated vegetables were introduced to the diet beginning at 6-7 weeks post-hatch.

**2.2| Genotyping**

Genotypic sex was determined for both *B. duperreyi* and *P. vitticeps* using polymerase chain reaction (PCR)-based molecular sex tests from extracted DNA collected from tissue samples. DNA was extracted from tissue samples. DNA purity was determined using a NanoDrop 1000 spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE, USA) and quantified using the Qubit 2.0 Fluorometric Quantitation (Invitrogen, Life technologies, Sydney, N.S.W., Australia). The sex-reversal status was determined for *B. duperreyi* by using PCR as described by Dissanayake et al. (Dissanayake et al., 2020), where the genotypic sex was identified based on Y-specific markers allowing identification of XX and XY samples. No XY females were observed, which is consistent with previous observations that recombination and/or mutation involving these loci is negligible and does not affect the accuracy of genotypic sex assignment. Genotypic sex (ZZ/ZW) for *P. vitticeps* was determined using a PCR-based molecular sex test that amplifies a W-chromosome-specific size polymorphism (Holleley et al., 2015), in which two bands amplify in ZW individuals and one control band amplifies in ZZ individuals. No ZW males were observed. All PCR products were visualized on a 1.5% agarose gel using SYBR Safe (Life Technologies, Carlsbad, USA), and all molecular sex tests were conducted blind to the phenotypic sex of the individuals. For both species, sex class accounted for genotype and phenotype and when genotype–phenotype discordance occurred individuals were classified as sex-reversed (Holleley et al., 2015).

**2.3 | Respirometry**

Metabolic rate (MR) was defined as the rate of oxygen consumption (V̇O2, mL min−1) of post-absorptive animal using a stop flow respirometry system (Stable System FMS, Las Vegas NV, USA). A gas analyser sub-sampler was used to pump outside air scrubbed of CO2 (using soda lime, Chem-Supply, AUS) and water vapour (using Drierite, W. A. Hammond Drierite Co. Ltd) to a mass flow controller that regulated flow rate to a nominal value of 130 ml min−1 (*B. duperreyi*) or 250 ml min−1 (*P. vitticeps*). After passing through the mass flow controller, air was pushed through an airtight cylindrical respirometry chamber, with dimensions designed specifically for each species (*B. duperreyi*: 75x20mm; *P. vitticeps*: 200x40mm). Air was pushed into the chamber and then through a flow meter ensuring that flow rates were constant. Air was then rescrubbed of water vapor, using Drierite, before being passed through H2O and O2 gas analysers. The fractional concentration of O in the ex-current air (FO2) was recorded at a frequency of 1 Hz. Following the manufacture protocols, both H2O and O2 analysers were calibrated prior to experiments.

Metabolic rate was measured within 3 weeks of hatching for all individuals. After a minimum of 24 h fasting period, body mass (0.01g) was measured of each individual lizard using a digital sale (Ohaus SP-202) before and after being placed in the respirometry chamber. Two incubators (LabWit, ZXSDR1090) were used to control the temperature of outside air being pulled into the respirometry system and then flowed through to the second incubator that controlled the temperature ( 1°C) in which animals in chambers were placed. Incubator temperatures were held at a constant temperature relevant to the thermal preference for each species (*B. duperreyi* 34°C (Du et al., 2010); *P. vitticeps* 33°C (Greer, 1989). At approximately 17:00 lizards were placed in respirometry chambers inside a dark incubator and remained in the chambers overnight for the duration of the experiment. As such, these animals were mainly in a quiescent state, but some activity may have occurred within the chamber. Each respirometry trial lasted approximately 14 h, and to ensure that animals were habituated within chambers, the first 2 h of data were discarded from analysis. The system contained seven chambers that lizards were placed in individually and one empty chamber designated as a control. The O2 consumption of each lizard was measured continuously for 5 min over a 70 min sampling window, and this sampling sequence was repeated every 70 min for the duration of the experiment. Immediately following each individual lizard measurement, the control chamber recorded for 5 min as a baseline of O2. During each 70 min sampling window O2 depletion for each individual was identified using the R package “metabR” (github.com/daniel1noble/metabR) and O2 depletion was averaged for each individual across the night to represent MR. The rate of O2 depleted by an individual was calculated following Eq. 4.21 *in* Lighton, 2008):

where the rate of O2 is the maximum percentage of O2 a sample below that baseline; Vchamber is the volume of the chamber (*B. duperreyi*: 23.56 mL; *P. vitticeps*: 251.33 mL); Vlizard was calculated as an average between the pre- and post-measurement mass of each individual, and t is the duration of time the chamber was sealed between air samples taken (70 min). The mass of each lizard was used as a proxy for its volume (1g = 1 ml) because of their high correlation and increased accuracy and precision in mass measurements(Friesen et al., 2017).

**2.4 | Growth and survival**

Measurements of snout-to-vent length (SVL) and mass were used to estimate growth rates. SVL and mass were initially measured during respirometry experiments and remeasured 6 months after the initial measurements. Growth rate was calculated by subtracting initial measurements (SVL or mass) from the final remeasurement and dividing the elapsed time between measurements. SVL growth rate was recorded in mm/d for both species, and mass growth rate was recorded in centigrams (cg/d) for *B. duperreyi* and (g/d) for *P. vitticeps*. The survival rate of hatchlings was determined by documenting the frequency of mortality between the hatch date and 6 months post-hatch date for both species.

