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The potential for disruptive selection on growth rates across genetically influenced alternative reproductive tactics

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Abstract:	A trade-off between survival to sexual maturity and mating success is common across alternative reproductive tactics (ARTs), and can lead to tactical disruptive selection on shared traits (i.e. positive selection gradient in one tactic, and negative selection gradient in another). We were interested in examining the theoretical possibility of tactical disruptive selection on intrinsic growth rate. The male ARTs in Xiphophorus multilineatus express two distinct life histories: "courters" optimize mating success by maturing later at larger size and coaxing females to mate, while "sneakers" optimize survival to sexual maturity by maturing earlier at a smaller size, using both coaxing and coercive mating behaviors. In addition to differences in mating behaviors, body length, body depth, and the pigment pattern vertical bars, courter males grow faster than sneaker males. We present a new hypothesis for differences in growth rates between genetically influenced ARTs. The "growth-maturity optimization" hypothesis suggests that ARTs with differences in the probability of surviving to sexual maturity may have different optimal growth rates, leading to tactical disruptive selection. We also present a simple model to suggest that when considering both a cost and benefit to faster growth, tactical disruptive selection on growth rates is theoretically possible. In our model, the value that determines when tactical disruptive selection on growth rate will occur is the increase in probability of survival to sexual maturity gained through faster growth multiplied by the cost of faster growth (reduced longevity). Finally, we present empirical evidence to support the prediction that faster growth has a cost in X.

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The potential for disruptive selection on growth rates across genetically influenced alternative reproductive tactics

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Abstract

A trade-off between survival to sexual maturity and mating success is common across alternative reproductive tactics (ARTs), and can lead to tactical disruptive selection on shared traits (i.e. positive selection gradient in one tactic, and negative selection gradient in another). We were interested in examining the theoretical possibility of tactical disruptive selection on intrinsic growth rate. The male ARTs in *Xiphophorus multilineatus* express two distinct life histories: "courters" optimize mating success by maturing later at larger size and coaxing females to mate, while "sneakers" optimize survival to sexual maturity by maturing earlier at a smaller size, using both coaxing and coercive mating behaviors. In addition to differences in mating behaviors, body length, body depth, and the pigment pattern vertical bars, courter males grow faster than sneaker males. We present a new hypothesis for differences in growth rates between genetically influenced ARTs. The "growth-maturity optimization" hypothesis suggests that ARTs with differences in the probability of surviving to sexual maturity may have different optimal growth rates, leading to tactical disruptive selection. We also present a simple model to suggest that when considering both a cost and benefit to faster growth, tactical disruptive selection on growth rates is theoretically possible. In our model, the value that determines when tactical disruptive selection on growth rate will occur is the increase in probability of survival to sexual maturity gained through faster growth multiplied by the cost of faster growth (reduced longevity). Finally, we present empirical evidence to support the prediction that faster growth has a cost in *X. multilineatus*: in a controlled laboratory setting, courter males that did not survive 1.2 years past sexual maturity grew faster as juveniles (14-70 days) than those that survived.

Introduction

Alternative reproductive tactics (ARTs) are common across taxa, and consist of discrete differences in suites of reproduction traits among individuals of the same sex (Taborsky et al. 2008). Selection against intermediate expression of reproductive traits is expected to lead to the evolution of the discrete differences between the tactics (Taborsky and Brockmann 2010). Such tactical disruptive selection occurs when traits shared by individuals of the same sex experience different selection gradients depending on the tactic in which they are expressed (Morris et al. 2013). In other words, a trait is under net disruptive selection as a result of directional selection in opposite directions in each tactic. Body size is a trait that is likely to be under tactical disruptive selection in many ARTs. For example, males that are of intermediate size in the bluegill sunfish are too small to win mates through male–male competition, but too large to be successful at gaining access to mates through sneaking (Gross 1982; 1984).

An important life history trait that is often overlooked in studies of ARTs, but may be experiencing tactical disruptive selection, is growth rate. Ecological and life history studies have often assumed that individuals should grow as fast as possible (i.e. selection on growth rates will be positive). Faster growth equals higher probability of reaching sexual maturity and larger body size, both of which are often adaptive. However, we now have a better understanding of the importance of growth-mortality tradeoffs in producing consistent differences in growth rates both across and within populations (Arendt 1997; Stamps 2007). Given that variation in growth rates within a population are heritable and that population variation in growth rates can be locally adaptive (Ardent 1997), we were interested in examining the potential for disruptive selection on growth rates across alternative reproductive tactics. We use ARTs in the swordtail fish, *Xiphophorus multilineatus,* as an example.

