Predation Environment Does Not Predict Life History in Morphologically-Constrained Fish Alfaro cultratus (Cyprinodontiformes: Poeciliidae)

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Predator Environment Does Not Predict Life History in the Morphologically-Constrained Fish *Alfaro cultratus* (Cyprinodontiformes: Poeciliidae)

Kaitlyn Beard Golden

A thesis submitted to the faculty of Brigham Young University in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Predator Environment Does Not Predict Life History in the Morphologically-Constrained Fish *Alfaro cultratus* (Cyprinodontiformes: Poeciliidae)

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Predation is known to have a significant effect on life history, eliciting predictable responses. Physical constraints of body shape and size may also limit life history divergence. There may be a trade-off between adapting to predation, and limits placed by constraints that decrease life history divergence. We test this idea in the Costa Rican livebearing fish *Alfaro cultratus*. This species has a keeled ventral surface and does not develop a distended abdomen when pregnant like other livebearers. We describe the life history of *A. cultratus* in 20 different populations across predator and non-predator environments. We found significantly lower reproductive allotment in predator environments relative to non-predator environments, but no significant difference in female or male size at maturity, number of offspring, or size of offspring. We found that *A. cultratus* exhibit isometric patterns of allocation for clutch dry mass in relation to female dry mass in predator and non-predator environments. We suggest that body shape constraints in this species limit the life history divergence we typically see in predator and non-predator environments in other species.

Keywords: Poeciliid, life history, Alfaro cultratus, allometry, constraints
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INTRODUCTION

A life history strategy defines how an organism utilizes and optimizes energy to survive and reproduce (Fisher, 1930; Williams, 1966; Stearns, 1977; Roff, 1992). The optimal strategy can be influenced by extrinsic factors such as mortality rate (Strauss, 1990; Jennions et al., 2006; Riesch, Martin, & Langerhans, 2013; Mukherjee et al., 2014; Olinger, Peoples, & Frimpong, 2016), resource availability (Reznick, Miles, & Winslow, 1992; Riesch et al., 2013; Moore, Riesch, & Martin, 2016; Zandonà et al., 2017), population density (Bronikowski et al., 2002; Schrader & Travis, 2012), and environmental conditions (e.g. salinity, gradient, elevation, etc.) (Zúñiga-Vega, Reznick, & Johnson, 2007; Jourdan et al., 2016; Rius et al., 2019). Predator environments have often been used to study the effects of mortality rate on life history strategies (Law, 1979; Reznick & Endler, 1982; Johnson & Belk, 1999; Gosline & Rodd, 2008) and have been found to affect a wide variety of taxa, including fish, anurans, and insects. Among other things, the presence of a predator can influence timing and size of maturation and stage changes (Chivers et al., 2001; Johnson, 2001; Hilton, Walde, & Leonard, 2002; Stoks et al., 2006; Peterson et al., 2019), growth rate (Lardner, 2000; Altwegg, 2002; Šupina, Bojková, & Boukal, 2016; Brown et al., 2018; DeWitt et al., 2019), and investment in offspring (Johnson & Belk, 2001; Gorini-Pacheco, Zandonà, & Mazzoni, 2017). Previous work consistently finds divergent life history patterns in predator and non-predator environments. For example, in the family Poeciliidae (livebearing fishes) many studies have shown a divergent pattern of smaller size at maturity, higher fecundity, smaller offspring, and greater reproductive allotment in high versus low predator environments (Reznick, 1990; Johnson, 2001; Jennions & Telford, 2002; Walsh & Reznick, 2009; Moore et al., 2016). Similarly, in anurans the timing and size of metamorphosis (Laurila, Kujasalo, & Ranta, 1998; Lardner, 2000) and timing of hatching (Laurila et al., 2002;
Capellán & Nicieza, 2007) change in response to the presence of a predator. Therefore, we expect to see patterns of life history divergence in response to predator environments in additional species.

