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Original Article

Effects of foraging and sexual selection on ecomorphology of a fish with alternative reproductive tactics

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The foraging ecology of fish is often considered to be the primary determinant of body shape due to tight links between morphology, swimming performance, and foraging efficiency. Fish foraging on littoral benthic macroinvertebrates typically have a deeper body shape than those foraging on pelagic zooplankton in the water column. However, morphological traits often have multiple ecological functions, which could result in performance trade-offs between functions. Here, we provide the first examination of body shape and diet in a species with alternative reproductive tactics, in this case, bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819). Bluegill males mature into either "parental" or "cuckolder" reproductive tactics. Parentals build nests and provide sole parental care and defense of the young. Cuckolders instead act as "sneakers" darting into the nests of parental males while mating is occurring and then later in life become "satellites," mimicking female appearance and behavior. Using stable carbon and nitrogen isotopic analysis of diet, we found that parentals and females consumed primarily pelagic zooplankton yet were the deepest in body shape. Sneakers consumed more littoral resources but were the most streamlined. Satellite males also consumed predominately littoral resources but had a deeper body form that was more similar to females than to size-matched juveniles. Our results differ from past studies of foraging ecomorphology and suggest that other selection pressures, such as sexual selection in species with alternative reproductive tactics, may also be an important factor influencing shape.

Key words: **alternative reproductive tactics, foraging, morphology, sexual selection, stable isotopes, sunfish.**

INTRODUCTION

Understanding the diversity of phenotypes and their function has long interested biologists (reviewed by Bolnick et al. 2011). The field of ecomorphology examines the links between morphological characteristics and a variety of ecological factors including foraging, predation, reproduction, and locomotion (Collar and Wainwright 2009; Cochran-Biederman and Winemiller 2010; Griffen and Mosblack 2011). It is arguably the relationship between morphology and foraging that has received the most attention, probably due to the strong selection pressures that are often associated with foraging efficiency. Studies of ecomorphology often examine variation in morphological features in relation to food acquisition tactics and overall resource use both within populations of a species and across multiple species within a taxa. Several taxa, including mammals (Saunders and Bailey 1992), invertebrates (Griffen and Mosblack 2011), reptiles (see Losos 2009), and fish (Robinson et al. 2000; Cochran-Biederman and Winemiller 2010), have shown strong, predictable relationships between specific morphological features and foraging. In some instances, the relationships between foraging and morphology have such consistent patterns that morphology has been accurately used as a predictor of resource use in previously unexamined populations and species (Saunders and Bailey 1992; Jastrebski and Robinson 2004; Griffen and Mosblack 2011).

Studies of foraging ecomorphology in fish have shown that a streamlined body shape (i.e., decreased overall body depth) is generally associated with increased burst swimming speed due to reduced drag moving through water (Ojanguren and Braña 2003).

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By comparison, increased body depth is instead associated with increased maneuverability and is common among fish occupying a structurally complex environment (Svanbäck and Eklöv 2002, 2003). Across species, streamlined fish are typically pelagic zooplanktivore feeders, whereas deep-bodied fish are found in littoral habitats feeding on a variety of benthic macroinvertebrates (Robinson et al. 2000; Collar and Wainwright 2009). Even within species that have specialized into littoral and pelagic foraging tactics (often referred to as "ecomorphs"), similar patterns of body shape variation exist between the tactics (Robinson et al. 2000; Robinson and Parsons 2002; Svanbäck et al. 2008).

Although many studies have focused on linking morphology to diet, a morphological trait may have multiple ecological functions. For example, cichlids use their fins not only for swimming and foraging but also during parental care to fan developing eggs and larvae in nests (Cochran-Biederman and Winemiller 2010), likely resulting in selection pressures related to both functions and influencing the observed fin morphology. If the optimal morphology for a trait varies across different ecological functions, then trade-offs between functions may exist. In mouthbrooding cichlids (*Haplochromis* spp.), for instance, there is variation in head morphology that has been linked to foraging tactic and mouthbrooding function, resulting in a trade-off between biting performance and the volume of the buccal cavity to brood offspring (tkint et al. 2012). In situations when natural selection (e.g., foraging efficiency) and sexual selection (e.g., reproductive success) have divergent selection pressures, successful individuals maximize fitness by balancing the costs and benefits of different morphological forms, resulting in an "optimal" morphology (tkint et al. 2012). Thus, although morphology may often be related to foraging, it is possible that other ecological factors, such as sexual selection, play a role in the evolution of morphology and should be considered when studying the relationship between the features of organisms, their behaviors, and the environment.

In this article, we set out to examine the interplay between different ecological functions and morphology by examining shape and diet variation among alternative morphs in bluegill (*Lepomis macrochirus* Rafinesque, 1819). Bluegill alternative male reproductive tactics are referred to as "parental" and "cuckolder" (Gross and Charnov 1980; Gross 1982). In the well-studied population in Lake Opinicon (Ontario, Canada, 44°34′N, 76°9′W), parental males mature at approximately 7 years of age, at which point they form breeding colonies and provide sole parental care for the offspring (Gross 1982). During the parental care period, the males exhibit a variety of behaviors, including fanning of the eggs and defensive opercular flares, lateral displays, and biting at a variety of brood predators (Gross and MacMillan 1981; Côté and Gross 1993). Cuckolders, by comparison, mature at a younger age and "steal" fertilization opportunities from parentals (Gross 1982). Cuckolders first use a "sneaker" tactic (2–3 years old), which involves darting into nests while the female is releasing her eggs. As cuckolders grow, they switch to a "satellite" tactic (4+ years) and mimic female appearance and behavior (Dominey 1980; Gross 1982). In addition to the variation in behavior among these male tactics, there is documented variation in size and shape (Gross 1982; Colborne et al. 2011). Females follow a single life history, maturing at 4 years of age (Gross 1982).

The divergent reproductive tactics of bluegill provide an exceptional opportunity to examine the relative influence of reproduction versus foraging on shape. If shape is primarily related to foraging, then bluegill with a deeper body shape should feed predominantly on littoral benthic macroinvertebrates (e.g., snails), whereas streamlined fish should consume mostly pelagic zooplankton. We have previously shown that parental males and females have the deepest body shapes (Colborne et al. 2011) and therefore now predict that these morphs will consume mostly littoral resources. Conversely, sneakers are streamlined in shape and should consume pelagic zooplankton if general patterns of foraging ecomorphology hold. In order to directly test this set of predictions, we use stable isotope analysis to assess diet of the bluegill morphs and link variation in diet to the body shapes of each morph.

MATERIALS AND METHODS

Fish collection

We collected a total of 142 bluegill from Lake Opinicon (Ontario, Canada, 44°34′N, 76°19′W). During the period of 8–26 June 2009, we used daily snorkel surveys of the littoral habitat to collect 102 bluegill using dip nets; sampling began on the first day parental males began to form colonies and continued until the first day after spawning had occurred. These fish sampled in 2009 were previously used in an examination of bluegill morphology and swim performance (Colborne et al. 2011). An additional 40 fish (parental males and females only) were collected from multiple locations in Lake Opinicon by angling with a small piece (2–3 cm) of earthworm suspended from the side of our research boat during the period of 24 May–30 June 2010 and were added to the original data set. Classification of fish into juveniles, females, parental males, satellites, or sneakers was initially based on observations of behavior in the field (i.e., immediately prior to collection; 2009 only) and the results of subsequent dissections. Juveniles have a gonadosomatic index (GSI; the ratio of gonad mass to body mass) of less than 1%, sneakers have a total body length of less than 100 mm and GSI of about 4%, and satellites have a total length of 100 mm or greater and a 3% GSI (Gross 1982; Colborne et al. 2011).