Two primary tactics have been described in *X. multilineatus*: larger "courter" males that use only courtship behaviors, and smaller "sneaker" males that use both courtship and sneak-chase mating behaviors depending on social context (Zimmerer and Kallman 1989). In addition to these distinct differences in mating behaviors, courters and sneaker males differ in age at sexual maturity, adult size, body depth and number of vertical bars for their size (Fig. 1). Once the males reach sexual maturity both types of males stop growing (Kallman 1989), and therefore age at sexual maturity and adult male size are positively correlated. Both larger male size and more vertical bars are known to contribute to the higher mating success of the courter males through sexual selection (Rios-Cardenas and Morris 2011). The mating advantage of the larger courter males (Morris et al. 2010), however, is countered by their later maturation; the smaller sneaker males have a higher probability of surviving to sexual maturity by maturing earlier (Bono et al. 2011). In other words, even though a courter male has a higher mating success than a sneaker male, fewer courter males survive to sexual maturity than sneaker males, which increases the number of courter males with a reproductive success of zero (Shuster and Wade 2003). This trade-off is expected to result in the ARTs having equal lifetime reproductive successes, thereby maintaining both types of males in the population (Ryan et al. 1992).

Evidence from both laboratory-reared (Kallman 1989) and wild-caught *X. multilineatus* males (Bono et al. 2011) suggest that larger courter males grow faster than sneaker males in this species (Table 1). Variation in both resources and predation risk have previously been identified as explaining consistent differences in growth rates; lower resource conditions selecting for slower growth (Iwasa 1991; Niewiarowski and Roosenburg 1993; Sinervo and

Adolph 1994), and higher predation risk selecting for faster growth (Abrams et al. 1996). Ardent and Reznick (2005) demonstrated that resources influenced variation in growth rates more so than predation when considering variation across populations of another live-bearing fish (*Poecilia reticulate*). Given that ARTs are found in the same population, and in *X. multilineatus* there is no evidence to suggest that the courter and sneaker males have access to different resources, variation in resources is unlikely to select for the differences in growth rates between the ARTs in this species. In addition, predators that are large enough to take a courter or sneaker male can be found across most of the range of *X. multilineatus* (Rios-Cardenas, unpublished data), suggesting that there is no advantage for one of the ARTs to grow faster to reach a size-refuge (as detected in *X. helleri*, Basolo and Wagner 2004; Hernandez-Jimenez and Rios-Cardenas 2012). Therefore, it appears that a different hypothesis is needed to explain variation in growth rates between the ARTs in *X. multilineatus*.

We propose a new hypothesis to explain differences in growth rates across genetically influenced ARTs, the "growth-maturity optimization" hypothesis. This hypothesis considers both the costs and benefits of faster growth in relation to differences in the probability of surviving to sexual maturity, and suggests that ARTs with genetically influenced differences in age at sexual maturity may have different optimal growth rates. Given that in *X. multilineatus* the courter males take longer to reach sexual maturity than sneaker males (Bono et al., 2011), faster growth rates could help these males compensate to some extent for their increased risk of mortality prior to reproducing. However, if faster growth rates carry a cost of reduced longevity, the benefit of reaching sexual maturity sooner for sneaker males (that mature earlier than courter males, but have a lower relative mating success, Morris et al. 2010) may not outweigh this cost. We develop a simple model that allows us to test the prediction that within certain parameter values, selection on growth rate will be negative for the ART that reaches sexual maturity sooner, and positive for the ART that matures later. In contrast to previous models of life history traits in threshold-based ARTs (Leonardsson & Lundberg 1986; Smallegange & Johansson 2014), our model therefore examines the potential for the evolution of phenotypic integration in existing genetically influenced ARTs. Increased growth rates have been shown to increase mortality not only in the presence of predators (trout, Biro et al. 2006), but also in laboratory-reared fish, where the influence of size based predation and nutrition on mortality was controlled (sticklebacks, Lee et al. 2013). Therefore, we also predicted that the increased growth rate of courters in *X. multilineatus* carries a cost of increased intrinsic mortality. To determine if there is a cost associated with faster growth rates in the swordtail fish *X. multilineatus*, we examined growth rates and mortality in laboratory conditions where the influence of maternal effects, nutrition, risk of predation, and investment in reproduction were controlled.

