Paternal Genetic Effects on Foraging Decision-Making Under the Risk of Predation

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Abstract

Foraging behavior under the risk of predation has interested biologists for decades. Here, we examine paternal genetic effects on foraging decisions of bluegill (*Lepomis macrochirus*) larvae sired by males adopting alternative life histories. We use split in vitro fertilization to generate maternal half-siblings sired by either a 'parental' male or a 'cuckolder' male. Immediately, upon the switch to exogenous feeding, we fed the larvae ad libitum for 2 d. We then starved the larvae for between 12 and 17 h, following which we subjected them to a dichotomous choice foraging trial, where one side of a test tank posed a risky foraging habitat and the other posed a safe foraging habitat. Equal amounts of food were simultaneously introduced to both sides of the tank and the proportion of individuals on either side was recorded. There were significantly fewer cuckolder offspring foraging on the risky side of the tank when compared with their parental half-siblings indicating that cuckolder offspring took fewer risks than parental offspring. These results demonstrate a paternal genetic effect (sire life history) on foraging behavior. We ruled out energetic state as a possible explanation for this difference because the half-siblings did not differ in body length or mass. Instead, previous research suggests that cuckolder offspring have higher conversion efficiency (efficiency of converting food into soma) than parental offspring and therefore the differences in foraging behavior observed here may, in part, be attributed to genetic differences in conversion efficiency.

Introduction

Biologists have long been intrigued by the foraging decisions made by individuals under the risk of predation (reviewed by Lima & Dill 1990; Lima 1998). Models of foraging behavior typically assume a trade-off between food intake and susceptibility to predation (i.e. vigilance), and empirical work has focused on the influence of energetic state on an individual's allocation of time to foraging vs. vigilance behavior. Generally, this empirical work has shown that individuals in a low energetic state (e.g. small body size or low condition) accept higher predation risks when foraging provided there is a greater chance for food profitability than individuals

in a high energetic state (e.g. Kohler & McPeek 1989; Holmes 1991; Bachman 1993; Krause 1993; Pettersson & Bronmark 1993; Moore 1994; Romey & Rossman 1995; Weary et al. 1996). For example, Bachman (1993) showed that Belding's ground squirrels (*Spermophilus beldingi*) with low body mass spend less time being vigilant and more time foraging after an alarm call than their heavier conspecific. Less attention has been given to other factors that may affect foraging decision-making such as conversion efficiency.

Conversion efficiency is a measure of an individual's ability to convert food into soma, and it is typically measured as the increase in body mass over a period of time divided by the mass of food

assimilated during that time (e.g. McPeek et al. 2001). Studies have demonstrated both genetic and environmental effects on conversion efficiency (Thomas et al. 1958; Gross et al. 1965; Leenstra & Pit 1988; Björnsson & Tryggvadóttir 1996; McPeek et al. 2001; Henryon et al. 2002). Here, we propose that conversion efficiency should also play a role in foraging decision-making, independent of an individual's state. Specifically, individuals with higher conversion efficiency, because of either experiencing an optimal environment or possessing genes that lead to higher conversion efficiency, should take fewer risks during foraging than individuals with lower conversion efficiency independent of their state because of their increased potential to convert food into soma (Fig. 1). For example, in many populations, there is a threshold level of growth that all individuals must maintain to minimize the probability of predation or to reach sexual maturation (Werner & Gilliam 1984). Because growth rate is in part a function of conversion efficiency, an individual with low conversion efficiency requires a higher food intake than an individual with high conversion efficiency to reach the same threshold size at a given time. Individuals who require more food must forage longer or in areas with higher food profitability and therefore they should accept a greater risk of predation (Lima & Dill 1990; Lima 1998).

