Increased sexual dimorphism evolves in a fossil stickleback following ecological release from fish piscivores

Allison Ozark[1], Akhil Ghosh[1], Raheyma Siddiqui[1], Matthew Stuart[1],
Samantha Swank[1], Michael A. Bell[2], Gregory J. Matthews[1], and Yoel E. Stuart[1]

[1] Loyola University Chicago, Chicago, IL, USA

[2] University of California Museum of Paleontology, Berkeley, CA, USA

Abstract

Everyone loves the stickle

Keywords: Stickle

1 Introduction

Ecological release theory suggests that a prey population's niche should expand when predation is relaxed or removed (reviewed in Herrmann, Stroud, and Losos (2021)). Niche changes in habitat and resource use should then drive phenotypic evolution as the population adapts to new conditions (Herrmann, Stroud, and Losos (2021)). For example, resource use expansion should result in trophic trait evolution (cite; e.g.,). Habitat expansion should result in locomotor change (cite; e.g.,). And release from enemies should result in reduction of costly defense traits (cite; e.g.,).

Niche expansion could manifest through a combination of increasing within- and between-individual niche widths (Bolnick et al. (2010); Herrmann, Stroud, and Losos (2021)), including divergence between the sexes (Bolnick and Doebeli (2003); Cooper, Gilman, and Boughman (2011)). Theory and empirical data suggest that a population presented with novel ecological opportunity might experience disruptive selection on males and females stemming from intraspecific competition over newly accessible resources, resulting in intersexual divergence in habitat use and associated phenotypes (Schoener 1968; Shine (1989); Bolnick and Doebeli (2003); Butler, Sawyer, and Losos (2007); Bolnick and Lau (2008); Cooper, Gilman, and Boughman (2011); but see Stuart et al. (2021); Blain (2022)). Such character displacement between the sexes is therefore one explanation for sexual dimorphism (de Lisle papers).

We tested this link between release from predators and the evolution of sexual dimorphism in a well-preserved, high resolution lineage of the fossil stickleback fish (Gasterosteus doryssus). The sex of the individual fossils, which is unobserved in practice, was imputed using multiple imputation by chained equations (MICE) (Buuren and Groothuis-Oudshoorn (2011)) with observed data used to train the imputation model based on extant stickleback with known sex. Then we tracked the multivariate evolution of sexual dimorphism over ~16,000 years for traits related to swimming, feeding and defense. The fossil sequence captures a bout of adaptive evolution following ecological release from predators, as follows. The fossil lineage appeared in the depositional environment as a fully armored form, with complete pelvic girdles, two pelvic spines, and three dorsal spines, on average (Michael A. Bell, Travis, and Blouw (2006); Stuart, Travis, and Bell (2020)). However, this habitat appears to have been missing fish piscivores (e.g., trout and other salmonids known to prey on modern stickleback; M. A. Bell (2009)), relaxing putative selection for armor (Reimchen papers, Bell papers, Bowne (1994); Roesti et al. 2023). The lineage thus adaptively evolved armor loss and reduction in several other traits as well (Hunt, Bell, and Travis (2008); Stuart, Travis, and Bell (2020); Siddiqui et al. in prep), and tooth wear data suggest that the population also began eating more planktonic prey, expanding to an open water lifestyle (Purnell et al. 2007).

Sexual Dimorphism is interesting because. . . . . .

Sexual Dimoprhism lit review: Saitta et al. (2020)

The remainder of this manuscript contains a description of the data in section 3 and a description of our models in 4. Section 5 presents a summary of our results, and we end with our conclusion and future work in section 6.

2   Methods and Materials

A major challenge in this work is inferring the sex of fossil specimens. This typically cannot be done directly, except for lineages whose sexes are distinguished by the presence or absence of sex-specific characters (Hone and Mallon (2017); Saitta et al. (2020)). Instead, paleobiologists resort to statistical detection of sex and sexual dimorphism, including tests for bimodality in trait distributions (e.g., Hone and Mallon (2017)) and divergence in growth curves (e.g., Saitta et al. (2020)).