The Model

Demonstrating disruptive selection on growth rates across ARTs would require detecting lower fitness with faster growth for one ART, as compared to higher fitness with faster growth for the other ART. The following model considers two ARTs that vary in their age at sexual maturity, and both age at sexual maturity and juvenile growth rates influence final adult size (both ARTs have determinant growth, and stop growing at sexual maturity). We assume that larger males have higher reproductive success, and that increasing growth rate would decrease age at sexual maturity, thereby decreasing risk of mortality prior to reproducing. In addition, we initially assume the ARTs have equal longevity, prior to considering any potential cost to longevity from faster growth rates, and we assume that the cost of faster growth is similar across the two ARTs. As we do not know if either of these assumptions hold true for *X. multilineatus*, in the end, we examine the effect of relaxing both assumptions on the potential for disruptive selection. We also assume there is a single locus (e.g. Mc4r), with two alternative alleles (functional, non-functional) that influences age at sexual maturity. While this is a simplification from the actual *X. multilineatus* system (there is additional variation in copy number of Mc4r within the courter males; Lampert et al. 2010), the model still captures the main differences between the two ARTs (courter and sneaker males). Our goal is for the model to provide proof of concept of disruptive selection on growth rates, as well as to identify the parameter space that could produce disruptive selection on growth rate across the two ARTs.

Parameters of the model were as follows:

Probability of survival to maturity for slow growth, p

Additional survival to maturity advantage of fast growth, a

Reproductive lifespan (years), l

Cost to reproductive lifespan of faster growth, c

Offspring produced per year, k

Lifetime reproductive success, w.

We made the assumptions that

$$0 \leq p + a \leq 1$$

$$c < l$$

If the lifetime reproductive success of slow growth, $w_s = plk$, and lifetime reproductive success of fast growth, $w_f = (p + a)(l - c)k$, we can then ask: when does faster growth increase lifetime fitness within any given tactic? Or, $w_f > w_s$.

In other words, under what conditions can the mutant "faster growth" allele invade? The model suggests that a tactic will have higher fitness with a faster growth rate when

$$a > p\frac{c}{(l - c)}$$

Or, when the survival advantage of fast growth is greater than probability of reaching maturity times the fraction that represents the cost of growing faster relative to the reproductive life span of fast-growing individuals.

Because there is an upper limit to the probability of juvenile survival (100%), we can imagine that there is a set of values where the fast growth tactic can never be advantageous. For example if the slow growth strategy already has a very high survival (e.g. 90%), then the maximum advantage that can be gained by growing faster is small (10%). This advantage may in some cases never be large enough to ever outweigh the costs of growing faster.

If we assume that

$$0 \leq a + p \leq 1$$

this means that the maximum value for survival is

$$a + p = 1.$$

The value of slow-growth survival to sexual maturity that sets our upper limit for where fast growth can invade (which we will call p_{max}) is therefore

$$p_{max} = 1 - a$$

or alternatively

$$a = 1 - p_{max}$$

We can then use this to solve for p_{max} when $w_f < w_{s.}$ (that is, when the fast growth tactic can never invade). Using what we know is true from above (that the fast growth tactic can invade when a>pc/(l-c)), we can conclude that the converse must also be true; the fast growth tactic can never invade when

$$a < p\,\frac{c}{(l - c)}$$

Substituting (1- p_{max}) for a and solving for p_{max}

$$\frac{(l - c)}{l} < p_{max}$$

In other words, if the survival of the slow growth tactic is higher than the ratio between fast reproductive lifespan ($l - c$) and slow reproductive lifespan (l), then the fast growth tactic can never invade. For example, if the fast growth lifespan is 80% of the slow growth lifespan, then survival probability of the slow growth tactic has to be less than 80% for the fast growth tactic to be able to invade.

If we assume that reproductive lifespan, cost of reduced reproductive lifespan for fast growth, and survival advantage to fast growth are the same in both tactics, but that the probability of survival to maturity and fecundity are different, then

Slow growing courters: $w_{sc} = p_c l k_c$

Fast growing courters: $w_{fc} = (p_c+a)(l–c)k_c$

Slow growing sneakers: $w_{sn} = p_n l k_n$

Fast growing sneakers: $w_{fn} = (p_n+a)(l-c)k_n$

This allows us to ask if differences in the probability of reaching sexual maturity and relative fecundity of tactics would result in tactical disruptive selection on growth rates. In other words we want to determine when $w_{fc} > w_{sc}$ and $w_{fn} < w_{sn}$ (i.e. when fast-growing courters do better than slow-growing courters, and slow-growing sneakers do better than fast-growing sneakers).

