

Evolution of mating systems and sexual size dimorphism in North American cyprinids

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Received: 17 October 2012 / Revised: 30 January 2013 / Accepted: 31 January 2013
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Abstract Mating systems evolve with sexual size dimorphism (SSD) in many animals. Mating systems with males larger than females occur when males compete for female access or guard territories, while mating systems with group mating tend to occur in species where females are the same size or larger than males. In addition to variation in SSD with mating system, sperm competition varies among mating systems in predictable patterns. We examined the evolution of mating systems with SSD and testes mass in 111 North American Cyprinidae fishes using phylogenetic comparative methods. Our results demonstrate that the evolution of mating systems in Cyprinidae fishes is from ancestral taxa that are group spawners with females the same size or larger than males to pair spawning systems where males tend to be larger than females. We used an additive model to predict male and female body size from testes mass and mating system. Only mating system varied predictably with SSD. Our results for analyses of hyperallometry (Rensch's rule) were that individual species of Cyprinidae can have hyperallometry for SSD, but the pattern is not present across all taxa.

Keywords Sexual selection · Sexual size dimorphism · Rensch's rule · Comparative phylogenetic analyses

Communicated by J. Frommen

Electronic supplementary material The online version of this article (doi:10.1007/s00265-013-1498-5) contains supplementary material, which is available to authorized users.

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Introduction

Mating system variation is the result of sexual selection whereby one sex becomes limiting (Emlen and Oring 1977). A result is sexual size dimorphism (SSD) that varies among mating systems with a common pattern of male-biased size allometry and increased male–male competition and/or female mating preferences for larger males (Andersson 1994; Dunn et al. 2001). Cox et al. (2003) suggested that observed SSD occurs through two adaptive hypotheses: (1) the intrasexual selection hypothesis, whereby male–male competition leads to selection for a larger body size, and (2) the fecundity advantage hypothesis, whereby natural selection drives females to have larger bodies in order to produce larger clutch sizes. Similarly, in Cyprinidae fishes, increased male body size is predicted to occur in taxa with mating systems displaying male guarding behavior and/or male territoriality (Pyron 1996). Increased female body size in fishes is usually a selective response to increased fecundity (Parker 1992) and has been correlated with changes in male body size (Young 2005). Consequently, the resulting SSD for any given taxon is the combination of sexual selection for males better able to mate guard and defend their territory and natural selection for increased fecundity in females.

Mating system variables that are correlated with SSD include levels of polygyny (Dunn et al. 2001) or territorial guarding (Pyron 1996). Males can obtain increased fitness by reduced investment in gametes and parental care, resulting in an increased number of males available to mate with receptive females (Clutton-Brock 2007). The evolution of SSD can occur through changes in male or female body size, which can be influenced by multiple mechanisms (Webb and Freckleton 2007). Rensch (1960) further defined a pattern of allometry with SSD (Abouheif and Fairbairn 1997; Reeve and Fairbairn 2001; Webb and Freckleton 2007). He predicted positive size allometry (hyperallometry) in taxa where males are larger and negative size allometry (hypoallometry) in taxa where females are the larger sex. Moreover, hyperallometry

appears to be more common in large-bodied species, while hypoallometry is more common in small-bodied species (Frydlová and Frynta 2010). These patterns, now referred to as *Rensch's rule*, have been identified in numerous taxa, including primates (Smith and Cheverud 2002), turtles (Stephens and Wiens 2009), birds (Dale et al. 2007), chameleons (Stuart-Fox 2009), mites (Colwell 2000), and salmonid fishes (Young 2005), and have been the focus of research efforts to identify developmental mechanisms that cause male and female morphology to diverge with sexual maturity (Badyaev 2002; Blanckenhorn et al. 2007).

Mating system diversity among fishes in the Cyprinidae family (Johnston and Page 1992) provides an ideal context for which to test hypotheses related to mating system evolution and co-evolution of mating system characters. Cyprinid mating systems vary from group spawning, in which females are larger than males, to pair spawning, in which males are larger than females (Pyron 1996). Pyron (1996) successfully predicted SSD in 58 cyprinid taxa using mating system variables for probability of sperm competition, male–male context, and male guarding. Our interest is in examining the evolution of SSD and mating systems for a larger number of taxa, including several where natural history information has not been published. Furthermore, we quantify testes mass from museum collections as an estimate of the probability of sperm competition (Parker 1992; Parker and Ball 2005). Although additional spermatozoa traits can influence fertilization success (Beausoleil et al. 2012), our comparative approach only included testes mass as an estimate of sperm production. While Pyron (2000) did not find evidence that testes mass and sexual size dimorphism evolved with mating systems in a comparative analysis of 37 minnow taxa, we tested for similar patterns in a larger diversity of taxa.

Our prediction is that species that are group spawners (many males participate in spawning events) will have female-biased SSD and that species with pair spawning (male guarding and/or male–male competition) will have male-biased SSD. In addition, we expected testes mass to predict the probability of sperm competition, with increased testes mass in species with group-spawning mating systems and males with similar size as females. We examined the evolution of SSD, testes mass, and mating systems using a phylogenetic comparative analysis. An additional goal was to predict mating systems from sexual size dimorphism for species that are lacking published mating system information.