We used a third approach to infer fossil sex and study the evolution of sexual dimorphism by taking advantage of the fact that G. doryssus is part of the extant threespine stickleback species complex (Gastersteus aculeatus). Along with the fossil data collected for this study, we also have data from extant populations of the Threespine Stickleback, Gasterosteus aculeatus, measuring the same traits for individuals whose sex could be determined directly. We then combined these sets of data and treat the sex of the fossil specimens as missing and used multiple imputation (Little and Rubin (2002)) to impute the sex of the fossils many times. Imputations were performed using the MICE (Buuren and Groothuis-Oudshoorn (2011)) algorithm and implemented in R (R Core Team (2022)) with M = 100 imputations performed.

After imputing the sex of the fossil data, each completed data set is then used to fit a modified Ornstein–Uhlenbeck (OU) (Uhlenbeck and Ornstein (1930)) model using a Bayesian framework to look for sexual dimorphism across a variety of stickleback phenotypes

3   Data

3.1   Fossil Specimen Data

We used Gasterosteus doryssus data that were previously reported by Stuart, Travis, and Bell (2020), Voje, Bell, and Stuart (2022), and Siddiqui et al. (in review). Briefly, the data were collected from fossil Series K from Quarry D (Cerasoni et al., in review), dug from

an open pit diatomite mine at 9.526° N, 119.094° W, near Fernley, Nevada, USA. Series K consisted of 18 samples taken at ~1000-year intervals, and mean sample times span ~16,363 years. Fish from series K were measured for 16 ecomorphological traits related to armor, swimming, and feeding (Table 1). Series K started at a previously documented horizon when a low armored lineage of stickleback with zero to one dorsal spines, zero pelvic spines, and highly reduced pelvises was completely replaced by a high armored lineage of stickleback with three dorsal spines, two pelvic spines, and complete (Bell et al. 2006; Bell 2009; Stuart et al. 2020). This lineage subsequently evolved reduction in armor, body size, and traits related to swimming and feeding (Bell et al. 2006; Stuart et al. 2020; Siddiqui et al. in review). The tempo and mode of armor reduction during this sequence suggests adaptive evolution by natural selection (Hunt et al. 2008), and we focus on the multivariate evolution of sexual dimorphism by this second lineage.

The fossil data consists of 814 specimens with unknown sex over 18 time periods spaced ~1000 years apart. Table 2 shows the sample size at each of the 18 time periods. There are at least 22 specimens at each time period with a high of 67 specimens in period 7.

Table 1: Traits and trait descriptions. 'sc' denotes size correction of trait against standard length. Names of bones follow Bowne (1994) unless otherwise noted.

Trait Name	Trait Code	Trait Description
Standard Length	sl	Distance from anterior tip of premaxilla to posterior end of last vertebra (hypural plate)
Dorsal Spine	mds	Number of dorsal spines from 0 to 3
Dorsal Fin Ray	mdf	Number of bones in the dorsal fin posterior to the third dorsal spine (i.e., soft dorsal fin rays)
Anal Fin Ray	maf	Number of bones in the anal fin posterior to the anal spine (i.e., soft dorsal fin rays)
Abdominal Vertebra	mav	Number of vertebrae anterior to the first vertebra contacting an anal fin pterygiophore (Aguirre et al. 2014)
Caudal Vertebra	mcv	Number of vertebrae posterior to and including the first vertebra contacting an anal fin pterygiophore (Aguirre et al. 2014)