Courter males will have positive selection on faster growth ($w_{fc} > w_{sc}$) when

$$a > p_c \frac{c}{(l - c)}$$

Similarly, sneakers will have negative selection on faster growth ($w_{fn} < w_{sn}$) when

$$a < p_n \frac{c}{(l - c)}$$

In other words,

$$p_c \frac{c}{(l - c)} < a < p_n \frac{c}{(l - c)}$$

$$p_c < \frac{ac}{(l - c)} < p_n$$

Therefore, for tactical disruptive selection to exist, there needs to be a difference between the tactics in the probability of reaching sexual maturity, and it is the value of the survival advantage times the relative reproductive lifespan cost that will determine when the selection on growth rate is negative for the males that mature early. A graphical representation of a particular case where the parameters would produce tactical disruptive selection is shown in Fig. 2.

Finally, if we relax the assumptions of equal reproductive lifespans and equal costs to fast growth in both tactics, we end up with

$$p_c \frac{c_c}{(l_c - c_c)} < a < p_n \frac{c_n}{(l_n - c_n)}$$

We can no longer simplify the inequality further now that $l_c \neq l_n$ and $c_c \neq c_n$. However we can still draw the general conclusion that the (tactic-specific) probability of survival times the relative longevity cost must be higher in sneakers than in courters for there to be disruptive selection. All else being equal, this relationship could then be attained in several ways:

1. Sneakers have higher probability of survival to maturity ($p_c < p_n$)
2. Courters have lower costs of fast growth ($c_c < c_n$)
3. Sneakers have shorter baseline reproductive lifespan ($l_c > l_n$)

(Note that the smaller the denominator ($l - c$), the larger the value of the fraction $\frac{c}{(l-c)}$.)

Growth Rate and Mortality

Material and methods

We examined the influence of growth rates on mortality for F3 males reared in environmental chambers, which controlled for temperature (22° C) and light (13:11 h L:D, see Murphy et al. 2014). Mothers of these males were raised individual on either low (LQ) or (HQ) diets (difference primarily in % protein, see Lyons et al. 2014), and then mated to males from the largest size class. As male size is influenced by number of copies of the Mc4r gene on Y-chromosome (Lampert et al. 2010), all of their sons were large as well. Offspring were isolated into individual tanks at 14 days of age, photographed to obtain standard length (SL), and reared on the LQ diet. At 70 days of age, individuals were photographed again for SL, and half of the offspring were assigned to the “social” treatment and half to “control”. Individuals in the social treatment were exposed to an adult courter male twice for three days (see Murphy et al. 2014 for more details). Using plastic Penn Plax (Hauppauge, NY, USA) breed-n-show boxes that were placed inside the fry’s home tank, juveniles received both visual and chemical (pheromone) cues from the adult males, but physical contact was prevented. Once males reached sexual maturity (mean = 187.4 days, SE = 28.9 days, range: 135–285 days) they remained isolated throughout their adult lives. Given that all the males were from the same size class (similar number of copies of Mc4r gene, Lampert et al. 2010), and raised in an environment without conspecifics or predators, a relationship between growth rate and mortality is unlikely to be attributed to variation in copy number of the Mc4r gene on the Y-chromosome, resources variation, reproductive effort, competition or predation.

Growth rates were measured over two different time periods so that any influence of the social treatment on growth rates could be detected: GR1 = 14 to 70 days of age, before social treatment was initiated; GR2 = 70 to 130 days of age, after social treatment but prior to the age when any of the individuals had reached sexual maturity and ceased growing. GR1 also provides a measure of growth prior to any known morphological differences between the ARTs, and is unlikely to include any investment in reproductive traits. The male's growth rates were calculated as size gain (SL_{age1}–SL_{age0}) over the number of days they grew (age1–age0). Males with mothers raised on HQ diets grew faster than males with mothers raised on LQ diets, and male offspring exposed to an adult male during juvenile development grew faster than controls (see Murphy et al. 2014, Table 1). Thirty-two of the 84 males died after sexual maturity, but before reaching the age of 1.8 years.

We compared both the early (GR1) and late (GR2) juvenile growth rate of the males that died to the males that survived to at least 1.8 years of age using a Generalized Linear Mixed Model (GzLMM) with a binomial distribution and a logit link, as the data set did not meet the assumptions of normality and homoscedasticity. We took into account the mother (as some of the males were siblings) as a random factor, which also controls for maternal effects. For the analysis of GR2 we also included the social treatment as a factor. All statistics were conducted using SPSS Statistics, Version 21.

