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Williams, Trevor J.; Johnson, Jerald B.; and Belk, Mark C., "Interaction between predation environment and diet constrains body shape in Utah chub, *Gila atraria* (Cypriniformes: Cyprinidae)" (2017). *Faculty Publications*. 5418.  
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Interaction between predation environment and diet constrains body shape in Utah chub, *Gila atraria* (Cypriniformes: Cyprinidae)

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Received 1 March 2017; revised 14 April 2017; accepted for publication 15 April 2017

Evolution typically occurs in response to a suite of selective pressures. Yet, many studies of natural selection in the wild only investigate a single selective agent at a time. This can be problematic when selective agents act in non-additive ways. Here we evaluate the interactive effects of diet and predation on the evolution of body shape in the cyprinid fish Utah chub (*Gila atraria*). We found that both factors and the interaction between them are significant predictors of body shape. This interaction is likely a result of different forms of selective pressures, where predation is a stabilizing selective force and diet is a disruptive selective force. Utah chub with more herbivorous diets exhibited a distended abdomen and shorter, shallower caudal peduncle relative to Utah chub with more carnivorous diets. These shapes correspond with common patterns of ecological divergence between limnetic and benthic morphotypes, and likely evolved due to diet specialization. Utah chub from predation environments are generally more streamlined and have larger caudal peduncles than Utah chub in non-predation environments, which may be an adaptive response to allow greater burst-swimming capability. However, Utah chub in predation environments also have deeper bodies than more-carnivorous Utah chub in non-predation environments. Therefore, Utah chub in predation environments exhibit an intermediate phenotype with an intermediate depth but larger caudal peduncle. Our results suggest that predation constrains the range of body shape variation that is expressed in response to diet. Hence, the interactive effects of multiple selective pressures appear to be important in determining overall phenotype.


INTRODUCTION

Body shape is an important target of natural selection, and has been the focus of several studies of adaptive evolution (Brönmark & Miner, 1992; Schluter, 1993; Rüber & Adams, 2001; Langerhans et al., 2003, 2004; Dayton et al., 2005; Aguilar-Medrano et al., 2011; Aguirre & Bell, 2012; Ingleby et al., 2014; Landy & Travis, 2015). Body shape is an especially important functional trait in fishes, primarily because it determines swimming ability and performance, which in turn can affect life-history, behaviour, and predator–prey interactions. Body shape can be affected by several selective agents, including competition (Schluter & McPhail, 1992; Schluter, 1993), stream flow (Aguirre & Bell, 2012; Meyers & Belk, 2014; Landy & Travis, 2015), resource availability (Keast & Webb, 1966; Mérigoux & Ponton, 1998; Rüber & Adams, 2001; Costa & Cataudella, 2007; Aguilar-Medrano et al., 2011), and predation (Langerhans et al., 2004; Wesner et al., 2011; Hassell et al., 2012; Ingleby et al., 2014; Landy & Travis, 2015; Ingleby & Johnson, 2016). Because of its link to so many aspects of fitness, body shape is a good trait to use to investigate the interactive effects of multiple agents of selection.

Two well studied selective drivers of fish body shape are diet and predation. Herein, we define ‘diet’ as the resources used for food consumption. The types of resources available for consumption within a habitat dictate the response of traits through selection to that environment (Rundle & Nosil, 2005). Selection
resulting from available food resources can therefore promote differences in functional morphology that in turn influence feeding ability (Wainwright, 1991; Wainwright & Richard, 1995). One well-known example of this was discovered in Darwin’s medium ground finch (Geospiza fortis; Gould, 1837), where a drought altered the availability of seed types and selected for larger birds with larger bills (Boag & Grant, 1981). Although, natural selection is not the only determinant of morphology, several studies have shown that the body form of an organism is an accurate predictor of its trophic ecology (Keast & Webb, 1966; Gatz, 1979a, b; Wainwright, 1991; Wainwright & Richard, 1995; Bower & Piller, 2015). This predictive power is one of the central tenets of ecomorphology: the study of the relationship between functional design of organisms and the environment (Karr & James, 1975; Bower & Piller, 2015). This predictive power is one of the central tenets of ecomorphology: the study of the relationship between functional design of organisms and the environment (Karr & James, 1975; Wainwright, 1991; Motta et al., 1995). Although many traits are correlated with feeding, one of the most pervasive in fish is relative intestine length and level of herbivory in the diet (Ribble & Smith, 1983; Kramer & Bryant, 1995a, b; Wagner et al., 2009). If the relationships determined by ecomorphology hold true, then intraspecific variation in morphology can act as preliminary evidence for ecological divergent selection. In other words, a species that exhibits variation in functional feeding traits may have acquired that variation through selection related to dietary differences.