Trait Name	Trait Code	Trait Description
Pterygiophore number	mpt	Number of pterygiophores anterior to but excluding the pterygiophore under the third dorsal spine, which is immediately anterior to and contiguous with the dorsal fin
Pelvic Spine length	lps.sc	Length from the base of one pelvic spine above its articulation with the pelvic girdle to its distal tip
Ectocoracoid	ect.sc	Length between the anterior and posterior tips of the shoulder girdle base (i.e., ectocoracoid)
Pelvic Girdle	tpg.sc	Length between the anterior to posterior tips along midline. If vestigial, the sum of longest anterior-posterior axis for the vestiges
Cleithrum length	cle.sc	Length from free dorsal tip to ventral tip of the cleithrum on the anterior margin of the shoulder girdle (i.e., cleithrum)
Premaxilla	pmx.sc	Length from the anterior tip of the premaxilla to the distal tip of the ascending process of the premaxilla
Dorsal Spine	Ds#.sc# = 1,2,or 3	Length from the base of a dorsal spine above the pterygiophore to its distal tip along the anterior edge
Pterygiophore	lpt.sc	Distance between the anterior to posterior tips of the pterygiophore immediately preceding the 3rd dorsal spine (when present)

3.2 Extant Specimen data

To span the gamut of stickleback diversity for our predictive model, we sampled modern stickleback from lakes containing generalist stickleback populations (Hendry et al. (2009); Bolnick (2011)) and from lakes containing benthic-limnetic species pairs (Baumgartner et al. 1988; Schluter and McPhail (1992)) (Table 2 (What is this?)). The generalist populations

Table 2: The number of stickleback fossils at each time point. Sample size at each time point ranges from a low of 22 to a high of 67.

time	count
1	43
2	41
3	51
4	41
5	46
6	48
7	67
8	55
9	42
10	33
11	37
12	22
13	41
14	43
15	46
16	47
17	56
18	55

were collected by YES in 2013 and previously described in Stuart et al. (2017). These samples were fixed in formalin, then stained for bone with Alizarin Red in 2013. Benthic and limnetic specimens were kindly loaned by D. Schluter and his lab at University of British Columbia. They collected benthic and limnetic individuals from Enos Lake in 1988 and from Emily Lake, Little Quarry Lake, Paxton Lake, and Priest Lake in 2018. The Enos specimens had been fixed whole in formalin and stored in 40% isopropanol. The specimens from the other lakes were initially preserved whole in 95% ethanol in the field before being gradually transferred to water then formalin in the lab and ultimately stored in 40% isopropanol. In 2019, we stained these specimens for bone using Alizarin Red.

We next replicated fossil data collection (Table 1) on these extant specimens. Standard length as well as pelvic-spine length on each side were measured with calipers. We used a dissection microscope to count dorsal spines, pelvic spines, dorsal-fin rays, and anal-fin rays. Right and left-side pelvic girdle lengths and ectocoracoid lengths were measured from ventral photographs taken using a Canon EOS Rebel T7 with a Tamron 16-300 mm MACRO lens mounted on a leveled Kaiser RS1 copy stand. Specimens were held in place for ventral photographs using a small tabletop vise with an attached scale bar. Lateral X-rays were used to measure dorsal spine length, number of pterygiophores anterior to the pterygiophore holding the third spine, length of the pterygiophore just anterior to the third spine, cleithrum length, and pre-maxilla ascending branch length. We also counted vertebrae from the X-

rays: abdominal vertebrae were counted anterior to the first vertebra with a haemal spine contacting an anal fin pterygiophore. Caudal vertebrae were posterior, including the first vertebra with the haemal spine contacting the anal fin pterygiophore (following Aguirre, Walker, and Gideon (2014). X-rays were taken with an AXR Hot Shot X-ray Machine (Associated X-ray Corporation) at the Field Museum of Natural History. Specimens were exposed at 35kV and 4mA. Small fish were exposed for 7s, medium fish for 8s, and large fish for 10s. We developed the film and scanned individual images of each fish using the B&W Negatives setting on an Epson Perfection 4990 Photo flatbed at 2400 dpi. Measurements from photographs and X-rays were taken with FIJI (Schindelin et al. 2012) and its plugin ObjectJ (https://sils.fnwi.uva.nl/bcb/objectj/). All photographs, X-rays, and ObjectJ files have been uploaded to Morphosource.org (accession # TBD). We dissected individuals from the generalist populations to determine sex from the gonads. Individuals from the species-pair lakes were sexed by Schluter and his lab, using a genotyping protocol (confirm and cite).