Results

There was a significant relationship between growth rate during male's first 70 days of life (GR1) and their mortality as adults in the laboratory (GzLMM, $F_{1,82}$= 4.949, P = 0.029). Males that survived grew on average 0.41 mm less between the ages of 14 and 70 days (mean growth rate = 0.119 mm/day, SD = 0.047 mm/day, N = 52) than the males that died (mean growth rate = 0.127 mm/day SD = 0.037 mm/day, N = 33). There was no significant influence of growth rate measured between 70 days and 130 days (GR2) on mortality of adults (GzLMM, $F_{2,81}$= 0.488, P = 0.487). Social treatment, which influenced growth rate in males (Murphy et al. 2014, see Table 1), did not influence mortality ($F_{2,81}$ = 2.241, P = 0.138).

Discussion

Our model suggests there is potential for tactical disruptive selection on growth rates between the genetically influenced ARTs in *X. multilineatus,* supporting the "growth-maturity optimization" hypothesis. We suggest that genes influencing variation in growth rate may be under different selection gradients depending on whether they are expressed in the ART that matures early (higher probability of reaching sexual maturity), or the ART that matures later (lower probability of reaching sexual maturity). First, we show that for there to be positive selection on a faster growth rate strategy, the survival advantage of fast growth should be greater than the relative reproductive lifespan cost times the probability of reaching maturity. Second, the model suggests that the possibility for tactical disruptive selection on growth rates depends on the value of the survival advantage of faster growth times the relative longevity cost of faster growth. In other words, faster growth within the tactic that maximizes mating success by maturing later (courter males in *X. multilineatus*) will improve probability of survival to sexual maturity as well as mating success due to larger adult size. However, in the tactic that maximizes their overall reproductive success by maturing earlier (sneaker males in *X. multilineatus*), the benefits of faster growth will in some cases not outweigh the costs of decreased reproductive lifespan. In addition, even when we relax the assumptions of equal costs to fast growth in both ARTs as well as equal reproductive lifespans, there are still areas of the parameter space that would result in disruptive selection on growth rates. We are currently collecting data on the relationship between growth rates, probability of reaching sexual maturity, and mating success for males from both tactics so that we can compare the selection gradients on growth rates (Innocenti and Morrow 2010), and determine if the predictions from our model for tactical disruptive selection on growth rate hold for the ARTs in *X. multilineatus*.

Our model of tactical disruptive selection relies on faster growth not only benefiting individuals by allowing them to reach sexual maturity sooner, but also imposing a cost. We detected a cost of reduced reproductive lifespan for faster growth rate for *X. multilineatus* courter males in the laboratory, where the confounding links between growth rate, nutrition and a size-related risk of predation were removed. Growth that influenced mortality was early in the juvenile stage (14-70 days old, GR1), when there are no distinguishable differences between courter and sneaker males. In addition, testes size was determined to be equivalent between the tactics after controlling for the relationship with soma mass (Smith and Ryan 2010). Therefore, while we only examined cost of growth rate in courter males, the assumption of this cost being equal across the ARTs is likely to hold upon further examination. These results support the growth-mortality tradeoff hypothesis (Metcalfe and Monaghan 2003; Stamps 2007), and suggest that even if a male can gain the benefits of reduced predation by being larger in this species (reaching a size-refuge due to faster juvenile growth rate), there would still be a cost for faster growth. Therefore, as long as faster growth resulted in an increased probability of mortality up and beyond the risk of mortality due to predation, the cost of reduced reproductive longevity due to faster growth could influence fitness.

A relationship between growth and mortality has been detected in several different species (reviewed in Mangel and Stamps 2001), and in some cases the mechanism responsible for the relationship has been documented as well. For example, faster growth rates produced by increased food intake can expose individuals to a greater risk of predation and thus produce higher mortality (Gotthard 2000; Biro et al. 2006). This could be occurring in *X. multilineatus,* as males that grew faster were bolder under risk of predation (see D'Amore et al. 2015). However, this would be an additional mechanism by which faster growth would be costly, as we can clearly rule out predation as a factor in our measure of cost; the fish in our study were raised individually in a predator-free environment. It is also unlikely that the cost we detected is due to investment in reproduction, as the time period of juvenile growth that influenced mortality was prior to the investment in reproductive traits (e.g. sperm). There are several other mechanisms, however, that could explain the growth-mortality tradeoff we detected. First, there may have been a positive effect of caloric restriction on increased life span (Merry 1995), given that the individuals that grew slower were likely to be eating less. Second, the relationship we detected could also be explained by the "selection for perfection" hypothesis (Chippindale et al. 2003). This hypothesis suggests that slower growth promotes higher ontogenetic fidelity, such that the risks of rapid growth are associated with developmental accidents. We find this hypothesis particularly interesting, as faster growth is correlated with higher fluctuating asymmetry (FA) in the vertical bar pigment pattern in *X. multilineatus* (Morris et al. 2012), as well as FA for wing size in *Drosophila* (Abbott et al. 2010). Third, there are several molecular processes that could explain why increased growth rates might lead to decreased longevity, including oxidative stress related to calorie intake (Merry 1995; Rollo 2002) and reduced investment in protein maintenance (Morgan et al. 2000). Finally, as we detected the relationship between mortality and early growth (GR1) prior to the social treatment, it is unlikely that the social treatment influenced the growth-mortality tradeoff, and these results suggest that faster growth early in development may be more costly than faster growth later in development. Regardless of the mechanism behind the relationship we detected, our results stress the importance of considering the costs of faster growth in studies of life-history evolution, as well as the potential for several different mechanisms to produce these costs.