Morphological analysis

All collected fish were taken to the Queen's University Biological Station and held in flow-through aquariums with water drawn directly from Lake Opinicon for no longer than 6 h before being euthanized with clove oil. We first assessed morphological variation in body shape among the 5 bluegill groups (n = 25 juveniles, 43 females, 36 parentals, 18 satellites, and 20 sneakers) by taking photographs of the left side of each fish with either a Canon PowerShot A95 (5.0 megapixels) or Olympus Stylus Tough-6000 (10 megapixels) digital camera. Using tpsDig software (Rohlf 2008), we placed 20 homologous landmarks on the image of each fish (see Colborne et al. 2011 for landmark locations). These homologous landmarks were then used to compare body shape, independent of size, across the 5 bluegill groups using partial warp analysis (Zelditch et al. 2004; Colborne et al. 2011).

Stable isotope analysis

Following photographing, we collected tissue samples for stable isotope analysis of diet. A sample of white muscle was removed from the right side of each fish immediately underneath the posterior portion of the dorsal fin. The liver was then removed and both tissue samples were stored at −20 °C. White muscle and liver tissues were selected because they are commonly used in stable isotope studies of fish diet (reviewed in Boecklen et al. 2011) and provide the opportunity to infer diet over different time frames because of tissue-specific differences in metabolic activity; white muscle reflects diet over a period of months, compared with several weeks for liver tissue (Hesslein et al. 1993; Perga and Gerdeaux 2005; Guelinckx et al. 2007).

Reference prey samples of littoral benthic invertebrates and pelagic zooplankton were also collected at regular intervals from multiple sites around Lake Opinicon during both sampling years to provide a resource baseline from which to compare the bluegill tissues. To verify that snails could be used as a general representative of the littoral habitat (Cabana and Rasmussen 1996; Post 2002), we collected the 5 most common littoral prey groups in Lake Opinicon (snails, amphipoda, isopoda, larval ephemeroptera, and larval odonata). The pelagic resource isotopic compositions reflect a pooled sample of shallow zooplankton collected using a 5-m vertical tow. The tow sample contained primarily copepods and cladocerans (e.g., *Daphnia* spp.), which were filtered to remove phytoplankton and algae.

The tissue and prey resource samples were prepared by freeze drying them at −50 °C for 24 h and grinding them into a fine powder using a mortar and pestle. Stable isotope ratios of carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N) were then determined using continuous-flow mass spectrometry (Costech elemental analyzer coupled to a Thermo Finnigan Delta^{plus} XL mass spectrometer) in the Laboratory for Stable Isotope Science (LSIS) at The University of Western Ontario (London, Ontario, Canada). Isotope ratios were expressed as the per mil (‰) difference from the standard reference material:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right)$$

where X is ^{13}C or ^{15}N, R is the ratio of ^{13}C:^{12}C or ^{15}N:^{14}N, and δ is the measure of heavy to light isotope in the sample.

The $\delta^{13}C$ values were calibrated to Vienna Pee Dee Belemnite (VPDB) using a 2-point curve anchored by international standards, either the combinations of NBS-22 (accepted value −30.03‰) and ANU-sucrose (IAEA-CH-6; accepted value −10.45‰) or USGS-40 (accepted value −26.39‰) and USGS-41 (accepted value +37.63‰). An internal keratin standard (accepted value −24.04‰) and USGS-40, USGS-41, and IAEA-CH-6 (when not part of the calibration curve) were used to monitor precision and accuracy. The $\delta^{13}C$ values obtained for standards were keratin, −24.1 ± 0.1‰ (n = 77); USGS-40, −26.4 ± 0.04‰ (n = 21); USGS-41, +37.6 ± 0.2‰ (n = 22); and IAEA-CH-6, −10.4 ± 0.1‰. Additionally, the mean $\delta^{13}C$ sample reproducibility for all tissue and resource samples was ±0.1‰ across 31 replicated samples. The $\delta^{15}N$ values were calibrated to atmospheric nitrogen using a 2-point curve calculated using either USGS-40 (accepted value −4.52‰) and IAEA-N2 (accepted value +20.30‰) or USGS-40 and USGS-41 (accepted value +47.57‰). To monitor the precision and accuracy, internal keratin (accepted value +6.36‰) and either USGS-41 or IAEA-N2 (when not part of the calibration curve) were used. The mean $\delta^{15}N$ values of the standards were keratin, +6.4 ± 0.2‰ (n = 76); USGS-41, +47.2 ± 0.4 (n = 22); and IAEA-N2, +20.5 ± 0.2‰ (n = 12). The $\delta^{15}N$ reproducibility for fish tissues and resource samples combined was ±0.2‰ (n = 31), within the ±0.2‰ range expected for sample reproducibility.

Tissues that are high in lipids (liver) may have lower $\delta^{13}C$ values compared with the isotopic compositions of pure protein samples (Smyntek et al. 2007; Boecklen et al. 2011). To compensate for this lipid effect, we corrected the carbon isotopic composition of each liver tissue sample using the mass balance correction model developed by Fry et al. (2003) and adapted by Smyntek et al. (2007) for freshwater organisms:

$$\delta^{13}C_{ex} = \delta^{13}C_{bulk} + 6.3\left(\frac{C:N_{bulk} - 4.2}{C:N_{bulk}} \right)$$

where $\delta^{13}C_{ex}$ is the predicted $\delta^{13}C$ value of the tissue sample without lipids, $\delta^{13}C_{bulk}$ is the measured $\delta^{13}C$ value of each individual, 6.3 represents the mean ‰ discrimination factor between lipids and protein, $C:N_{bulk}$ is the observed atomic ratio of C:N of each sample, and 4.2 represents the mean C:N ratio of lipid extracted tissues across a variety of taxa (Smyntek et al. 2007). We did not mathematically correct the stable isotope composition of white muscle tissue because the lipid levels in white muscle are sufficiently low (C:N ratio < 4) that correction is considered not to be required (Pörtner 2002; Boecklen et al. 2011).

Statistical analysis

Partial warp scores for each bluegill were used in a discriminant function analysis (DFA) to compare shape variation among the morphs (juveniles, females, parentals, sneakers, and satellites). When significant differences among morphs were identified by the DFA, an analysis of variance (Anova) with Tukey's post hoc comparisons was used for each significant DFA axis to identify which morphs differed. In addition, patterns of body shape variation were visualized using thin-plate splines generated by tpsRegr software (Rohlf 2009).

Stable isotope analysis of diet was completed by first comparing the prey resources to assess the suitability of $\delta^{13}C$ and $\delta^{15}N$ at differentiating between resources in the littoral and pelagic habitats. The isotopic compositions of 5 common littoral macroinvertebrate resource groups were compared using a 1-factor Anova. We then compared the 2 sampling years for temporal variation using the 2 most abundant prey types (littoral snails and pelagic zooplankton) using 2-tailed t-tests. Following this, the differences in stable isotope compositions of prey resources were compared between habitats using a 2-tailed t-test. Due to the large degree of overlap in $\delta^{15}N$ values between the littoral and pelagic resource groups (see Results), we did not consider $\delta^{15}N$ further in our interpretation of the results for the bluegill tissues.

The differences in $\delta^{13}C$ values among bluegill morphs were then examined using a 1-factor Anova with Tukey's post hoc comparisons, when appropriate, for each tissue type (white muscle and liver) separately. Additionally, estimates of the % littoral contribution to the diet of each fish were made using a two-end-member-mixing model based on Post (2002):

$$\%\,\text{Littoral} = \frac{\delta^{13}C_{consumer} - \delta^{13}C_{base\,2}}{\delta^{13}C_{base\,1} - \delta^{13}C_{base\,2}} \times 100$$

where $\delta^{13}C_{consumer}$ is the observed $\delta^{13}C$ value for each fish, $\delta^{13}C_{base\,1}$ represents the mean $\delta^{13}C$ value of littoral snails, and $\delta^{13}C_{base\,2}$ is the mean $\delta^{13}C$ value of pelagic zooplankton.