The extant data used here consists of a total of 367 specimens all with known sex. Of these, there are 202 and 165 female and male specimens, respectively.

3.3   Outlier analysis.

To check for outliers, we calculated within-group means and standard deviations for each trait separately for K series fossil specimens (pooled across samples) and for extant specimens (pooled across lakes). We noted trait values greater than 3.5 standard deviations from the mean as potential outliers. We checked whether these potential outliers were a result of data entry and collection error and corrected them if they were. We turned the remaining outlier trait values to NAs. (confirm) (Wait, what? Why? Anything that was 3.5 SD above the mean was recorded as missing? How do you justify this?)

Missing data imputation, including fossil sex

Quantification and evolution of sexual dimorphism

What covariates do we have in the data: length, what else,

4   Models

4.1   Imputation Model

Let $\boldsymbol{W}$ be an $(n_{extant} + n_{fossil}) \times 1$ vector of the covariate gender of the stickleback fish, $\boldsymbol{X}$ be an $(n_{extant} + n_{fossil}) \times K$ matrix of the K continuous phenotypes of interest, and $\boldsymbol{Y}$ be

an $(n_{extant} + n_{fossil}) \times L$ matrix of the L discrete phenotypes of interest. Because the gender of the fossilized stickleback fish is unobservable, we further define $\boldsymbol{W} = (\boldsymbol{W}_{extant}^T, \boldsymbol{W}_{fossil}^T)^T$ where $\boldsymbol{W}_{extant}$ and $\boldsymbol{W}_{fossil}$ are the $n_{extant} \times 1$ and $n_{fossil} \times 1$ vectors of the observed extant gender and missing fossil gender, respectively.

We impute the missing gender for the fossil data by sampling from the posterior predictive distribution $P(\boldsymbol{W}_{fossil} | \boldsymbol{W}_{extant}, \boldsymbol{X}, \boldsymbol{Y})$ using the multiple imputation by chained equations (MICE) algorithm (Buuren and Groothuis-Oudshoorn (2011)) with predictive mean matching. Traditionally, the choice for the number of completed dats sets is a relatively small number such as $M = 5$ or $M = 10$. However, Zhou and Reiter (2010) recommend a larger number of imputed data sets if the data users intend on performing Bayesians analysis after imputation, which in this case, we do. Therefore, the imputation algorithm is run to obtain a total of $M = 100$ completed datasets. In addition to this, Zhou and Reiter (2010) suggests rather than using Rubin's combining rules to combine across imputed data sets, instead pool all of the draws from the posterior distributions across all of the imputed data sets to estimate the posterior distributions of parameters of interest. We proceed with our Bayesian analysis in this manner.

Akhil's stuff about validating the imputation model goes here.

4.2 Completed Data Model

We should note somewhere that we are only using the W_{fossil} in the modeling part. We drop the W_{extant}. So just note that W_{ti} is really $W_{fossil,ti}$. Not sure how to say this, but we need to make it clear that we are only using the fossil data for the OU modeling.

4.2.1 Continuous Phenotypes

For a given imputed dataset, let W_{ti} be the imputed gender, $\boldsymbol{X}_{ti}$ be the $K \times 1$ vector of continuous phenotypes, and $\boldsymbol{Y}_{ti}$ be the $L \times 1$ vector of discrete phenotypes for $t = 1, \ldots, T$ and $i = 1 \ldots, n_t$).