**2.5 | Statistical analysis**

All statistical analysis were conducted using the R environment, ver. 4.1.0 ([www.r.-project.org](http://www.r.-project.org)). Bayesian linear mixed effect models from the package *brms* (Bürkner, 2017) were used to analyse O2 data for each species. We used Bayesian modelling approaches because of their flexibility with respect to parameter estimation. It is also easier to interpret and manipulate posterior probabilities for each parameter in the model. Default priors *(See Supplementary Material for Details)* were used and 4 MCMC chains of 5000 were run with a burn in of 1000 and a thinning interval of 5 for the “brms” models. All models were checked for proper mixing and convergence by visually inspecting trace plots. For each species two models were fitted, the first in which homoscedasticity of the data was assumed and the second in which heteroscedasticity was accounted for within the data. The first model for estimating metabolism was fitted using the following structure:

where is the metabolic rate () for measurement *i* (i = 1 to , number of measurements) on individual *j* (j = 1 to , number of individuals) and day *k* (k = 1 to , number of days). Contrasts for the different sex classes (), where and are for concordant sexes and sex-reversed animals, respectively. A linear slope 4 was estimated for measurement time (, z-transformed) and a random intercept () and slope for () were included for individual *j* across measurement occasions. A linear slope for log transformed mass (, centered on mean, sc) and mass scaling relationships were estimated separately for the different sex classes (i.e., , , and respectively). Deviations were sampled from a multivariate normal distribution (~, where ID is a (co)variance matrix with a random intercept and slope variance and their covariance. A random-effect for day () (~ ) was also included in the model to account for variation across days in metabolic rate. In all models, we retained data for each measurement throughout the night to improve analytical power. Given that animals were quiescent, our MR data is expected to be representative of Standard Metabolic Rate (SMR). Nonetheless, some movement did occur in our chambers. As such, we also fit the same models described above but kept the lowest 10% of oxygen consumption values during trials – data that should be quite close to SMR. We found no changes in our results when using the full dataset compared to the dataset that only used the lowest 10% (*see* Fig. S2; Tables S1 & S2 in *Supp*). Therefore, all V̇O2 measurements from trials (MR) were kept for further analysis.

Differences in growth rates were compared across sex class using Bayesian linear models while accounting for individual mean metabolism. This allowed us to test if there was a relationship between metabolism and growth rate (mass or svl) across sex class. Fisher’s exact tests were used to determine if there was an association between sex class and frequency of hatchling mortality after six months.

For all Bayesian models, posterior estimates were from four MCMC chains, and we present posterior means and their 95% credible intervals. To test for the Like Genotype (genotype - sex-reversed) or Like Phenotype (phenotype - sex-reversed) framework for each species, contrasts were calculated by subtracting the posterior distributions of each sex class. To test if the magnitude of these differences varied significantly, probabilities of parameter estimates were considered statistically significant when the 95% CIs did not include 0, and the pMCMC values were less than 0.05. Data, code, and additional resources are available at: <https://github.com/daniel1noble/energy_sex_reversal.git>.

**3 | Results**

**3.1 | Energetic consequences of sex-reversal**

*Bassiana duperreyi* - A total of 760 measurements for 40 individuals (male XX: n = 13, female XX: n = 15, male XY: n = 12) were recorded. There was a strong scaling relationship between log metabolic rate and log mass (Table 1), and scaling slopes varied significantly depending sex class (significant interaction between sex class × logmass – Fig. 2A). Sex-reversed male XX *B. duperreyi* had a mass-specific metabolic rate that was most like their phenotypic counterparts (male XY - maleSR XX; pMCMC = 0.33; Table 3) and lower than their genotypic counterparts (female XX - maleSR XX; pMCMC < 0.01). For phenotypic males (maleSR XX & male XX), the scaling relationship between logmass and metabolism changed similarly across differently sized individuals (Fig. 2B; Table S3). Pairwise comparisons across sex class indicated no differences in body mass across our treatments (Fig. 2A; Table S4). The homogeneous variance model was the most parsimonious ([heteroscedastic model – homoscedastic model] loo: -5.5, SE = 6.87), accounting for 77% (95% CI:0.75 - 0.78) of the variation in metabolic rate.

*Pogona vitticeps* - A total of 1365 measurements for 96 individuals (femaleSR ZZ: n = 28, female ZW: n = 30, male ZZ: n = 38) were recorded. There was a strong scaling relationship between log metabolic rate and log mass (Table 2), and scaling slopes varied significantly depending sex class (significant interaction between sex class × logmass - Fig. 2C). Sex-reversed female *P. vitticeps* (femaleSR ZZ) had a mass-specific metabolic rate that was overall higher than their genotypic counterparts (male ZZ - femaleSR ZZ; pMCMC < 0.01), but lower than their phenotypic counterparts (female ZW - femaleSR ZZ; pMCMC = 0.04; Table 3). The mass scaling relationship of metabolism for femaleSR ZZ was more like ZZmales than ZW females (Fig. 2D; Table S3). As a consequence, large female ZZ have significantly lower metabolism compared to female ZW of comparable size (see Figure 2D; Table S3). Pairwise comparisons of body mass across sex class in *P. vitticeps* indicated no differences in body mass across treatments (Fig. 2C; Table S4). The heteroscedasticity variance model was the most parsimonious ([heteroscedastic model – homoscedastic model] loo: -189.8, SE = 33.96), accounting for 84% (95% CI:0.83 - 0.85) of the variation in metabolic rate.