One of the expected outcomes of disruptive selection on heritable traits is the evolution of dimorphism (Rueffler et al. 2006). Intralocus tactical conflict (IATC) can constrain the evolution of tactic dimorphism such that males of one or both tactics are not at their phenotypic optimum (Morris et al. 2013). When homologous traits such as intrinsic growth rate are not at their adaptive optimum, tactical disruptive selection can generate IATC. The concept of intralocus conflict has been examined extensively in the context of the sexes (IASC, Bonduriansky and Chenoweth, 2009), and as ARTs can be considered one of the many different types of alternative phenotypes, some of the same mechanisms that help resolve IASC can help resolve IATC. For example, relocation of tactically antagonistic genes to the chromosomes influencing the ART, as well as gene duplication followed by the subsequent divergence of their function are both mechanisms that could resolve intralocus conflict (Morris et al. 2013). We suggest that the multiple copies of the Mc4R gene on the Y-chromosome could function to resolve tactical disruptive selection on growth rates in *X. multilineatus* by regulating both growth and reproduction. Suppression of the Mc4r gene, responsible for delaying sexual maturity in swordtail fishes (Lampert et al. 2010) and increasing growth rates in zebrafish (Zhang et al. 2012), is also known to stimulate appetite in other fish species (e.g. goldfish, Cerdá-Reverter et al. 2003; rainbow trout, Schjolden et al. 2009; Mexican cavefish, Aspiras et al. 2015). This system, therefore, has the potential to provide us with interesting insights into the extent to which linking delayed maturation and faster growth rates through increased appetite with a gene on the Y-chromosome could resolve IATC, allowing for the growth rates of the ARTs to diverge due to disruptive selection.

We limited our model to genetically influenced ARTs, however even within this sub-class of ARTs, the extent to which this outcome is expected to be specific to *X. multilineatus* needs further investigation. Evidence that genes on the Y-chromosome influence differences between the ARTs is growing (e.g. chinook salmon *Oncorhynchus tshawytscha* Heath et al. 2002; cichlid *Lamprologus callipterus,* Ocaňa et al. 2014). In the cichlid, dwarf males grow faster than larger dominant males early in life, and then slower as they reach sexual maturity (Ocaňa et al. 2013). There is at least one interesting difference between the cichlid system and *X. multilineatus* that could be explored in relation to the predictions of our model, as well as used to extend the model we have presented. The cichlid males that are going to become larger and dominant do not wait to mature until they are large, but instead have a sequentially reversible reproductive strategy (sneaky when smaller and dominant when they reach the optimal size threshold for nest building).

In conclusion, we present a new hypothesis for the adaptive evolution of variation between ARTs in growth rates. Our model suggests there is potential for tactical disruptive selection on growth rates, and predicts that growth rates are more likely to be under negative selection in alternative reproductive tactics that have higher probabilities of reaching sexual maturity (e.g. small sneaker males), and under positive selection in tactics with lower probabilities of reaching sexual maturity (e.g. large courter males). The important value to determine when tactical disruptive selection will occur is the probability of survival to sexual maturity gained through faster growth multiplied by the cost of faster growth (reduced longevity). Our empirical results provide evidence for a cost to faster growth, adding to the growing evidence for a growth-mortality tradeoff. Finally, to evolve variation in growth rates due to tactical disruptive selection, it will be important for growth rates to be genetically correlated to the alternative reproductive tactics. We suggest that variation in the number of copies of the Mc4r gene on the Y-chromosome could link delayed maturation with increased growth rate, and should be examined as mechanism that could partially resolve IATC on growth rate in swordtail fishes.

