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## Geographic Overlap of Potentially Hybridizing Species in the Fish Family Poeciliidae in Their Native Ranges

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GEOGRAPHIC OVERLAP OF POTENTIALLY HYBRIDIZING SPECIES IN THE FISH  
FAMILY POECILIIDAE IN THEIR NATIVE RANGES

By

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I dedicate this thesis to Robert Allen Blume – my boyfriend, my inspiration, and my favorite person in the universe.

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## ABSTRACT

Understanding the factors that influence a species' geographic range and the overlap between the ranges of distinct species remains a central question in both ecology and evolution. Here we investigate the influences of hybridization and the breakdown of reproductive isolation and a key innovation, matrotrophy (the provision of energy for embryonic development after fertilization), on species ranges and range overlaps in the fish family Poeciliidae. We assessed whether pairs of species that hybridize have different amounts of range overlap than pairs of species with similar divergence times that do not hybridize. We also assessed whether matrotrophic species have larger ranges than lecithotrophic species (lecithotrophic species provide all energy for embryonic development before fertilization). To investigate our hypotheses, we reviewed the literature on poeciliid fishes and plotted the ranges of all extant species in ArcGIS. The data we worked on was compiled by M. Tobler and Z. Culumber in 2019 and consisted of museum collection records for individuals of distinct species. We quantified the ranges for 407 different fish species. We then we added data on the estimated time of divergence between sister taxa, based on the phylogenetic tree (Furness *et al.* 2019). We found that the areas of overlap between sister taxa depended upon time since divergence. However, the slopes of range overlap and divergence time were of opposite sign between species pairs that hybridize and species pairs of similar divergence times that do not hybridization and range overlap (km<sup>2</sup>). Based on our results, we believe that the species that are closely related but not hybridizing have smaller areas of overlap because they are still in the stage of primary differentiation, are experiencing secondary contact after prior geographic separation that no longer exists or are in a stable hybrid zone. When comparing the ranges of closely related placentals and non-placentals, we found that multiple closely related species that shared the same reproductive strategy did not have any range overlap. This lends support to the theory that placentation evolved separately in different geographic areas. A future question that researchers could answer using these data would be what is causing the geographic overlap between species. Another future biogeographic study may be an evaluation of whether water features are leading to a decline in species diversity based on habitat preferences or their normal range.

# CHAPTER 1

## GEOGRAPHIC OVERLAP OF HYBRIDIZING SPECIES IN THE FISH FAMILY POECILIIDAE IN THEIR NATIVE RANGES

### Introduction

Understanding the factors that influence a species' geographic range and the overlap between the ranges of distinct species remains a central question in both ecology and evolution. Species adapted to similar conditions could overlap extensively (Rauchenberger 1988). Very few species have the same exact distributions, which may be the result of their speciation events or ongoing interspecific competition (Mouillot and Gaston 2009). Sister species often have similar range sizes, but less similar than other biological traits (Mouillot and Gaston 2009).

Prior work on the geographic ranges of poeciliid species has been geographically restricted and focused on species interactions, dietary niche width, and trophic position (García-Andrade *et al.* 2021). These studies mostly focused on a small scale in individual habitats instead of encompassing the broad global scale of the biosphere (Hayden *et al.* 2019). A notable exception is the work of Bagley *et al.* (2013), who described how fluctuations in climate and sea level during the last ice age heavily influenced the current biogeography of the Least Killifish, *Heterandria formosa*. A similar analysis was conducted by Schlupp *et al.* (2002) for the historical ranges of *Poecilia latipinna* and *Poecilia mexicana*, which are the progenitors of the unisexual Amazon molly, *Poecilia formosa*. They found that the original ranges overlapped much more than the present ranges and that the two species have been reducing their overlap over time (Schlupp *et al.* 2002). The driving force for the reduced overlap was posited to be the strong selection on males to avoid mating with the unisexual individuals (Schlupp *et al.* 2002). Historical changes in range make it difficult to fully understand the historical biogeography of species and apply it to current ranges of species.

Human factors can also impact species populations (Mercado-Silva *et al.* 2012). Populations are shifting geographically because of climate change (Mercado-Silva *et al.* 2012). Fish species are highly susceptible to anthropogenic disturbance, and novel hybrid zones have formed (Mercado-Silva *et al.* 2012). Breeding seasons are shifting, and sex ratios are changing –

which in turn increases hybridization, which could affect species range sizes (Mercado-Silva *et al.* 2012).

There can be consequences to the hybridization of species (Genovart 2009). Species with high dispersal and colonization have the potential to hybridize more, and these new hybrids are often more adaptable (Chunco 2014). Individuals from one species may introgress with individuals from a more common species, leading sometimes to extinction or, in rare cases, saving a species (Schumer *et al.* 2016; Schumer *et al.* 2017). More commonly, hybridization can lead to decreased fitness and are under selective forces through either or both lethality and sterility (Lu *et al.* 2020).

Hybridization is facilitated when closely related species without complete reproductive isolation from each other overlap in their ranges. Thus, we might expect pairs of hybridizing species to overlap more than pairs of similar levels of relatedness that do not hybridize. Conversely, if imperfect pre-mating isolation caused the facilitation of hybridization, but selection does not favor hybrids, that selection could drive reductions in range overlap between pairs of species. In this case the result would be less overlap between pairs of species capable of hybridizing than between pairs of similar relatedness that are not capable of hybridizing.

There are hybridogenic and gynogenetic poeciliid species in the genus *Poeciliopsis* that could have differing range sizes from other non-hybridizing species. There is a literature on hybridization as a source of new adaptive genetic variation, but this work focused on species that have small geographic range sizes (Ungerer *et al.* 1998).

The primary purpose of this research is to ascertain whether pairs of hybridizing species overlap more than pairs of non-hybridizing ones. This study is on the entire family Poeciliidae, with a focus on the genera *Xiphophorus*, *Poecilia*, *Limia*, *Poeciliopsis*, and *Gambusia*. *Xiphophorus* is known to commonly hybridize (Cui *et al.* 2013; Fisher *et al.* 2006). We also used data on time since divergence between species from Furness *et al.* (2019) to determine the divergence times between pairs of species that are known to hybridize and pairs of sister species that do not hybridize.

We hypothesized that pairs of hybridizing species will have more geographic range overlap than pairs of species of similar levels of relatedness that do not hybridize, and that hybrid species would have greater range sizes than species that are not known to hybridize with any others. This is based on the hypothesis that the amount of contact a species has with a closely

related species increases the chances of hybridization (Wang and Keena 2021). However, the inverse result could occur due to hybrid species being under strong selective pressures (Piotrowski *et al.* 2012). If imperfect pre-mating isolation facilitates hybridization, but selection is working against hybrids, that selection could drive reductions in range overlap between pairs of species (Uy *et al.* 2018). In this case the result would be less overlap between pairs of species capable of hybridizing than between pairs of similar relatedness that are not capable of hybridizing.

If we see broad range sizes in species known to hybridize with other species, this may be because they have high adaptability to a variety of habitats. Inversely, if we see small range sizes in species known to hybridize with other species, they may be highly adapted to an extremely specific type of habitat. Due to the phylogenetics of the Poeciliidae family, this will be vital to understanding the correlation between hybridization and geographic range size.

## **Methods**

The dataset we worked on was compiled by M. Tobler and Z. Culumber in 2019 that consisted of museum records for individuals of different poeciliid fish species. Each species had a label with the catch location including the latitude and longitude coordinates, along with the scientific literature the data came from, the country of the catch location, and information about the water source at the catch location. We removed any data points from the dataset with illogical geographic locations in areas where the species were neither native nor introduced. For example, if an individual's coordinates placed it in Greenland when it has only been previously found in Mexico, it was removed from the dataset. Since there are no significant data on all introductions or sites, we used scientific literature as support for introduction locations of each species. Since there have been different classifications of taxa historically, we removed any misclassifications from the dataset as well.

To investigate our hypotheses, we reviewed literature on poeciliids and plotted the ranges of all extant species in ArcGIS (ESRI 2020; Figure 1). We quantified the ranges for the 407 different fish species in our dataset and calculated the range areas for those species (Figure 2). We conducted data analyses on these ranges to answer our research questions.