To examine the possible relationship between diet (i.e., stable isotopic composition) and morphology across the morphs (i.e., DFA axes), we used separate linear regressions analyses for white muscle and liver tissues (dependent factor: $\delta^{13}C$ value; independent factor: DFA axis score or body length). Only the first 2 DFA axes, which together represented 84% of the total variation in morphology (see below), were considered in these analyses. Analysis of covariance (ANCOVA) was used to examine the relationship between body length (a surrogate of bluegill age; Neff et al. 2004) and body shape using bluegill morphs that overlapped in body length (dependent

factor: DFA 1 or DFA 2; fixed factor: morph; covariate: body length).

To simultaneously compare the relationship among $\delta^{13}C$ values (diet) and 3 possible explanatory variables (body length, DFA 1, and DFA 2), we applied an all-possible-subset regression procedure and the best model was selected on the basis of the Akaike information criteria score recommended for small sample sizes (AIC_c; Burnham and Anderson 1998). The model with the lowest score was considered to have the best fit unless the score was within 2 units of a simpler model (i.e., one with fewer explanatory variables), in which case the model with the fewest explanatory variables was considered the best fit (see Burnham and Anderson 1998; Berner et al. 2011).

All analyses were completed using JMP v. 10.0 (SAS Institute Inc., Cary, NC), at α level = 0.05. All means are reported as ±1 SE, except for stable isotope compositions, which are reported as means ± 1 SD.

RESULTS

Bluegill morphological variation

DFA revealed significant differences in body shape among the 5 morphs (MANOVA, Wilks' $\lambda = 0.008$, $P < 0.001$; Figure 1), with 64% and 20% of the total variation being explained by the first 2 axes. The bluegill morphs were all significantly different in shape based on DFA 1 (Anova, $F_{4,137} = 273.4$, $P < 0.001$; Tukey's, all $P \leq 0.01$), except between females and satellite males, which were marginally nonsignificant (Tukey's, $P = 0.06$). Thin-plate spline visualizations of DFA 1 showed that parental males had the deepest body shape, followed by females, satellites, and juveniles, with sneakers being the most streamlined in shape (Figure 1). The morphs also varied significantly on DFA 2 (Anova, $F_{4,138} = 87.7$, $P < 0.001$), with the thin-plate splines showing that shape variation on this axis was localized to head and caudal peduncle areas (Figure 1). Based on thin-plate splines of the DFA 2 scores, females had more streamlined heads and thicker caudal peduncles than all other morphs (Tukey's: $P < 0.05$; Table 2).

Diet variation among bluegill morphs

Among the 5 primary littoral macroinvertebrate prey groups (amphipoda, larval odonata, larval ephemeroptera, isopoda, and gastropoda), there were similar $\delta^{13}C$ values (Anova, $F_{4,32} = 2.04$, $P = 0.11$). There was significant variation in $\delta^{15}N$ values among the common littoral prey groups (Anova, $F_{4,32} = 7.07$, $P < 0.001$); however, post hoc comparisons indicated that snails did not differ significantly from any of the other prey groups (Tukey's, all $P \geq 0.10$), except odonata ($P = 0.04$). Therefore, our gastropod (snail) samples were representative of the littoral prey isotope values for both $\delta^{13}C$ and $\delta^{15}N$ (see Supplementary material). Across the 2 sampling years, there was no significant variation in $\delta^{13}C$ values for either littoral (*t*-test, $t_{16} = 0.52$, $P = 0.61$) or pelagic (*t*-test, $t_8 = -0.79$, $P = 0.45$) prey groups, indicating that $\delta^{13}C$ prey values were temporally consistent in our data set. In contrast, the $\delta^{15}N$ prey values differed between years for both littoral ($t_{16} = -3.19$, $P = 0.006$) and pelagic

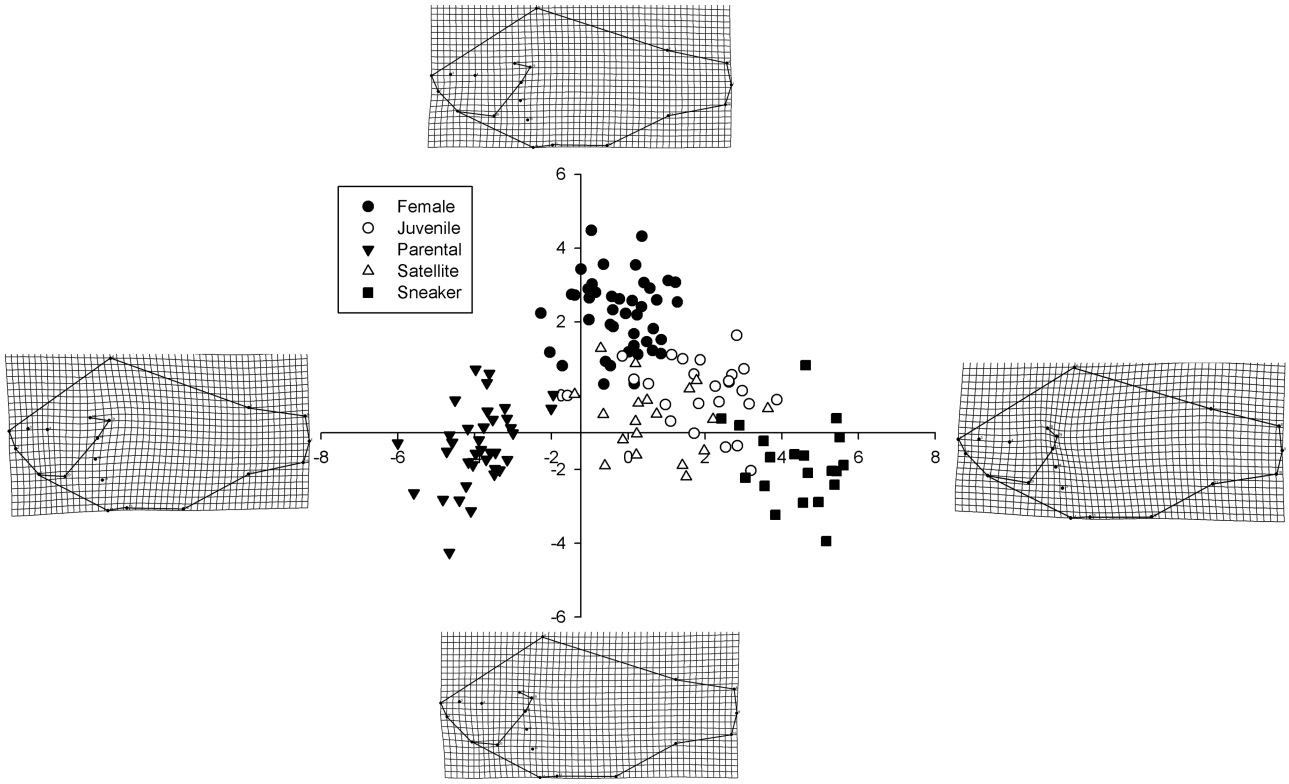

Figure 1
DFA of body shape among 5 morphs of bluegill (*Lepomis macrochirus*): juveniles, sneakers, satellites, females, and parental males. The first 2 discriminant function axes (DFA 1 and DFA 2) are depicted on the *x* and *y* axes, respectively. Thin-plate splines on each axis display the overall body shape associated with the extreme values for DFA 1 and DFA 2.