There are limits, however, to divergent evolution in predator environments. Divergent evolution requires that populations are able to adapt to environmental pressures. That said, there are genetic, phylogenetic, morphological, and physiological constraints to adaptations (Gould, 1980). Morphological constraints are particularly important in life history evolution as they can change the space available for reproduction. This has been frequently studied in turtles (Clark, Ewert, & Nelson, 2001; Ryan & Lindeman, 2007; Rollinson & Brooks, 2008; Macip-Rios et al., 2012). For example, the small African tortoise *Homopus signatus*, produces single-egg clutches. Although producing one large egg is best for the fitness and survival of the offspring, *H. signatus* is constrained by a small body size and pelvic canal limiting how large the egg can be (Hofmeyr, Henen, & Loehr, 2005). Similar patterns were found in other species of turtles where the pelvic girdle (also influenced by evolutionary pressures on locomotion) limited egg size, especially in small individuals (Congdon & Gibbons, 1987). Thus, morphology can constrain a life history trait due to space, size, and shape of an organism.

Morphology is also important in survival; tradeoffs between the optimal morphology for survival and reproduction may be present in some species. Size and shape can be very important in predator avoidance. The humpback chub, *Gila cypha*, have a large dorsal cranial hump that increases the depth of their body and therefore protects against gape limited predators (Portz & Tyus, 2004). Tradeoffs may be present as morphologies may be advantageous in some selective pressures, but not in others. In the family Poeciliidae, fishes invest more into offspring when predators are present; however, this investment comes at a cost of decreased swimming
performance (Ghalambor, Reznick, & Walker, 2004). Thus swimming performance and the optimal morphology for reproduction appear to be competing selective pressures (Zúñiga-Vega et al., 2007; Wesner et al., 2011; Hassell et al., 2012; Ingle et al., 2016; Quicazan-Rubio et al., 2019). Selective pressures acting on morphology can limit the optimal adaptation in life history or vice versa in an environment. However, we don’t know how morphological adaptations limit life history adaptations in predator environments.

An additional question is how predation and morphological constraints influence lifetime reproductive allocation. The terminal investment hypothesis predicts that organisms will invest more in reproduction as they age and chances for future reproduction decrease (Williams, 1966). Specifically, in environments that experience high mortality (such as predator environments) individuals may allocate energy to current reproduction over future reproduction; however, in low mortality environments (such as non-predator environments) individuals may allocate more to future reproduction than current reproduction, consistent with the terminal investment hypothesis (Law, 1979; Michod, 1979; Billing, Rosenqvist, & Berglund, 2007; Belk, Nance, & Johnson, 2011; Billman et al., 2014; Nickley, Saintignon, & Roberts, 2016). Thus, reproductive allocation may change in response to mortality pressures presented in predator environments as high mortality limits the chance of survival and opportunities for future reproduction.

Morphological constraints may also influence within-lifetime reproductive allocation. In Brachyrhaphis parismina (a poeciliid fish), populations showed isometric allocation of reproductive allotment to female body mass with age (Belk et al., 2011). This is possibly due to a narrow-bodied shape that may constrain reproductive allocation from being greater than proportionate to body size. Thus, mortality rates and morphological constraints can influence reproductive investment.
In this study, we test the ideas that 1) life history traits that are limited by morphological constraints may not vary in different predator environments, and 2) within lifetime reproductive allocation, consistent with the terminal investment hypothesis, may be limited by predator environments and morphological constraints. Therefore, we should find isometric allocation rather than hyper-allometric allocation in highly morphologically constrained species. To test these ideas, we used the fish *Alfaro cultratus* from the family Poeciliidae (Regan, 1908). Poeciliids provide an optimal study system as they are livebearers, have a short generation time, and are found in many different environments (Reznick & Endler, 1982). *Alfaro cultratus* is an ideal species for this study as it is an extremely narrow-bodied poeciliid with a keeled ventral surface (Figure 1). Additionally, *A. cultratus* do not develop a distended abdomen during pregnancy. Distinguishing between pregnant and non-pregnant females externally is very difficult (*personal observation*). The body morphology of this fish is likely a constraint for reproduction as it does not allow additional space provided when the abdomen expands in pregnancy as exemplified in other poeciliids.
METHODS