Adaptive functional morphology as a result of predation environment has also been thoroughly studied (Werner & Hall, 1988; Brönmark & Miner, 1992; Langerhans et al., 2004; Nowlin et al., 2006; Langerhans, 2009, 2010; Ingleby et al., 2014; Ingleby & Johnson, 2016). Typically, fish exhibit one of two morphologies that aid in predator evasion. These strategies are related to the gape-width limitation hypothesis, which infers that prey larger than a predator’s gape cannot be consumed (Hoyle & Keast, 1987; Hambright, 1991; Nowlin et al., 2006). Therefore, the total mouth width of piscivorous predators determines the body depth of prey that can be consumed. If prey are unable to outgrow a predator’s gape they typically exhibit a body form that enhances burst-swimming capabilities during the C-start. This body form is expressed by shallow anterior body and head and an enlarged caudal peduncle (Langerhans & DeWitt, 2004; Langerhans et al., 2004; Langerhans, 2009). Alternatively, fish that are capable of outgrowing a predator’s gape typically do so by increasing body depth (Hoyle & Keast, 1987; Werner & Hall, 1988; Hambright, 1991; Brönmark & Miner, 1992; Nowlin et al., 2006). Fish that have larger body depths will either not be targeted by predators, or will increase handling time and the probability of escape (Hoyle & Keast, 1987). Although, these adaptive strategies are predictable and widespread throughout nature (Langerhans & DeWitt, 2004), little research has documented how selection from multiple selective pressures interact to determine body shape (but see Crowl, 1990; Landy & Travis, 2015).

In theory, two types of selective interactions can occur: evolutionary synergism or evolutionary antagonism. In evolutionary synergism, multiple evolutionary pressures select for the same phenotype. For example, both water velocity and increased competition due to population density select for a streamlined body shape with a small caudal region that enhances steady swimming ability in mosquitofish (Gambusia affinis; Baird and Girard 1853) (Langerhans et al., 2003; Langerhans, 2008). Evolutionary antagonism occurs when two or more selective pressures push the phenotypic mean in opposite directions. For example, evolutionary antagonism should occur in populations of mosquitofish where flow selects for steady swimming but predation selects for unsteady swimming. Although, evolutionary change due to a single selective force can be accurately predicted (Langerhans, 2008, 2010), evolutionary antagonism can result in various outcomes and is therefore less predictable. One possible result of antagonism is phenotypic compromise, in which an intermediate mean for a single trait provides greater fitness than either maximum. Evidence for phenotypic compromise has been found in aquatic snails for age at maturity (Crowl, 1990) in response to selection from habitat stability and predation, as well as shell shape (DeWitt, Robinson, & Wilson, 2000; Lakowitz, Brönmark, & Nyström, 2008) in response to two different predators. Another possible result of antagonism is the coevolution of multiple traits, such as morphology and behaviour to maximize fitness (DeWitt, Sih, & Hucko, 1999). In the case of fish body shape, optimal phenotypes resulting from predation may be incompatible with the optimal phenotype selected for by diet. For example, herbivorous fish sometimes exhibit a distended abdomen due to the large intestines they require for plant digestion. This distended abdomen may not be beneficial if the fish is unable to outgrow its predator’s gape width and where selection promotes a body shape that is more efficient or powerful for escaping predators. Therefore, it is likely that the interaction between these forces will result in evolutionary antagonism.