(t_8 = 6.84, P < 0.001) prey groups, indicating that $\delta^{15}N$ values of prey resources varied between sampling years. Sampling years were subsequently pooled for further analysis of $\delta^{13}C$, but not $\delta^{15}N$. Across the habitat types, the mean $\delta^{13}C$ value of littoral prey resources (represented by snails: −22.3 ± 1.9‰, n = 18) was significantly higher compared with the value of pelagic zooplankton prey (−29.2 ± 1.3‰, n = 10; t-test, t_{26} = −10.3, P < 0.001), indicating that $\delta^{13}C$ values could be used to compare littoral and pelagic resource use by bluegill. In contrast, the $\delta^{15}N$ values of littoral prey resources were higher than pelagic prey in 2009 (t_9 = −3.67, P = 0.005), but lower than pelagic prey in 2010 (t_{15} = 6.35, P < 0.001). Thus, we excluded $\delta^{15}N$ from further interpretation, focusing instead on the $\delta^{13}C$ values.

The 5 bluegill morphs showed significant differences in $\delta^{13}C$ values among morphs in both white muscle (Anova, $F_{4,133}$ = 23.0, P < 0.001) and liver tissues (Anova, $F_{4,136}$ = 18.2, P < 0.001; Figure 2). For both tissue types, parental males and females were similar in $\delta^{13}C$ (Tukey's, all $P \geq 0.08$) but had significantly lower $\delta^{13}C$ values compared with the other 3 morphs (Tukey's, all $P \leq 0.004$; Table 1). The $\delta^{13}C$ values of sneakers, satellites, and juveniles were not significantly different from each other (Tukey's, all $P \geq 0.52$). Overall, parental males and females had mean diets composed of greater than 80% pelagic resources, whereas juveniles, sneakers, and satellites had mean diets composed of 40–60% littoral resources (Table 1). See Supplementary material for a summary of the stable isotope compositions for each individual.

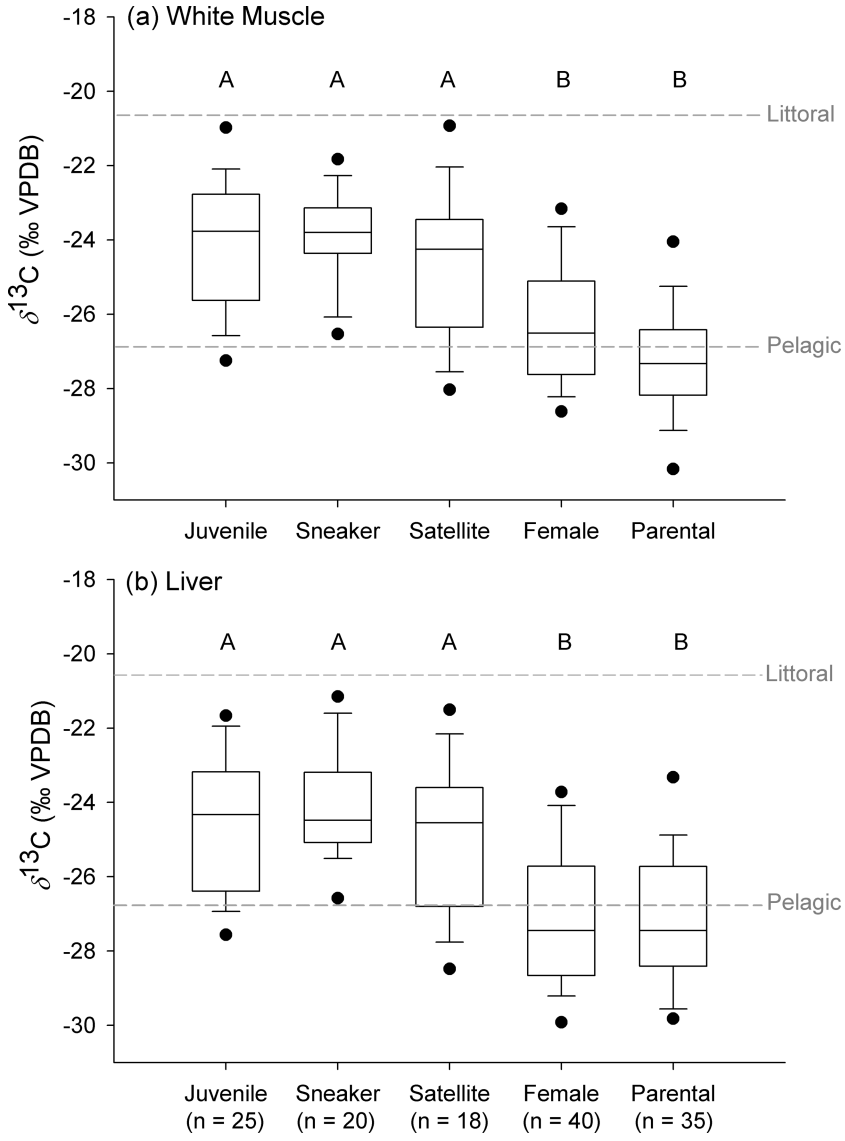

Figure 2
Boxplots of $\delta^{13}C$ values (per mil deviation of measured ^{13}C:^{12}C relative to VPDB) among 5 morphs of bluegill (*Lepomis macrochirus*): juveniles, sneakers, satellites, females, and parental males. The stable carbon isotope compositions of (a) white muscle and (b) liver tissues are presented separately. Boxes represent the interquartile range (inner 50% of observations) separated by the median, whiskers represent the 90th and 10th percentiles, and the dots are the compositions falling outside the whisker range. Capital letters above the boxplots denote homogeneous subsets as identified by Anova and Tukey's post hoc comparisons of morphs (α = 0.05).

Table 1

Summary of the mean (±SE) values of size, shape, and diet measurements for 5 morphs of bluegill (*Lepomis macrochirus*)

Reproductive morph	*n*	Body length (mm)	DFA 1 score	DFA 2 score	White muscle $\delta^{13}C$	Liver $\delta^{13}C$	White muscle (% littoral)	Liver (% littoral)
Juvenile	25	117.4 ± 3.7^{A}	1.91 ± 0.19^{A}	0.08 ± 0.20^{A}	-24.2 ± 0.3^{A}	-24.6 ± 0.4^{A}	55	49
Sneaker	20	83.3 ± 4.2^{B}	4.43 ± 0.22^{B}	-1.83 ± 0.22^{B}	-23.8 ± 0.4^{A}	-24.2 ± 0.4^{A}	61	55
Satellite	18	123.0 ± 4.4^{A}	0.51 ± 0.23^{C}	-0.63 ± 0.24^{AC}	-24.6 ± 0.4^{A}	-25.1 ± 0.4^{A}	48	41
Female	40	164.4 ± 3.0^{C}	-0.22 ± 0.15^{C}	2.21 ± 0.15^{D}	-26.3 ± 0.3^{B}	-27.2 ± 0.3^{B}	18	13
Parental	35	186.2 ± 3.1^{D}	-3.87 ± 0.16^{D}	-1.34 ± 0.17^{BC}	-27.3 ± 0.3^{B}	-27.2 ± 0.3^{B}	12	14

Capital letters beside error terms denote homogeneous subsets as identified by Anova and Tukey's post hoc comparison of morphs for each variable ($\alpha = 0.05$).

Morphology and body length

The morphs differed in body length (Anova, $F_{4,134} = 129.2$, $P < 0.001$), with all morphs differing except satellite males and juveniles (Tukey's, $P = 0.87$). Examining these latter 2 morphs, there was a significant relationship between DFA 1 values and body length (ANCOVA, $F_{1,39} = -6.58$, $P < 0.001$; Figure 3). However, over the size range of these 2 groups, the DFA 1 scores were consistently higher for juveniles compared with satellite males (ANCOVA, $F_{1,39} = 5.14$, $P < 0.001$). There was no interaction between morph and body length in this analysis (ANCOVA, $F_{1,39} = 0.01$, $P = 0.99$). Similarly, for a given body length, juvenile DFA 2 scores were greater than satellites (ANCOVA, $F_{1,39} = 3.73$, $P < 0.001$), but there was no relationship between DFA 2 scores and body length (ANCOVA, $F_{1,39} = 1.53$, $P = 0.13$) and no interaction between morph and length (ANCOVA, $F_{1,39} = -0.58$, $P = 0.57$).