Study Sites and Collections. We collected from 8 different sites in Costa Rica during February and May 2006 and May 2007. Additionally, we collected *A. cultratus* from 12 different sites in northeast Costa Rica during April 2019 (Figure 2). Fish were collected using a handheld seine (1.3 m × 5 m; 8 mm mesh size). We tried to collect approximately 100 females (Table 1) from each site to ensure that we had enough mature and immature individuals for analysis without taking more than a fraction of the local population. All fish were humanely euthanized and preserved in ethanol in the field, then transported back to the laboratory for analysis. We recorded predator sites as locations where the piscivorous species *Parachromis dovii* (Johnson & Belk, 2001) and/or *Parachromis managuensis* were found during seining. Non-predator sites were recorded as locations where *A. cultratus* was found only with non-piscivorous fishes. Here, we analyze 11 predator sites (1 from 2006, 3 from 2007, 7 from 2019) and 9 non-predator sites (2 from 2006, 2 from 2007, 5 from 2019). We term these sites as ‘predator environments’ or ‘non-predator environments’. Predator and non-predator environments are expected to vary in predation risk but also may be confounded with other environmental factors such as resource availability, temperature, elevation, flow, and density (Johnson, 2002; Jourdan et al., 2016; Olinger et al., 2016). Thus, predator environments are characterized by the presence or absence of a predator but are called environments to encompass the many different factors that may be causally or incidentally correlated with the presence or absence of a predator.

Life History. We measured five life history traits: 1) male size at maturity; 2) female size at maturity; 3) number of offspring; 4) size of offspring; and 5) reproductive allotment. All traits were measured from alcohol-preserved specimens using methods described in Johnson & Belk (2001). In brief, we did this as follows. We determined male size at maturity as the mean standard
length of all mature males (male poeciliids grow little if at all after maturation) (Turner, 1942; Johnson & Belk, 2001; Belk et al., 2011). To score female size at maturity for each population, we first divided females into 2 mm size classes. We identified size at maturity as the size class where at least half of the females were mature with developing embryos. Developing embryos were classified using Haynes classification method (stages 1-11). Stage 1 and 2 are immature and unfertilized eggs, and stage 3 and above are developing embryos. Stage 3 is a fully yolked and fertilized egg and stage 11 is a mature embryo with the yolk sac entirely or almost entirely absorbed (Haynes, 1995). In cases where population samples of mature females were small, the actual value may be slightly smaller or larger than reported because we lacked adequate sampling. We counted number of offspring as the number of developing embryos contained in each mature female. We determined size of offspring as the lean dry mass of the brood divided by the number of offspring in each brood. We measured reproductive allotment as the lean dry mass of the brood compared to the lean dry mass of the female. Female dry mass (digestive tract removed) and brood dry mass were measured after they were separated and dried for 24 hours in a 55 °C desiccating oven.

Allometry Analysis. We modeled reproductive allotment as the relationship between the natural log of clutch dry mass and the natural log of female dry mass in predator and non-predator environments. We used the slopes of these models as allometric coefficients (Table 2). We included developmental stage of offspring as a covariate and collection location as a random effect in the models. We determined patterns of allometry using ordinary least squares regression (Kilmer & Rodríguez, 2017). When the slope was equal to one, this indicated isometry and not terminal investment. When the slope was greater than one, this indicated terminal investment— the mass of the clutch is proportionately larger than predicted by body size. Females exhibit indeterminate
growth; thus, we use size of females as a surrogate of age. All analyses were done using R Studio (RStudio Team, 2019).

*Life History Trait Analysis.* We ran general linear models for each life history trait to assess the effect of predation. We included covariates for the life history models as described in Johnson & Belk (2001). When analyzing number of offspring, we included female dry mass as a covariate. When analyzing offspring size and reproductive allotment, we used female dry mass and development stage of embryos as covariates. We did not include any covariates for male or female size at maturity. Brood dry mass is our measure of reproductive allotment. We log transformed reproductive allotment and number of offspring in the analysis to satisfy assumptions of the linear model. All output for reproductive allotment and number of offspring was back transformed to the original scale before being included in graphs or tables. We included location in each model as a random effect. Additionally, we calculated population least squares means for reproductive allotment, number of offspring, and size of offspring for comparable estimates (Table 1). All analyses were done using R Studio version 3.5.2 (RStudio Team, 2019).
RESULTS