To determine the interactive effects of two selective pressures, we compared how both diet and predation affect body shape among populations of Utah chub (Gila atraria; Girard 1856). Utah chub is a common, widespread minnow within the Bonneville Basin and Upper Snake River Drainage in western North America (Sigler & Sigler, 1996). These fish exhibit a general fusiform shape. However, there is large variation in shape, colour and size among and within populations (Fig. 1; Sigler & Sigler, 1996; Johnson & Belk, 2006). The current geographic range of Utah chub
represents a natural experiment, with Utah chub in the upper Snake River drainage sympatric with and preyed upon by Cutthroat trout (*Oncorhynchus clarkii*; Richardson, 1836) in many locations, whereas many Bonneville Basin populations are free of piscivorous predators (Fig. 2). Previous work has shown divergence in life history strategies between predation and non-predation environments (Johnson & Belk, 1999). Therefore, it is likely that populations diverge in body shape as a result of adaptation to predation environment. However, within populations, diet varies between individuals on a more herbivorous more carnivorous spectrum, which could result in intrapopulational divergence due to diet specialization (Robinson & Wilson, 1994; Skúlason & Smith, 1995; Schluter & Rambaut, 1996; Smith & Skúlason, 1996). Utah chub are omnivorous fishes that feed upon a wide variety of foods including but not limited to benthic and pelagic aquatic invertebrates and plant material including green algae (Sigler & Sigler, 1996). Selection due to predation environment is likely stabilizing or directional. Alternatively, diet specialization due to competition could result in disruptive selection. For fish, this type of disruptive selection from diet has commonly resulted in benthic and limnetic morphotypes or forms (Robinson et al., 1993; Robinson & Wilson, 1994; Skúlason & Smith, 1995; Schluter & Rambaut, 1996; Smith & Skúlason, 1996). This difference in selection types makes Utah chub an ideal system to study the effects of interactive selective pressures.

In this study, we have two major objectives: (1) to compare shape of Utah chub to general predictions from previous studies on effects of predation and diet, and (2) to determine the interactive effects of diet and predation on Utah chub body shape. We predicted that more herbivorous chub will exhibit distended abdomens while more carnivorous chub will exhibit a more streamlined body shape. Additionally, we predicted that Utah chub that lived predation environments would increase body depth to reduce predation. Although the interactive effect is less predictable, because adaptive phenotypes for variable diets and predation environments are often incompatible, it is likely that evolutionary antagonism and phenotypic compromise will result.

**METHODS**

**STUDY SYSTEM**

To measure the effects of different selective pressures on body shape in Utah chub, we collected fish

**Figure 1.** Examples of phenotypic variation among Utah chub populations. (a) Heart Lake, WY, (b) Fish Springs, UT, (c) Fish Springs, UT, (d) Locomotive Springs, UT.
from multiple locations across their native range. We selected eight locations based on whether piscivorous predators were present or not (Fig. 2). Past research indicates that these populations have been isolated from each other since the late Pleistocene as Lake Bonneville declined (Oviatt, Currey & Sack, 1992; Johnson, 2002; Johnson & Belk, 2006). With no gene flow since isolation, evolutionary change is likely a result of differential selection and neutral evolution among populations (Johnson, 2002). The same specimens we used in this study were used in an earlier study to compare variation in life history of Utah chub in predation and non-predation environments (Johnson & Belk, 1999). We define a predation environment as the sum total of all selective forces within environments that contain predators. Although predation is usually the selective pressure investigated, forces other than just those due to predation act in these environments as well and also contribute to adaptive phenotypes.

To explore the effect of diet on Utah chub morphology, we characterized diet in our analysis by using relative intestine length as a surrogate for trophic feeding position. Generally, herbivores have longer intestines than omnivores, which have longer intestines than carnivores (Al-Hussaini, 1949; Montgomery, 1977; Ribble & Smith, 1983; Felley, 1984; Kramer & Bryant, 1995a, b; Motta et al., 1995; Hugueny & Pouilly, 1999; Pouilly et al., 2003; Elliott & Bellwood, 2003; German & Horn, 2006; Karachle & Stergiou, 2010). This relationship is apparent among disparate taxonomic groups and across numerous continents and habitats (Keast & Webb, 1966; Gatz, 1979a, b; Ribble & Smith, 1983; Wikramanayake, 1990; Winemiller, 1991; Kramer & Bryant, 1995a, b; Motta et al., 1995; Mérigoux & Ponton, 1998; Hugueny & Pouilly, 1999; Pouilly et al., 2003; Elliott & Bellwood, 2003; German & Horn, 2006; Wagner et al., 2009; Karachle & Stergiou, 2010) The preponderance of evidence supporting the correlation between relative intestine length and herbivory in fish, despite habitat or taxonomic affinity indicates its predictive power and allows relative intestine length to be used as a surrogate for diet in this study. We measured intestine length from the posterior end of the stomach to the end of the intestine and calculated relative intestine length by taking the ratio of that measurement with standard length. Individuals were sexed by direct observation of gonads.