**3.2 | Effects of sex-reversal on growth and survival**

Growth rates for both SVL and mass supported the Null prediction among *B. duperreyi,* where there were no detectible differences across sex class (Table 3). Similarly, in *P. vitticeps* the Null prediction was supported when comparing SVL and mass growth rates across sex class (Table 3). For both species, there was no relationship between metabolism and growth rate estimates (Table S5 & S6). Sex-reversed male *B. duperreyi* had the lowest rates of survival (77%; Table S7) in comparison to concordant females (87%) and concordant males (100%), but this relationship was non-significant (p = 0.29). Similarly, sex-reversed *P. vitticeps* individuals had the lowest rates of survival (75%; Table 3) in comparison to concordant females (83%) and concordant males (95%), but this relationship was also not significant (p = 0.06).

**4 | Discussion**

We examined two species with different modes of sex-reversal to test whether metabolism, growth, and survival differed between sex-reversed individuals and others of the same phenotypic and genotypic sex. Metabolic responses differed between the two species, with clear support for the Like Phenotype hypothesis when males reverse sex (maleSR XX; *Bassiana duperreyi*) and equivocal support for each hypothesis when females reverse sex (femaleSR ZZ; *Pogona vitticeps*). For both species, regardless of whether individuals reversed sex, phenotypic females required more energy than phenotypic males as individuals grew larger. While sex-reversed animals appeared to have reduced survival, albeit not significantly so, there is no clear evidence in either species for growth advantages over their phenotypic sex. Together our results suggest that traits associated with energy use and growth may not be strongly tied to genes on the sex chromosomes. Other mechanisms, such as hormonal pathways or differences in immune function, may better explain the stronger signal for phenotypic sex differences (Cox et al., 2017; Kelly et al., 2018; van Doorn and Kirkpatrick, 2010). Assuming similar patterns occur in natural populations, energetic processes may have varying impacts on the species' life-history traits, which could provide insight into what constrains the distribution of sex-reversal in nature.

R). ,responses to elevated levels of or corticosterone,increasing s for female izards, these same hormonesare (DuRant et al., 2008; John-Alder, 1990; Meylan et al., 2010). in hormonal pathways between sexesthe concordant sex,but hormonal responses may transpire differently depending on the phenotype that undergoes sex-reversal.However, how efor male and female lizards remains poorly understood (*but see* Lovern et al., 2001) and requires further attention when accounting for sex-reversed individuals as they mature

We showed that metabolic scaling relationships of sex-reversed individuals differed depending on the GSD system. In the ZZ/ZW system of *P. vitticeps*, larger sex-reversed females (femaleSR ZZ;> +1.5SD above mean mass) have lower metabolism (15%) than concordant females (female ZW) of similar size (Fig. 2D; Table S3), whereas we observed no such differences for small sized hatchlings. Given that selection for larger hatchling lizards in the wild is common in lizards (i.e. ‘bigger is better’ hypothesis; Ferguson and Fox, 1984; Sinervo et al., 1992; Warner and Andrews, 2002), this would imply energetic differences between adult sex-reversed and concordant female *P. vitticeps*. As such, we predict that adult femaleSR ZZ may have more residual energy than female ZW to allocate towards storage, production, or activity after resting metabolic costs have been paid. Such surplus in energy reserves for femaleSR ZZ may explain why sub-adult (<1year) and adult femaleSR ZZ *P. vitticeps* are more similar to male ZZ in behaviour and morphology, including higher activity, levels of aggression, and larger body size in captivity(Holleley et al., 2015; Li et al., 2016). However, further work is needed to investigate if these different strategies of energy allocation exist and how they translate to the observed differences between phenotypic females in body mass, body size, and fecundity in wild populations of *P. vitticeps* (Wild et al., 2022).Given that our results indicate that the magnitude of metabolic differences varies across sexes as individuals get larger (Fig. 2). Investigating ontogenetic changes associated with sex-reversal will provide promising insights into the consequences of such effects.

In contrast to *Pogona vitticeps, B. duperreyi* showed strong support for the like-phenotype hypothesis. One simple explanation for this finding is that traits linked to metabolism are of little or no consequence for males. Alternatively, traits linked to metabolism for sex-reversed males (maleSR XX) in this species may not be associated with sex chromosomes and are linked to hormonal levels relevant to the phenotypic sex. This hypothesis is plausible if phenotypic males share similarities in their gonadal steroid levels, specifically testosterone. If this hypothesis is true, then it is likely that steroid levels would have a comparable effect on their metabolism compared to females, and the strengths of these signals could differ across life stages or seasons (Marler and Moore, 1989; Oppliger et al., 2004; Zena et al., 2019). Some support for this idea exists in *Anolis carolinensis*. Plasma testosterone concentrations in males are upwards to 4 times higher than similar-sized females 2 weeks post-hatch, and this difference in testosterone persists throughout juvenile growth where male testosterone can be 3 to 10 times higher than females (Lovern et al., 2001). If these hormonal differences were to exist between phenotypes in *B. duperreyi* thismay provide a mechanism for why maleSR XX are more like their phenotypic sex.