Life history in *A. cultratus* did not differ significantly in predator versus non-predator environments for all traits except reproductive allotment. For reproductive allotment, individuals in predator environments had a significantly lower value than those in non-predator environments (ANCOVA, $F = 5.7$, df = 1, $P = 0.017$, slope = -0.15, $R^2 = 0.46$). The statistical significance of this relationship is entirely due to one population with high brood dry mass in the non-predator category (i.e., *Quebrada Serena*). Size of offspring, number of offspring, and size at maturity for males and females did not differ significantly in predator versus non-predator environments (Table 3; Figure 3; Figure 4).

Similarly, the allometric coefficients for reproductive allotment did not differ between predator and non-predator environments. Individuals in both environments displayed isometric reproductive allocation with age, inconsistent with the terminal investment hypothesis (Table 2; Figure 5).
DISCUSSION

We did not see divergence in four life history traits or allometric coefficients for reproductive allotment in *A. cultratus* for different predator environments. All life history traits showed no significant difference between predator environments except for reproductive allotment which did differ significantly. However it differed in a direction opposite to what theory predicts (Reznick, 1990)—we found lower allotment in predator environments than in non-predator environments. This significant result and allotment patterns are driven by our collection from Quebrada Serena (site 3). With the removal of this site, the difference in reproductive allotment is no longer significant. In this site we collected 94 total females, 65 of which were mature, the largest number of mature females found from any sampled population. We sampled this location using the same method as every other location. The catch per unit effort (CPUE) in this location was 4.3 for *A. cultratus*. We had an average of 4.1 CPUE for *A. cultratus* for all locations with a range of 0.7 to 7.2 CPUE. This site appears to be unique in that all mature females had a large number of offspring (greater than 8). Environmental factors (canopy cover, substrate type, stream depth, stream width, pH, and temperature) were taken at the site but did not vary significantly from the values found at other sites we collected from during the same year. Thus, it is possible that life history phenotype observed at this site is due to another selective pressure. One possible explanation is resource availability. High resource availability has been found to influence a high fecundity (Reznick & Yang, 1993) and with the high fecundity found at this site this may be a likely explanation. The nearby landscape, including perhaps runoff from a nearby factory, may be contributing to an unusually high resource environment. The allometric coefficient for reproductive allotment also did not vary but showed an isometric pattern of
allocation in both environments. This isometric pattern of investment is not consistent with the
terminal investment hypothesis, thus terminal investment is not seen in this species.

There are several possible explanations for the lack of divergence in life history in A. cultratus. It is possible that there may not be differences in environmental selective pressures among the sites. In environments where multiple factors are highly correlated, using one factor such as predator presence, is sufficient in representing a suite of putative selective agents at sites (Johnson, 2002). If environmental factors are not highly correlated, then using one factor such as predation may not adequately represent variation among environments. It is possible that the sites used for predator and non-predator environments in our study had similar mortality rates despite the presence or absence of predators and therefore showed no differences in life history. Lack of phenotypic divergence may also be attributed to gene flow between populations that can limit the ability of populations to adapt to selective pressures in their environment and therefore decrease differences between populations (Storfer, 1999). We currently have no measure of gene flow for this species. Another alternative is that there is limited additive genetic variation. Unfortunately, we have no direct measure of additive genetic variation for A. cultratus. None of these explanations were examined in full in this study, but they may be a good direction for future research.