**Figure 2.** Map showing sampling localities for the eight populations in the study. Predation environments are represented by filled circles, non-predation environments are represented by open circles. Populations are numbered as follows: 1 – Heart Lake, 2 – Jackson Lake, 3 – Two Ocean Lake, 4 – Bear Lake, 5 – Locomotive Springs, 6 – Big Spring, 7 – Rush Lake, 8 – Fish Springs.

**GEOMETRIC MORPHOMETRICS**

Prior to dissection and preservation, we photographed the left lateral view of adult Utah chub from each of eight locations. Fish that were not aligned properly (e.g. upturned tail, etc.) were not used in the analysis. We included 142 individuals (n = 9 to 27 per location), and used geometric morphometrics methods (Rohlf & Slice, 1990; Rohlf & Marcus, 1993; Bookstein, 1997) to characterize body shape. Geometric morphometrics quantify shape by calculating the deformation of homologous landmarks on each individual from an average consensus (Rohlf & Slice, 1990). We identified 12 landmarks as follows as indicated in Fig. 3.
We considered landmarks 3, 5 and 10 as sliding semi-landmarks. Semi-landmarks only move along the axis perpendicular to the two associated landmarks, so they only represent shape variation on one axis rather than two axes (Bookstein, 1997). Shape variables were calculated by first aligning each specimen with the orthogonal least-squares method (Rohlf & Slice, 1990). Partial warps and uniform components (i.e. the weight matrix) were calculated, and we used a principal components analysis of the weight matrix (TPSRelW; Rohlf, 2015) to generate relative warps (RWs). We used RWs as response variables in statistical analysis. Twenty RWs were generated from the 12 landmarks; however, we only used the first 17 RWs generated to account for loss of dimensionality from the use of sliding semi-landmarks. The first 17 RWs account for 99.8% of shape variation.

**Statistical Analysis**

We used a multivariate linear mixed model to determine effects of predation environment and diet on fish body shape. With this model we were able to simultaneously analyze all shape variables, characterized by the 17 RWs, while accounting for fixed and random effects. We included predation environment as a fixed categorical effect (two levels), sex as a fixed categorical variable (two levels), relative intestine length and body size (i.e. centroid size) as continuous covariates and collection location (i.e. population) as a random effect. In 'natural experiments' such as this one, treating location as a random effect allows tests of fixed effects (i.e., predation environment) that are not confounded with location-specific variation. The order (or identity) of shape variables is then indexed by an 'index variable' inserted as a predictor variable which preserves the ordered nature of the RWs in the same way that time is often used as an index in repeated measures analysis. Therefore, it is the interaction of the other main effects with the index variable that tests for differences in shape between levels of main effects (Wesner et al., 2011; Hassell et al., 2012; Meyers & Belk, 2014). We included the two-way interactions between the index variable and predation environment, and index variable and relative intestine length, and the three-way interaction between the index variable, predation environment and relative intestine length in the model. Statistical analyses were conducted in SAS using the MIXED procedure (SAS version 9.4, SAS Institute Inc., Cary, NC, USA).

To illustrate the effects of predation and diet, we plotted the least square means of the RW scores (± SE) of high and low levels of relative intestine length (representing more herbivorous and more carnivorous phenotypes respectively) from both predation environments on RWs 1 and 2 (Fig. 4). It is generally accepted that relative intestine lengths less than one correspond to carnivory while relative intestine lengths greater than three correspond with herbivory (Karachle & Stergiou, 2010). However, various studies have reported different exact values for these cut-offs (Kramer & Bryant, 1995b and sources cited). In this study, we consider Utah chub with relative intestine lengths close to one to be mainly carnivorous and Utah chub with relative intestine lengths greater than two to be mainly herbivorous. These values correspond well with those reported in Kramer & Bryant (1995b) for fish the size of Utah chub, noting that the most herbivorous Utah chub are still likely partly omnivorous. Least squares means (and associated SEs) plotted in Fig. 4 were calculated using relative intestine length as a covariate at these values. RWs 1 and 2 accounted for 37.97% and 19.32% of variation in shape, respectively. Additionally, we generated thin-plate spline deformations that represented observed extremes in body shape along RWs 1 and 2 and placed those on the ends of the axes in Fig. 4 (TPSRelw; Rohlf, 2015).