Methods

Testes mass data were obtained from museum specimens, whereby individual fishes were dissected (Pyron 2000). We used only collections that had been preserved for at least 10 years to avoid shrinkage differences (Vervust et al. 2009),

and representing the reproductive season of the species (females had ripe ova; males had tubercles), and only mature individuals. All collections were initially preserved in formalin and later, once fixation occurred, stored in alcohol. The standard length (SL) of all individuals was measured to 0.1 mm. Moisture was blotted from testes and bodies and the wet mass was determined to 0.001 g on an electronic balance (testes mass was added to body mass for calculations). Information about mating systems was from published sources or predicted from SSD (Table 1). We categorized mating system into pair spawning or group spawning (Pyron 1996) because details of the mating behavior of most cyprinids are not available. For the taxa where mating system information was unavailable, we used a discriminant function analysis to predict pair spawning or group spawning from SSD. As sexual size dimorphism is a strong predictor of mating systems in cyprinid fishes (Pyron 1996), taxa with SSD scores higher than 0.02 were assigned as pair spawners; all others, as group spawners. SSD was calculated as the difference between log-transformed male standard length and log-transformed female standard length (Pyron 1996). Hormiga et al. (2000) demonstrated a cladistic test for examining the evolution of SSD separately in males and females. Their approach was to reconstruct the ancestral body size for males and females using parsimony to identify the sequence of evolutionary events. We used a similar approach to identify the evolutionary origins and the sequence of changes in SSD for Cyprinidae fishes.

We used comparative phylogenetic methods to control for non-independence for all of our analyses (Garland and Ives 2000; Garland et al. 2005). A composite phylogeny for Cyprinidae taxa was assembled from the molecular hypotheses of Simons et al. (2003), Mayden et al. (2006), Pramuk et al. (2007), Moyer et al. (2009), Bufalino and Mayden (2010), and Schönhuth and Mayden (2010). Male and female mean standard length, testes mass, and mating system score (pair or group spawning) were assigned to each taxon.

We used the PDAP PDTREE (version 1.15; Midford et al. 2002) package in the software Mesquite (version 2.73; Maddison and Maddison 2010) for comparative phylogenetic analyses (other than the additive model described below). Divergence times for all taxa were not known due to limitations in molecular clock and fossil record data; thus, we used constant branch lengths. The body size of males and females, SSD, testes mass, and mating system were reconstructed on the cladogram using parsimony. We visually examined ancestral character changes of male and female body size on cladograms to detect which gender resulted in changes in SSD (Hormiga et al. 2000). This allowed us to examine whether origins for SSD occur simultaneously with changes in body size of males or females, or both. We used Pagel's (1994) maximum likelihood approach in Mesquite (Maddison and Maddison 2010) to test

Table 1 Taxa, testes mass, mean SL of males and females, log-transformed difference in SL of males and females, spawning mode, source of material (abbreviations from Sabaj Pérez 2010), mean of testes mass to body mass ratio, and the source of mating system information