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Table 1. Growth rates of *X. multilineatus* males across different genotypes and environments

Wild-caught	Y-L Courter (N = 7) 0.17 ± 0.011 mm/day	Y-s Sneaker (N = 30) 0.16 ± 0.018 mm/day	Bono et al. 2011*
Laboratory	NA	Y-s Sneaker (N = 3) 0.15 ± 0.035 mm/day	Marcus and McCune 1999
Laboratory (14-70 days)	HQ diet mothers Y-L Courter (N = 34) 0.14 ± 0.006 mm/day	LQ diet mothers Y-L Courter (N = 50) 0.13 ± 0.005 mm/day	Murphy et al. 2014§
Laboratory (70-130 days)	Social Experience Y-L Courter (N = 42) 0.12 ± 0.006 mm/day	Controls Y-L Courter (N = 42) 0.11 ± 0.004 mm/day	Murphy et al. 2014§

* Estimates of growth rates based on otolith ring counts (days to sexual maturity, Morris and Ryan 1990) and adult male size (size at sexual maturity). Morris et al. (2012) detected an asymmetry in otolith ring counts between the right and left side that matched asymmetry in the vertical bar pigment pattern. Therefore, to present the best estimate here, we re-estimated growth rates based on the otolith with the largest count. § Mothers of the males in this study were reared on high (HQ) or low quality (LQ) diets, and some males were exposed to an adult male during development (Social Experience) while others were not (Controls). Note that the slower growth rates in this study are likely due to all males being reared on the low quality diet.

Figure Legends

Figure 1. Males in *Xiphophorus multilineatus* are classified as one of two alternative reproductive tactics: (A) sneaker or (B) courter males. The tactics differ not only in their mating behaviors (courters do not use sneak-chase behavior, Zimmerer and Kallman 1989), but also in their growth rates and age at sexual maturity (Kallman 1989; Bono et al. 2011), as well as relative mating success (Morris et al. 2010). Males breed true (sneaker males have sneaker sons) due to variation in the Mc4r gene on the Y chromosome (Lampert et al. 2010) and can be distinguished morphologically due to differences in adult size, body depth and vertical bars (Zimmerer and Kallman 1988). The widths of the bars in the diagram represent the investment into each of these life-history traits. Time was included along the bottom of the diagram to stress the difference in time to sexual maturity, when males stop growing (Kallman, 1989). We initially assume in the model that the baseline reproductive life spans for the two ARTs, prior to a cost of growing faster, is equal. Our model also examines the possibility of unequal baseline reproductive lifespans (see text). As courter males reach sexual maturity later and grow faster (producing a cost of shorter longevity), we have portrayed them with shorter adult or "reproductive" lifespans in this figure. Photos by K. de Queiroz.

Figure 2. Changes in lifetime reproductive success (w) as a function of probability of reaching sexual maturity (p), tactic (courter = dashes; sneaker = dots) and growth rate (red = faster growth; blue = slower growth). Faster growth was assumed to incur a one-year reduction in longevity (c) for both tactics. Courter males were given a 0.130 yearly reproductive advantage (k) over sneaker males (after Morris et al. 2010; 2 per year for sneakers (k_n), 2.6 for courters (k_c)). Note that if growing faster increases the probability of reaching sexual maturity by 20% (a), for males that already have a high probability of reaching sexual maturity (p_n = 30%) this

decreases lifetime reproductive success (w_n) from 1.2 to 1 for sneakers (arrow “B”), while for males that have a lower probability of reaching sexual maturity ($p_c = 10\%$) this would **increase** lifetime reproductive success (w_c) from 0.52 to 0.78 for courters (arrow “A”).

Figure 1.