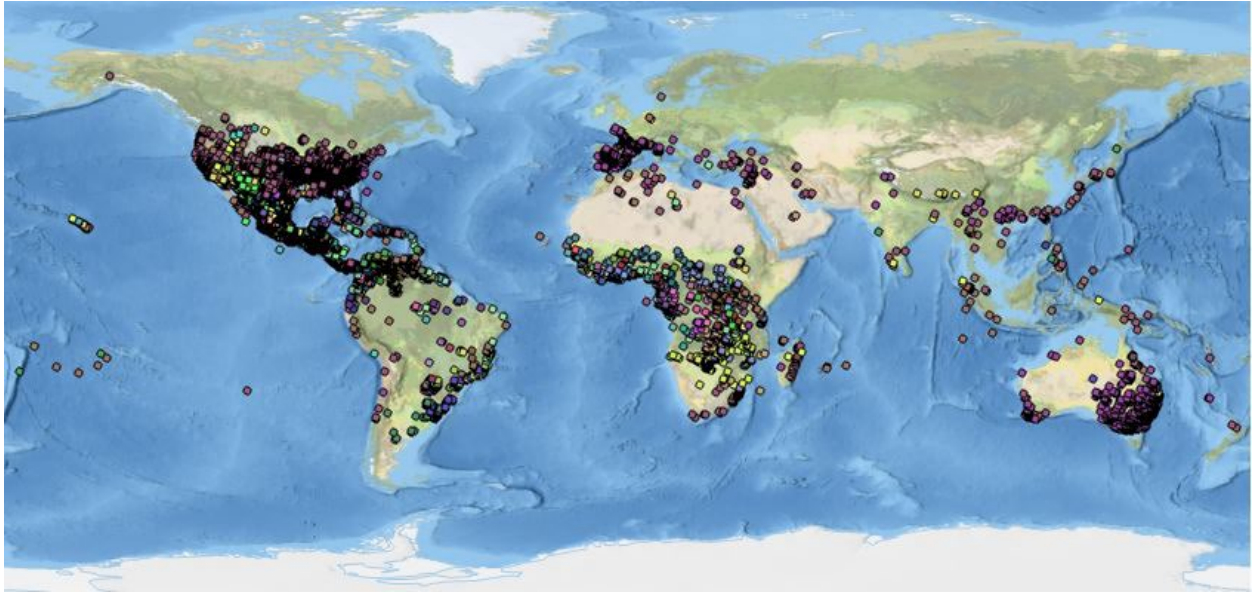


Figure 1. A map showing each data point of the 407 distinct species in the museum records, including the 275 species in the family Poeciliidae and other egg-laying species in the order *Cyprinodontiformes*. Since the native ranges of live bearing poeciliids are in the neotropics, this includes introduced populations across the rest of the world.

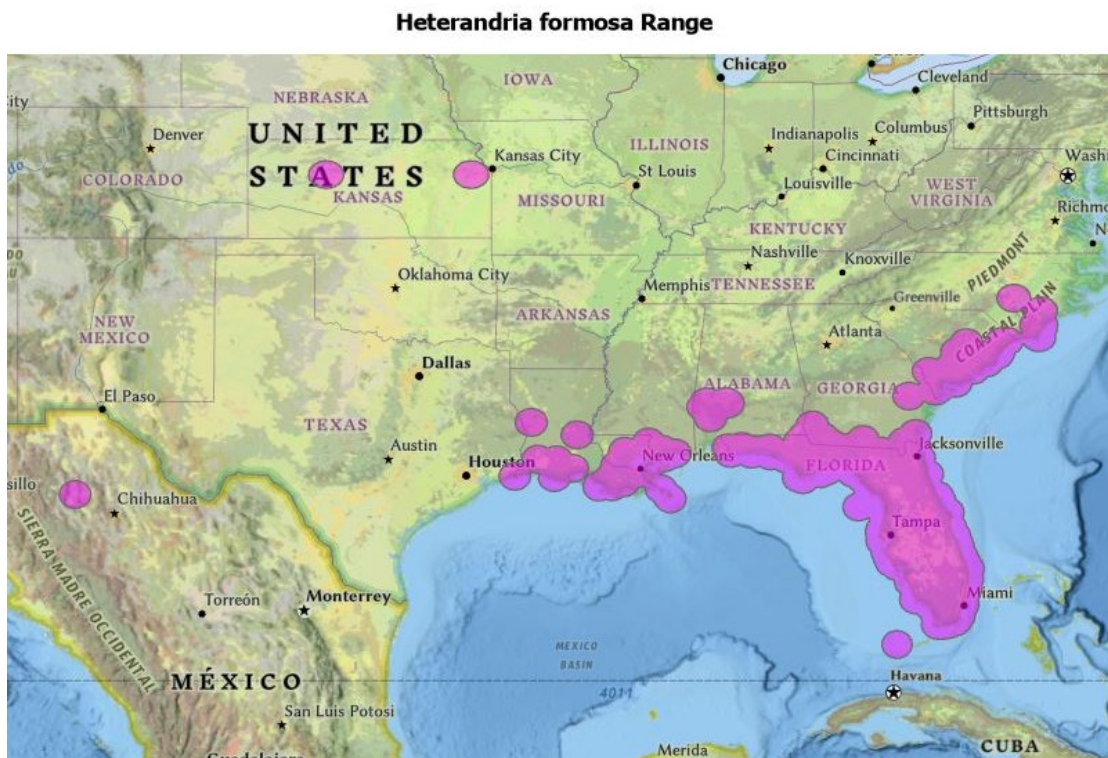


Figure 2. Map of the total range of *Heterandria formosa*. Each of the 407 species in the dataset had individual maps including their total range.

To assess whether there are differences in the size of range overlap between hybridizing and non-hybridizing species, we quantified overlapping ranges and whether species are known to hybridize or not in the wild. We had presence-only data on eleven different hybrids of *Gambusia*, *Poeciliopsis*, and *Xiphophorus* species. We took the native ranges of the individual species and found where the two ranges overlapped using the “Intersect” tool in ArcGIS (ESRI 2020). It was important that the species we considered hybridizing were species that would hybridize naturally in their native ranges, instead of species that are capable of hybridizing with one another in a laboratory or aquarium setting. There is a multitude of data on popular aquarium poeciliids that aquarists have made hybrid crosses of (Maciaszek *et al.* 2019). However, these crosses may not naturally occur in the field due to sexual selection or lack of range overlap.

We then quantified the area of the intersecting ranges using the same methods as we used for the total species’ ranges (Figure 3). The maps also contain the points located inside and outside of the intersect ranges with the locations of known hybrids.



Figure 3. A map of the intersect for the ranges of *Gambusia affinis* and *Gambusia speciosa*, two species of mosquitofish. The points on the map located in and outside of the blue intersect ranges are the locations of known hybrids.

We evaluated whether areas of overlap between species known to hybridize are different from areas of overlap between species that are closely related but not known to hybridize by analyzing

and comparing the range areas of each. These non-hybridizing species that we expected have the potential to hybridize were species that share the same genus and are closely related phylogenetically.

Next, we conducted a Phylogenetic Generalized Least Squares analysis of range size as a function of hybridization to look for a relationship between the hybridization and geographic range size. To do so, we used the poeciliid timetree (Reznick *et al.* 2017). We pruned the tree to include only poeciliid species and updated the taxonomic names. We then made the tree ultrametric with its tips perfectly aligned, by adjusting very minor branch length rounding. We used the discrete variable of hybridization, then subset data for all species with complete data across variables, so that the models that we compared all have the same species and sample sizes (Table 1). This allowed us to determine the impact of the hybridogenic species, while controlling for non-independence of the residuals.

*Table 1.* Species within the *Poeciliid* timetree from Reznick *et al.* (2017). We quantified the range sizes (km<sup>2</sup>) using ArcGIS (ESRI 2020).