An additional explanation is that morphology is indeed a real constraint. Our results are consistent with the hypothesis that life history divergence is constrained by morphology, and we suggest that these morphological constraints are driven by adaptations for swimming performance. Morphological adaptations in fish are critical to increasing thrust and decreasing drag despite swimming style (e.g. stead or unsteady) (Webb, 1984). Small differences in morphology can have a large effect on locomotion (Webb, 1982), with body shape and fins both
playing important roles in swimming performance (Blake, 2004; Langerhans & Reznick, 2010). For *Alfaro cultratus*, both the ventral keel and the narrow, streamlined body shape likely contribute to swimming ability. First, a keeled ventral surface has been shown to be important in swimming performance (George & Westneat, 2019). In scombroid fishes, the presence of a keel on both sides of a caudal peduncle decreases drag and is more efficient than a cylinder or vertically elliptical peduncle (Walters, 1962). A keeled surface increases the surface area that is used for thrust (Graham & Lowell, 1987). Specifically, a ventral keel creates a negative pressure that increases stabilization and resistance to rolling (Van Wassenbergh *et al.*, 2015). The ventral keeled surface of *Alfaro cultratus* may contribute to swimming performance by increasing stability for steady swimming. Second, a narrow-bodied morphology can likewise be beneficial for steady swimming. The body morphology of a fish influences energy demands by favoring either steady or unsteady swimming (Ohlberger, Staaks, & Hölker, 2006). A streamlined body shape reduces turbulence and energetic costs (Araújo, Layman, & Brian Langerhans, 2017a). Thus, the thin, streamlined body shape of *Alfaro cultratus* likely contributes to steady swimming, allowing for cruising at low energy costs (Figure 1). Both the ventral keel and the streamlined morphology of *A. cultratus* appear to be adapted for steady swimming. However, many fish experience morphological tradeoffs when specialization occurs (Webb, 1984; Langerhans & Reznick, 2010). Thus, these features may be beneficial for increased swimming performance, but could also have costs.

One possible cost may be that of the optimal life history. Body morphology influences swimming performance and predator avoidance (McPeek, Schrot, & Brown, 1996; Kolar & Wahl, 1998; Langerhans *et al.*, 2004; Langerhans, 2009; Araújo, Layman, & Brian Langerhans, 2017b). Pregnancy, in many species of poeciliids, can drastically change swimming performance
causing predator avoidance to decline as pregnancy progresses (Ghalambor et al., 2004; Belk & Tuckfield, 2010). This may be caused by a morphological convergence across species during pregnancy which limits burst swimming near the end of pregnancy as the abdomen becomes distended and reproductive investment is favored over predator escape speed (Ghalambor, Walker, & Reznick, 2003; Wesner et al., 2011; Ingley et al., 2014). The narrow body of *A. cultratus* appears to limit a distended abdomen during pregnancy. This may occur because the thin body and ventral keel are important for stabilized swimming and stabilized swimming may be favored in all environments in this species.

Why would stabilized swimming always be present? Previous studies have found that in high-predator environments unsteady swimming is favored but in low-predator environments steady swimming is favored (Langerhans, 2009; Langerhans & Reznick, 2010). Maintaining the same morphology in both predator and non-predator environments is thought to be costly as morphological divergence across predator regimes is commonly found in prey fish (Langerhans et al., 2004). The optimal morphology in a predator environment must be suboptimal in a non-predator environment or else we would expect to see the same morphology in both (Langerhans et al., 2004). A lack of difference between mortality environments, gene flow, and no additive genetic variation are possible explanations for this lack of divergence. However, other selective pressures such as stream flow and resources acquisition may also influence this morphology. Little is known about the habitat preference and foraging habits of *A. cultratus*. However, if foraging occurs in high flows, this may influence a steady swimming morphology despite suboptimal escape maneuvers that are limited in direction because of high flows (Anwar et al., 2016). Further work is needed to directly assess body shape, swimming performance, and selective pressures in this species.
In some species, life history characteristics also change in response to morphological adaptations to selective pressures. For example, some species maintain a more streamlined body morphology during pregnancy in all environments by superfetation, the simultaneous carrying of multiple broods (Zúñiga-Vega et al., 2007; Fleuren, Van Leeuwen, & Pollux, 2019). However, this life history characteristic is not found in *A. cultratus*. Instead we see little variation among populations and individuals in life history characteristics. Many poeciliids show significant differences in life history traits between predator and non-predator environments (Reznick & Endler, 1982; Johnson & Belk, 2001). However, there do appear to be some more narrow-bodied species and populations that show less divergence in life history traits. In addition to *A. cultratus*, this pattern was seen in the species *Brachyrhaphis parismina* who have a more narrow-body shape than most poeciliids and likewise show little divergence in life history characteristics across populations (Belk et al., 2011). Thus, it seems that *A. cultratus* do not change their life history allocation in response to predation, instead maintain consistent life history responses in all predator environments.