Overall,

there has been little attention focused on how growth or survival differs in sex-reversed individuals compared to their phenotypic or genotypic sex. While we did not detect a significant difference in growth or survival, in both species, sex-reversed hatchlings had a higher frequency of mortality over a 6-month period than the other sexes. High mortality has been previously observed in sex-reversed individuals in laboratory experiments (Mikó et al., 2021) and in the wild (Wild et al., 2022). The lack of clear evidence for differences in metabolism, growth, and survival for sex-reversed individuals (maleSR XX or femaleSR ZZ) over their concordant phenotypic sex (male XY or female ZW) in our study provides insight into the factors that may explain the occurrence of sex-reversal in the wild. While egg incubation differed between the species for logistical reasons – for *B. duperreyi,* 90% occurred in the field, while in *P. vitticeps* all eggs were incubated in the laboratory – we do not expect this to impact the relative differences we observed between sex-reversed and concordant individuals in these two species. In both species, incubation temperatures mimicked nest temperatures documented in the wild (Castelli et al., 2021; Dissanayake et al., 2021b), and all hatchlings were reared under common laboratory conditions for the first 6-months of life when all measurements were taken. Further investigation is required to understand the cause of this low survivorship and the demographic consequences these results have for the emergence of sex-reversal(Cotton and Wedekind, 2009). Overall, the lack of explicit support in our data for the Like Genotype hypothesis in metabolism, growth, or survivorship reveals clues on the mechanisms that drive sex-reversal in nature.

**Literature cited**

**Angilletta  Michael J, J.** (2001). Variation in metabolic rate between populations of a geographically widespread lizard. *Physiological and Biochemical Zoology* **74**, 11–21.

**Angilletta Jr, M. J. and Angilletta, M. J.** (2009). *Thermal adaptation: a theoretical and empirical synthesis*. New York, NY, USA: Oxford University Press.

**Arnqvist, G., Rönn, J., Watson, C., Goenaga, J. and Immonen, E.** (2022). Concerted evolution of metabolic rate, economics of mating, ecology, and pace of life across seed beetles. *Proceedings of the National Academy of Sciences* **119**, e2205564119.

**Bachtrog, D., Mank, J. E., Peichel, C. L., Kirkpatrick, M., Otto, S. P., Ashman, T.-L., Hahn, M. W., Kitano, J., Mayrose, I. and Ming, R.** (2014). Sex determination: why so many ways of doing it? *PLoS Biol* **12**, e1001899.

**Bókony, V., Ujhegyi, N., Mikó, Z., Erös, R., Hettyey, A., Vili, N., Gál, Z., Hoffmann, O. I. and Nemesházi, E.** (2021). Sex Reversal and Performance in Fitness-Related Traits During Early Life in Agile Frogs. *Front Ecol Evol* **9**, 1–14.

**Boratyński, Z., Koskela, E., Mappes, T. and Oksanen, T. A.** (2010). Sex‐specific selection on energy metabolism–selection coefficients for winter survival. *J Evol Biol* **23**, 1969–1978.

**Bradshaw, S. D.** (1997). *Homeostasis in desert reptiles*. New York, NY, USA: Springer Science & Business Media.

**Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B.** (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

**Bull, J. J.** (1980). Sex Determination in Reptiles. *Source: The Quarterly Review of Biology* **55**, 3–21.

**Bull, J. J.** (1983). *Evolution of sex determining mechanisms*. San Francisco, CA, USA: Benjamin Cummings.

**Bürkner, P.-C.** (2017). brms: An R package for Bayesian multilevel models using Stan. *J Stat Softw* **80**, 1–28.

**Burton, T., Killen, S. S., Armstrong, J. D. and Metcalfe, N. B.** (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences* **278**, 3465–3473.

**Castelli, M. A., Georges, A., Cherryh, C., Rosauer, D. F., Sarre, S. D., Contador‐Kelsall, I. and Holleley, C. E.** (2021). Evolving thermal thresholds explain the distribution of temperature sex reversal in an Australian dragon lizard. *Divers Distrib* **27**, 427–438.

**Charlesworth, D. and Charlesworth, B.** (1980). Sex differences in fitness and selection for centric fusions between sex-chromosomes and autosomes. *Genet Res*  **35**, 205–214.

**Codding, B. F., Bird, R. B. and Bird, D. W.** (2011). Provisioning offspring and others: risk–energy trade-offs and gender differences in hunter–gatherer foraging strategies. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2502–2509.

**Congdon, J. D.** (1989). Proximate and evolutionary constraints on energy relations of reptiles. *Physiol Zool* **62**, 356–373.

**Cotton, S. and Wedekind, C.** (2009). Population consequences of environmental sex reversal. *Conservation Biology* **23**, 196–206.

**Cox, R. M., Cox, C. L., McGlothlin, J. W., Card, D. C., Andrew, A. L. and Castoe, T. A.** (2017). Hormonally mediated increases in sex-biased gene expression accompany the breakdown of between-sex genetic correlations in a sexually dimorphic lizard. *Am Nat* **189**, 315–332.

**Dissanayake, D. S. B., Holleley, C. E., Hill, L. K., O’Meally, D., Deakin, J. E. and Georges, A.** (2020). Identification of Y chromosome markers in the eastern three-lined skink (*Bassiana duperreyi*) using in silico whole genome subtraction. *BMC Genomics* **21**, 1–12.

**Dissanayake, D. S. B., Holleley, C. E., Deakin, J. E. and Georges, A.** (2021a). High elevation increases the risk of Y chromosome loss in Alpine skink populations with sex reversal. *Heredity* 1–12.

