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COMPARATIVE PHYLOGENETIC ANALYSIS OF MALE ALTERNATIVE REPRODUCTIVE TACTICS IN RAY-FINNED FISHES

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Abstract.—Using comparative phylogenetic analysis, we analyzed the evolution of male alternative reproductive tactics (MARTs) in ray-finned fishes (Actinopterygii). Numerous independent origins for each type of MART (involving sneaker males, female mimics, pirates, and satellite males) indicate that these behaviors have been highly labile across actinopterygiian evolution, consistent with a previous notion that convergent selection in fishes can readily mold the underlying suites of reproductive hormones into similar behaviors. The evolutionary appearance of MARTs was significantly correlated with the presence of sexually selected traits in bourgeois males ($P = 0.001$) but not with the presence of male parental care. This suggests that MARTs often arise from selection on some males to circumvent bourgeois male investment in mate monopolization, rather than to avoid male brood care per se. We found parsimony evidence for an evolutionary progression of MARTs wherein sneaking is usually the evolutionary precursor to the presumably more complex MARTs of female mimicry and cooperative satellite behavior. Nest piracy appears not to be part of this evolutionary progression, possibly because its late onset in the life cycle of most ray-finned fishes reduces the effects of selection on this reproductive tactic.

Key words.—Cuckoldry, mate monopolization, mating behaviors, satellites, sexual selection, sneakers.

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Ray-finned fishes (Actinopterygii) display a great diversity of male reproductive tactics, probably more so than any other vertebrate clade. These behaviors range from mass group spawning (where scramble competition and sperm competition are major determinants of male fitness) to distinct pairings between one or a few females and particular territorial or ''bourgeois'' males (where the effectiveness of mate appropriation has a key impact on male fitness). Under the bourgeois tactic, mate monopolization may occur via monogamous pair bonding or polygamous harems, but in either case the male acts to control the reproductive potential of prospective mate(s) to the relative fitness detriment of other males (Emlen and Oring 1977; Gross 1996; Taborsky 2001). Furthermore, often associated with the bourgeois strategy in various fish species are a variety of parasitic and cooperative male alternative reproductive tactics (henceforth MARTs) by which some males in effect sidestep or even co-opt bourgeois males' often substantial investments in attracting females and defending territories and mates. In other words, effective MARTs can break the monopoly that bourgeois males otherwise hold on fitness-enhancing resources (Taborsky 1994, 1998).

These MART behaviors, three of which are parasitic and one cooperative, have been extensively cataloged and reviewed (Taborsky 1994, 1998, 2001; Gross 1996), and the definitions used throughout this analysis are from Taborsky (1994). By definition, males displaying parasitic reproductive behaviors attempt to steal fertilization events from territorial males. Sneaker males do so by means of speed or stealth that gives them access to a spawning opportunity. Female mimics do so by duping territorial males and thereby gaining access to spawning sites in which they deposit sperm. Pirate males steal fertilizations by being massive enough to evict a territorial male from his spawning location. The eviction is often temporary because the pirate may depart after one or a few spawning events, leaving the bourgeois male to guard what may be a mixed-parentage brood. Cooperative reproductive behaviors by males are rarer and less diverse in actinopterygiian fishes, but no less intriguing. Cooperative males, often known as satellites, are tolerated by a bourgeois male and may contribute to female acquisition, territory defense, and parental care in exchange for fertilization opportunities. In general, males displaying most MART adaptations (with the exception of piracy) lack the sexually selected ornaments exhibited by territorial males (Taborsky 2001).

Due to diligent field observations and molecular genetic appraisals of parentage (reviewed in Avise et al. 2002), documentations of species-specific MARTs abound in the literature, and the hormonal and genetic controls of these reproductive tactics are becoming increasingly clarified in laboratory experiments (Borg 1994; Foran and Bass 1998, 1999; Bass and Grober 2001; Knapp 2004; Fitzpatrick et al. 2005). However, little is understood about phylogenetic patterns of MART evolution in fishes, a shortcoming that we begin to redress here.

The recent publication of a provisional supertree for the Actinopterygii (Mank et al. 2005) makes possible a comparative appraisal of MART evolution across this large and diverse fish clade. Here we use a comparative phylogenetic approach to analyze evolutionary patterns and to assess the evolutionary lability of MARTs. We also test for correlated evolution between MARTs and two other possibly relevant reproductive traits (male parental care, and sexual selection as assessed by the presence of male ornaments).

MATERIALS AND METHODS

We searched the published literature for accounts of the following: mating behavior including patterns of mate pairing

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and MARTs; paternity identification, primarily from genetic appraisals (Avise et al. 2002), as an indicator of cryptic MARTs; male ornaments or traits presumably indicative of sexual selection; and presence and mode of parental care.