| Species | Testes mass (g) | Male SL (mm) | Female SL (mm) | Log male SL–female SL | Spawning mode | Source of material | Testes/body mass | Mating system source |
|----------------------------------|-----------------|--------------|----------------|-----------------------|---------------|---------------------|------------------|---|
| <i>Agosia chrysogaster</i> | 0.034 | 55 | 57.7 | −0.021 | Group | INHS | 0.007 | Pyron (2000) |
| <i>Campostoma anomalum</i> | 0.336 | 80.2 | 80.9 | −0.004 | Group | INHS | 0.018 | Pyron (2000) |
| <i>Campostoma oligolepis</i> | 0.083 | 73.1 | 85.2 | −0.067 | Group | INHS | 0.009 | Johnston and Page (1992) |
| <i>Campostoma ornatum</i> | 0.014 | 57 | 47.5 | 0.079 | Group | INHS | 0.004 | Johnston and Page (1992) |
| <i>Clinostomus funduloides</i> | 0.083 | 55.6 | 57 | −0.011 | Group | INHS | 0.018 | Pyron (2000) |
| <i>Codoma ornata</i> | 0.031 | 5.3 | 4.5 | 0.071 | Pair | UMMZ | 0.011 | Pyron (2000) |
| <i>Couesius plumbeus</i> | 0.087 | 8.5 | 9.4 | −0.044 | Group | UMMZ | 0.010 | Pyron (2000) |
| <i>Cyprinella camura</i> | 0.042 | 66.7 | 65.9 | 0.005 | Pair | INHS | 0.007 | Johnston and Page (1992) |
| <i>Cyprinella galactura</i> | 0.061 | 81.5 | 71.8 | 0.055 | Pair | INHS | 0.005 | Pyron (2000) |
| <i>Cyprinella lutrensis</i> | 0.02 | 53.8 | 44.6 | 0.081 | Group | INHS | 0.006 | Pyron (2000) |
| <i>Cyprinella spiloptera</i> | 0.035 | 86.2 | 70.1 | 0.090 | Pair | OMNH | 0.008 | Pyron (2000) |
| <i>Cyprinella venusta</i> | 0.055 | 59 | 48.7 | 0.083 | Group | OMNH | 0.012 | Pyron (2000) |
| <i>Cyprinella whipplei</i> | 0.092 | 49 | 38 | 0.110 | Group | INHS | 0.011 | Pyron (2000) |
| <i>Dionda episcopa</i> | 0.046 | 50.5 | 46.7 | 0.034 | Group | UMMZ | 0.020 | Pyron (2000) |
| <i>Erimystax dissimilis</i> | 0.04 | 78.8 | 67 | 0.070 | Pair | INHS | 0.007 | Same as <i>Erimystax monachus</i> (Jenkins and Burkhead 1993) |
| <i>Exoglossum maxilingua</i> | 0.046 | 8 | 6.4 | 0.097 | Pair | UMMZ | 0.004 | Pyron (2000) |
| <i>Gila atraria</i> | 0.29 | 8.2 | 9.6 | −0.068 | Group | UMMZ | 0.023 | Pyron (2000) |
| <i>Gila coerulea</i> | 0.2 | 85 | 113 | −0.124 | Group | INHS | 0.012 | Johnston and Page (1992) |
| <i>Hemitremia flammea</i> | 0.05 | 46.8 | 49.2 | −0.022 | Group | INHS | 0.028 | Predicted |
| <i>Hesperoleucas symmetricus</i> | 0.024 | 46 | 56.4 | −0.089 | Group | INHS | 0.016 | Mayden and Simons (2002) |
| <i>Hybognathus hankinsoni</i> | 0.011 | 38.4 | 43.1 | −0.050 | Group | INHS | 0.013 | Lane et al. (1996) |
| <i>Hybognathus nuchalis</i> | 0.012 | 66 | 66.8 | −0.005 | Group | INHS | 0.003 | Mayden and Simons (2002) |
| <i>Hybognathus placitus</i> | 0.025 | 54.4 | 54.9 | −0.004 | Group | INHS | 0.007 | Pyron (2000) |
| <i>Hybognathus regius</i> | 0.023 | 58.5 | 62.5 | −0.029 | Group | INHS | 0.008 | Lane et al. (1996) |
| <i>Hybopsis amblops</i> | 0.006 | 51.1 | 64.7 | −0.102 | Group | INHS | 0.003 | Pyron (2000) |
| <i>Hybopsis hypsinotus</i> | 0.024 | 58 | 50.5 | 0.060 | Group | INHS | 0.007 | Johnston and Page (1992) |
| <i>Hybopsis rubifrons</i> | 0.026 | 61.8 | 60.1 | 0.012 | Pair | INHS | 0.007 | Johnston and Page (1992) |
| <i>Lavinia exilicauda</i> | 0.117 | 64.5 | 68 | −0.023 | Group | INHS | 0.022 | Johnston and Page (1992) |
| <i>Lepidomeda vittata</i> | 0.06 | 96 | 96 | 0.000 | Group | Blinn et al. (1998) | 0.045 | Blinn et al. (1998) |
| <i>Luxilus albeolus</i> | 0.16 | 103 | 67 | 0.187 | Pair | INHS | 0.007 | Johnston and Page (1992) |
| <i>Luxilus cardinalis</i> | 0.031 | 67.2 | 63.3 | 0.026 | Pair | INHS | 0.006 | Johnston and Page (1992) |
| <i>Luxilus chrysocephalus</i> | 0.32 | 118.9 | 78.6 | 0.180 | Group | INHS | 0.009 | Johnston and Page (1992) |
| <i>Luxilus coccogenis</i> | 0.004 | 55.1 | 61.8 | −0.050 | Group | INHS | 0.003 | Johnston and Page (1992) |
| <i>Luxilus cornutus</i> | 0.07 | 77 | 60 | 0.108 | Pair | OMNH | 0.004 | Pyron (2000) |
| <i>Luxilus pilsbryi</i> | 0.01 | 55.9 | 67.2 | −0.080 | Group | INHS | 0.005 | Johnston and Page (1992) |
| <i>Luxilus zonistius</i> | 0.07 | 76.3 | 66 | 0.063 | Pair | INHS | 0.009 | Johnston and Page (1992) |
| <i>Lythrurus ardens</i> | 0.02 | 65.4 | 54.9 | 0.076 | Group | INHS | 0.006 | Johnston and Page (1992) |
| <i>Lythrurus bellus</i> | 0.008 | 46.7 | 40 | 0.067 | Group | INHS | 0.007 | Johnston and Page (1992) |
| <i>Lythrurus fasciolaris</i> | 0.014 | 50.4 | 49 | 0.012 | Pair | INHS | 0.007 | Johnston and Page (1992) |
| <i>Lythrurus fumeus</i> | 0.012 | 44.4 | 44.8 | −0.004 | Pair | INHS | 0.012 | Johnston and Page (1992) |
| <i>Lythrurus matutinus</i> | 0.01 | 51.1 | 48.1 | 0.026 | Pair | INHS | 0.007 | Johnston and Page (1992) |
| <i>Lythrurus umbratilis</i> | 0.009 | 47.1 | 41.1 | 0.059 | Group | INHS | 0.005 | Pyron (2000) |
| <i>Machybopsis storeriana</i> | 0.052 | 91.1 | 100.5 | −0.043 | Group | INHS | 0.006 | Lane et al. (1996) |
| <i>Margariscus margarita</i> | 0.004 | 67.9 | 72.7 | −0.030 | Pair | UWZM | 0.001 | Pyron (2000) |
| <i>Nocomis asper</i> | 0.231 | 100.33 | 105.1 | −0.020 | Pair | INHS | 0.007 | Maurakis and Roston (1998) |