**Dissanayake, D. S. B., Holleley, C. E. and Georges, A.** (2021b). Effects of natural nest temperatures on sex reversal and sex ratios in an Australian alpine skink. *Sci Rep* **11**, 1–11.

**Du, W.-G., Elphick, M. and Shine, R.** (2010). Thermal regimes during incubation do not affect mean selected temperatures of hatchling lizards (Bassiana duperreyi, Scincidae). *J Therm Biol* **35**, 47–51.

**DuRant, S. E., Romero, L. M., Talent, L. G., and Hopkins, W. A**. (2008). Effect of exogenous corticosterone on respiration in a reptile. *Gen and Comp Endo* ***156***, 126-133.

**Ernest, S. K. M., Enquist, B. J., Brown, J. H., Charnov, E. L., Gillooly, J. F., Savage, V. M., White, E. P., Smith, F. A., Hadly, E. A. and Haskell, J. P.** (2003). Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecol Lett* **6**, 990–995.

**Eyer, P.-A., Blumenfeld, A. J. and Vargo, E. L.** (2019). Sexually antagonistic selection promotes genetic divergence between males and females in an ant. *Proceedings of the National Academy of Sciences* **116**, 24157–24163.

**Ferguson, G. W. and Fox, S. F.** (1984). Annual Variation of Survival Advantage of Large Juvenile Side-Blotched Lizards, Uta stansburiana: Its Causes and Evolutionary Significance. *Evolution*, 342-349.

**Fisher, R. A.** (1931). The evolution of dominance. *Bio Rev* **6**, 345–368.

**Friesen, C. R., Johansson, R. and Olsson, M.** (2017). Morph‐specific metabolic rate and the timing of reproductive senescence in a color polymorphic dragon. *J Exp Zool A Ecol Integr Physiol* **327**, 433–443.

**Geffroy, B.** (2022). Energy as the cornerstone of environmentally driven sex allocation. *Trends in Endocrinology and Metabolism* **33**, 670–679.

**Greer, A. E.** (1989). *The biology and evolution of Australian lizards*. Sydney, NSW, AUS: Surrey Beatty and Sons.

**Grossen, C., Neuenschwander, S. and Perrin, N.** (2011). Temperature‐dependent turnovers in sex‐determination mechanisms: a quantitative model. *Evolution* **65**, 64–78.

**Harolow, P. S.** (1996). A harmless technique for sexing hatchiling lizards. *Herpetol Rev* **27**, 71.

**Harrison, P. W., Wright, A. E., Zimmer, F., Dean, R., Montgomery, S. H., Pointer, M. A. and Mank, J. E.** (2015). Sexual selection drives evolution and rapid turnover of male gene expression. *Proceedings of the National Academy of Sciences* **112**, 4393–4398.

**Hayward, A. and Gillooly, J. F.** (2011). The cost of sex: quantifying energetic investment in gamete production by males and females. *PLoS One* **6**, e16557.

**Holleley, C. E., O’Meally, D., Sarre, S. D., Marshall Graves, J. A., Ezaz, T., Matsubara, K., Azad, B., Zhang, X. and Georges, A.** (2015). Sex reversal triggers the rapid transition from genetic to temperature-dependent sex. *Nature* **523**, 79–82.

**Jameson, E. W., Heusner, A. A. and Arbogast, R.** (1977). Oxygen consumption of Sceloporus occidentalis from three different elevations. *Comp Biochem Physiol A Physiol* **56**, 73–79.

**John-Alder, H. B.** (1990). Effects of Thyroxine on Standard Metabolic Rate and Selected Intermediary Metabolic Enzymes in Field-Active Lizards *Sceloporus undulatus*. *PhysiologicalZoology* **63**, 600–614.

**Kearney, M. and Porter, W. P.** (2004). Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* **85**, 3119–3131.

**Kelly, C. D., Stoehr, A. M., Nunn, C., Smyth, K. N. and Prokop, Z. M.** (2018). Sexual dimorphism in immunity across animals: a meta-analysis. *Ecol Lett* **21**, 1885–1894.

**Kwok, A. B. C., Wardle, G. M., Greenville, A. C. and Dickman, C. R.** (2016). Long‐term patterns of invertebrate abundance and relationships to environmental factors in arid Australia. *Austral Ecol* **41**, 480–491.

**Letnic, M. and Dickman, C. R.** (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews* **85**, 501–521.

**Li, H., Holleley, C. E., Elphick, M., Georges, A., Shine, R. and Shine, R.** (2016). The behavioural consequences of sex reversal in dragons. *Proceedings of the Royal Society B: Biological Sciences* **283**, 1–7.

**Lighton, J. R. B.** (2008). *Measuring metabolic rates: a manual for scientists*. New York, NY, USA: Oxford University Press.

**Lipinska, A., Cormier, A., Luthringer, R., Peters, A. F., Corre, E., Gachon, C. M. M., Cock, J. M. and Coelho, S. M.** (2015). Sexual dimorphism and the evolution of sex-biased gene expression in the brown alga Ectocarpus. *Mol Biol Evol* **32**, 1581–1597.

**Lovern, M. B., McNabb, F. M. A. and Jenssen, T. A.** (2001). Developmental effects of testosterone on behavior in male and female green anoles (Anolis carolinensis). *Horm Behav* **39**, 131–143.

**Marler, C. A., and Moore, M. C.** (1989). Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). *Phys. Zool.* **6** , 1334-1350.