Bluegill morphology and stable isotopes

Across all morphs, linear regression indicated that there was a positive relationship between DFA 1 scores and $\delta^{13}C$ values in both white muscle ($F_{1,136} = 80.68$, $R^2 = 0.37$, $P < 0.001$) and liver ($F_{1,139} = 48.44$, $R^2 = 0.26$, $P < 0.001$; Figure 4) tissues, with higher $\delta^{13}C$ values (littoral diet) being associated with higher DFA 1 scores (i.e., streamlined body shape). In contrast, DFA 2 scores were not related to $\delta^{13}C$ values in white muscle (linear regression, $F_{1,136} = 2.66$, $R^2 = 0.02$, $P = 0.11$) but were related to liver $\delta^{13}C$ (linear regression, $F_{1,139} = 8.01$, $R^2 = 0.05$, $P = 0.005$). Body length was negatively related to $\delta^{13}C$ values of white muscle (linear regression, $F_{1,133} = 95.85$, $R^2 = 0.42$, $P < 0.001$) and liver (linear regression, $F_{1,136} = 77.54$, $R^2 = 0.36$, $P = 0.005$), with increased body length being associated with lower $\delta^{13}C$ values (pelagic diet).

Model selection based on AIC_c scores indicated that, for white muscle, the model predicting $\delta^{13}C$ values with the lowest AIC_c scores contained body length alone (Table 2). In comparison, the model for liver $\delta^{13}C$ values with the lowest AIC_c score included both body length and DFA 2; however, using the parsimony criterion, the best model included only body length for the liver $\delta^{13}C$ values.

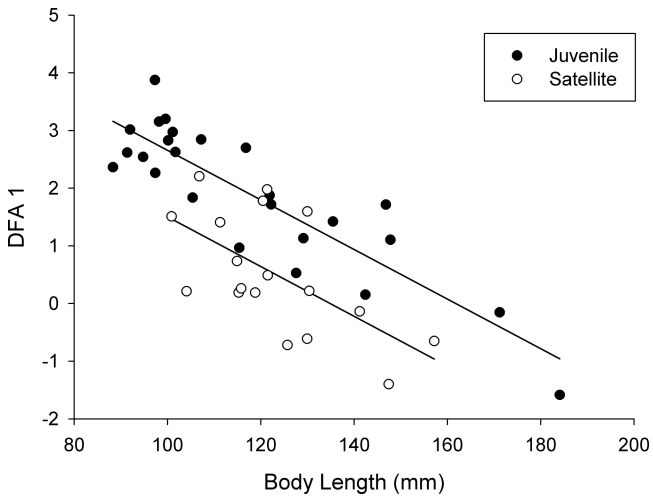

Figure 3

Relationship between morphology (DFA 1) and body length (mm) of juvenile and satellite male bluegill (*Lepomis macrochirus*). The DFA 1 scores were generated using a DFA of partial warp scores generated for each individual. The lines are based on regressions, but statistical analyses used ANCOVA (see text for details).

DISCUSSION

Diets varied among the bluegill groups: juveniles, sneakers, and satellites consumed primarily littoral resources (benthic macroinvertebrates), whereas females and parentals consumed mostly pelagic resources (zooplankton). This pattern was stable over a period of weeks to months because the stable isotopic compositions were similar in the liver and white muscle tissues (Pinnegar and Polunin 1999; Dalerum and Angerbjörn 2005; Phillips 2012). Based on the general relationships between morphology and diet observed among a wide range of fish species (Robinson et al. 2000; Svanbäck et al. 2008; tkint et al. 2012), we expected a littoral diet to be associated with a deeper body shape. However, we found that bluegill parental males and females had the deepest body shapes but had diets of primarily pelagic zooplankton. Conversely, the sneakers were the most streamlined of the morphs but had some of the highest $\delta^{13}C$ values (i.e., most littoral diet). Furthermore, the models comparing the relationship between diet ($\delta^{13}C$ values) to length and shape (DFA 1 and DFA 2) did not identify the main axis of shape variation (DFA 1) as a significant predictor of diet. Based on these results, it appears that foraging ecomorphology alone does not explain shape and resource use among bluegill morphs, at least in our study population of bluegill.

Many studies of fish ecomorphology have focused on individuals that have passed through the period of size-dependent predation (i.e., after the juvenile stage of life). Predation may influence both habitat and resource use by restricting smaller fish to the littoral habitat until they reach a body size that exceeds the gape of most predators (Chipps et al. 2004; Zandonà et al. 2011). Indeed,

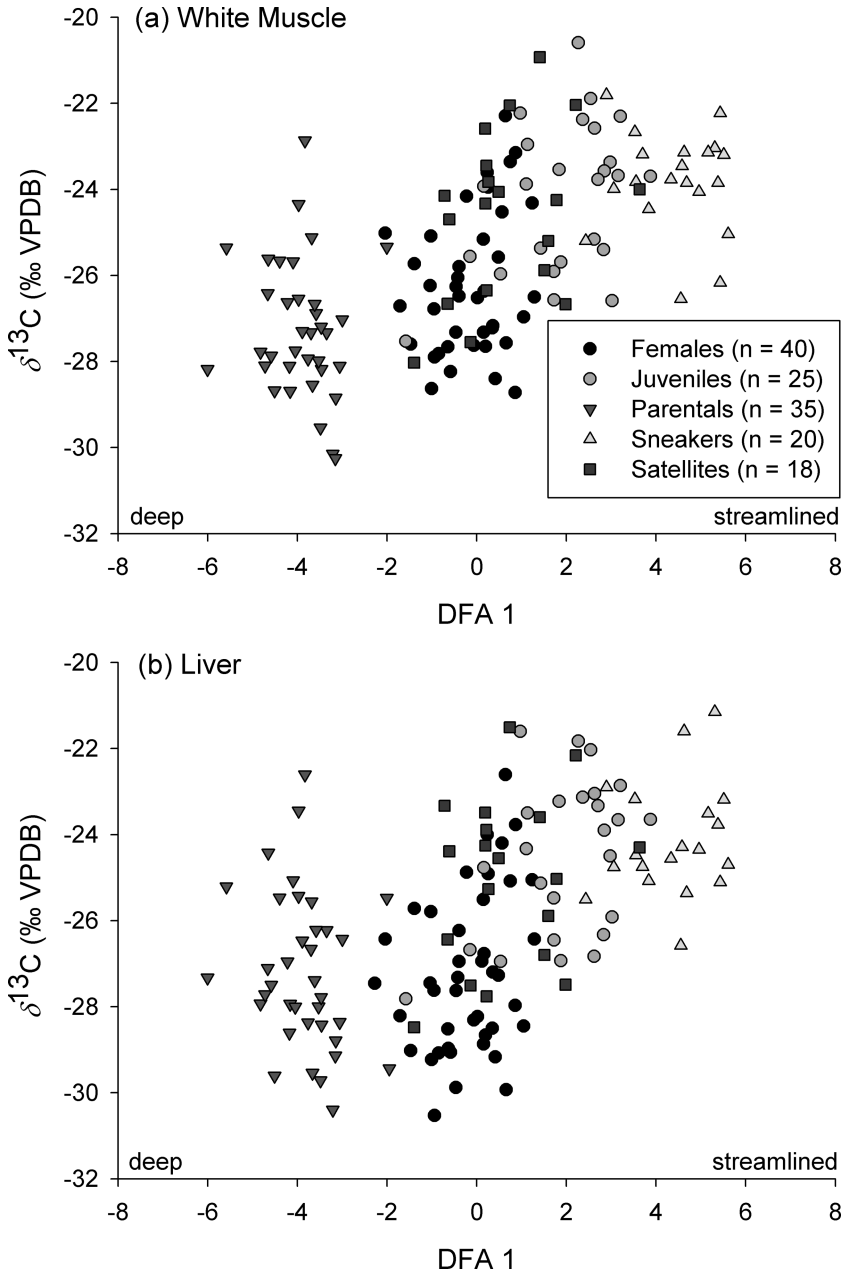

Figure 4
Relationship between $\delta^{13}C$ values (per mil ratio of sample ^{13}C:^{12}C compared with VPDB) and morphology (DFA 1) of (a) white muscle or (b) liver tissues of 5 morphs of bluegill (*Lepomis macrochirus*): juveniles, sneaker males, satellite males, females, and parental males. DFA 1 scores were generated using DFA of partial warp scores generated for each individual (see text for description).