Table 1 (continued)

| Species | Testes mass (g) | Male SL (mm) | Female SL (mm) | Log male SL–female SL | Spawning mode | Source of material | Testes/body mass | Mating system source |
|---------------------------------|-----------------|--------------|----------------|-----------------------|---------------|-----------------------------|------------------|--|
| <i>Nocomis biguttatus</i> | 0.319 | 122 | 75.2 | 0.210 | Pair | UMMZ | 0.010 | Pyron (2000) |
| <i>Nocomis leptocephalus</i> | 0.805 | 160 | 90.6 | 0.247 | Pair | INHS | 0.009 | Wallin (1992) |
| <i>Nocomis micropogon</i> | 0.013 | 138 | 111 | 0.095 | Pair | Jenkins and Burkhead (1993) | 0.003 | Maurakis et al. (1991) |
| <i>Notemigonus crysoleucas</i> | 0.06 | 57 | 60 | −0.022 | Group | INHS | 0.023 | Johnston and Page (1992) |
| <i>Notropis albizonatus</i> | 0.007 | 47.9 | 49 | −0.010 | Group | INHS | 0.007 | Predicted |
| <i>Notropis amabilis</i> | 0.017 | 51.3 | 46.3 | 0.045 | Pair | INHS | 0.008 | Predicted |
| <i>Notropis ammophilus</i> | 0.0043 | 40 | 40.5 | −0.005 | Pair | INHS | 0.005 | Suttkus and Boschung (1990) from Hubbs and Walker (1942) |
| <i>Notropis amoenus</i> | 0.005 | 52.5 | 57.1 | −0.036 | Group | INHS | 0.003 | Johnston and Page (1992) |
| <i>Notropis ariommus</i> | 0.016 | 59.5 | 49.3 | 0.082 | Pair | INHS | 0.006 | Predicted |
| <i>Notropis atherinoides</i> | 0.013 | 63 | 69 | −0.040 | Group | OMNH | 0.014 | Pyron (2000) |
| <i>Notropis bairdi</i> | 0.03 | 42 | 48 | −0.058 | Group | OMNH | 0.027 | Pyron (2000) |
| <i>Notropis bifrenatus</i> | 0.004 | 41.6 | 40.6 | 0.011 | Group | UMMZ | 0.004 | Pyron (2000) |
| <i>Notropis blennioides</i> | 0.022 | 54 | 67.7 | −0.098 | Group | INHS | 0.009 | Pyron (2000) |
| <i>Notropis boops</i> | 0.015 | 48 | 48.7 | −0.006 | Group | INHS | 0.009 | Predicted |
| <i>Notropis buccatus</i> | 0.009 | 33.3 | 33.5 | −0.003 | Group | INHS | 0.004 | Johnston and Page (1992) |
| <i>Notropis buechanani</i> | 0.006 | 33.9 | 35.6 | −0.021 | Group | INHS | 0.011 | Predicted |
| <i>Notropis chalybaeus</i> | 0.009 | 39.9 | 42.6 | −0.028 | Group | INHS | 0.009 | Johnston and Page (1992) |
| <i>Notropis chiliticus</i> | 0.046 | 46.4 | 46.6 | −0.002 | Group | INHS | 0.032 | Johnston and Page (1992) |
| <i>Notropis cummingsae</i> | 0.012 | 47.5 | 48.3 | −0.007 | Group | INHS | 0.010 | Fletcher (1993) |
| <i>Notropis dorsalis</i> | 0.007 | 48.6 | 51 | −0.021 | Group | INHS | 0.005 | Predicted |
| <i>Notropis greenei</i> | 0.004 | 46.2 | 45.3 | 0.009 | Group | INHS | 0.004 | Predicted |
| <i>Notropis heterodon</i> | 0.018 | 46.1 | 48.3 | −0.020 | Group | INHS | 0.013 | Lane et al. (1996) |
| <i>Notropis heterolepis</i> | 0.01 | 48 | 45.3 | 0.025 | Group | INHS | 0.007 | Lane et al. (1996) |
| <i>Notropis hypselopterus</i> | 0.004 | 41.3 | 35.4 | 0.067 | Pair | INHS | 0.004 | Predicted |
| <i>Notropis lirus</i> | 0.004 | 44.2 | 43.4 | 0.008 | Group | INHS | 0.005 | Predicted |
| <i>Notropis lutipinnis</i> | 0.136 | 55.2 | 54.5 | 0.006 | Group | INHS | 0.056 | Wallin (1992) |
| <i>Notropis nazas</i> | 0.05 | 44.2 | 42.1 | 0.021 | Group | INHS | 0.039 | Predicted |
| <i>Notropis nubilus</i> | 0.02 | 48.8 | 53.3 | −0.038 | Group | INHS | 0.011 | Johnston and Page (1992) |
| <i>Notropis petersoni</i> | 0.026 | 53.9 | 57.2 | −0.026 | Group | INHS | 0.012 | Predicted |
| <i>Notropis photogenis</i> | 0.013 | 74.2 | 73.1 | 0.006 | Group | INHS | 0.004 | Predicted |
| <i>Notropis rubellus</i> | 0.03 | 46 | 48.2 | −0.020 | Group | INHS | 0.027 | Pyron (2000) |
| <i>Notropis rubricroceus</i> | 0.0086 | 35.4 | 38.9 | −0.041 | Group | INHS | 0.014 | Johnston and Page (1992) |
| <i>Notropis shumardi</i> | 0.014 | 44.3 | 37.7 | 0.070 | Pair | INHS | 0.011 | Predicted |
| <i>Notropis spectrunculus</i> | 0.007 | 51.3 | 49.8 | 0.013 | Group | INHS | 0.006 | Predicted |
| <i>Notropis stilbius</i> | 0.008 | 53.2 | 58.3 | −0.040 | Pair | INHS | 0.005 | Mayden and Simons (2002) |
| <i>Notropis stramineus</i> | 0.015 | 47.8 | 46.6 | 0.011 | Group | INHS | 0.009 | Platania and Altenbach (1998) |
| <i>Notropis telescopus</i> | 0.011 | 46.6 | 51.5 | −0.043 | Group | INHS | 0.010 | Predicted |
| <i>Notropis texanus</i> | 0.006 | 51.2 | 56.7 | −0.044 | Group | INHS | 0.003 | Pyron (2000) |
| <i>Notropis volucellus</i> | 0.007 | 42.1 | 42.2 | −0.001 | Group | INHS | 0.007 | Pyron (2000) |
| <i>Notropis xaenocephalus</i> | 0.01 | 46.7 | 54.8 | −0.069 | Group | INHS | 0.008 | Predicted |
| <i>Notropis zonatus</i> | 0.104 | 81.4 | 69 | 0.072 | Pair | INHS | 0.010 | Predicted |
| <i>Opsopoeodus emiliae</i> | 0.007 | 42.1 | 37.5 | 0.050 | Pair | TU | 0.004 | Pyron (2000) |
| <i>Phenacobius crassilabrum</i> | 0.087 | 73.4 | 71.1 | 0.014 | Group | INHS | 0.018 | Johnston and Page (1992) |
| <i>Phenacobius mirabilis</i> | 0.034 | 65.5 | 65.6 | −0.001 | Group | INHS | 0.008 | Pyron (2000) |
| <i>Phenacobius uranops</i> | 0.025 | 72.4 | 76.4 | −0.023 | Group | INHS | 0.007 | Predicted |
| <i>Phoxinus eos</i> | 0.013 | 35.7 | 36.9 | −0.014 | Group | INHS | 0.002 | Johnston and Page (1992) |