Species	Range size (km <sup>2</sup> )	Hybridizes
<i>Gambusia affinis</i>	2765533.66	1
<i>Gambusia atrora</i>	15174.83	0
<i>Gambusia holbrooki</i>	909452.75	1
<i>Gambusia nicaraguensis</i>	181159.9	1
<i>Gambusia nobilis</i>	33331.15	1
<i>Gambusia panuco</i>	94791.67	0
<i>Gambusia puncticulata</i>	81578.32	1
<i>Gambusia rhizophorae</i>	33031.96	1
<i>Gambusia sexradiata</i>	295821.29	1
<i>Gambusia speciosa</i>	45679.85	1
<i>Gambusia vittata</i>	57070.38	0
<i>Gambusia yucatana</i>	285733.19	1
<i>Poeciliopsis baenschi</i>	42125.35	0
<i>Poeciliopsis balsas</i>	68721.1	0
<i>Poeciliopsis fasciata</i>	164046.03	1
<i>Poeciliopsis gracilis</i>	354132.01	0
<i>Poeciliopsis hnlickai</i>	66120.79	0
<i>Poeciliopsis infans</i>	137766.66	0
<i>Poeciliopsis latidens</i>	51999.22	1
<i>Poeciliopsis monacha</i>	37811.33	1



Table 1. continued

Species	Range size (km <sup>2</sup> )	Hybridizes
<i>Poeciliopsis pleurospilus</i>	126420.9	0
<i>Poeciliopsis presidionis</i>	81579.24	0
<i>Poeciliopsis prolifica</i>	126889.7	0
<i>Poeciliopsis scarlli</i>	65922.65	0
<i>Poeciliopsis turneri</i>	20497.61	0
<i>Poeciliopsis turrubarensis</i>	253313.6	0
<i>Xiphophorus alvarezi</i>	33111.61	1
<i>Xiphophorus birchmanni</i>	14015.9	1
<i>Xiphophorus hellerii</i>	343795.75	1
<i>Xiphophorus nigrensis</i>	9658.07	0

To determine whether species that hybridize with one another have differing range overlap from species that are not known to hybridize, we first made a list of all the pairs of lecithotrophic species within the genera *Gambusia*, *Poeciliopsis*, and *Xiphophorus* that show overlap in their native ranges (Table 2). For species to hybridize naturally, they require range overlap. Hybrid pairs were a grouping of two species known to hybridize (either historically or currently), based on the collection data and robust evidence in scientific literature. Non-hybrid pairs were a grouping of two species that have no historical or present record of hybridizing with any other species but shared the same genera as the hybrid pairs and have similar time since divergence (hybrid  $\bar{x}$  = 10.23 mya, non-hybrid  $\bar{x}$  = 14.44 mya). We then added data for whether they produce hybrids in the wild as a categorical (0 or 1) variable. Next, we added data on the amount of range overlap (km<sup>2</sup>) using ArcGIS (ESRI 2020) to quantify this. For the next step, we added data on the time since the pair of species diverged from each other, using a poeciliid time tree generated (Furness *et al.* 2019). Lastly, we fit a Generalized Linear Model (GLM) with a Gamma likelihood and log link to estimate whether range overlap exhibited log-linear relationships with a) whether species hybridize or not, and b) the time since divergence (mya) between the pair of species. We tested hypotheses using likelihood ratio tests and conducted model diagnostics using simulated residuals via the DHARMA (Hartig 2022) package and conducted all analyses using R (R Core Team 2022).

Table 2. Pairs of lecithotrophic species within the genera *Gambusia*, *Poeciliopsis*, and *Xiphophorus* that show range overlap in their native ranges. Hybrid pairs were a grouping of two species known to hybridize, non-hybrid pairs were a grouping of two species that have no record of hybridizing with any other species but shared the same genera as the hybrid pairs and have similar time since divergence. Whether they produce hybrids in the wild was a categorical (0 or 1) variable. We quantified the amount of range overlap (km<sup>2</sup>) using ArcGIS (ESRI 2020). We calculated time since the pair of species diverged from each other using a poeciliid time tree (Furness *et al.* 2019).

Species pair	Hybridizes	Range overlap (km <sup>2</sup> )	Time since divergence (mya)	Source
<i>Gambusia affinis x georgei</i>	1	10240.1	11.64	fishnet2
<i>Gambusia affinis x heterochir</i>	1	7347.61	11.64	fishnet2
<i>Gambusia affinis x marshi</i>	1	21806.51	14.13	Minckley 1964
<i>Gambusia affinis x nobilis</i>	1	33294.6	11.64	fishnet2
<i>Gambusia affinis x rhizophorae</i>	1	30711.41	14.13	
<i>Gambusia affinis x speciosa</i>	1	45546.01	11.64	Girard 1859
<i>Gambusia atrora x panuco</i>	0	15109.91	8.99	
<i>Gambusia atrora x vittata</i>	0	15173.44	8.99	
<i>Gambusia holbrooki x rhizophorae</i>	1	29158	14.13	
<i>Gambusia nicaraguensis x sexradiata</i>	1	25547.12	16.54	fishnet2
<i>Gambusia puncticulata x yucatanana</i>	1	6742.68	4.69	Regan 1914
<i>Poeciliopsis baenschi x balsas</i>	0	6144.8	21.97	
<i>Poeciliopsis baenschi x infans</i>	0	26574.27	21.97	
<i>Poeciliopsis baenschi x presidionis</i>	0	70.24	19.97	
<i>Poeciliopsis baenschi x prolifica</i>	0	6743.3	21.97	
<i>Poeciliopsis baenschi x scarlli</i>	0	24990.41	19.97	
<i>Poeciliopsis baenschi x turneri</i>	0	20497.61	19.97	
<i>Poeciliopsis baenschi x turrubarensis</i>	0	12821.34	19.97	
<i>Poeciliopsis catemaco x gracilis</i>	0	12833.98	2.42	
<i>Poeciliopsis gracilis x hnlickai</i>	0	46364.85	2.42	
<i>Poeciliopsis gracilis x infans</i>	0	608.43	21.97	
<i>Poeciliopsis gracilis x pleurospilus</i>	0	89270.46	3.9	
<i>Poeciliopsis gracilis x scarlli</i>	0	12340.94	15.27	
<i>Poeciliopsis gracilis x turrubarensis</i>	0	48694.65	15.27	
<i>Poeciliopsis hnlickai x pleurospilus</i>	0	17548.45	3.9	
<i>Poeciliopsis hnlickai x turrubarensis</i>	0	3153.86	15.27	
<i>Poeciliopsis infans x pleurospilus</i>	0	1981.36	21.97	
<i>Poeciliopsis infans x scarlli</i>	0	14599.77	21.97	
<i>Poeciliopsis latidens x fasciata</i>	1	849.96	4.9	Mateos 2005
<i>Poeciliopsis monacha x latidens</i>	1	39097.59	21.97	fishnet2
<i>Poeciliopsis scarlli x turneri</i>	0	15354.63	15.27	

Table 2. continued

Species pair	Hybridizes	Range overlap (km <sup>2</sup> )	Time since divergence (mya)	Source
<i>Xiphophorus birchmanni x malinche</i>	1	6742.68	2.82	fishnet2
<i>Xiphophorus hellerii x alvarezi</i>	1	31559.7	0.93	fishnet2
<i>Xiphophorus multilineatus x nigrensis</i>	0	21.57	0.37	

## Results

The PGLS analysis using hybridization as a discrete variable did not reveal a significant effect of hybridization on range size ( $F_{26} = 2.34$ ,  $p = 0.14$ ; Figure 4).