in some species, distinct foraging ecomorphs develop only after the period of intense size-dependent predation has passed. For example, arctic charr (*Salvelinus alpinus*) in Lake Thingvallavatn, Iceland, have 4 distinct ecomorphs that diverge in resource use starting at 70 mm body length, which is well above the 35 mm body length threshold for their most common predator (Malmquist et al. 1992). The extent to which predation delays the divergence into ecomorphs, however, is not yet well understood, and it is likely that other ecological factors, including early juvenile swim performance and foraging efficiency, are also important factors influencing morphology (Fischer-Rousseau et al. 2010). Nevertheless, previous studies of bluegill have found a predation threshold such that fish less than 100 mm in length are restricted to the littoral habitat (Mittelbach 1981). Unlike other studies of ecomorphology, the length variation among bluegill morphs includes fish that are well within the size-dependent predation risk threshold. For example, sneaker males in our sample had a mean body length of 83 mm. Sneakers also had a diet of approximately 60% littoral resources despite having a streamlined body shape. The resource use of sneakers is thus consistent with size-dependent predation driving habitat use.

Although body length may be an important predictor of diet for sneakers, it does not account for all of the variation that we observed among morphs. For example, satellite males and juveniles were similar in body length and showed increases in body

Table 2

Stepwise regression and AIC model selection for predictors of diet measured by $\delta^{13}C$ values among 5 morphs of bluegill (*Lepomis macrochirus*)

	Model variables	AIC_c	R^2
$\delta^{13}C$ white muscle	**BL**	**514.20**	**0.42**
	BL + DFA 1	514.66	0.43
	BL + DFA 2	516.54	0.42
$\delta^{13}C$ liver	BL + DFA 2	551.79	0.37
	BL	**552.18**	**0.36**
	BL + DFA 1 + DFA 2	553.71	0.38

Predictors of $\delta^{13}C$ values in either white muscle or liver comprised body length (BL) and 2 measures of shape from a discriminant function analysis (DFA 1 and DFA 2). All possible model combinations were considered; only the 3 models with the greatest explanatory power based on AIC_c scores for each tissue type are presented with their respective R^2 values. The best model based on AIC_c and parsimony criteria are shown in bold (see text for details of selection criteria).

depth with length, yet juveniles were consistently more streamlined than satellites. This difference in body shape indicates that, although allometric growth may increase body depth as overall size increases, it is not the only factor and at least some shape variation may instead be related to sexual selection. Satellite males gain access to mating opportunities by mimicking female appearance (Dominey 1980), and even though satellite males were on average smaller in length than the females in our sample, they were of a similar body shape. Thus, the shape variation between satellite males and juveniles may be the result of selection on satellite males to mimic the body shape of females (Dominey 1980). Additionally, for sneaker males, burst swimming speed is critical to gain proximity to females during spawning and avoid detection by guarding parental males (Stoltz and Neff 2006). Of all the bluegill morphs, sneakers have the fastest burst swim speed, when adjusted for size, which is likely mediated by their streamlined body shape (Colborne et al. 2011). Parental males had the deepest body form, a shape that increases maneuverability (Webb 1984; Collar and Wainwright 2009), which may increase their ability to thwart sneaker spawning attempts or brood predators during parental care (Gross and MacMillan 1981; Gross 1982). The possibility that sexual selection plays an important role in body shape variation among morphs in bluegill deserves further investigation.

Our data also suggest trade-offs exist between reproduction and foraging on female shape. We found that, even though females foraged primarily on pelagic zooplankton, their body shape was deeper than juveniles and sneakers, and consequently, females are probably less efficient at capturing plankton (Robinson et al. 2000). Females were larger than juveniles and sneakers in our sample, so the increased depth could be partly a result of allometric growth. However, the females had more streamlined head regions than any other group we examined, suggesting that the body depth is not solely from allometry. Similar results have been found in perch (*Perca fluviatilius*; Svanbäck and Eklöv 2002). The increased overall body depth in females may instead be the result of selection on fecundity. Fish show nonlinear increases between body size and the volume of eggs that can be carried (Bernardo 1996); therefore, increasing body depth can significantly increase fecundity. Indeed, bluegill females in Lake Opinicon produce an average of about 6000 eggs each breeding season (Gross and Charnov 1980) and larger body size is directly related to the number of eggs females produce (Gross 1980). Selection for increased fecundity in bluegill might therefore lead to a slightly less optimal overall body shape when it comes to foraging.

In conclusion, the field of ecomorphology provides a solid foundation linking morphology and foraging ecology. Although we found morphological and resource use variation among the bluegill morphs, our results were inconsistent with previous studies of shape and foraging ecology alone. We instead argue that foraging ecomorphology interacts with other ecological selection pressures, including size-dependent predation and sexual selection. We suggest that in order to understand the relationships between morphology, function, and adaptation, it is essential to consider the interplay between natural and sexual selection.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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Supplementary Material

Summary of common invertebrate prey resource stable isotope values for both the littoral and pelagic habitats in Lake Opinicon, Ontario.

Invertebrate Group	N	Collection Habitat	$\delta^{13}C$	$\delta^{15}N$
Amphipoda	8	Littoral	–21.5 ± 1.9	+3.6 ± 0.7
Ephemeroptera	3	Littoral	–23.5 ± 1.4	+5.7 ± 1.8
Isopoda	5	Littoral	–22.8 ± 3.1	+3.7 ± 0.3
Odonata	3	Littoral	–24.3 ± 1.7	+5.8 ± 0.4
Gastropoda (snails)	18	Littoral	–22.3 ± 1.9	+4.4 ± 0.8
Zooplankton (cladocera and copepoda)	10	Pelagic	–29.2 ± 1.3	+4.9 ± 1.3

Summary of the mass, length, DFA scores, and stable isotope compositions for each bluegill (*Lepomis macrochirus*).