Divergent evolution in different predation environments was not seen in *Alfaro cultratus*. This may be due to a tradeoff in adaptations as the development of one trait may constrain the evolution of other traits. The ability of *A. cultratus* to adapt to predation pressures may be constrained by a morphology adapted to stabilized swimming performance.
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Table 1. Descriptive statistics for life history characteristics of *Alfaro cultratus* for 20 populations. Brood size, number of offspring, and size of offspring are least squares means that come from the linear models reported in the text. Brood size and number of offspring least squares means have been back transformed represent true numeric values. Number of females for populations in 2006 and 2007 are reported only as the number that were mature out of the number dissected; for 2019 populations these include all females collected.

| Location                  | Year | Site Number | Number of Males | Mean length of adult males (mm) | Size range of adult males (min - max) | Number of Females | Minimum size of gravid females (mm) | Brood Dry Mass (mg) | Number of Offspring | Offspring Size (mg) | Mean Female Dry Mass (mg) |
|---------------------------|------|-------------|-----------------|---------------------------------|--------------------------------------|-------------------|-------------------------------------|---------------------|---------------------|----------------------|------------------------|
| Non-Predator Sites        |      |             |                 |                                 |                                      |                   |                                     |                     |                     |                      |                        |
| Rio Queque                | 2019 | 1           | 6               | 34.14                           | 30-42.8                              | 33/54             | 32                                  | 0.009               | 9.714               | 0.00101              | 0.115                  |
| Rio Balsa Tributary       | 2019 | 2           | 40              | 34.4                            | 28.1-41.7                            | 56/156            | 34                                  | 0.008               | 7.491               | 0.00114              | 0.142                  |
| Quebrada Serena           | 2019 | 3           | 48              | 33.33                           | 28.2-43                              | 65/94             | 34                                  | 0.019               | 18.145              | 0.00110              | 0.136                  |
| Quebrada Sahino           | 2019 | 4           | 14              | 33.86                           | 30-42                               | 49/90             | 32                                  | 0.009               | 6.200               | 0.00159              | 0.078                  |
| Rio Sucio                 | 2019 | 5           | 13              | 34.78                           | 28.2-42.6                            | 32/50             | 34                                  | 0.011               | 13.397              | 0.00083              | 0.098                  |
| Trib. To Rio Sixaola      | 2007 | 6           | 14              | 26.486                          | 21.7-38.1                            | 24/33             | 30                                  | 0.008               | 7.431               | 0.00123              | 0.099                  |
| Trib. to Rio Parismina    | 2007 | 7           | 11              | 36.291                          | 28.9-41.5                            | 20/21             | 30                                  | 0.009               | 7.765               | 0.00124              | 0.247                  |
| Rio Salto                 | 2006 | 8           | 21              | 31.433                          | 25.3-52.7                            | 27/82             | 28                                  | 0.012               | 11.862              | 0.00151              | 0.100                  |
| Quebrada Perez            | 2006 | 9           | 7               | 39.643                          | 30-46.5                             | 12/57             | 42                                  | 0.022               | 27.744              | 0.00069              | 0.184                  |
| Predator Sites            |      |             |                 |                                 |                                      |                   |                                     |                     |                     |                      |                        |
| Rio Zapote (Side Channel) | 2019 | 10          | 18              | 33.35                           | 25.9-47.6                            | 32/96             | 34                                  | 0.019               | 17.888              | 0.00107              | 0.128                  |
| Quebrada Las Latas        | 2019 | 11          | 57              | 30.34                           | 23-43.2                             | 59/108            | 28                                  | 0.009               | 9.001               | 0.00108              | 0.131                  |
| Rio Ricardo               | 2019 | 12          | 22              | 37.65                           | 31.9-43.8                            | 43/76             | 34                                  | 0.011               | 10.840              | 0.00106              | 0.125                  |
| Quebrada Piedra           | 2019 | 13          | 20              | 35.28                           | 23.9-44.6                            | 60/106            | 34                                  | 0.011               | 10.243              | 0.00113              | 0.115                  |
| Rio San Rafael Tributary  | 2019 | 14          | 35              | 32.37                           | 26.8-41.4                            | 55/114            | 30                                  | 0.008               | 6.395               | 0.00127              | 0.130                  |
| Quebrada Huevo            | 2019 | 15          | 26              | 33.37                           | 27.7-41.5                            | 46/130            | 32                                  | 0.013               | 9.412               | 0.00147              | 0.124                  |
| Rio Saino                 | 2019 | 16          | 24              | 30.58                           | 25.5-38.3                            | 43/98             | 34                                  | 0.014               | 12.120              | 0.00119              | 0.097                  |
| Rio Herediana             | 2007 | 17          | 13              | 40.523                          | 35.5-46.8                            | 27/104            | 40                                  | 0.012               | 13.657              | 0.00092              | 0.220                  |
| Rio Sabalo                | 2007 | 18          | 17              | 35.465                          | 25.7-47.3                            | 17/90             | 42                                  | 0.006               | 6.921               | 0.00086              | 0.244                  |
| Trib. to Rio Sarapiqui    | 2007 | 19          | 21              | 34.814                          | 26.4-45.8                            | 49/92             | 32                                  | 0.010               | 10.993              | 0.00100              | 0.179                  |
| Isla Grande               | 2006 | 20          | 13              | 30.339                          | 25.3-41.6                            | 19/73             | 32                                  | 0.004               | 9.254               | 0.00086              | 0.096                  |
Table 2. Allometric coefficient table for predator and non-predator environments. Isometry is seen in predator and non-predator environments as evidenced by confidence intervals that span a slope of 1.