Table 1 (continued)

| Species | Testes mass (g) | Male SL (mm) | Female SL (mm) | Log male SL–female SL | Spawning mode | Source of material | Testes/body mass | Mating system source |
|----------------------------------|-----------------|--------------|----------------|-----------------------|---------------|----------------------------|------------------|----------------------------|
| <i>Phoxinus erythrogaster</i> | 0.012 | 46 | 45.6 | 0.004 | Group | INHS | 0.009 | Johnston and Page (1992) |
| <i>Phoxinus neogaeus</i> | 0.05 | 50.3 | 50 | 0.003 | Group | INHS | 0.020 | Johnston and Page (1992) |
| <i>Phoxinus oreas</i> | 0.015 | 43.8 | 49.1 | −0.050 | Group | INHS | 0.010 | Johnston and Page (1992) |
| <i>Pimephales notatus</i> | 0.017 | 71.6 | 58.5 | 0.088 | Pair | INHS | 0.004 | Pyron (2000) |
| <i>Pimephales promelas</i> | 0.029 | 52.8 | 46.1 | 0.059 | Pair | INHS | 0.010 | Cole and Smith (1987) |
| <i>Pimephales vigilax</i> | 0.028 | 56.6 | 41.6 | 0.134 | Pair | OMNH | 0.009 | Pyron (2000) |
| <i>Platygobio gracilis</i> | 0.023 | 53.2 | 82.8 | −0.192 | Group | INHS | 0.007 | Predicted |
| <i>Pteronotropis hubbsi</i> | 0.007 | 43.5 | 40 | 0.036 | Pair | INHS | 0.007 | Fletcher and Burr (1992) |
| <i>Pteronotropis signipinnis</i> | 0.002 | 44.6 | 39.9 | 0.048 | Pair | INHS | 0.002 | Albanese (2000) |
| <i>Pteronotropis welaka</i> | 0.06 | 36.1 | 34.7 | 0.017 | Group | Johnston and Knight (1999) | 0.002 | Johnston and Knight (1999) |
| <i>Ptychocheilus grandis</i> | 0.06 | 293 | 384 | −0.117 | Group | Beamesderfer (1992) | 0.004 | Johnston and Page (1992) |
| <i>Rhinichthys atratulus</i> | 0.01 | 59.6 | 59 | 0.004 | Group | INHS | 0.003 | Pyron (2000) |
| <i>Rhinichthys cataractae</i> | 0.01 | 57.7 | 63.6 | −0.042 | Group | INHS | 0.004 | Johnston and Page (1992) |
| <i>Rhinichthys osculus</i> | 0.05 | 48.6 | 43.2 | 0.051 | Group | INHS | 0.025 | Mueller (1984) |
| <i>Richardsonius balteatus</i> | 0.068 | 64.8 | 57.7 | 0.050 | Group | UMMZ | 0.014 | Pyron (2000) |
| <i>Semotilus atromaculatus</i> | 0.419 | 123 | 103 | 0.077 | Pair | UMMZ | 0.014 | Pyron (2000) |
| <i>Semotilus corporalis</i> | 0.014 | 69.9 | 69.7 | 0.001 | Pair | INHS | 0.003 | Ross and Reed (1978) |
| <i>Semotilus lumbee</i> | 0.26 | 56.4 | 107 | −0.278 | Pair | INHS | 0.089 | Johnston and Page (1992) |
| <i>Semotilus thoreauianus</i> | 0.012 | 72 | 65.3 | 0.042 | Pair | INHS | 0.002 | Predicted |
| <i>Tiaroga cobitis</i> | 0.04 | 49.8 | 51.7 | −0.016 | Pair | UMMZ | 0.020 | Pyron (2000) |

The species where mating systems were predicted are listed under “Mating system source”

for independent evolution of SSD (categorized) and mating system (pair or group spawning). This analysis was repeated with and without taxa, in which we estimated mating system, to verify that results were not solely due to our mating system predictions using SSD.