Mating systems with alternative life histories may be ideal to test the effect of conversion efficiency on foraging decision-making under the risk of predation because in several species there are differences in conversion efficiency between the life histories. For example, many salmonids have two male life histories: (i) a resident male that remains in freshwater
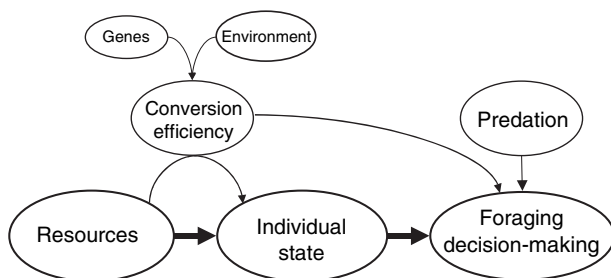
and matures precociously; and (ii) a migrant male that migrates from freshwater to saltwater and delays maturation (Jonsson & Jonsson 1993). Morinville & Rasmussen (2003) examined the conversion efficiency of resident and migrant brook trout (*Salvelinus fontinalis*) by calculating both growth rate and consumption rate for individuals. They found that, in the year before migration (age 1 + year old individuals), brook trout that became migrants consumed 40% more food than their resident conspecifics of the same age, but grew to a similar size. In Atlantic salmon (*Salmo salar*), Aubin-Horth & Dodson (2004) examined growth rate of residents and migrants by back-calculation of growth rings on otoliths. They showed that the larger males became residents and that the size difference between future residents and migrants in these salmon was already apparent at the end of the endogenous (yolk-sac) feeding period (also see Hutchings & Jones 1998; Garant et al. 2002,2003). These two studies suggest that individuals that become residents have higher conversion efficiency than those that become migrants.

Bluegill (*Lepomis macrochirus*) are also characterized by discrete alternative male life histories, which are termed 'parental' and 'cuckolder' (Gross & Charnov 1980; Gross 1982), and offspring of these males appear to differ in their genetic conversion efficiency. We have previously used split clutch in vitro fertilization to generate maternal half-siblings that were sired by either a parental male or a cuckolder male (Neff 2004). We found that, at the end on the endogenous feeding period, offspring of cuckolder males were 5% longer on average than their half-siblings sired by parental males. Because the offspring had equivalent food sources (i.e. the yolk-sac provided by a shared mother) and length is highly correlated with mass in bluegill larvae ($r_s = 0.994$, n = 253, p < 0.001; Neff & Lister, unpublished data), these data indicate that larvae sired by cuckolder males have genes that lead to high conversion efficiency.

Here, we use split clutch in vitro fertilization to generate maternal half-siblings sired by either parental or cuckolder males. Shortly after the switch to exogenous feeding, we examine the foraging decisions of the maternal half-siblings under the perceived risk of predation. We assume that these differences in conversion efficiency persist into the exogenous feeding period, as has been shown for other fishes with similar alternative life histories (e.g. Morinville & Rasmussen 2003) and test the hypothesis that conversion efficiency affects foraging decision-making, independent of an individual's state (body length or mass). We predicted that the

Fig. 1: Model of the effects of an individual's state and conversion efficiency on foraging decision-making under the risk of predation. Most previous research has focused on the flow of resources to an individual's state, such as body size, to decision-making. Conversion efficiency, which has both genetic, environmental and genetic by environmental components, also should play a role in foraging decision-making independent of state

offspring of cuckolders would take fewer risks when foraging than parental offspring because cuckolder offsprings have higher genetic conversion efficiency and therefore require less food to maintain a required level of growth.

Methods

Study Species

Bluegill are endemic to North America (Lee et al. 1980). They are characterized by a discrete alternative life history in males. In Lake Opinicon (Ontario, Canada: 44°16′N, 76°30′W), parentals sexually mature at about 7 yrs of age and provide sole parental care for the developing eggs and larvae in their nest (Gross 1982). Other males called cuckolders mature precociously at 2 yrs of age, and using a parasitic tactic, steal fertilizations from parentals during spawning. Cuckolders do not provide care to their young, but instead leave this to the parentals they parasitize. About 21% of males mature precociously, while the other 79% follow the parental life history (Gross 1982). Breeding experiments have shown that these life histories have a genetic component; on average, about 70% of a parental's sons become parentals, whereas only 50% of a cuckolder's sons become parentals (M. R. Gross, Toronto, University of Toronto, unpublished data; reported in Alcock 1989, p. 412).

During the May to Jul. breeding season, parentals nest in colonies along the littoral zone of Lake Opinicon. Parental care lasts up to 10 d, after which the larvae leave the nest as a group and head for safer open waters (Werner 1967). However, as the larvae leave the colony they must pass through Eurasian water milfoils (*Myriophyllum spicatum*), which are abundant around most colonies in Lake Opinicon (Elliott et al. 1997). During this passage, about 20% of larvae are consumed by a major predator, *Hydra canadensis*, which congregate around colonies on the *M. spicatum* (Elliott et al. 1997). Surviving larvae remain in the safer open waters for several weeks until they outgrow the vulnerable prey size range of *H. canadensis* (Elliott et al. 1997; Garvey et al. 2002).