Define the last element of $\boldsymbol{X}_{ti}$ ($X_{K,ti}$) as the length of the stickleback. For $k = 1, \cdots, K-1$, we will assume

$$X_{k,ti} \overset{iid}{\sim} \begin{cases} \mathcal{N}(\mu_{k,ft} & +\beta_k(X_{K,ti} - \mu_{K,ft}), & \sigma_k^2), & W_{ti} = \text{Female} \\ \mathcal{N}(\mu_{k,mt} & +\beta_k(X_{K,ti} - \mu_{K,mt}), & \sigma_k^2), & W_{ti} = \text{Male} \end{cases} \tag{1}$$

$$X_{K,ti} \overset{iid}{\sim} \begin{cases} \mathcal{N}(\mu_{K,ft}, & \sigma_K^2), & W_{ti} = \text{Female} \\ \mathcal{N}(\mu_{K,mt}, & \sigma_K^2), & W_{ti} = \text{Male} \end{cases} \tag{2}$$

where $\mu_{k,ft}$ and $\mu_{k,mt}$ represent the time-t specific mean of phenotype k for female and male stickleback fish, respectively, and β_k is an additional parameter to account for the biological phenomenon that other continuous phenotypes for a particular animal are positively correlated with their length **CITATION NEEDED**. We further set

$$\mu_{k,gt} = \theta_{k,g} + u_{k,gt}, \tag{3}$$

for $g \in \{f, m\}$ where $\theta_{k,g}$ is the overall mean of phenotype X_k for each gender, and $u_{k,gt}$ measures the difference between $\mu_{k,gt}$ and $\theta_{k,g}$. We then fit $\boldsymbol{u}_{k,g} = \{u_{k,g1}, \cdots, u_{k,gT}\}$ to an Ornstein-Uhlenback (OU) process (Uhlenbeck and Ornstein (1930)) where we assume $u_{k,gT}$ have a marginal mean of 0. Because each time period is ~1000 years, we will discretize the OU process without loss of generality. For $t = 2, \ldots, T$, we assume

$$u_{k,gt} \overset{iid}{\sim} \mathcal{N}(\kappa_k u_{k,g(t-1)}, \tau_k^2). \tag{4}$$

$\kappa_{k,g}$ represents the correlation between $\mu_{k,gt}$ and $\mu_{k,g(t+1)}$, and it also follows that $\mathrm{cor}(u_{g,t}, u_{g,t+h}) = \kappa^h$ for $h \in \mathbb{N}$. In addition, we assume

$$u_{k,g1} \overset{iid}{\sim} \mathcal{N}\left(0, \frac{\tau_k^2}{1 - \kappa_k^2}\right). \tag{5}$$

This model choice is to preserve stationarity; i.e. $p(u_{k,gs}) = p(u_{k,gt})$ for $s \neq t$.

4.2.2 Discrete Phenotypes

For the discrete phenotypes, we will assume

$$Y_{l,ti} \sim \begin{cases} Poisson(\lambda_{l,ft}), & W_{ti} = \text{Female} \\ Poisson(\lambda_{l,mt}), & W_{ti} = \text{Male} \end{cases}, \tag{6}$$

for $l = 1, \cdots, L$. Similar to the continuous phenotypes, we set

$$\log(\lambda_{l,gt}) = \gamma_{l,g} + v_{l,gt}. \tag{7}$$

We use the log function to allow $v_{l,gt}$ to take all values on the real number line so we can properly fit an OU process to these effects. We further assume

$$v_{l,gt} \overset{iid}{\sim} \mathcal{N}(\phi_l v_{l,g(t-1)}, \omega_l^2), \tag{8}$$

and

$$v_{l,g1} \stackrel{iid}{\sim} \mathcal{N}\left(0, \frac{\omega_l^2}{1 - \phi_l^2}\right)..\tag{9}$$

Because we are fitting a dataset with a stochastic structure on the means of the phenotypes, we analyze the data via a Bayesian analysis. Bayesian data analysis is also more naturally used when we have to impute data (**CITATION**).