We tested for independent effects in an additive model with female and male SL, testes mass, and mating system using phylogenetic least squares regressions (PGLS) in the R (v2.15.0) package “caper” (Orme et al. 2012; R Development Core Team 2010). PGLS uses a branch length transformation (Pagel’s λ) that maximizes the fit of the phylogeny to Brownian motion (Pagel 1999; Freckleton et al. 2002). In addition, we performed a PGLS analysis to determine the effect of mating system (pair or group) on testes mass. All variables were log-transformed before analysis. We calculated phylogenetic signal (Pagel’s λ) for SSD and testes mass in the “caper” package and we used fitDiscrete from the “geiger” package (Harmon et al. 2008) to calculate phylogenetic signal for the categorical mating system variable. The presence of allometry in SSD (Rensch’s rule) with changes in body size was tested by comparing the slope of a PGLS regression for male SL on female SL to a null model 1:1 slope by calculating 95 % confidence intervals (Sokal and Rohlf 1995).

Results

We collected testes mass and SSD scores for 111 taxa and spawning mode for 90 taxa (Table 1 and Electronic supplementary material). We attempted to locate large sample sizes for each species, but museum collections frequently did not have large numbers of mature individuals. The mean sample size per species was 8.3 (SD=3.9) and ranged from 1 to 20 (one taxon had a sample size of 1). A discriminant function analysis of SSD correctly classified 73 % of 90 taxa using discrete mating systems. We assigned spawning mode using SSD to the 21 taxa where mating system information was not available using a SSD value of 0.02 (males larger than females) as species with pair spawning and species with SSD values <0.02 as group spawning (Pyron 1996). Six of the 21 taxa with unknown mating systems were assigned mating systems of pair spawning and 15 taxa as group spawning (Table 1). We traced the evolution of SSD and mating system on the composite cladogram of all 111 taxa (Fig. 1). The ancestral spawning mode for cyprinids is group spawning and the ancestral SSD score is females larger than males. Character changes in SSD from females the same size or larger than males to males larger than females occurred 10 times on the cladogram. There were no reversals

from males larger than females to males the same size or smaller. Character changes from group spawning to pair spawning occurred 16 times on the cladogram (not shown in Fig. 1), with a single reversal in *Luxilis pilsbryi* Fowler. We examined ancestral changes in male and female body size separately from SSD score and found that changes occurred at the same nodes and in the same direction (male and female SL reconstructions) for 9 of 13 character changes when these characters were traced separately. Of the 10 character changes in SSD that resulted in males larger than females, only two or three of these changes occurred simultaneously with increased male body size. Female SL decreased multiple times in reconstructions, but only a few occurred with increased SSD (males larger than females; Fig. 1). The evolution of SSD does not occur by independent changes in the body size of males or females.

Modeling the relationship between male and female standard length allows all predictors to be interpreted in terms of SSD. As a result, SSD was negatively correlated with testes mass (Table 2). Phylogenetic signal (λ) was present for all variables: SSD value were 0.729, 0.515 for testes mass, and 0.812 for mating system, indicating that traits are frequently present in taxa because of ancestral relationships (Blomberg et al. 2003). Moreover, SSD was significantly correlated with mating system. Finally, we found in a phylogenetic model that there was no difference in testes mass between pair spawners and group spawners with all species included ($F_{2,108}$, $p=0.42$) or with only species where we did not estimate mating systems ($F_{2,89}$, $p=0.35$). Male and female SLs were positively correlated with a slope of 0.98 (Fig. 2), indicating a lack of significant allometry in male body size and an absence of Rensch's rule (Fairbairn 1997).

Discussion

Females are larger than males in most animals, likely due to selection for increased fecundity (Darwin 1871; Andersson 1994). A pattern of hyperallometry is expected in taxa where sexual selection is stronger for males (Walker and McCormick 2009) as they compete for access to females and attempt to maintain their reproductive dominance (Shuster and Wade 2003; Grosenick et al. 2007). In Cyprinidae fishes, males are larger than females in species where males guard territories or compete for females (Pyron 1996). However, we did not find evidence for Rensch's rule as has been previously found in intraspecific and interspecific studies (Abouheif and Fairbairn 1997; Young 2005; Dale et al. 2007). Although hyperallometry may be present in individual fish taxa, such as the spotfin shiner *Cyprinella spiloptera* Cope (Pyron et al. 2007) and two blennioids (family Blenniidae; Lengkeek et al. 2008), an overall family-wide pattern was not present in Cyprinidae fishes. Intraspecific variation in hyperallometry may be

common (Pyron et al. 2007), providing additional complexity to interpreting patterns in higher taxa. For example, Abouheif and Fairbairn (1997) and Webb and Freckleton (2007) found evidence for hyperallometry only in analyses where species with female-biased SSD were separated from species with male-biased SSD. Furthermore, when Webb and Freckleton (2007) analyzed all 61 minnow species from Pyron's (1996) allometry study, they found no evidence for either hyperallometry or hypoallometry, similar to our current results. We interpret these results as evidence for correlated evolution of male and female body length, with a few exceptions where males evolved larger body size than females. Similar to our findings, there was no evidence that SSD was the result of a separate evolution of male or female body size in *Phrynosoma* lizards, which lack male-male competition and male territoriality (Zamudio 1998).