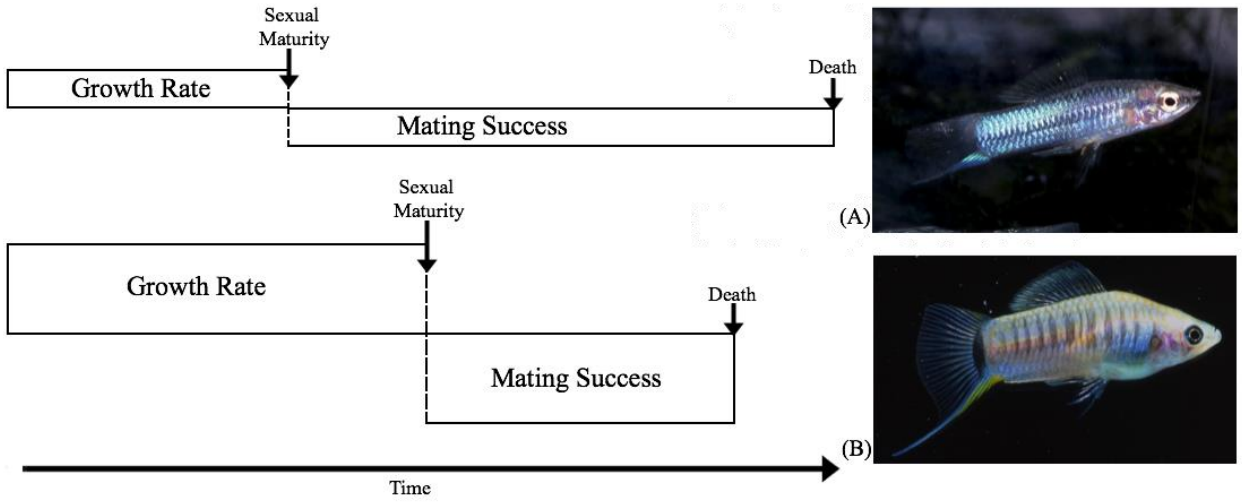
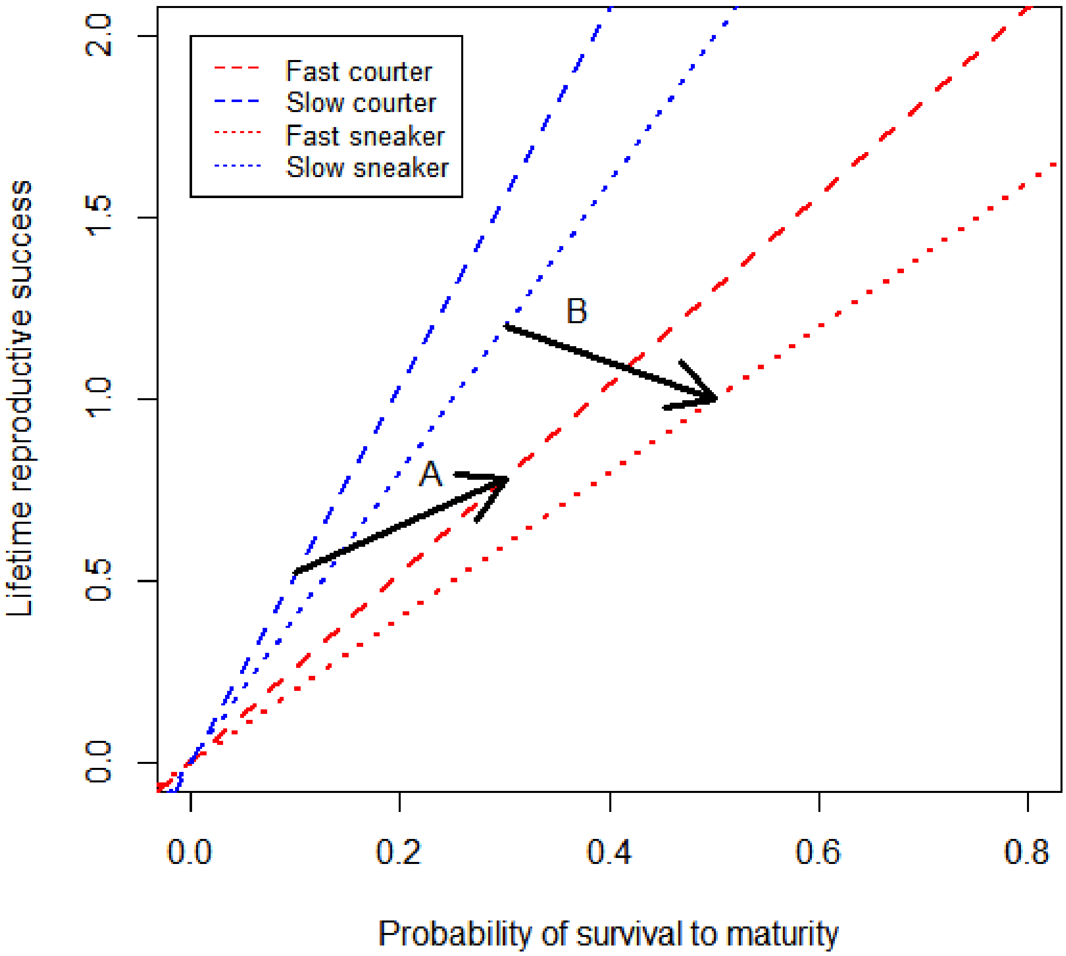

Sexual Maturity
Growth Rate
Death
Mating Success
(A)
Sexual Maturity
Growth Rate
Death
Mating Success
(B)
Time

Figure 2


Fast courter
Slow courter
Fast sneaker
Slow sneaker
A
B
Lifetime reproductive success
0.0
0.5
1.0
1.5
2.0
Probability of survival to maturity
0.0
0.2
0.4
0.6
0.8