Priors: For $k = 1, \cdots, K$ and $l = 1, \cdots, L$,

$$
\begin{aligned}
\sigma_k &\stackrel{iid}{\sim} \mathcal{N}(0, 100)I_{\{\sigma>0\}} \\
\tau_k &\stackrel{iid}{\sim} \mathcal{N}(0, 100)I_{\{\tau>0\}} \\
\kappa_k &\stackrel{iid}{\sim} \mathcal{N}(0, 1)I_{\{-1<\kappa_g<1\}} \\
\beta_k &\stackrel{iid}{\sim} \mathcal{N}(0, 5) \\
\theta_{k,g} &\stackrel{iid}{\sim} \mathcal{N}(0, 10000)\omega_l \quad\quad\quad\quad \stackrel{iid}{\sim} \mathcal{N}(0, 100)I_{\{\tau>0\}} \\
\phi_l &\stackrel{iid}{\sim} \mathcal{N}(0, 1)I_{\{-1<\kappa_g<1\}} \\
\gamma_{l,g} &\stackrel{iid}{\sim} \mathcal{N}(0, 10000)
\end{aligned}
\tag{10}
$$

$$\tag{11}$$

All models were built using R Core Team (2022)

Cornuault (2022) Bayesian OU model.

Bayesian Analysis after multiple imputation Zhou and Reiter (2010): They recommend using a large number of imputations. 5 or 10 is too small. We are using M = 100.

5   Results

6   Discsusson, Future work and conclusions

We predicted that release from predators would result in niche expansion and increased sexual dimorphism, based on several studies of modern stickleback. For example, in lakes where sculpin competitors are absent and stickleback (Roesti et al. 2023) See Spoljaric and Reimchen 2008, page 512 right column for references and discussion of differences between benthic males and limnetic females. Male stickleback are benthic and littoral (Wootton 1976).... Reimchen papers in general good for this section.

Acknowledgements

Supplementary Material

All code for reproducing the analyses in this paper is publicly available at https://github.com/Akhil-Ghosh/SticklebackProject

References

Aguirre, Windsor E, Kendal Walker, and Shawn Gideon. 2014. "Tinkering with the Axial Skeleton: Vertebral Number Variation in Ecologically Divergent Threespine Stickleback Populations." *Biol. J. Linn. Soc. Lond.* 113 (1): 204–19.

Bell, M A. 2009. "Implications of a Fossil Stickleback Assemblage for Darwinian Gradualism." *J. Fish Biol.* 75 (8): 1977–99.

Bell, Michael A, Matthew P Travis, and D Max Blouw. 2006. "Inferring Natural Selection in a Fossil Threespine Stickleback." *Paleobiology* 32 (4): 562–77.

Blain, S A. 2022. *Evolutionary Outcomes of Interactions Among Phenotypes in Post-Glacial Lakes.* University of British Columbia, Canada.

Bolnick, Daniel I. 2011. "Sympatric Speciation in Threespine Stickleback: Why Not?" *Int. J. Ecol.* 2011: 1–15.

Bolnick, Daniel I, and Michael Doebeli. 2003. "Sexual Dimorphism and Adaptive Speciation: Two Sides of the Same Ecological Coin." *Evolution* 57 (11): 2433–49.

Bolnick, Daniel I, Travis Ingram, William E Stutz, Lisa K Snowberg, On Lee Lau, and Jeff S Paull. 2010. "Ecological Release from Interspecific Competition Leads to Decoupled Changes in Population and Individual Niche Width." *Proc. Biol. Sci.* 277 (1689): 1789–97.

Bolnick, Daniel I, and On Lee Lau. 2008. "Predictable Patterns of Disruptive Selection in Stickleback in Postglacial Lakes." *Am. Nat.* 172 (1): 1–11.

Bowne, P S. 1994. "Systematics and Morphology of the Gasterosteiformes." In *The Evolutionary Biology of the Threespine Stickleback*, edited by M A Bell and S A Foster. Oxford, UK: Oxford University Press.

Butler, Marguerite A, Stanley A Sawyer, and Jonathan B Losos. 2007. "Sexual Dimorphism and Adaptive Radiation in Anolis Lizards." *Nature* 447 (7141): 202–5.

