



Superfotation increases total fecundity in a viviparous fish regardless of the ecological context



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ABSTRACT

Superfotation is the ability of females to simultaneously carry multiple broods of embryos at different developmental stages. This is an uncommon reproductive strategy that has evolved independently several times in viviparous fishes. The ecological conditions that favor higher degrees of superfotation (the presence of more simultaneous broods) still remain unclear. In this study we tested hypotheses about the potential effects of three particular ecological factors (water flow velocity, population density, and adult mortality) on superfotation. We used data on six populations of one fish species from the family Poeciliidae (*Poeciliopsis baenschi*) and a multimodel inference framework to test these hypotheses. We found no clear associations between the degree of superfotation and these ecological factors. Instead, we found a positive relationship between the total number of embryos carried by females and superfotation. Females increased their total fecundity as they overlapped more broods and this pattern was independent of the particular ecological conditions. Thus, in *P. baenschi* superfotation may facilitate a greater reproductive output. In addition, this positive relationship between total number of embryos and superfotation was stronger in small- and medium-sized females, whereas large females produced few or no simultaneous broods regardless of their total fecundity. The observed lack of association between superfotation and ecological variables is noteworthy because previous studies on other congeneric species have found that superfotation may vary as a function of water flow velocity or food availability. Our results indicate that the effect of particular selective factors on the degree of superfotation may differ among closely related species.

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1. Introduction

Superfotation is the ability of females to simultaneously carry more than one brood of developing young at different developmental stages (Turner, 1937; Scrimshaw, 1944; Pires et al., 2011). It is a rare reproductive strategy that occurs in a few mammals such as the brown hare (*Lepus europaeus*), the European badger (*Meles meles*) and the American mink (*Neovison vison*; Roellig et al., 2010, 2011; Corner et al., 2015), and that has evolved independently in three unrelated families of fishes (Clinidae, Poeciliidae, and Zenarchopteridae; Reznick and Miles, 1989; Gunn and Thresher, 1991; Reznick et al., 2007; Zúñiga-Vega et al., 2010). The reproductive strategy known as “sequential brooding”, which occurs in some species of the bivalve family Sphaeriidae, is equivalent to

superfotation because these organisms exhibit brood masses that contain developmentally discrete subsets of embryos, with each subset encapsulated in a different brood sac (Cooley and Foighil, 2000). Within the fish family Poeciliidae, superfotation has also evolved independently several times, with species from some genera (e.g. *Xiphophorus* and *Alfaro*) completely lacking superfotation and species from other genera (e.g. *Poeciliopsis* and *Heterandria*) exhibiting varying degrees of superfotation (from two up to eight simultaneous broods; Travis et al., 1987; Pollux et al., 2009; Pires et al., 2010). Moreover, the degree of superfotation varies considerably among populations of some poeciliid species (Pires et al., 2007; Zúñiga-Vega et al., 2007; Frías-Alvarez et al., 2014). This wide inter- and intraspecific variation in both the presence and degree of superfotation suggests that it must confer some fitness benefits under particular environmental conditions.

Some ecological factors have been proposed as potential drivers of variation in superfotation in fishes (reviewed in Zúñiga-Vega et al., 2010). Environments that promote hydrodynamic and

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streamlined phenotypes such as high-velocity water systems or high-predation habitats, where fish must swim fast to avoid predators, might select for increased superfetation (Thibault and Schultz, 1978; Reznick and Miles, 1989). This hypothesis is based on the idea that superfetating females split their reproductive effort into smaller broods and, hence, they never carry many large, advanced-stage embryos such as non-superfetating females do. Thus, superfetation may provide a way to maintain a high reproductive output while reducing the amount of space required to carry developing broods. In this way, superfetating females should be able to produce the same number of offspring as non-superfetating females, while maintaining a more streamlined phenotype. This ‘morphological constraint’ hypothesis has been tested using three poeciliid species with contradictory results. Zúñiga-Vega et al. (2007) found strong support in *Poeciliopsis tur-rubarensis*. Females inhabiting fast-moving rivers produced more simultaneous broods and were thinner and more elongated than females inhabiting slow-moving rivers. In contrast, Frías-Alvarez and Zúñiga-Vega (2016) found no support for this hypothesis in *P. gracilis* and *P. infans*. The velocity of the water current did not clearly predict interpopulation variation in superfetation or body shape.