Although sexual selection is proposed to be the ultimate cause of variation in growth rate, differences in the developmental growth of males and females is said to be the proximate cause of SSD (Blanckenhorn 2005; Walker and McCormick 2009). Blanckenhorn (2005) recommends a combination of comparative phylogenetic analyses and manipulative experiments on individual species to identify causes for SSD evolution. Although the role of sex-specific growth plasticity in shaping morphological features has been demonstrated in reef fish (Walker and McCormick 2009), manipulative experiments of sexual selection are currently lacking in cyprinid fish.

The plesiomorphic state for cyprinid mating systems is group spawning (Johnston and Page 1992; Pyron 1996; Mayden and Simons 2002). Although 34 of the 111 taxa in this study are pair spawners, no examples of reversals to group spawning occurred in reconstructions using parsimony. In addition, the pair spawning behavior is distributed widely across the clade, with multiple independent origins. Thus, based on a cladogram of 111 taxa, evolution of group spawning from pair spawning does not occur. This suggests the presence of phylogenetic constraints to reversals for male competition and territorial behaviors or constraints for the evolution of characters for sperm competition. Blanckenhorn (2005) suggests that this approach of inferring selective pressures in the past from current observations is problematic. For example, male-biased SSD may evolve as a result of male competition or mate guarding behavior being sexually selected. However, the evolution of mating systems may also result as a consequence of SSD as social mating system is predictive of size allometry (Dale et al. 2007). In addition, our characterization of mating systems into two alternative mating systems likely oversimplifies their complexity and influences our results, as does our classification of mating systems from SSD.

We found a negative correlation for testes mass with SSD. Species with small testes tended to have males larger than females, as predicted based on the probability of sperm

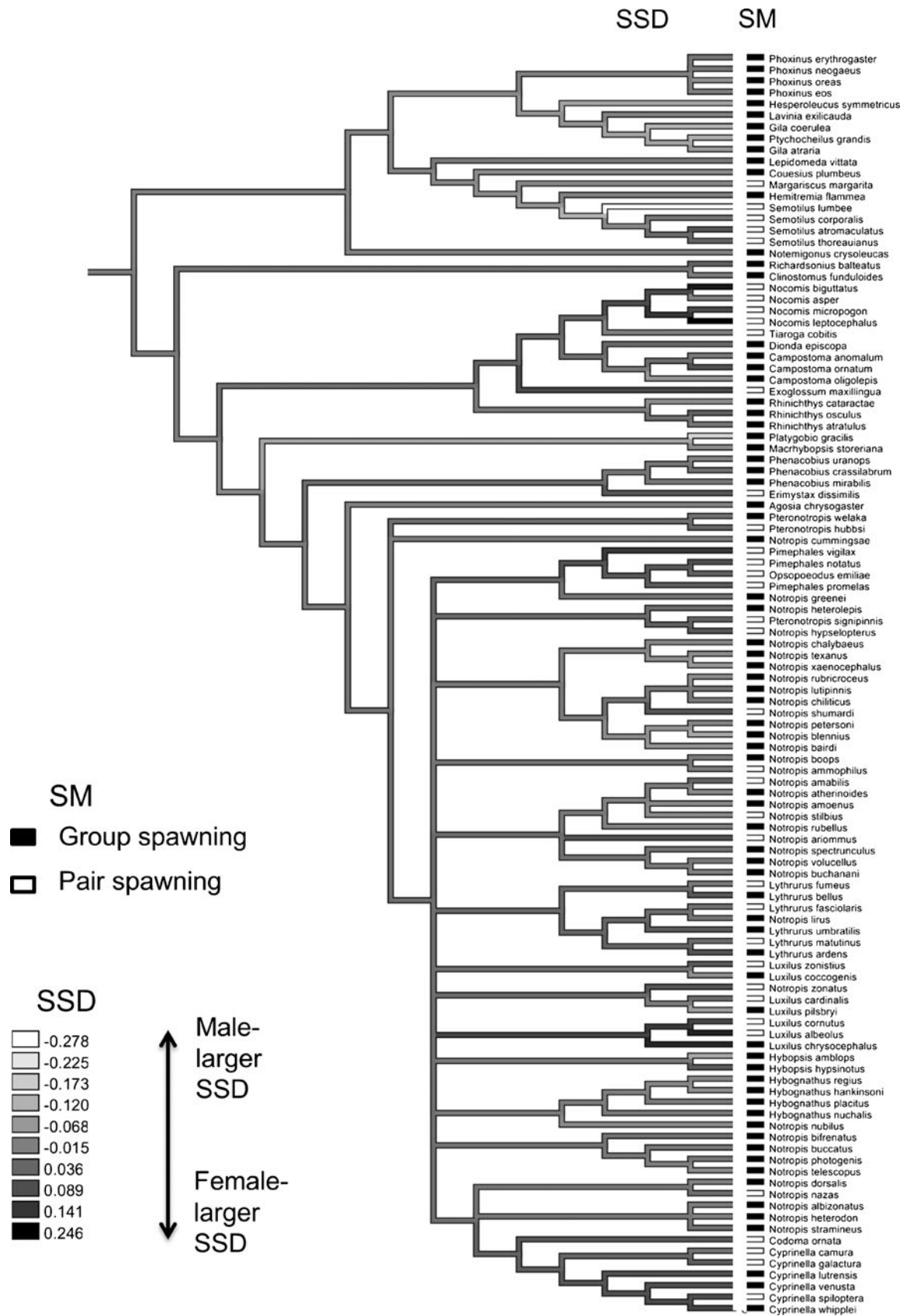


Fig. 1 Composite Cyprinidae phylogeny constructed as described in text. SSD score (log male SL–log female SL) is depicted on the cladogram. Spawning mode is shown *at the end of bars*