| Predator | Allometric Coefficient (AC) | SE   | 95% CI      | AC > 1 | Intercept |
|----------|------------------------------|------|-------------|--------|-----------|
| Yes      | 1.052                        | 0.061| 0.932 - 1.172 | No     | -3.161    |
| No       | 1.083                        | 0.081| 0.924 - 1.243 | No     | -2.753    |
Table 3. ANCOVA table output for the five life history traits with the effect of predation. Female dry mass and development stage are covariates for reproductive allotment and offspring size. Development stage is a covariate for number of offspring. Location is included as a random effect for each.

| Life History Trait        | F     | df | P-value | Slope  | R2         | Intercept |
|---------------------------|-------|----|---------|--------|------------|-----------|
| Reproductive Allotment    | 5.730 | 1  | 0.017   | -0.150 | 0.455      | -5.702    |
| Number of Offspring       | 1.118 | 1  | 0.291   | -0.070 | 0.401      | 1.659     |
| Offspring Size            | 2.975 | 1  | 0.085   | -0.000 | 0.089      | 0.001     |
| Female Size at Maturity   | 1.011 | 1  | 0.315   | 0.317  | 0.002      | 32.284    |
| Mean Male Size at Maturity| 1.266 | 1  | 0.261   | 0.286  | 0.003      | 33.308    |
Figure 1. Photos of the lateral and dorsal view of a female *Alfaro cultratus*. Dorsal view shows streamlined body shape.
Figure 2. Map of Costa Rica collection locations. Localities are numbered according to the site number found in Table 1. Predator sites are open circles; non-predator sites are closed circles.
Figure 3. Plot of population least squares means for reproductive allotment (brood dry mass), number of offspring, and size of offspring in predator and non-predator environments. Populations means points are jittered for better visualization.
Figure 4. Plot of size at maturity for males and females in predator and non-predator environments. Sizes represent the population maturity size. The size where at least ½ females contain developing embryos is the female size at maturity. For males this is the mean size of mature males. Populations points are jittered for better visualization.
Figure 5. Graph of allometric coefficients (AC) for predator and non-predator environment. Non-predator points are open circles and predator sites are closed circles. The non-predator AC (1.052) is the dashed line and the predator AC (1.083) is the solid line.