Buuren, Stef van, and Karin Groothuis-Oudshoorn. 2011. "Mice: Multivariate Imputation by Chained Equations in r." *Journal of Statistical Software* 45 (3): 1–67. https://doi.org/10.18637/jss.v045.i03.

Cooper, Idelle A, R Tucker Gilman, and Janette Wenrick Boughman. 2011. "Sexual Dimorphism and Speciation on Two Ecological Coins: Patterns from Nature and Theoretical Predictions." *Evolution* 65 (9): 2553–71.

Cornuault, Josselin. 2022. "Bayesian Analyses of Comparative Data with the Ornstein–Uhlenbeck Model: Potential Pitfalls." *Systematic Biology* 71 (6): 1524–40. https://doi.org/10.1093/sysbio/syac036.

Hendry, A P, D I Bolnick, D Berner, and C L Peichel. 2009. "Along the Speciation Continuum in Sticklebacks." *J. Fish Biol.* 75 (8): 2000–2036.

Herrmann, Nicholas C, James T Stroud, and Jonathan B Losos. 2021. "The Evolution of 'Ecological Release' into the 21st Century." *Trends Ecol. Evol.* 36 (3): 206–15.

Hone, David W E, and Jordan C Mallon. 2017. "Protracted Growth Impedes the Detection of Sexual Dimorphism in Non-Avian Dinosaurs." *Palaeontology* 60 (4): 535–45.

Hunt, Gene, Michael A Bell, and Matthew P Travis. 2008. "Evolution Toward a New Adaptive Optimum: Phenotypic Evolution in a Fossil Stickleback Lineage." *Evolution* 62 (3): 700–710.

Little, R. J. A., and D. B. Rubin. 2002. *Statistical Analysis with Missing Data*. Wiley Series in Probability and Mathematical Statistics. Probability and Mathematical Statistics. Wiley. http://books.google.com/books?id=aYPwAAAAMAAJ.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Saitta, Evan T, Maximilian T Stockdale, Nicholas R Longrich, Vincent Bonhomme, Michael J Benton, Innes C Cuthill, and Peter J Makovicky. 2020. "An effect size statistical framework for investigating sexual dimorphism in non-avian dinosaurs and other extinct taxa." *Biological Journal of the Linnean Society* 131 (2): 231–73. https://doi.org/10.1093/biolinnean/blaa105.

Schluter, D, and J D McPhail. 1992. "Ecological Character Displacement and Speciation in Sticklebacks." *Am. Nat.* 140 (1): 85–108.

Shine, R. 1989. "Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence." *Q. Rev. Biol.* 64 (4): 419–61.

Stuart, Yoel E, J William Sherwin, Ambika Kamath, and Thor Veen. 2021. "Male and Female Anolis Carolinensis Maintain Their Dimorphism Despite the Presence of Novel

Interspecific Competition." *Evolution* 75 (11): 2708–16.

Stuart, Yoel E, Matthew P Travis, and Michael A Bell. 2020. "Inferred Genetic Architecture Underlying Evolution in a Fossil Stickleback Lineage." *Nat. Ecol. Evol.* 4 (11): 1549–57.

Stuart, Yoel E, Thor Veen, Jesse N Weber, Dieta Hanson, Mark Ravinet, Brian K Lohman, Cole J Thompson, et al. 2017. "Contrasting Effects of Environment and Genetics Generate a Continuum of Parallel Evolution." *Nat. Ecol. Evol.* 1 (6): 158.

Uhlenbeck, G. E., and L. S. Ornstein. 1930. "On the Theory of the Brownian Motion." *Phys. Rev.* 36 (September): 823–41. https://doi.org/10.1103/PhysRev.36.823.

Voje, Kjetil L, Michael A Bell, and Yoel E Stuart. 2022. "Evolution of Static Allometry and Constraint on Evolutionary Allometry in a Fossil Stickleback." *J. Evol. Biol.* 35 (3): 423–38.

Zhou, X., and J. Reiter. 2010. "A Note on Bayesian Inference After Multiple Imputation." *The American Statistician* 64 (2): 159–63.