**Meylan, S., Haussy, C., and Voituron, Y.** (2010). Physiological actions of corticosterone and its modulation by an immune challenge in reptiles. *Gen and Comp Endo* ***169***, 158-166.

**Mikó, Z., Nemesházi, E., Ujhegyi, N., Verebélyi, V., Ujszegi, J., Kásler, A., Bertalan, R., Vili, N., Gál, Z. Hoffmann, O. I., & Bókony, V.** (2021). Sex reversal and ontogeny under climate change and chemical pollution: are there interactions between the effects of elevated temperature and a xenoestrogen on early development in agile frogs? *Environmental Pollution* **285**, 117464.

**Mueller, P. and Diamond, J.** (2001). Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. Proceedings of the National Academy of Sciences **98,** 12550-12554.

**Noble, D. W. A., Stenhouse, V. and Schwanz, L. E.** (2018). Developmental temperatures and phenotypic plasticity in reptiles: A systematic review and meta‐analysis. *Bio Rev* **93**, 72–97.

**Noy-Meir, I.** (1973). Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 25–51.

**Oppliger, A., Giorgi, M. S., Conelli, A., Nembrini, M., and John-Alder, H. B**. (2004). Effect of testosterone on immunocompetence, parasite load, and metabolism in the common wall lizard (*Podarcis muralis*). *Can. Jour. Zool.****82***, 1713-1719.

**Peterson, C. C., Walton, B. M. and Bennett, A. F.** (1999). Metabolic costs of growth in free-living Garter Snakes and they energy budgets of ectotherms. *Funct Ecol* **13**, 500–507.

**Quinn, A. E., Georges, A., Sarre, S. D., Guarino, F., Ezaz, T. and Graves, J. A. M.** (2007). Temperature sex reversal implies sex gene dosage in a reptile. *Science (1979)* **316**, 411.

**Quinn, A. E., Radder, R. S., Sarre, S. D., Georges, A., Ezaz, T. and Shine, R.** (2009). Isolation and development of a molecular sex marker for Bassiana duperreyi, a lizard with XX/XY sex chromosomes and temperature-induced sex reversal. *Molecular Genetics and Genomics* **281**, 665–672.

**Radder, R. S., Pike, D. A., Quinn, A. E. and Shine, R.** (2009). Offspring sex in a lizard depends on egg size. *Current Biology* **19**, 1102–1105.

**Ricklefs, R. E. and Wikelski, M.** (2002). The physiology / life- history nexus. **17**, 462–468.

**Robert Burger, J., Hou, C., A. S. Hall, C. and Brown, J. H.** (2021). Universal rules of life: metabolic rates, biological times and the equal fitness paradigm. *Ecol Lett* **24**, 1262–1281.

**Sarre, S. D., Georges, A. and Quinn, A.** (2004). The ends of a continuum : genetic and temperature- dependent sex determination in reptiles. *BioEssays* 639–645.

**Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B. and Charnov, E. L.** (2004). Effects of body size and temperature on population growth. *Am Nat* **163**, 429–441.

**Schwanz, L. E., Georges, A., Holleley, C. E. and Sarre, S. D.** (2020). Climate change, sex reversal and lability of sex-determining systems. *J Evol Biol* **33**, 270–281.

**Sears, M. W.** (2005). Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology* **140**, 171–177.

**Shine, R., Elphick, M. J. and Donnellan, S.** (2002). Co‐occurrence of multiple, supposedly incompatible modes of sex determination in a lizard population. *Ecol Lett* **5**, 486–489.

**Sinervo, B., Doughty, P., Huey, R. B., Zamudio, K., Sinervo, B. and Zamudio, K.** Allometric Engineering: A Causal Analysis of Natural Selection on Offspring Size. *Science* **258**, 1927-1930.

**Somjee, U., Shankar, A. and Falk, J. J.** (2022). Can Sex-Specific Metabolic Rates Provide Insight into Patterns of Metabolic Scaling? *Integr Comp Biol* **62**, 1460–1470.

**Tsuji, J. S.** (1988). Thermal Acclimation of Metabolism in Sceloporus Lizards from Different Latitudes. *Source: Physiological Zoology* **61**, 241–253.

**van Doorn, G. S. and Kirkpatrick, M.** (2010). Transitions between male and female heterogamety caused by sex-antagonistic selection. *Genetics* **186**, 629–645.

**Warner, D. A. and Andrews, R. M.** (2002). Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society* **76**, 105–124.