**RESULTS**

Predation, diet, centroid size and sex all had significant effects on Utah chub body shape after accounting for the interaction with the index variable (Table 1).
Additionally, the interaction between the index variable, predation and relative intestine length was significant, consistent with the hypothesis that predation and diet interact in determining Utah chub body shape (Table 1). Populations from predation environments had more streamlined body shapes and longer caudal peduncles in comparison to non-predation environments, which exhibited more robust body shapes and shorter caudal peduncles (Fig. 4). This result is largely aligned along RW2. Fish with longer relative intestine lengths show a deeper belly body shape, while fish with short relative intestine lengths have a shallower belly (Fig. 4). Variation in relative intestine length aligns with RW1. The significant interaction term indicates that the mean shape corresponding with relative intestine length differs between environments with and without piscivorous predators. In non-predation environments, more herbivorous Utah chub exhibit distended abdomens and shorter caudal peduncles whereas more carnivorous Utah chub have a streamlined shape and long caudal peduncle. Alternatively, more herbivorous and more carnivorous Utah chub in predation environments have similar shapes, with a streamlined body but greater depth than more carnivorous Utah chub from non-predation environments. The least squares means also show a larger range for non-predation environments than for predation environments (0.059 and 0.025 across RW 1 for predator-free and predation environments respectively). Overall, non-predation environments cover more morphospace than do predation environments on RWs 1 and 2 (range on RWs 1 and 2 is 0.177 and 0.108, respectively, for non-predation environments and 0.116 and 0.098 for predation environments). Additionally, fish within populations showed considerable variation in relative intestine length and body shape, with many populations containing fish with both relatively short and relatively long intestines (Fig. 5).

**DISCUSSION**

Of the explanatory variables measured, the largest amount of variation in Utah Chub body shape was explained by differences due to diet (Fig. 4, RW 1). More herbivorous fish exhibit a distended abdomen, whereas more carnivorous fish were much more streamlined (Fig. 4). These findings are congruent with those of previous studies and match predictions based on ecomorphological hypotheses (Winemiller, 1991; Hugueny & Pouilly, 1999; Pouilly et al., 2003; Karachle & Stergiou, 2010). Although this could indicate a plastic response to varying resource availability, it could also signify diversification and incipient diet specialization. Several fish species manifest resource polymorphisms and multiple morphotypes depending on diet and microhabitat use (Schluter & McPhail, 1992; Robinson et al., 1993; Robinson & Wilson, 1994; Skúlason & Smith, 1995; Schluter & Rambaut, 1996; Smith & Skúlason, 1996). Typically, a benthic and a limnetic form arise as a result of open niche space (Robinson et al., 1993) or intraspecific competition and subsequent character displacement (Schluter & McPhail, 1992). The literature is replete with examples of convergence on these forms from various taxa, indicating that evolution within and between species in this manner may be a general phenomenon in fish (Robinson & Wilson, 1994; Skúlason & Smith, 1995; Schluter & Rambaut, 1996; Smith &
Utah chub in predation environments are more constrained in body shape, when compared to non-predation environments. In general, they displayed a more streamlined body with relatively large caudal peduncles, traits typically seen in benthic feeders. More carnivorous Utah chub are fusiform with longer caudal peduncles, a body shape that is well adapted for efficient swimming and catching zooplankton in the pelagic zone.

Utah chub in predation environments are more constrained in body shape, when compared to non-predation environments. In general, they displayed a more streamlined body with relatively large caudal peduncles, a shape that is congruent with 'unsteady swimming' (Langerhans et al., 2004; Langerhans, 2009). This body shape may aid in predator evasion while Utah chub are still below a gape-size that would allow consumption. However, when comparing the differences in body shape between more carnivorous Utah chub in different predation environments, Utah chub in predation environments have a deeper body than those in non-predation environments (Fig. 4).