Split In Vitro Fertilization

Experiments were conducted at the Queen's University Biological Station on Lake Opinicon. During the breeding season of 2003, colonies were located by daily snorkeling. On the day of spawning, parentals, cuckolders and gravid females were collected using dip nets and transported to holding tanks in an aquarium facility. All aquaria were supplied with fresh lake water via a flow-through system. Shortly after collection, maternal half-siblings were generated using split in vitro fertilization. Eggs were stripped from each female by applying gentle pressure to the abdomen and milt was collected from males in 0.5-ml syringes in a similar manner. For each female, broods were divided approximately in half; one half was fertilized with sperm from a cuckolder and the other half with sperm from a parental. Fertilization was accomplished by placing eggs and milt together in 50 ml of lake water in a 500-ml mason jar for 2 min. The jars were then filled with water and an air feed was placed in each jar to oxygenate the water. Water changes of about 250 ml were performed twice daily at about 8:00 and 19:00 EST until embryos became freely swimming larvae, which occurred 9–10 d after fertilization. Each brood was then transferred to individual 19-l aquariums and fed zooplankton of size 0.1–0.3-mm ad libitum for 2 d. The size range of zooplankton was selected based on the natural diet of bluegill larvae (see Keast 1980). Broods were used only once in the trials.

All trials commenced at 21:00 EST when between 4 and 41 larvae ($\bar{x}$ 25 ± 1.4 SE) were placed in a 1.5-l (*ca.* 15 × 10 × 10 cm) plastic aquarium containing gravel to a depth of 1 cm and filled with 1.2-l lake water at ambient temperature. Each test aquarium was divided into three sections by drawing two lines with a marker on the outside of the aquarium. The two outer sections measured 5.5 cm in length and the center section measured about 4 cm in length. The larvae were then left for 12–17 h without food after which we conducted one of three types of experiments between the hours of 9:00 and 14:30 EST.

Preliminary Trials

We conducted risk free trials (n = 10) to establish the baseline distribution of larvae in our experimental aquarium. For the preliminary trials, we used larvae of mixed parentage (i.e. cuckolder and parental offspring) because of limitations in the number of half-sib families we were able to produce. After the starvation period (12–17 h), we simultaneously added zooplankton at a mean concentration of 5.2 plankton per 50-μl lake water 2 cm from either side of the aquarium using two pipettes. This process was repeated every minute throughout the trial for a total of 20.5 min. Beginning 30 s after the first

application of food, we recorded the number of larvae in each of the three sections of the tank and this count was repeated every 60 s for the duration of the trial and these numbers were averaged. We then conducted a one-sample t-test on the proportion of larvae per trial on the left minus right sides to determine if there were equal numbers on either side (null hypothesis of difference = 0).

Next, we conducted 'risk' trials (n = 10) without food to confirm that larvae perceived one habitat as risky and the other as safe. Trials were run using the same arrangement as above but with the following modifications. A 'risky' patch was created by placing three 8-cm tall *M. spicatum* at one end of the test aquarium. We expected that the plants would create the perception of risk and deter larvae from foraging in that area (see above and Werner 1967). The side containing the *M. spicatum* was alternated in successive trials. To determine if bluegill larvae avoid the *M. spicatum*, we conducted a one-sample t-test on the difference between the proportion of larvae per trial on the open vs. *M. spicatum* sides.

Risk and Foraging

We conducted risk trials with food added to the aquarium (n = 16 paired half-sibling families) to quantify differences in foraging behavior under the risk of predation between cuckolder and parental offspring. This experiment was conducted similarly to the previous risk trials except that each trial contained full-siblings. Zooplankton were added as in the risk-free trials. The number of larvae feeding in each section of the tank was recorded every 60 s for 20.5 min and these numbers were averaged. At the end of each trial, larvae were preserved in 70% ethanol for later phenotypic measurements and analysis of state.