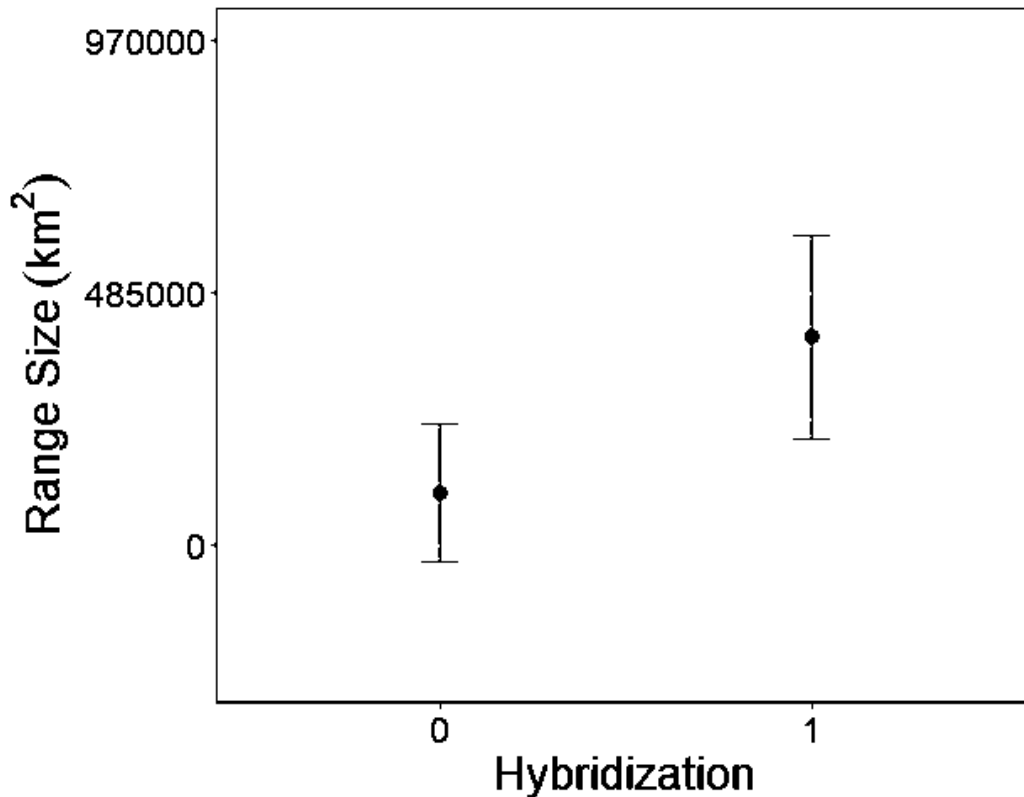
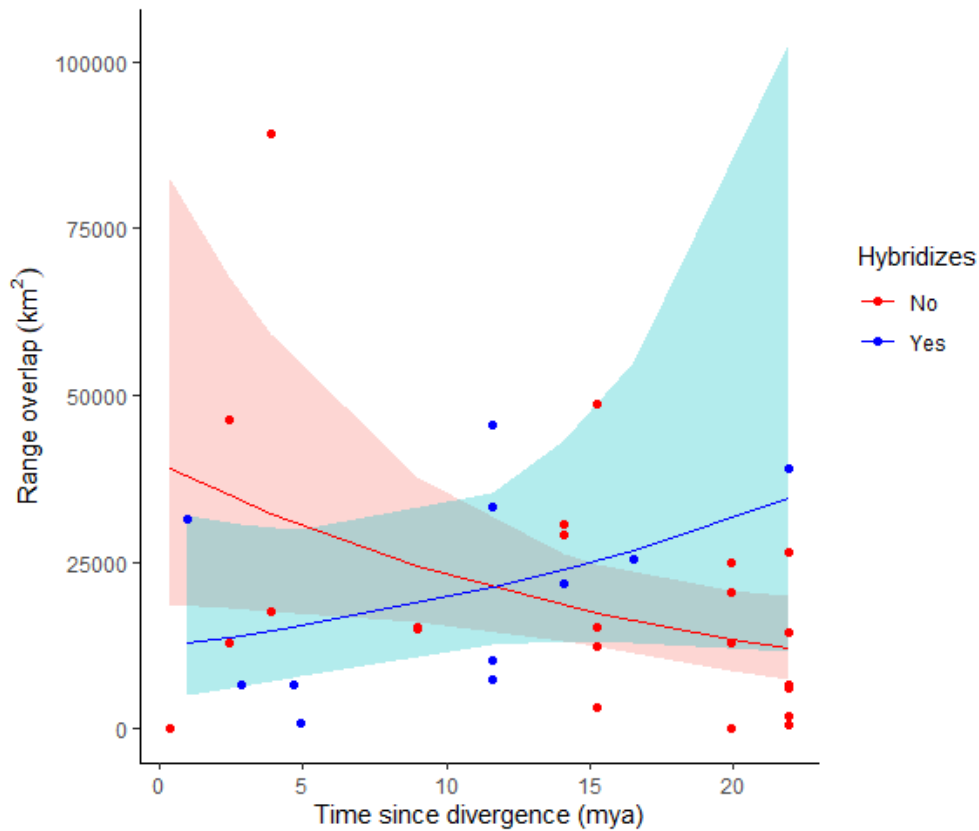


Figure 4. The results of our Phylogenetic Generalized Least Squares analysis, including hybridizing poeciliid species ( $n = 15$ ) and non-hybridizing species ( $n = 15$ ). Species that hybridize do not have a significantly different range size from species that do not hybridize. Error bars represent standard error.

The results of our Generalized Linear Model found heterogeneity in the slopes ( $R^2 = 0.09$ ,  $t = 26.26$ ,  $p < 0.001$ ; Figure 5). A Shapiro-Wilk's test show that the residuals did not violate the normality assumption ( $W = 0.95$ ,  $p = 0.18$ ). When assessing the independence of the data, the

residuals showed no trend against fitted values. In addition, a mixed model using species identity as a random effect still found heterogeneity in the slopes ( $t = 3.86$ ,  $p < 0.001$ ). Species pairs that are known to hybridize displayed increased range overlap ( $\text{km}^2$ ) as time since divergence (mya) increased ( $t = 44.95$ ,  $p < 0.001$ ). By contrast, species pairs that are not known to hybridize displayed a decreased range overlap ( $\text{km}^2$ ) as time since divergence (mya) increased ( $t = 45.94$ ,  $p < 0.001$ ). Each slope, both hybridizing ( $t = 45.94$ ,  $p < 0.001$ ) and non-hybridizing ( $t = 3.93$ ,  $p = 0.003$ ), were significant in the mixed model using species identity as a random effect. There was not a significant relationship between range overlap ( $\text{km}^2$ ) and time since divergence (mya) ( $\chi^2 = 3.76$ ,  $p = 0.29$ ). Also, there was not a significant relationship between range overlap ( $\text{km}^2$ ) and whether a species hybridizes ( $\chi^2 = 3.74$ ,  $p = 0.15$ ).



*Figure 5.* The results of our Generalized Linear Model (+ 95% confidence intervals), including known hybridizing poeciliid species pairs ( $n = 11$ ) and non-hybridizing species pairs ( $n = 23$ ). The blue line represents species pairs that are known to hybridize with one another, which have a larger range overlap ( $\text{km}^2$ ) as time since divergence (mya) increases. The red line represents species pairs that do not hybridize with each other, which have a smaller range overlap ( $\text{km}^2$ ) as time since divergence (mya) increases.

## Discussion

One limitation of this study was the sampling density. There were few species that are known to hybridize, based on the presence-only data used in this study. Due to this limitation, there were species (such as *Gambusia affinis* and *Poeciliopsis baenschi*) that were present in multiple hybridizing and non-hybridizing species pairs. This leads to non-independence of the data used in the Generalized Linear Model. However, the Phylogenetic Generalized Least Squares analysis corrected for this non-independence.

Species pairs that recently diverged but can still hybridize can have small range overlaps for one of three reasons: they may be still in the stage of primary differentiation, they are experiencing secondary contact after prior geographic separation, or they are inhabiting a stable hybrid zone (Abbott *et al.* 2013; Anderson and Weir 2021). Wang *et al.* (2014) found evidence that suggested parapatric speciation (when two species are genetically similar in areas of range overlap) may largely contribute to divergence between species. Anacker and Strauss (2014) found evidence that divergence between species does not increase with range overlap. There are theories and empirical evidence that barriers to gene flow are broken down due to recombination and gene flow in secondary contact zones (Abbott *et al.* 2013). In addition, studies done on cryptic bird species in the genus *Troglodytes* found that low fitness in hybrids is correlated with limited range overlap in the parental species (Mikkelsen and Irwin 2021). Another study conducted on ground crickets in the genus *Allonemobius* discovered that areas of large range overlap between two hybridizing species leads to a reduction in hybridization compared to areas of small range overlap (Howard 1986).