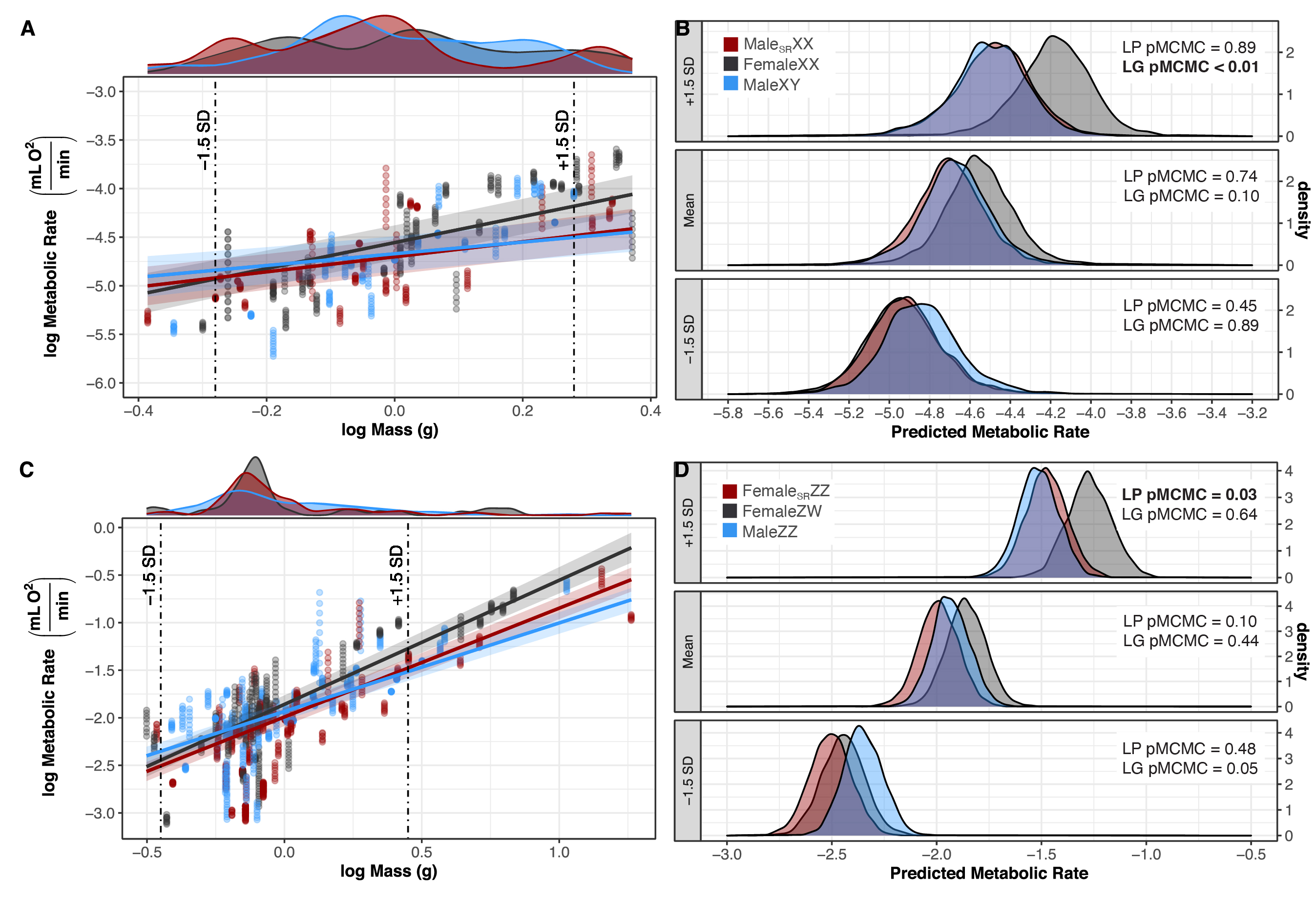
**White, C. R., Alton, L. A., Bywater, C. L., Lombardi, E. J. and Marshall, D. J.** (2022). Metabolic scaling is the product of life-history optimization. *Science* **377**, 834-839.

**Wild, K. H., Roe, J. H., Schwanz, L., Georges, A. and Sarre, S. D.** (2022). Evolutionary stability inferred for a free ranging lizard with sex‐reversal. *Mol Ecol* **31**, 2281–2292.

**Zena, L. A., Dillon, D., Hunt, K. E., Navas, C. A., Bícego, K. C., and Buck, C. L**. (2019). Seasonal changes in plasma concentrations of the thyroid, glucocorticoid and reproductive hormones in the tegu lizard *Salvator merianae*. *Gen and Comp Endo****273***, 134-143.



**Figure 1.** The Like Phenotype/Genotype Framework for testing the metabolic consequences of sex-reversal for ZZ/ZW and XX/XY genetic sex determination systems with different patterns of genetic sex determination. Colours indicate sex class for each species. Body mass and metabolic rates have been log transformed to approximate linear relationships. Each pattern of genetic sex determination contains three competing hypotheses for the relationship between body mass and metabolic rates: Null – no differences; Like Phenotype – similarities between reversed sex and concordant phenotype; Like Genotype – similarities between reversed sex and concordant genotype.



**Figure 2.** Comparison of log metabolic rate (V̇O2 mL min) across log body mass (g) by sex class for *Bassiana duperreyi* (A-B; n = 40) and *Pogona vitticeps* (C-D; n = 96). Sex-reversed individuals (maleSR XX or femaleSR ZZ) are denoted by red colour, phenotypic females (female XX or femaleZW) are denoted in black, phenotypic males (male XY or maleZZ) are denoted in blue. Fitted lines were obtained from predicted values from the brms model for each species and confidence bands were constructed from the SE of prediction values for each sex (A,C). Density plots above each regression plot denote the distribution in body mass (log mass) by sex for each species. To visualize how log metabolic rate changes across log body mass, panels (B and D) show the distribution of predicted metabolic rate at three areas of log body mass (mean, +1.5SD, and -1.5SD) denoted by the dash-dot line in panels A and C for each sex and species. In panels A and C pMCMC indicate contrast differences between Like Phenotype (LP) or Like Genotype (LG) for each distribution.