							White Muscle		Liver	
Fish Number	**Morph**	**Collection Year**	**Body Length (mm)**	**Mass (g)**	**DFA 1**	**DFA 2**	**δ^{13}C**	**δ^{15}N**	**δ^{13}C**	**δ^{15}N**
1	Female	2009	192.2	113.5	0.16	0.32	–26.4	+8.9	–26.8	+7.6
2	Female	2009	186.9	145.0	-0.43	2.69	–26.1	+9.9	–27.3	+7.8
3	Female	2009	183.6	117.2	0.34	2.41	–27.2	+10.2	–28.5	+8.5
4	Female	2009	152.5	70.6	0.66	1.81	–27.6	+8.4	–29.9	+6.8
5	Female	2009	195.9	168.8	-2.28	2.24	--	--	–27.5	+7.3
6	Female	2009	151.7	61.3	0.02	1.19	–26.5	+8.8	–28.2	+7.5
7	Female	2009	128.9	41.5	1.04	3.12	–27.0	+7.9	–28.5	+6.2
8	Female	2009	135.6	49.6	0.23	2.19	–23.6	+8.8	–24.0	+7.5
9	Female	2009	177.0	105.4	0.15	1.68	–25.2	+9.7	–25.5	+8.6
10	Female	2009	153.7	63.3	0.48	1.46	–25.6	+8.7	–27.3	+7.0
11	Female	2009	149.0	63.6	0.75	2.59	–23.4	+9.0	–25.1	+7.4
12	Female	2009	133.2	44.0	0.86	1.51	–23.2	+7.4	–23.8	+5.4
13	Female	2009	141.7	48.2	0.86	1.14	–28.7	+7.0	–28.0	+5.4
14	Female	2009	151.7	66.4	1.24	3.07	–24.3	+9.1	–25.1	+7.0
15	Female	2009	148.4	62.4	0.64	1.22	–22.3	+8.2	–22.6	+6.0
16	Female	2009	152.6	82.5	0.56	2.91	–24.5	+9.4	–24.2	+7.1
17	Female	2009	117.8	28.6	1.28	2.53	–26.5	+9.3	–26.4	+7.4
18	Female	2009	168.2	104.5	-0.23	2.62	–24.2	+9.5	–24.9	+8.2
19	Female	2009	142.4	80.8	-0.46	0.81	–26.3	+9.1	–27.6	+7.3
20	Female	2009	155.1	110.4	0.15	1.35	–27.3	+9.3	–28.9	+7.7
21	Female	2010	185.0	90.5	0.11	2.57	--	--	–26.9	+7.7
22	Female	2010	178.0	77.9	-0.64	0.31	--	--	–29.0	+7.7
23	Female	2010	165.0	80.4	-0.40	2.33	–26.5	+9.1	–26.2	+7.3

24	Female	2010	170.0	107.6	-0.96	4.47	–26.8	+10.0	–27.6	+8.2
25	Female	2010	166.0	90.5	-0.85	2.80	–27.8	+10.2	–29.1	+8.9
26	Female	2010	153.0	73.2	0.41	3.06	–28.4	+9.9	–29.2	+8.4
27	Female	2010	184.0	82.2	0.25	1.12	–24.0	+8.7	–24.9	+9.2
28	Female	2010	176.0	83.0	-1.02	2.06	–25.1	+8.7	–25.8	+7.2
29	Female	2010	175.0	64.5	-0.40	1.87	–25.8	+10.3	–27.0	+8.4
30	Female	2010	156.0	103.2	-1.39	2.72	–25.7	+10.0	–25.7	+8.5
31	Female	2010	184.0	93.3	-0.47	1.93	–27.3	+9.2	–29.9	+6.8
32	Female	2010	165.0	89.0	-0.64	3.56	–27.7	+9.8	–28.5	+7.9
33	Female	2010	190.0	67.6	0.36	4.32	–27.2	+9.5	–27.2	+7.1
34	Female	2010	150.0	106.7	-2.04	1.17	–25.0	+9.8	–26.4	+7.9
35	Female	2010	165.0	83.2	-1.04	2.90	–26.2	+8.9	–27.5	+7.9
36	Female	2010	175.0	114.7	-0.07	2.23	–27.6	+10.4	–28.3	+8.7
37	Female	2010	187.0	61.1	0.20	3.54	–27.7	+10.0	–28.7	+8.3
38	Female	2010	185.0	77.8	-0.94	3.02	–27.9	+9.7	–30.5	+6.9
39	Female	2010	158.0	93.8	-1.01	2.65	–28.6	+9.5	–29.2	+7.9
40	Female	2010	191.0	118.6	-1.71	0.80	–26.7	+9.6	–28.2	+7.8
41	Female	2010	--	118.0	-1.48	2.74	–27.6	+9.6	–29.0	+7.8
42	Female	2010	--	69.3	-0.59	0.93	–28.2	+9.7	–29.1	+8.0
43	Female	2010	--	139.9	-1.23	3.43	–28.1	+9.8	–23.7	+8.0
44	Juvenile	2009	101.1	19.5	2.97	0.13	–23.4	+9.4	–24.5	+8.0
45	Juvenile	2009	98.2	15.5	3.15	-0.22	–23.7	+9.7	–23.7	+8.3
46	Juvenile	2009	101.7	16.4	2.63	0.36	–22.6	+9.2	–23.1	+8.1
47	Juvenile	2009	99.6	15.2	3.20	-2.03	–22.3	+9.8	–22.9	+7.8
48	Juvenile	2009	88.3	11.5	2.36	-0.17	–22.4	+9.2	–23.1	+7.1
49	Juvenile	2009	105.4	22.7	1.84	-0.22	–23.5	+9.1	–23.2	+7.8
50	Juvenile	2009	107.2	19.8	2.84	-1.36	–23.6	+8.9	–23.9	+7.9
51	Juvenile	2009	115.4	22.6	0.97	-0.24	–22.2	+9.1	–21.6	+7.6
52	Juvenile	2009	97.4	15.9	2.26	0.26	–20.6	+9.0	–21.8	+7.5

53	Juvenile	2009	94.8	13.9	2.54	-1.40	–21.9	+8.2	–22.0	+7.9
54	Juvenile	2009	97.3	14.2	3.88	-0.11	–23.7	+8.4	–23.7	+7.7
55	Juvenile	2009	116.8	27.4	2.70	0.56	–23.8	+8.7	–23.3	+7.6
56	Juvenile	2009	147.8	69.2	1.11	-0.70	–23.9	+8.8	–24.3	+7.7
57	Juvenile	2009	171.2	92.0	-0.15	1.07	–25.6	+9.0	–26.7	+8.0
58	Juvenile	2009	146.8	52.9	1.72	0.58	–25.9	+9.2	–25.5	+7.7
59	Juvenile	2009	127.6	39.3	0.53	0.32	–26.0	+8.9	–27.0	+8.1
60	Juvenile	2009	121.9	39.0	1.88	0.97	–25.7	+9.9	–26.9	+8.4
61	Juvenile	2009	100.2	17.3	2.83	1.64	–25.4	+9.9	–26.3	+8.3
62	Juvenile	2009	91.4	14.3	2.62	0.40	–25.2	+9.8	–26.8	+8.4
63	Juvenile	2009	129.2	41.9	1.13	1.11	–23.0	+9.4	–23.5	+7.0
64	Juvenile	2009	92.0	14.7	3.02	0.72	–26.6	+9.7	–25.9	+8.0
65	Juvenile	2009	122.2	33.7	1.72	-1.03	–26.6	+9.9	–26.5	+9.3
66	Juvenile	2009	135.5	39.6	1.42	1.00	–25.4	+8.5	–25.1	+6.8
67	Juvenile	2009	142.4	56.6	0.15	0.44	–23.9	+8.8	–24.8	+7.9
68	Juvenile	2009	184.1	124.2	-1.58	0.01	–27.5	+9.1	–27.8	+8.7
69	Parental	2009	206.3	203.3	-3.46	-1.54	–28.2	+10.6	–28.4	+9.7
70	Parental	2009	180.7	135.4	-3.97	0.71	–24.4	--	–23.5	+9.3
71	Parental	2009	194.4	144.0	-4.40	-2.84	–25.7	+9.7	–25.5	+9.9
72	Parental	2009	191.0	129.5	-5.58	-2.64	–25.4	+10.4	–25.2	+9.9
73	Parental	2009	191.5	117.6	-4.10	-3.13	–25.7	+9.1	–25.1	+9.1
74	Parental	2009	180.9	111.6	-3.15	-1.74	–28.9	+8.0	–28.8	+7.5
75	Parental	2009	195.0	132.5	-3.97	-1.57	–26.6	+9.8	–25.4	+9.7
76	Parental	2009	209.4	153.9	-3.00	-1.02	–27.0	+9.2	–26.4	+9.4
77	Parental	2009	200.8	143.9	-3.83	-1.46	–22.9	+10.3	–22.6	+10.1
78	Parental	2009	198.3	152.2	-4.22	-2.45	–26.6	+10.0	–27.0	+10.4
79	Parental	2009	201.5	169.4	-3.35	-2.02	–27.3	+9.6	–26.2	+10.3
80	Parental	2009	198.5	148.0	-4.65	-1.07	–25.6	+9.9	–24.4	+9.4
81	Parental	2009	220.2	154.4	-3.53	-0.65	–28.0	+10.1	–28.0	+9.7