There is a degree of genetic relatedness between two species where hybridization occurs, and outside this zone there is no hybridization (Turner and Liu 1977). If two closely related “incipient species” hybridize, then they may merge and become a single species once again (Arias *et al.* 2008). Therefore, there is no hybridization – as a recognizable phenomenon between distinct species – until there is a minimal level of reproductive isolation (Bettles *et al.* 2005). Likewise, if very distantly related species with a high degree of reproductive isolation will not produce hybrid offspring because the two species either would not recognize each other as potential mates or, if they did mate, no offspring would result because they are too divergent (Chapman and Burke 2007). Therefore, there can be hybridization after a certain degree of reproductive isolation or genetic divergence where the two species have become distinct species

but have not experienced so much divergence or reproductive isolation that they do not recognize the other species as a potential mate or cannot physically produce hybrid offspring (Turbek *et al.* 2017; Mandeville *et al.* 2015; Bigelow 1965; Tubaro and Lijtmaer 2002; Lipshutz 2018; Malone and Fontenot 2008).

Future questions that researchers could answer using these data would be what may be causing the geographic overlap between species, and whether more overlap of species farther away from geographic boundaries (such as land masses) leads to more hybridization. Habitat association may have a significant effect on range sizes as well for species that are habitat specialists/generalists or have restricted/broad habitat types that they can inhabit. Also, human impacts and development could be the cause of the large, introduced ranges for species such as mosquitofish. In addition, predator-prey or competitive relationships are important to the population dynamics of these species and could be the cause of range overlap. Another future biogeographic study may be an evaluation of whether water features are leading to a decline in species diversity based on habitat preferences or their normal range.

## CHAPTER 2

# GEOGRAPHIC OVERLAP OF PLACENTAL SPECIES IN THE FISH FAMILY POECILIIDAE IN THEIR NATIVE RANGES

### Introduction

Understanding the factors that influence a species' geographic range and the overlap between the ranges of distinct species remains a central question in both ecology and evolution. The goal of this research is to ask whether placental species have larger (or smaller) areas of range overlap than non-placental species. While all members of the Poeciliidae family give birth to live young, there is extensive variation in the provisioning of developing young (Reznick *et al.* 2002). In lecithotrophic species, the mother provides all energy for development before fertilization of ova. In matrotrophic species, the mother provides much of the energy for development after fertilization (Olivera-Tlahuel *et al.* 2018). Placentation has evolved multiple times within the family (Pollux *et al.* 2009). Matrotrophy presents the potential for sexual conflict during development, in which maternal and paternal genes have divergent “interests” (Lemus *et al.* 2017). Prevailing theories believe that sexual conflict drives rapid evolution of reproductive isolation, with less potential for genetic introgression (Rice and Holland 1997; Zeh and Zeh 2000; Zeh and Zeh 2001; Zeh and Zeh 2008; Mank and Avise 2009; Schrader *et al.* 2013).

There have been multiple papers appearing sporadically over the last three decades about the adaptive significance of matrotrophy (Bassar *et al.* 2014, Reznick *et al.* 2007; Reznick *et al.* 2021; Reznick *et al.* 1996; Zúñiga-Vega *et al.* 2016; Marsh-Matthews and Deaton 2006; Marsh-Matthews *et al.* 2001). Not much is known about the evolution of the placenta, but poeciliid fish species allow us to discover more about how this feature came about. No studies have discovered the true cause of the origin of placentation, but the hypotheses supported in literature include adaptive hypotheses, and the conflict hypothesis (Pollux *et al.* 2009). The conflict hypothesis is that there is a mother-offspring conflict for nutrients, which led to the development of the placenta (Pollux *et al.* 2009). Within the adaptive hypotheses, there is the locomotor costs hypothesis (Pollux *et al.* 2009). This hypothesis posits that because bearing live young is costly to females, matrotrophy reduces the reproductive cost of producing eggs (Pollux *et al.* 2009).

Another adaptive hypothesis is the resource-availability hypothesis, or the Trexler-DeAngelis theory (Pollux *et al.* 2009).

In 2003, Trexler and DeAngelis proposed a theory that matrotrophic species evolved as an adaptation to resource conditions in the environment around them. To have a higher fitness (survival and fecundity) due to less of an energetic demand, these species developed a placenta to provide nutrients to their offspring throughout the development process (Trexler and DeAngelis 2003). This means that stable habitats that have excessive amounts of resources produce conditions favorable to matrotrophic species (Trexler and DeAngelis 2003). Inversely, more variable habitats with low amounts of food available are more favorable for lecithotrophic species (Trexler and DeAngelis 2003). This is because matrotrophic species need a constant supply of nutrients for their embryos to develop, while lecithotrophic species can store nutrients when they have access to more food resources (Trexler and DeAngelis 2003; Trexler *et al.* 2010). Tests of this theory have been inconclusive – there is minimal support for the idea that poeciliids evolved placental reproduction due to resource availability (Reznick and Pollux 2011).

Placentation can change the balance of pre-mating and post-mating reproductive isolation (Furness *et al.* 2019). Indeed, there is an inverse relationship between courtship and ornamentation and matrotrophy: species with ornamented males and courtship tend to be lecithotrophic (Furness *et al.* 2019). This means that there is a multitude of opportunities for pre-mating isolation in those species and less opportunity (or so we have posited) for matrotrophic species to have pre-mating isolation (Furness *et al.* 2019). From this, we might predict that placental species are much less likely to produce hybrids because all isolation is post-mating and likely based on offspring inviability.

Understanding the range overlaps of these species can illuminate this issue. If reproductive isolation evolves more rapidly and readily between placental populations, we should see less genetic introgression between pairs of placentals than non-placentals. (Elliot and Crespi 2006; Morrison 2017). If there is less introgression between placental pairs, then there should be smaller range overlaps. Conversely, there could be larger range overlaps if sister species have similar niches but do not hybridize. By characterizing the locations where placental and non-placental species overlap, this allows us to understand the potential for various levels of introgression between non-placental pairs and placental pairs.



Therefore, we believe there will be greater evidence of interspecific hybridization and introgression between non-placental species than placental species. If reproductive isolation evolves more rapidly between placentals, we expect there to be less evidence of introgression in these pairs. This permits greater overlap because overlap will not lead as readily to hybridization. Non-placentals might evolve isolation more slowly and thus selection would force the parentals apart more. In addition to this expectation, we also predict that placental species (matrotrophs) might have smaller range sizes than non-placental species (lecithotrophs). Matrotrophs presumably are limited to stable high productivity environments as pregnant females rely on a continuous supply of nutrition during pregnancy to provision their offspring, while lecithotrophs would presumably not face this limitation and hence could be found in a wider range of habitats (Itonaga *et al.* 2012, Hubbs and Delco 1962; Olivera-Tlahuel *et al.* 2015; Pires *et al.* 2011; Morrison *et al.* 2017; Saleh-Subaie *et al.* 2021; Weldele *et al.* 2014; Riesch *et al.* 2013; Ostrovsky *et al.* 2015; Riesch *et al.* 2010).