The foraging behavior of offspring from the two life histories were compared using mixed-model analyses of variance with sire life history entered as a fixed factor, female identity (maternal line) entered as a random factor, and mean mass or body length of the offspring for each family entered as a covariate. The dependent variable was the mean proportion of larvae on the *M. spicatum* side of the tank (= # on *M. spicatum* side/[# on *M. spicatum* side + # on open side]). We also conducted an independent t-test to compare the mean proportion of larvae on the *M. spicatum* side in the preliminary trials (no food added) and the proportion of larvae on the *M. spicatum* side in the behavioral trials (data from cuckolder and parental offspring combined). We expected that

there should be more larvae on the *M. spicatum* side in the trials with food than the trials without food.

About 1 month after, the larvae were preserved, and they were photographed using a Retiga 1300 digital camera (W. Nuhsbaum, Inc., McHenry, IL, USA) from Qimaging mounted on a Zeiss Axioskop 2 Mot microscope. SCION IMAGE BETA 4.0.2 software was used to determine the total body length (mm). The larvae were then dried in an oven at 55°C for 18 h and weighed using a Mettler Toledo microbalance (Mettler-Toledo, Inc., Columbus, OH, USA) (0.001 mg). Body length and mass measurements were used as measures of an individual's state (see Lima 1998). A mixed-model analyses of variance were used with either body length or mass entered as the dependent variable, sire life history was entered as a fixed factor, and female identity (maternal line) and the interaction term were entered as random factors.

All means are reported plus or minus 1 SE. All statistical tests were performed using SPSS (v. 10.0) or JMP (v. 5.1).

Results

Preliminary Trials

When given an equivalent amount of food on both sides of the tank, there was no significant difference in proportion of larvae foraging on either side (left = 0.42 ± 0.02, right = 0.42 ± 0.02; t = 0.014, df = 9, p = 0.99). The proportion of larvae found in the center section of the tank was 0.17 ± 0.01. When *M. spicatum* was placed on one side of the test tank (and no food was added), a greater proportion of the larvae were on the open side than on the *M. spicatum* side (open = 0.75 ± 0.02, *M. spicatum* = 0.14 ± 0.02; t = 17.9, df = 9, p < 0.001). The proportion of larvae found in the center section of the tank was 0.12 ± 0.01. Thus, as expected, the bluegill larvae were reluctant to enter the area containing *M. spicatum*.

Risk and Foraging

After the starvation period, we found that cuckolder offspring took fewer risks while foraging under the perceived risk of predation than parental offspring. The proportion of cuckolder offspring observed on the *M. spicatum* side relative to the open side of the tank was significantly less than that of parental offspring (cuckolder: 24%; parental 33%; ANOVA: sire life history, F = 12.1, df = 1, 6, p = 0.013; Fig. 2).
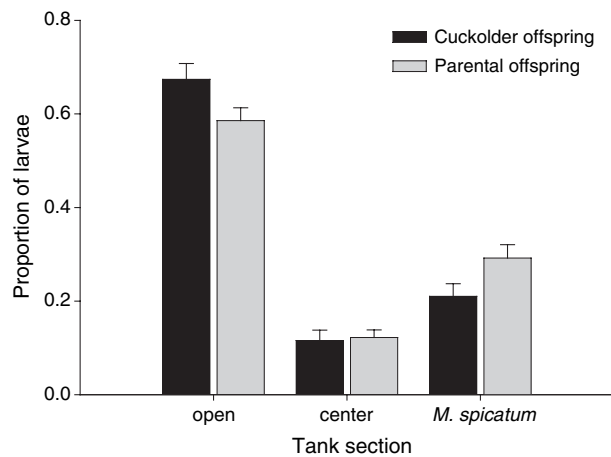
Fig. 2: Mean proportion of larval bluegill (*Lepomis macrochirus*) observed in the open, center and *M. spicatum* sections of the test tank. When food was added, a greater proportion of parental off-springs were in the risky, *M. spicatum* section than cuckolder off-spring, indicating that parental offsprings were willing to take greater risks when foraging. A similar proportion of cuckolder and parental offspring was in the center section. Error bars denote 1 SE

Fig. 3: Mean offspring body length for half-sibling larval bluegill (*Lepomis macrochirus*) sired by either a cuckolder or parental male. The dots denote the means of each family and the lines join maternal half-sibling data. Some females produced larger offspring on average than other females independent of sire life history (significant female identity effect) and within females' half-sibling families, half the females produced larger offspring on average with the cuckolder sire, whereas the other half produced larger offspring on average with the parental sire (significant interaction effect between female identity and sire life history). The triangles and dashed line denote the means for all cuckolder or parental families

There was no significant effect of female identity (F = 2.61, df = 7, 6, p = 0.13) or the mean mass of the offspring (F = 3.62, df = 1,6, p = 0.10) on the proportion of larvae on the *M. spicatum* side. Similar results were found when mean body length of the offspring was used as the covariate instead (sire life history: F = 8.74, df = 1, 6, p = 0.025; female identity: F = 3.85, df = 7, 6, p = 0.060; body length: F = 4.77, df = 1, 6, p = 0.072).