Our results indicate that predation constrains body shape variation in Utah chub and suggests evolutionary antagonism. Whereas Utah chub in non-predation environments are able to diverge into limnetic and benthic forms, Utah chub in predation environments may not exhibit the limnetic form as readily as non-predation environments due to predation pressure. In other fish species (e.g. pumpkinseed sunfish, freshwater stickleback) it has been shown that intermediate phenotypes between limnetic and benthic forms are less fit and selected against (Schluter, 1995; Robinson, Wilson, & Shea, 1996; Robinson & Wilson, 1996). In Utah chub, where divergence into limnetic and benthic forms also occurs, disruptive selection likely selects against intermediate phenotypes as well. However, in predation environments, selection due to predation likely promotes stabilizing selection on an intermediate phenotype. This intermediate phenotype consists of a streamlined body shape, but a greater depth than more carnivorous Utah chub in non-predation environments. Hence, body shape in Utah chub appears

**Table 1.** Summary statistics for multivariate mixed model analysis

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num D.F.</th>
<th>Den D.F.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Index variable</td>
<td>16</td>
<td>846</td>
<td>4.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Predation environment</td>
<td>1</td>
<td>112</td>
<td>5.59</td>
<td>0.0198</td>
</tr>
<tr>
<td>Relative intestine length</td>
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<td>268</td>
<td>15.35</td>
<td>0.0001</td>
</tr>
<tr>
<td>Centroid size</td>
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<td>173</td>
<td>0.37</td>
<td>0.5460</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>936</td>
<td>11.46</td>
<td>0.0007</td>
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<tr>
<td>Relative intestine length × index variable</td>
<td>16</td>
<td>846</td>
<td>8.03</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Predation environment × index variable</td>
<td>16</td>
<td>846</td>
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<td>&lt;0.0001</td>
</tr>
<tr>
<td>Centroid size × index variable</td>
<td>16</td>
<td>846</td>
<td>7.32</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Sex × index variable</td>
<td>16</td>
<td>846</td>
<td>5.91</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Predation environment × relative intestine length × index variable</td>
<td>17</td>
<td>705</td>
<td>3.02</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
to be a phenotypic compromise, where fish that contain aspects of both burst-swimming and larger depth have the greatest fitness. In Utah chub, the conflicting demands of selection from diet and predation result in evolutionary antagonism. Different pressures select for different phenotypes of body shape, which due to functional constraints, cannot be optimized for each selective pressure (Langerhans et al., 2004; Langerhans, 2008, 2010; Ingle et al., 2014; Ingle & Johnson, 2016). The resultant phenotype is therefore a compromise, which likely increases total fitness when compared to the optimal phenotypes of each selective pressure.

The significant interaction between diet and predation seen in Utah chub appears to be caused by two opposing types of selection. Our results indicate the presence of diet specialization in Utah chub, which would be promoted by disruptive selection among individuals segregating into benthic and limnetic morphotypes (Robinson & Wilson, 1994; Robinson et al., 1996; Schluter & Rambaut, 1996). This pressure is working on intrapopulation variation to promote ecological divergence (Robinson & Wilson, 1996). Since predation is likely stabilizing, though, it is able to constrain the total amount of variation due to diet specialization that is typically seen in non-predation environments. Our study indicates that selection due to diet and predation is important in determining body shape in Utah chub. It also suggests that evolutionary antagonism and phenotypic compromise are occurring as a result of competing selective demands. Whether or not the interactive constraint displayed herein is a general trend, or whether evolutionary antagonism rather than synergism is more common, are both unknown. Further studies into the interaction of selective pressures will shed light on these questions and give a better understanding of how natural selection works in the wild.

ACKNOWLEDGEMENTS

Funding was provided by the Department of Biology at Brigham Young University. Utah Division of Wildlife Resources, U. S. Fish and Wildlife Service - Fish Springs Wildlife Refuge, Wyoming Game and Fish Department, Grand Teton National Park and Yellowstone National Park provided permits and logistical support at various stages of the field work. For help with field work and laboratory analysis we thank A. Baker, J. Bianchi, B. Boggess, J. Jackson, J. Johnson, S. Jordan, E. Linder, C. Patillo, K. Polizotto, J. Tolman and others. We thank M. Maxwell for help with the figures and on early drafts of the writing. We also thank two anonymous reviewers for their helpful comments and suggestions on the manuscript. This study was supported by a grant from BYU Department of Zoology to M.C.B., a Sigma Xi grant-in-aid of research and a Clarence C. Cottam Award to J.B.J, and a Brigham Young University Graduate Studies High Impact Doctoral Research Assistantship to T.J.W.

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