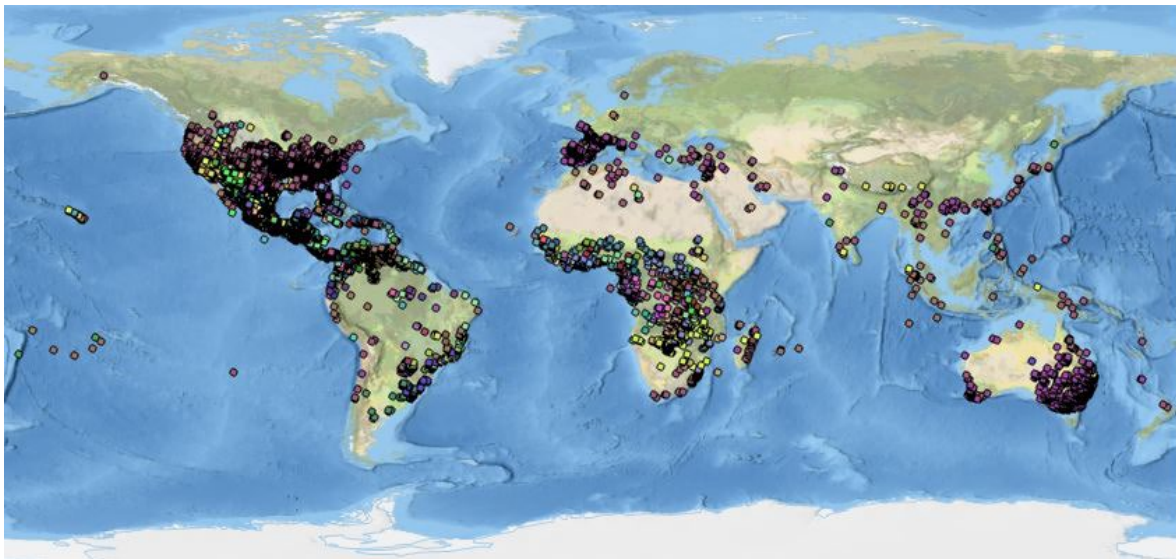
## Methods

We used the figure from Furness *et al.* (2019) to differentiate between placental and non-placental species. We also used the matrotrophy index (MI) from Reznick *et al.* (2002) and Olivera-Tlahuel *et al.* (2015) to determine the origins of placentation, where species with an MI > 1 are placental. MI was calculated using the dry mass of offspring when they were born, divided by the dry mass of the egg after it was fertilized (Reznick *et al.* 2002; Olivera-Tlahuel *et al.* 2015).

We then created maps using ArcGIS (ESRI 2020) by plotting each data point. We separated each of the 407 distinct species in our dataset into differently colored datapoints (Figure 6). We created maps of the ranges for each species, which included their native and introduced ranges. We used Rosen and Bailey's publication from 1963 to delimit the native ranges. In addition, only museum records from recent decades were included in the native ranges. Each species had two maps associated with it – one of the total ranges of that species, and another that represents the species' native and introduced ranges (Figure 7; Figure 8). We created a buffer around the data points of twenty-five nautical miles out from those points. Twenty-five nautical miles was an estimate of the natural range of each of these species, based on their dispersal abilities that have been studied in scientific literature. Species that are known

to be isolated between drainages at exceedingly small spatial scales, such as *Xiphophorus nigrensis*, *X. multilineatus*, *X. montezumae*, *X. nezahualcoytl*, *X. cortezi*, *X. malinche*, and *X. continens*, had their range buffers reduced to ten or even one nautical mile. We were then able to quantify these ranges by calculating the area of the total buffer for each species in square miles.

We then conducted a Phylogenetic Generalized Least Squares (PGLS) analysis of range size as a function of reproductive mode to look for a relationship between the continuous variable of placentation and geographic range size, using range size as a proxy for habitat heterogeneity. To do so, we used a poeciliid timetree (Reznick *et al.* 2017). We pruned the tree to include only poeciliid species and updated the taxonomic names. We then made the tree ultrametric with its tips perfectly aligned, by adjusting very minor branch length rounding. We used the continuous variable of the natural log-transformed matrotrophy index (LMNI) from Pollux *et al.* (2014), then subset data for all species with complete data across variables, so that the models that we compared all have the same species and sample sizes (Table 3). This allowed us to determine the impact of the placentation, while controlling for non-independence of the residuals.



*Figure 6.* A map created using ArcGIS to plot each data point. Each color represents each of the 407 distinct species in the dataset, including the 275 species in the family Poeciliidae and other egg-laying species in the order *Cyprinodontiformes*. Since the native ranges of live bearing poeciliids are in the neotropics, this includes introduced populations across the rest of the world.

**Heterandria formosa Range**



Figure 7. Map of the total range of the species *Heterandria formosa*. Each of the 407 species in the dataset had individual maps including their total range.



Figure 8. Map of the native and introduced ranges of *Heterandria formosa*.

Table 3. Species within the poeciliid timetree from Reznick *et al.* (2017). We obtained the continuous variable of the natural log-transformed matrotrophy index (LMNI) from Pollux *et al.* (2014). We quantified the range sizes (km<sup>2</sup>) using ArcGIS (ESRI 2020).

Species	Range size (km <sup>2</sup> )	LMNI
<i>Alfaro cultratus</i>	53029.33	-0.544727175
<i>Alfaro huberi</i>	129740.14	-0.446287103
<i>Belonesox belizanus</i>	381012.12	-0.356674944
<i>Brachyrhaphis cascajalensis</i>	33657.69	-0.083381609
<i>Brachyrhaphis holdridgei</i>	35475.43	-0.415515444
<i>Brachyrhaphis parismina</i>	18130.56	-0.776528789
<i>Brachyrhaphis rhabdophora</i>	50335.63	-0.265268478
<i>Brachyrhaphis roseni</i>	38160.73	-0.510825624
<i>Brachyrhaphis terrabensis</i>	17737.61	-0.507497834
<i>Carlhubbsia kidderi</i>	112001.89	-0.673344553
<i>Carlhubbsia stuarti</i>	27631.78	-0.139262067
<i>Cnesterodon decemmaculatus</i>	147554.3	-0.217360944
<i>Gambusia affinis</i>	2765533.66	-0.476424197
<i>Gambusia atrora</i>	15174.83	-0.183922838
<i>Gambusia geiseri</i>	107435.6	-0.621757184
<i>Gambusia holbrooki</i>	909452.75	-0.441610555
<i>Gambusia hurtadoi</i>	8460.66	-0.301105093
<i>Gambusia manni</i>	31190.21	-0.287682072
<i>Gambusia vittata</i>	57070.38	-0.30652516
<i>Gambusia wrayi</i>	10906.51	-0.414001439
<i>Girardinus metallicus</i>	34412.91	-0.328504067
<i>Heterandria formosa</i>	394363.57	3.555348061
<i>Neoheterandria elegans</i>	6742.68	-0.223143551
<i>Neoheterandria tridentiger</i>	66490.67	-0.46203546
<i>Phallichthys amates</i>	158922.58	-0.616186139
<i>Phallichthys tico</i>	20828.55	-0.673344553
<i>Phalloceros caudimaculatus</i>	225604.02	0.760805829
<i>Phalloptychus januarius</i>	25207.44	3.124565145
<i>Poecilia (Acanthophaeclus) reticulata</i>	508256.58	-0.412887101
<i>Poecilia (Allopoecilia) caucana</i>	103281.61	-0.264232709
<i>Poecilia (Limia) dominicensis</i>	24389.31	-0.642702449
<i>Poecilia (Limia) vittata</i>	41610.53	-0.021040716
<i>Poecilia (Micropoecilia) branneri</i>	22674.93	4.459096067
<i>Poecilia (Micropoecilia) parae</i>	41566.75	1.908921497

Table 3. continued

Species	Range size (km <sup>2</sup> )	LMNI
<i>Poecilia (Micropoecilia) picta</i>	57934.97	-0.242592452
<i>Poecilia (Mollienesia) gillii</i>	282569.28	-0.228605342
<i>Poecilia (Mollienesia) gracilis</i>	282569.28	-0.236988958
<i>Poecilia (Mollienesia) latipinna</i>	754080.49	0.022251567
<i>Poecilia (Mollienesia) mexicana</i>	968402.64	-0.469236216
<i>Poecilia (Mollienesia) orri</i>	134209.23	-0.256184423
<i>Poecilia (Mollienesia) petenensis</i>	133891.14	0.144543391
<i>Poecilia (Mollienesia) sphenops</i>	801241.45	-0.382892686
<i>Poecilia (Mollienesia) velifera</i>	88477.64	-0.391562203
<i>Poecilia (Pamphorichthys) hollandi</i>	6742.68	3.245490508
<i>Poecilia (Pamphorichthys) minor</i>	6742.68	0.489052105
<i>Poecilia (Poecilia) vivipara</i>	278634.63	-0.392259223
<i>Poeciliopsis baenschi</i>	42125.35	0.457424847
<i>Poeciliopsis elongata</i>	6742.68	4.232656178
<i>Poeciliopsis fasciata</i>	164046.03	-0.210721031
<i>Poeciliopsis gracilis</i>	354132.01	-0.371063681
<i>Poeciliopsis infans</i>	137766.66	-0.15082289
<i>Poeciliopsis latidens</i>	51999.22	-0.15082289
<i>Poeciliopsis lucida</i>	48301.61	0.693147181
<i>Poeciliopsis monacha</i>	37811.33	-0.494296322
<i>Poeciliopsis occidentalis</i>	297077.12	0.113328685
<i>Poeciliopsis paucimaculata</i>	9250.14	2.054123734
<i>Poeciliopsis presidionis</i>	81579.24	3.068052935
<i>Poeciliopsis prolifica</i>	126889.7	1.686398954
<i>Poeciliopsis retropinna</i>	40395.48	4.762173935
<i>Poeciliopsis scarlli</i>	65922.65	-0.139262067
<i>Poeciliopsis turneri</i>	20497.61	3.723280881
<i>Poeciliopsis turrubarensis</i>	253313.6	-0.415515444
<i>Poeciliopsis viriosa</i>	88942.09	-0.072570693
<i>Priapella compressa</i>	43052.74	-0.328504067
<i>Priapella intermedia</i>	56053.14	-0.510825624
<i>Priapichthys annectens</i>	46843.52	-0.562118918
<i>Priapichthys darienensis</i>	24372.25	-0.478035801
<i>Scolichthys greenwayi</i>	31288.92	-0.186329578
<i>Xenodexia ctenolepis</i>	19079.17	1.217875709
<i>Xenophallus umbratilis</i>	26182.01	-0.356674944
<i>Xiphophorus alvarezii</i>	33111.61	-0.544727175