Analysis of the offspring phenotypic measurements revealed that, although there were significant female identity and female identity by sire life history interaction effects, there was no difference between offspring sired by parents vs. cuckolders in either body length (parental: 5.31 ± 0.02 mm; cuckolder: 5.33 ± 0.02 mm) or mass (parental: 46.1 ± 0.6 mg; cuckolder: 46.1 ± 0.5 mg; Table 1, Fig. 3).
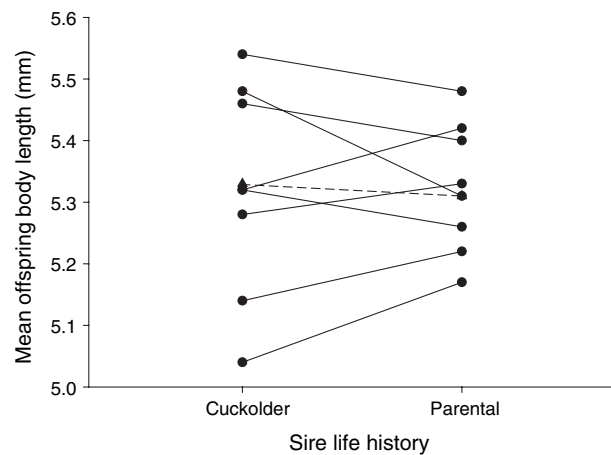
Comparing the risk and foraging results to those from the preliminary trials with no food added, there were significantly more larvae on the *M. spicatum* side when there was food added than when there was no food (t = 3.77, df = 24, p = 0.001), but there was no difference in the proportion of larvae observed in the center sections across these two trial types (t = 0.15, df = 24, p = 0.88).

Discussion

Most research on foraging decision-making under the risk of predation has focused on the state of an

Measurement	Treatment	ss	df	F	p	σ^2
Body length	Sire life history	0.012	1, 7	0.152	0.707	–
($r^2 = 0.518$)	Female identity	4.122	7, 7	5.821	0.017	0.0136 (39)
	Sire life history × Female identity	0.708	7295	6.244	<0.001	0.0047 (14)
	error	4.746	–	–	–	0.0162 (47)
Mass ($r^2 = 0.443$)	Sire life history	0.002	1, 7	0.280	0.610	–
	Female identity	0.638	7, 7	10.517	0.003	0.0023 (40)
	Sire life history × Female identity	0.061	7295	2.751	0.009	0.0003 (5)
	error	–	–	–	–	0.0032 (55)

Table 1: Summary of the mixed-model ANOVA results for sire life history, female identity and interaction effects on offspring body length or mass of bluegill (*Lepomis macrochirus*) larvae. The data comprise the sum of squares (ss), degrees of freedom (df), F statistic, p-value, and variance component (σ^2) for the random effects with percent of total in parentheses. The proportion of variance (r^2) captured by the model is presented below the dependent variables

NB: for mass, the sum of squares and the variance components are ×10^{-2}.

individual as a major determinant of such decision-making. Generally, this research has shown that individuals in a low state (e.g. small body size) take more risks to obtain food than individuals in a high state (e.g. large body size). Here, we found that individuals sired by alternative life histories in bluegill made different decisions when foraging under the risk of predation, independent of their body size. Larvae sired by parental males took more risks when foraging than larvae sired by cuckolder males. Previous research has shown that larvae sired by cuckolder males have higher conversion efficiency during the endogenous feeding period than larvae sired by parental males (see Introduction). Assuming that this difference in conversion efficiency continues during exogenous feeding, as has been shown for other fish with alternative life histories (Morinville & Rasmussen 2003; Aubin-Horth & Dodson 2004), the data presented here support a role for conversion efficiency in foraging decision-making under the risk of predation.