82	Parental	2009	184.6	134.5	-3.70	-1.73	–27.3	+8.5	–26.7	+7.8
83	Parental	2009	202.7	151.9	-3.06	-0.87	–28.1	+10.0	–28.4	+9.8
84	Parental	2009	201.3	143.2	-4.83	-2.82	–27.8	+9.9	–27.9	+9.8
85	Parental	2009	198.0	132.9	-3.47	-1.98	–27.2	+9.9	–27.8	+9.7
86	Parental	2009	194.8	128.2	-4.66	-4.26	–26.4	+10.7	–27.1	+10.7
87	Parental	2009	184.6	124.4	-3.21	-0.33	–30.2	+8.9	–30.4	+8.5
88	Parental	2010	175.0	91.6	-3.15	-0.62	–30.3	+8.5	–29.1	+7.6
89	Parental	2010	187.0	94.4	-3.68	0.34	–25.1	+9.3	–25.6	+8.7
90	Parental	2010	184.0	150.6	-4.51	-0.13	–28.7	+10.3	–29.6	+9.6
91	Parental	2010	190.0	113.5	-1.95	0.02	--	--	–29.4	+8.9
92	Parental	2010	203.0	119.3	-4.17	-1.80	–28.7	+9.3	–27.9	+9.0
93	Parental	2010	197.0	144.4	-3.67	-0.43	–28.6	+8.7	–29.5	+7.7
94	Parental	2010	158.0	128.7	-4.72	-1.51	–28.1	+9.5	–27.7	+9.3
95	Parental	2010	160.0	150.8	-4.18	-0.90	–28.1	+10.4	–28.6	+10.0
96	Parental	2010	180.0	131.9	-3.58	-1.54	–26.9	+9.7	–26.2	+9.5
97	Parental	2010	144.0	111.5	-2.01	-0.35	–25.3	+7.9	–25.5	+7.1
98	Parental	2010	155.0	137.9	-3.89	-1.20	–27.3	+10.0	–26.5	+9.6
99	Parental	2010	156.0	138.9	-4.59	-1.27	–27.9	+8.4	–27.5	+8.0
100	Parental	2010	171.0	156.3	-3.49	-2.13	–29.5	+9.3	–29.7	+9.0
101	Parental	2010	184.0	140.1	-3.77	-0.86	–27.9	+10.3	–28.4	+10.0
102	Parental	2010	185.0	138.5	-3.62	0.60	–26.7	+9.8	–27.4	+8.7
103	Parental	2010	178.0	165.1	-4.05	-1.88	–27.8	+9.4	–28.0	+10.1
104	Parental	2010	165.0	126.2	-6.00	-1.29	–28.2	+9.0	–27.3	+9.1
105	Satellite	2009	115.3	31.8	0.19	-0.70	–24.3	+8.1	–24.3	+6.9
106	Satellite	2009	118.8	32.3	0.19	0.87	–22.6	+8.8	–23.5	+8.3
107	Satellite	2009	141.2	53.4	-0.14	-1.20	–27.6	+9.1	–27.5	+8.9
108	Satellite	2009	120.5	33.8	1.78	0.41	–24.3	+8.4	–25.0	+7.9
109	Satellite	2009	125.7	37.7	-0.72	1.28	–24.2	+8.8	–23.3	+7.9
110	Satellite	2009	115.8	28.4	0.26	-0.21	–23.8	+9.4	–25.3	+8.4

111	Satellite	2009	104.1	22.0	0.21	-1.61	–23.5	+9.8	–23.9	+9.1
112	Satellite	2009	130.0	43.4	1.60	0.18	–25.2	+9.2	–25.9	+8.6
113	Satellite	2009	157.2	76.0	-0.65	-0.51	–26.7	+8.9	–26.4	+8.5
114	Satellite	2009	147.4	65.0	-1.40	0.03	–28.0	+9.7	–28.5	+9.5
115	Satellite	2009	121.5	31.0	0.49	-0.13	–24.1	+7.7	–24.6	+7.8
116	Satellite	2009	114.9	24.8	0.74	-0.50	–22.1	+8.4	–21.5	+7.2
117	Satellite	2009	129.9	44.7	-0.61	-1.90	–24.7	+10.4	–24.4	+8.6
118	Satellite	2009	121.4	32.5	1.98	-1.50	–26.7	+10.0	–27.5	+7.7
119	Satellite	2009	100.9	27.4	1.51	-2.20	–25.9	+10.2	–26.8	+8.2
120	Satellite	2009	111.3	23.7	1.41	-1.89	–20.9	+9.5	–23.6	+8.4
121	Satellite	2009	106.8	25.0	2.21	-0.64	–22.0	+9.1	–22.2	+8.3
122	Satellite	2009	130.4	42.3	0.22	-1.04	–26.4	+9.6	–27.8	+9.0
123	Sneaker	2009	85.5	9.9	3.84	-3.23	–24.5	+10.3	–25.1	+8.5
124	Sneaker	2009	104.5	21.7	2.89	-0.81	–21.8	+9.7	–22.9	+8.4
125	Sneaker	2009	82.9	9.5	4.33	-1.59	–23.8	+8.1	–24.6	+7.8
126	Sneaker	2009	78.6	10.2	4.58	-1.63	–23.5	+9.3	–24.3	+8.5
127	Sneaker	2009	94.0	12.1	4.55	-2.90	–26.6	+9.5	–26.6	+8.7
128	Sneaker	2009	85.3	9.9	4.96	-2.88	–24.1	+9.0	–24.4	+7.6
129	Sneaker	2009	64.6	4.8	4.68	-2.10	–23.9	+8.9	–25.4	+8.3
130	Sneaker	2009	80.8	8.9	3.70	-1.67	–23.2	+9.6	–24.8	+8.3
131	Sneaker	2009	100.3	17.9	3.06	-2.23	–24.0	+10.1	–24.8	+8.7
132	Sneaker	2009	104.4	21.5	2.43	-0.62	–25.2	+10.1	–25.5	+8.7
133	Sneaker	2009	83.1	9.9	5.31	-2.04	–23.0	+9.8	–21.2	+8.0
134	Sneaker	2009	76.1	7.0	5.43	-0.61	–22.2	+9.7	--	--
135	Sneaker	2009	70.5	5.2	5.43	-2.05	–26.2	+9.3	–25.1	+7.8
136	Sneaker	2009	83.7	9.8	5.51	-1.13	–23.2	+9.8	–23.2	+8.2
137	Sneaker	2009	70.9	4.9	5.61	-1.88	–25.0	+9.7	–24.7	+7.7
138	Sneaker	2009	83.8	8.4	5.16	-3.94	–23.1	+9.9	–23.5	+8.7
139	Sneaker	2009	67.3	4.6	3.53	-1.23	–22.7	+9.5	–23.2	+8.4

140	Sneaker	2009	82.8	10.4	5.38	-2.42	–23.9	+9.3	–23.8	+7.8
141	Sneaker	2009	81.2	8.5	3.55	-2.45	–23.8	+8.6	–24.5	+8.8
142	Sneaker	2009	84.8	10.6	4.62	0.82	–23.1	+9.3	–21.6	+7.5

Note: -- denotes an entry for which the data is unavailable and was excluded from all statistical analyse