Table 3. continued

Species	Range size (km <sup>2</sup> )	LMNI
<i>Xiphophorus clemenciae</i>	23064.76	-0.314710745
<i>Xiphophorus cortezi</i>	32.29	-0.400477567
<i>Xiphophorus couchianus</i>	23871.6	-0.400477567
<i>Xiphophorus hellerii</i>	343795.75	-0.494296322
<i>Xiphophorus maculatus</i>	181184.93	-0.168418652
<i>Xiphophorus nezahualcoyotl</i>	20193.17	-0.673344553
<i>Xiphophorus nigrensis</i>	9658.07	-0.342490309
<i>Xiphophorus pygmaeus</i>	81.32	-0.261364764
<i>Xiphophorus variatus</i>	132975.02	-0.248461359
<i>Xiphophorus xiphidium</i>	35764.62	-0.15082289

To answer our research question, we made a list of all the closely related species pairs in our dataset based on molecular phylogeny (Table 4). Placental pairs were a grouping of two species who are both matrotrophs with a matrotrophy index greater than one. Non-placental pairs were a grouping of two species who are both lecithotrophs with a matrotrophy index less than one. The matrotrophic species chosen for the analysis have no current or historical record of hybridizing with any other species. Then we added data on the amount of range overlap between the sister species using ArcGIS (ESRI 2020). Next, we added data on the time since the pair of species diverged from each other using a poeciliid time tree (Furness *et al.* 2019). The placental and non-placental species had similar time since divergence (placental  $\bar{x}$  = 15.84 mya, non-placental  $\bar{x}$  = 10.83 mya). Then we added data on whether the species reproduce through lecithotrophy or matrotrophy. Lastly, we fit a Generalized Linear Model with a Gamma distribution and a log link function of the form using the data on range overlap, the mode of reproduction, and the time since divergence between the pair of species.

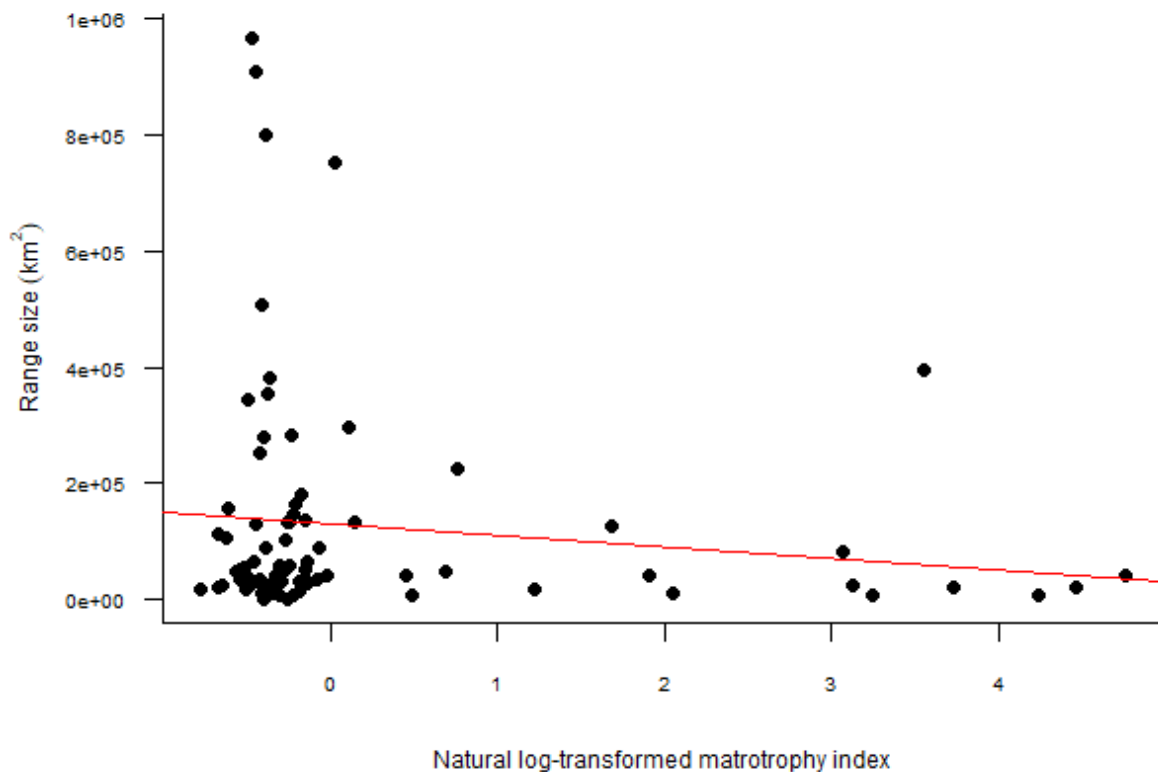
*Table 4.* Closely related species pairs with minimal time since divergence (mya) based on molecular phylogeny. Placental pairs were a grouping of two species who are both matrotrophs, non-placental pairs were a grouping of two who are both lecithotrophs. Whether they are matrotrophic or lecithotrophic was a categorical (0 or 1) variable. We quantified the amount of range overlap (km<sup>2</sup>) using ArcGIS (ESRI 2020). We calculated time since the pair of species diverged from each other using a poeciliid time tree (Furness *et al.* 2019). The pairs *Poeciliopsis retropinna x elongata*, *Poeciliopsis latidens x fasciata*, and *Xiphophorus helleri x alvarezi* are sister taxa (Furness *et al.* 2019).

Species pair	Placental	Range overlap (km <sup>2</sup> )	Time since divergence (mya)
<i>Gambusia affinis x georgei</i>	0	10240.1	11.64
<i>Gambusia affinis x heterochir</i>	0	7347.61	11.64
<i>Gambusia affinis x marshi</i>	0	21806.51	14.13
<i>Gambusia affinis x nobilis</i>	0	33294.6	11.64
<i>Gambusia affinis x rhizophorae</i>	0	30711.41	14.13
<i>Gambusia affinis x speciosa</i>	0	45546.01	11.64
<i>Gambusia holbrooki x rhizophorae</i>	0	29158	14.13
<i>Gambusia nicaraguensis x sexradiata</i>	0	25547.12	16.54
<i>Gambusia puncticulata x yucataana</i>	0	6742.68	4.69
<i>Poeciliopsis elongata x retropinna</i>	1	10510.87	15.52
<i>Poeciliopsis latidens x fasciata</i>	0	849.96	4.9
<i>Poeciliopsis lucida x occidentalis</i>	1	9691.6	3.95
<i>Poeciliopsis lucida x presidionis</i>	1	15879.38	21.97
<i>Poeciliopsis lucida x prolifica</i>	1	28130.87	5.06
<i>Poeciliopsis lucida x turneri</i>	1	5151.72	21.97
<i>Poeciliopsis monacha x latidens</i>	0	39097.59	21.97
<i>Poeciliopsis occidentalis x presidionis</i>	1	19068.1	21.97
<i>Poeciliopsis occidentalis x prolifica</i>	1	44145.83	5.06
<i>Poeciliopsis paucimaculata x retropinna</i>	1	8327.62	18.98
<i>Poeciliopsis presidionis x prolifica</i>	1	72304.46	21.97
<i>Poeciliopsis prolifica x turneri</i>	1	5861.81	21.97
<i>Xiphophorus birchmanni x malinche</i>	0	6742.68	2.82
<i>Xiphophorus hellerii x alvarezi</i>	0	31559.7	0.93