We also found effects of offspring body size and female identity (dam) on foraging behavior, although neither of these effects was statistically significant. Consistent with other research, bluegill larvae that were longer or heavier took fewer risks during foraging. The female identity effect was independent of offspring body size and therefore suggests a maternal additive genetic effect on foraging decision-making. The genetic basis of this effect may be similar to that captured by sire life history.

Our data also provide insight into the genetic architecture of growth rate in bluegill. The risk trials involved a split in vitro design that enabled us to partition variance in growth rate during early development to maternal effects (environmental and maternal additive genetic or 'good genes'), sire life history effects (paternal additive genetic) and the interaction between these two factors (non-additive genetic; Lynch & Walsh 1998; Neff & Pitcher 2005). We found a strong maternal effect that accounted for 39–40% of the explained variance in offspring body length or mass (see Table 1). It is likely that this maternal effect predominately represents an environmental effect associated with differences in egg quality such as size as has been shown in other fishes (e.g. Heath et al. 1999). We also found a significant interaction between female identity and sire life history, which accounted for 14% of the explained variance in offspring body length and 5% of the explained variance in mass. This latter effect is indicative of non-additive genetic effects such as overdominance or epistasis (Lynch & Walsh 1998).

Perhaps surprisingly, there was no direct effect of sire life history on offspring length or mass. This may seem at odds with our assumption that differences in conversion efficiency continue into the exogenous feeding period (see Introduction). It is possible that the strong interaction with female identity masked any sire life history effect in our study (see Table 1, Fig. 3). Alternatively, the difference in foraging activity between the two offspring types that we revealed here indicates that parental offsprings spend more time feeding (and less time being vigilant) than cuckolder offspring. Thus, parental offspring may grow at a similar rate to, or faster than, cuckolder offspring during the exogenous feeding period because they consume more food. Such an effect has been demonstrated in a interspecific comparison of damselfly larvae (McPeek et al. 2001). In predatory-free *ad lib* feeding trials, the authors found that *Enallagma* spp. larvae ate more food and grew faster than *Ischnura* spp. larvae. Interestingly, in predatory risk trials, the authors also found that the *Ischnura* spp. larvae had higher conversion efficiency than the *Enallagma* spp. larvae. Unfortunately, in our study, we did not measure the actual feeding rate of the bluegill larvae during the 2 d of ad libitum feeding and therefore we cannot confirm a similar effect in our study.

Our results may provide insight into unexplained behavioral patterns found in other studies of bluegill. Werner et al. (1983) showed that bluegill make variable foraging decisions when under the risk of predation from piscivorous largemouth bass (*Micropterus salmoides*). They found that some bluegill chose to forage in safer but less profitable vegetative habitat, whereas other bluegill chose to forage in more profitable but dangerous open water habitat. Although Werner et al. (1983) postulated that individuals collected from the open water habitat should have had a higher growth rate than those in the vegetative habitat, they found no size difference between individuals collected from the two habitats. Our results suggest that such variation in foraging behavior may reflect differences in conversion efficiency. If individuals with low conversion efficiency take more risks when foraging than those with high conversion efficiency, as we found in the current study, then the bluegill in the open water may have lower conversion efficiency than the bluegill in the vegetative habitat and although the former individuals are in more profitable habitat, they do not grow faster.

Why does it appear that species with alternative life histories consistently differ in their conversion efficiency between the male types? Many of these

alternative life histories likely have evolved as a conditional strategy, whereby the 'decision' to adopt either life history is based on an individual's state (Gross 1996). It is therefore conceivable that the direct effect of genetic conversion efficiency on an individual's state (see Fig. 1) can indirectly affect which life history is adopted and will thereby contribute to the inheritance of alternative life histories. Individuals that inherit high conversion efficiency are more likely to attain a higher state and adopt the associated life history, all else being equal, than individuals that inherit low conversion efficiency. Modeling has shown that such inheritance does not preclude evolutionary stability of a conditional strategy (Repka & Gross 1995; Gross & Repka 1998). In the cases of the salmonids and bluegill, interestingly, it appears that the precocious maturing individuals are the ones that have the higher conversion efficiency and presumably the higher growth potential.

In conclusion, our data suggest that conversion efficiency can affect foraging behavior of individuals under the risk of predation. Genetic diversity underlying conversion efficiency also may contribute to the inheritance of condition-dependent alternative life histories through its role in governing individual state. More research is warranted in these areas to better elicit the role of conversion efficiency.

Acknowledgements

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