High adult mortality represents another potential ecological driver of increased superfetation. This hypothesis assumes that superfetation is a mechanism to increase the rate of offspring production because females overlap consecutive broods, thereby reducing the amount of time that they need to produce a particular total number of young (Burley, 1980). In this way, brood overlap could result in more frequent production of offspring. Increased rates of offspring production at the potential cost of losing future reproductive opportunities would be advantageous if adult survival probabilities are low or uncertain (Promislow and Harvey, 1990; Reznick et al., 1996; Benton and Grant, 1999; Roff, 2002). Thus, superfetation should be favored in environments with intense and unpredictable adult mortality (Travis et al., 1987). Until present, no study has used reliable estimates of adult mortality to test this hypothesis.

Environments where reproduction is costly, such as sites with high population density, might also select for increased superfetation. This hypothesis assumes that superfetation reduces the peak cost of reproduction because females split a single large reproductive bout into two or more smaller broods (Downhower and Brown, 1975). By this mechanism, superfetating females are presumably able to maintain a relatively low and constant energy investment on developing embryos throughout pregnancy. In contrast, females without superfetation should experience a higher peak demand of energy because at some point they will need to simultaneously carry and provide resources to many embryos during demanding and/or advanced stages of development. This reduction in reproductive allocation that potentially occurs as a result of superfetation, is stronger in matrotrophic species, where females actively transfer nutrients to developing embryos and, hence, where embryos increase in mass and volume throughout development (as opposed to lecithotrophic species, where females do not provide nutrients to embryos after fertilization and, hence, where embryo mass and volume decrease slightly throughout development; Pollux et al., 2009). Superfetation would spread reproductive investment more evenly over time, reducing the peak demand at any particular time without affecting total reproductive output (Zúñiga-Vega et al., 2010). High-density populations likely increase intraspecific competition, reducing per capita resource availability and, therefore, may promote mechanisms to reduce the costs of reproduction such as superfetation (Lindström et al., 2005; Svanbäck and Bolnick, 2007; Leips et al., 2009). To our knowledge, no study has attempted to find a relationship between spatial

variation in population density and the degree of superfetation.

In this study, we gathered demographic and reproductive data as well as information on water flow velocity to search for ecological correlates of spatial variation in the degree of superfetation of a viviparous fish of the family Poeciliidae. In particular, we tested the predictions outlined above to assess whether site-specific water flow velocity, adult mortality rates, and population density are associated with differences among populations in the number of simultaneous broods. Additionally, we tested the hypothesis that superfetation facilitates a greater reproductive output (Burley, 1980; Travis et al., 1987) by searching for an association between the number of simultaneous broods carried by females and the total number of embryos that they produce.

2. Materials and methods

2.1. Study system and field methods

We studied six populations of *Poeciliopsis baenschi*, a viviparous poeciliid fish endemic to Western Mexico (Miller et al., 2005). Our study sites are located in six geographically isolated river drainages (Table 1; Fig. S1 – Online Supplementary Material). Average values of population density and adult mortality rates per week were obtained from previous studies conducted in our specific study locations (Zúñiga-Vega et al., 2012a, 2012b; Molina-Moctezuma et al., 2013). We visited these sites during the dry seasons (November–May) of 2009, 2010, and 2012 to collect reproductive females and to measure water velocity. We used a flow meter (Flowwatch; JDC Electronic SA) to record water velocity at the exact point of the river where fish were observed and collected. On each visit, we recorded water velocity at three distinct spots and then calculated an average per site across replicates and visits (Table 1).

Pregnant females were collected using a seine net (1.3 m depth × 5 m length, 8 mm mesh size) and were anesthetized at the time of capture using tricaine methanesulfonate (MS-222). Then, we sacrificed them by immersion in 95% ethanol. We took a digital photograph of the lateral profile of each female. Our total sample size across all six populations was 364 females (sample sizes per study site and month are shown in Table 1).

2.2. Reproductive data

We dissected all 364 females to count the number of simultaneous broods. We extracted the ovary from each female and identified each brood as a group of embryos that shared the same developmental stage according to Haynes (1995). Groups of embryos at stages 1, 2 and 3 were excluded from our counts because these stages correspond to non-fertilized ova. We also recorded the total number of embryos carried by each female (across all broods). We measured female dry mass (ovary and digestive tract removed) after desiccating females for 24–48 h at 55 °C.

2.3. Fineness index

We estimated how streamlined female bodies are by means of the fineness index (FI; Langerhans and Reznick, 2010). This index is an appropriate measure of streamlining and a good predictor of swimming performance because it has a direct connection to biomechanics and hydrodynamics (Blake, 2004; Langerhans and Reznick, 2010; Haas et al., 2015). We calculated an FI for each female as: $FI = 1 - |1 - (FR/4.5)|$. In this equation FR stands for fineness ratio, which is calculated as body length/maximum body depth. We used the digital photographs to measure body length and depth for each female using the software tpsDIG2 (Rohlf, 2016). We evaluated repeatability of this FI by measuring each individual by two

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