**Table 1**. Model coefficients for testing whether sex affects the slope of metabolic rate for *Bassiana duperreyi*, where the intercept is concordant females. Metabolic rate and mass were log transformed and time was z-transformed. Columns l-95% CI and u-95% CI, are the lower and upper bound of the 95% credible interval for each parameter, estimated from the posterior distribution.

| Parameter | | Estimate | | l-95% CI | | u-95% CI | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| *Fixed Effects* |  | |  | |  | |
| **Intercept (FemaleXX)** | **-4.56** | | **-4.90** | | **-4.20** | |
| MaleSRXX | -0.15 | | -0.32 | | 0.02 | |
| MaleXY | -0.12 | | -0.29 | | 0.06 | |
| **logMass** | **1.34** | | **0.87** | | **1.81** | |
| ztime | 0.01 | | -0.02 | | 0.05 | |
| **MaleSRXX:logMass** | **-0.56** | | **-0.90** | | **-0.23** | |
| **MaleXY:logMass** | **-0.74** | | **-1.07** | | **-0.41** | |
| *Random Effects* |  | |  | |  | |
| Lizard Identity (id) |  | |  | |  | |
| **Intercept** | **0.25** | | **0.19** | | **0.33** | |
| **Slope** | **0.09** | | **0.07** | | **0.13** | |
| Sampling Session (day) |  | |  | |  | |
| **Intercept** | **0.38** | | **0.17** | | **0.83** | |
| **Residuals** | **0.26** | | **0.25** | | **0.28** | |

**Table 2**. Model coefficients form hetero testing whether sex affects the slope of metabolic rate for *Pogona vitticeps,* which heteroscedasticity was accounted for within the data. The intercept is concordant females. Metabolic rate and mass were log transformed and time was z-transformed. Columns l-95% CI and u-95% CI, are the lower and upper bound of the 95% credible interval for each parameter, estimated from the posterior distribution.

| Parameter | Estimate | l-95% CI | u-95% CI |
| --- | --- | --- | --- |
| *Fixed Effects* |  |  |  |
| **Intercept (FemaleZW)** | **-1.86** | **-2.04** | **-1.67** |
| FemaleSRZZ | -0.13 | -0.28 | 0.03 |
| MaleZZ | -0.07 | -0.22 | 0.07 |
| **logMass** | **1.30** | **1.11** | **1.49** |
| **ztime** | **0.06** | **0.04** | **0.08** |
| **FemaleSRZZ:logMass** | **-0.16** | **-0.32** | **-0.01** |
| **MaleZZ:logMass** | **-0.37** | **-0.55** | **-0.21** |
| *Random Effects* |  |  |  |
| Lizard Identity (id) | 0.22 | 0.18 | 0.27 |
| **Intercept** | **0.30** | **0.25** | **0.35** |
| **Slope** | **0.07** | **0.06** | **0.09** |
| Sampling Session (day) |  |  |  |
| **Intercept** | **0.28** | **0.19** | **0.42** |
| Residuals |  |  |  |
| **Sigma\_Intercept** | **-1.60** | **-1.64** | **-1.56** |
| **Sigma\_logMass** | **-1.40** | **-1.54** | **-1.26** |
| **Sigma\_ztime** | **0.22** | **0.18** | **0.27** |

**Table 3**. Posterior distributions for log metabolic rate (Log MR) and growth rate (SVL or mass) estimates when testing if sex-reversed individuals show support for Like Genotype or Like Phenotype Framework for *Bassiana duperreyi* and *Pogona vitticeps*. Estimates were comparisons from subtracting the model posterior distribution of the median for sex-reversed individuals by either their phenotypic or genotypic counterparts, depending on the framework being tested. Growth rate models (SVL and mass) posteriors were extracted while accounting for log metabolic rate on each growth estimate by sex. Full model results can be found in Tables S5 & S6.

| Species | Test | Contrast | Estimate | | l-95% CI | | u-95% CI | | pMCMC Value | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *B. duperreyi* | Log MR | MaleSR XX - Male XY | | 0.18 | | -0.17 | | 0.53 | | 0.33 |
| **MaleSR XX - Female XX** | | **-0.56** | | **-0.90** | | **-0.23** | | **< 0.01** |
| SVL (mm/d) | MaleSR XX - Male XY | | 3.77 | | -8.53 | | 15.57 | | 0.52 |
| MaleSR XX - Female XX | | -4.06 | | -15.80 | | 7.71 | | 0.47 |
| Mass (cg/d) | MaleSR XX - Male XY | | -0.43 | | -4.92 | | 3.88 | | 0.85 |
| MaleSR XX - Female XX | | -2.59 | | -6.54 | | 1.13 | | 0.18 |
| *P. vitticeps* | Log MR | **FemaleSR ZZ - Female ZW** | | **-0.16** | | **-0.32** | | **-0.01** | | **0.05** |
| **FemaleSR ZZ - Male ZZ** | | **0.21** | | **0.09** | | **0.32** | | **< 0.01** |
| SVL (mm/d) | FemaleSR ZZ - Female ZW | | -1.50 | | -4.60 | | 1.78 | | 0.37 |
| FemaleSR ZZ - Female ZW | | -1.16 | | -3.99 | | 1.68 | | 0.43 |
| Mass (g/d) | FemaleSR ZZ - Female ZW | | -0.91 | | -4.44 | | 2.80 | | 0.61 |
| FemaleSR ZZ - Male ZZ | | -1.81 | | -5.00 | | 1.25 | | 0.25 |