Table 2 Results for additive phylogenetic models predicting SSD, including the estimate, standard error associated with each variable, the *t* value, and the *p* value (from the relevant phylogenetically controlled analyses using PGLS, see “Methods” for details)

| Variable | Estimate | Standard error | <i>t</i> value | <i>p</i> value |
|---|----------|----------------|----------------|----------------|
| All species (including those with mating systems estimated from SSD) are included | | | | |
| Male SL | 0.98 | 0.02 | 39.3 | <0.001 |
| Testes mass | -0.03 | 0.01 | -2.4 | 0.018 |
| Mating system | -0.05 | 0.01 | -3.4 | <0.001 |
| Species with mating systems estimated from SSD not included | | | | |
| Male SL | 0.98 | 0.02 | 38.3 | <0.001 |
| Testes mass | -0.03 | 0.01 | -2.3 | 0.022 |
| Mating system | -0.04 | 0.02 | -2.6 | 0.01 |

All species are included in the upper analyses ($n=111$). Species with mating systems estimated from SSD are not included in the bottom analyses ($n=90$). See text for details

competition (Parker 1992; Dunn et al. 2001). Although the correlation was significant, the relationship explained relatively low variation. Other methods for quantifying sperm quality or morphology have the potential to provide stronger estimates of SSD (Lüpold et al. 2008). In addition, several of the taxa we sampled resulted in low sample sizes, potentially biasing the results.

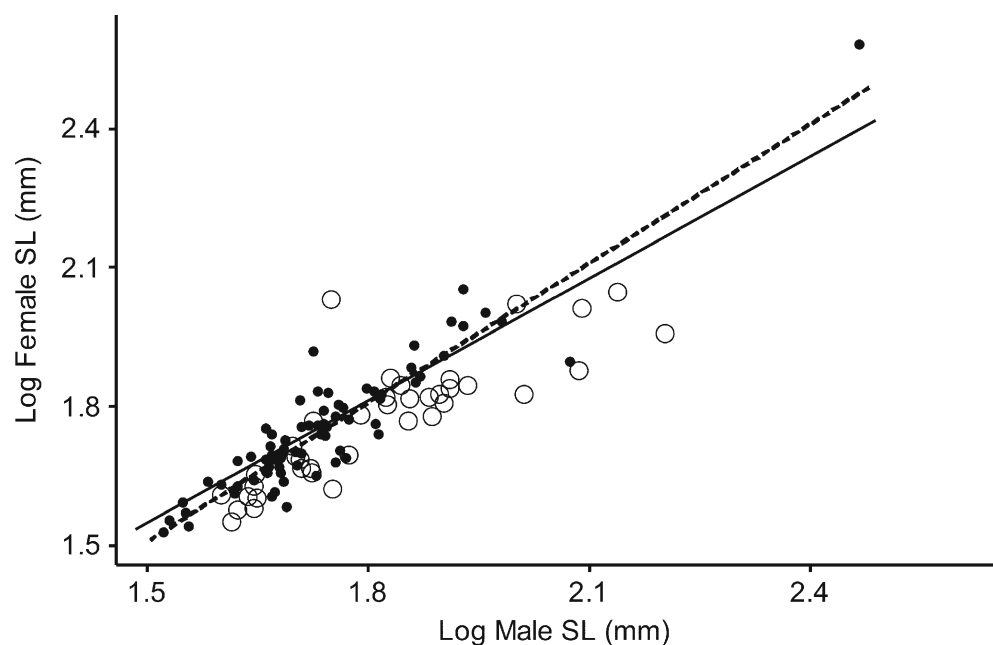
Intraspecific variation can lead to a great amount of disparity within a data set, ultimately affecting a predicted relationship. In our analyses, we were unable to control for this variation in our measured variables. Variation within a single species is expected to exist throughout nature and can result from a number of forces, including environmental and seasonal conditions. Wong-Muñoz et al. (2011) identified seasonal variation in SSD that fit predictions for mating system covariation. Consequently, details of intraspecific variation in mating system variables across geographic

ranges (Blanckenhorn et al. 2007) and seasons will allow verification of these patterns in other taxa.

Conclusions

Our results demonstrate that the evolution of mating systems in Cyprinidae fishes is predictable, from ancestral taxa that are group spawners with females the same size or larger than males to recent taxa that retain their ancestral mating system unless males are territorial. This provides support that mating systems and sexual size dimorphism evolve in predictable patterns, but not testes mass. We predicted mating systems for 21 species that were lacking information based on SSD. These patterns for mating system evolution in the cladogram are likely valid, but need to be verified empirically. Additionally, we did not find evidence for hyperallometry in

Fig. 2 Regression (PGLS) of log female standard length on log male standard length. *Open circles* are species with group-spawning mating systems and *filled circles* are pair-spawning species. The *dashed line* is the 1:1 line



Cyprinidae fishes, although individual species of Cyprinidae can have hyperallometry for SSD (Rensch's rule).

Acknowledgments We are grateful to Mike Retzer at the Illinois Natural History survey for fish loans.

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