## Results

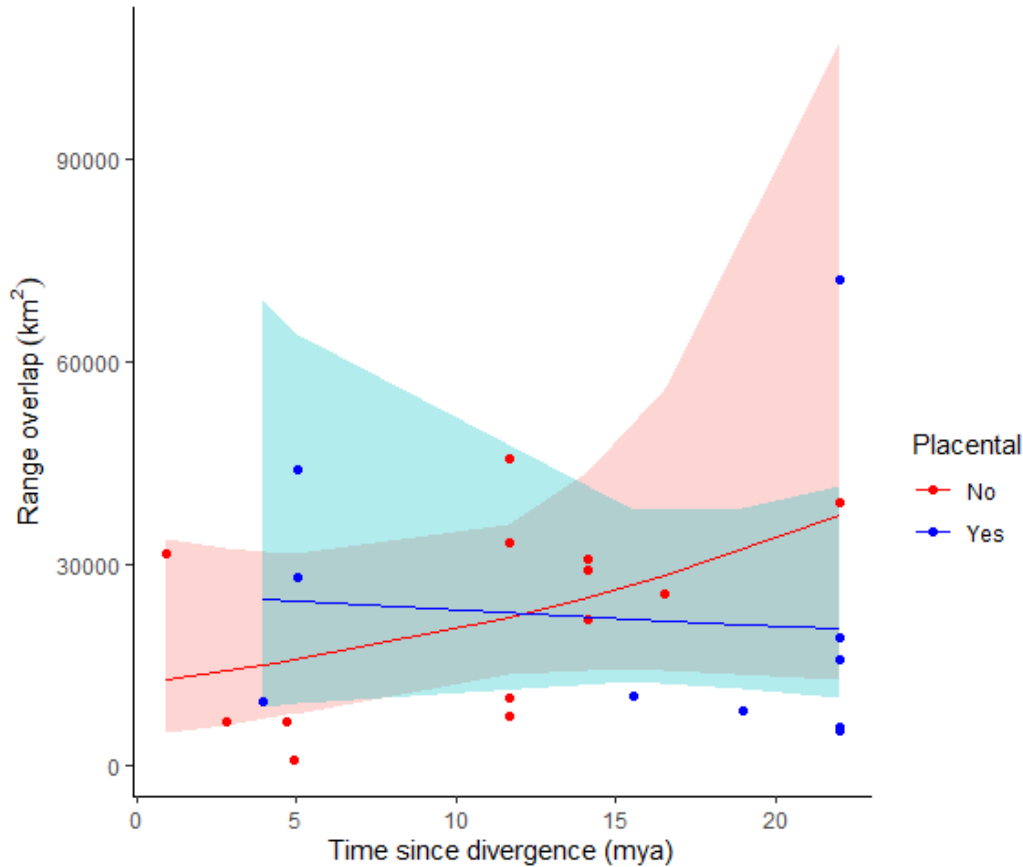
The PGLS analysis using the natural log-transformed matrotrophy index as a continuous variable did not reveal a significant effect of placentation on range size ( $F_{77} = 1.11$ ,  $p = 0.29$ ;

Figure 9). The results of our Generalized Linear Model found heterogeneity in the slopes ( $R^2 = 0.07$ ,  $t = 17.83$ ,  $p < 0.001$ ; Figure 10). A Shapiro-Wilk's test shows that the residuals did not violate the normality assumption ( $W = 0.98$ ,  $p = 0.85$ ). When assessing the independence of the data, the residuals showed no trend against fitted values. However, a mixed model using species identity as a random effect did not find heterogeneity in the slopes ( $t = 0.8$ ,  $p = 0.4$ ). We found that pairs of closely related species that are both lecithotrophic displayed increased range overlap as time since divergence increased ( $t = 55.84$ ,  $p < 0.001$ ). Closely related species that were both matrotrophic showed a relationship between divergence time and area of overlap ( $t = 32.36$ ,  $p < 0.001$ ). The lecithotrophic slope ( $t = 5.05$ ,  $p < 0.001$ ), but not the matrotrophic slope ( $t = 2.3$ ,  $p = 0.07$ ), was significant in the mixed model using species identity as a random effect. There was not a significant relationship between range overlap ( $\text{km}^2$ ) and time since divergence (mya) ( $\chi^2 = 2.02$ ,  $p = 0.57$ ). Also, there was not a significant relationship between range overlap ( $\text{km}^2$ ) and whether a species is placental ( $\chi^2 = 2.02$ ,  $p = 0.36$ ).



*Figure 9.* The results of our Phylogenetic Generalized Least Squares analysis, including poeciliid species at varying levels of maternal provisioning ( $n = 90$ ). Species that are placental do not have a significantly different range size ( $\text{km}^2$ ) from species that are not placental.





*Figure 10.* The results of our Generalized Linear Model (+ 95% confidence intervals), including placental poeciliid species pairs ( $n = 10$ ) and non-placental species pairs ( $n = 13$ ). The blue line represents species pairs that are placental. The red line represents species pairs that do not hybridize with each other. Species pairs that are placental do not have a significantly different range overlap ( $\text{km}^2$ ) as time since divergence (mya) increases than species pairs that are not placental.

## Discussion

We did not find greater evidence of interspecific hybridization and introgression between non-placental species than placental species. Our results may be due to what Reznick *et al.* found in 2002 that matrotrophic species (such as *Poeciliopsis prolifica*, *P. turneri*, and *P. presidionis*) have sister taxa that are lecithotrophic. In addition, the lecithotrophs included in the analysis were also species that are known to hybridize with each other. Therefore, the most closely related species may not be capable of hybridizing due to their different reproductive strategies for maternal provisioning. When comparing the ranges of closely related placentals and non-placentals, we found that multiple closely related species that shared the same reproductive

strategy did not have any range overlap. This lends support to the theory that placentation evolved separately in different geographic areas.

In our PGLS analysis, the proxy for habitat heterogeneity or heterogeneity in productivity was range – the larger the range, the more varied the habitats or locations for the species (Brown 1984). If matrotrophy requires a productive habitat, then one might expect smaller ranges because lecithotrophy works in a variety of habitats. The use of range as a proxy may not be the best solution – a species might be a habitat specialist but still have a broad range because that habitat is widespread, which allows them to inhabit large areas. But individual cases of habitat specialization do not obviate a general pattern. In future studies, quantifying habitat heterogeneity or heterogeneity in productivity and using it to find support for the Trexler and DeAngelis theory in matrotrophic and lecithotrophic poeciliid fish species could be the next step in this field of research.

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## **BIOGRAPHICAL SKETCH**

### **Experience**

Close Encounters Naturalist at the Brandywine Zoo (May 2012 – August 2013)

Fish Survey Intern at the Delaware Center for the Inland Bays (May 2017 – June 2017)

Education Intern at the Salisbury Zoo (May 2017 – July 2017)

Guest Speaker at Ursuline Academy (March 2018 – December 2021)

Facility Monitor at Bellevue State Park (April 2018 – October 2018)

Education Staff at Challenger Learning Center (September 2019 – August 2020)

Teaching Assistant at Florida State University (August 2020 – Present)

### **Education**

B.S. in Wildlife 2017 (Purdue University)

M.S. in Biology expected 2022 (Florida State University)

### **Skills**

Microsoft Office

ArcGIS

Data Collection

Data Analysis

Habitat Surveys

Education

Transportation

Wildlife Identification

Field Safety

Habitat Management