MARTs considered here involve sneakers, satellites, female mimics, and pirates (see Introduction). We only included species that have been characterized in the current literature for mating tactics and behavior. For each characterization from the current literature, we assessed the described MART and assigned the category based on the definitions laid out in Taborsky (1994). Where a species was documented as exhibiting more than one mating tactic, all described behaviors were recorded and included in the phylogenetic analysis. Where a family included species that exhibited different tactics, or suites of tactics, each species was recorded and analyzed in the phylogenetic reconstruction. More than 150 references, available in the Supplemental Material online only at http://dx.doi.org/10.1554/06-042.1.s1, comprise this database.

The data on sexually selected traits and male parental investment were originally compiled in Mank et al. (2005) and can be accessed there. To reduce problems of ascertainment bias and repeatability, we limited our appraisal of sexually selected traits to published accounts of male ornaments repeatedly shown to be under sexual selection in various fish taxa (Mank et al. 2006). These include elongate fins (Harrington 1997; Marcus and McCune 1999; Kuwamura et al. 2000), breeding tubercles (Kortet et al. 2003, 2004), and sexual dichromatism defined as nuptial colors expressed more noticeably in males than in females (Reimchen 1989; Houde and Endler 1990; Stott and Poulin 1996; Amundsen and Forgren 2001). We omitted from our database sexually dimorphic traits such as gonopodia and body-size differences that likely result at least in part from natural selection and are thus poor proxies for the presence of sexual selection. Finally, taxa in which males tend embryos or larvae subsequent to mating were deemed for current purposes to have male parental care, whether or not female parental care was also involved.

We then mapped this information onto an actinopterygiian supertree phylogeny constructed (via matrix-representation with parsimony; Ragan 1992) from 58 previously published source cladograms which themselves had been based on molecular data or morphological evidence (Mank et al. 2005). We first estimated numbers of independent origins as well as transitions among MART character states under maximum parsimony criteria using MacClade 4 (Maddison and Maddison 2000). We then tested for patterns of correlated evolution between MARTs and other reproductively associated characters using the maximum likelihood program DISCRETE (Pagel 1994, 1997). Each statistical evaluation of correlated evolution was conducted using a likelihood ratio test of the null model of evolution (i.e., with no correlation between traits) to the alternative correlated model. Each resultant likelihood ratio test has a χ^2 distribution with four degrees of freedom (since there are four more parameters in the null model than in the correlated model; Pagel 1994).

Although DISCRETE can incorporate different branch lengths (ages of clades) into the analysis, the amalgamated nature of our supertree (as well as the limited temporal information in the original source cladograms, due in part to the limited actinopterygiian fossil record) precluded estimates of absolute divergence times. Thus, we used the standard convention (Mank et al. 2005; Weiblen et al. 2000) of coding all branch lengths in DISCRETE as equal to one.

RESULTS

We scrutinized published descriptions of mating and reproductive behaviors for 296 species in 86 taxonomic families distributed throughout the Actinopterygii. Figure 1 shows the phylogenetic distribution of MARTs based on this information, as well as the maximum parsimony reconstructions of ancestral states. For clarity of depiction, all of the assessed MARTs have been compressed into a single category in Figure 1. However, the parsimony analysis was performed with each MART behavior coded individually. Most (81%) of the taxonomic families surveyed in this analysis were monomorphic regarding male mating tactics, with all species exhibiting identical mating behaviors. Of the 16 families that showed diversity in male mating behavior, the vast majority of this diversity was comprised of different alternative mating tactics (satellite, sneaker, female mimic, pirate), or suites of tactics in different confamilial species. In other words, for families with a diversity of tactics, the diversity is due to multiple alternative tactics evolving.

Maximum parsimony reconstruction resulted in several instances of equivocal ancestral states (shown with hatched shading in Fig. 1), so the numbers provided indicate the range of evolutionary transitions spanning the minimum and maximum estimate. Our analysis suggests that various MART behaviors arose independently on at least 26–43 separate occasions during the course of actinopterygiian evolution (Fig. 2A). In 21–27 of these cases, the MART is most-parsimoniously interpreted to have evolved directly from mate monopolization, but the other 5–16 evolutionary origins for MARTs seem at face value to trace directly to group spawning (Fig. 2A). However, if we assume that distinct pairing or mate monopolization is normally a direct prerequisite for MART evolution (see Taborsky 1994, 2001), then these latter inferred transitions to MARTs might actually have entailed an intermediate but transient stage of female monopolization that was not detected in the parsimony analysis.

Inferred transitions from mate monopolization (which we henceforth assume to be a requisite ancestral state, as described above) to particular types of MARTs are shown in Figure 2B. According to maximum parsimony reconstruction, by far the most common evolutionary transition has been to sneaking (15–20 independent origins). On various occasions, sneaking was also the inferred transitional state between mate monopolization and both female mimicry (three to six evolutionary transitions) and cooperative satellite behavior (three to four evolutionary switches). The parsimony analysis also suggests that mate monopolization can progress directly to satellite and female mimic character states without involving sneaking as an intermediate stage (Fig. 2B). However, it is also possible that these latter transitions also progressed through a transitional sneaking state that subsequently was lost.

Finally, we also tested for correlated evolution between

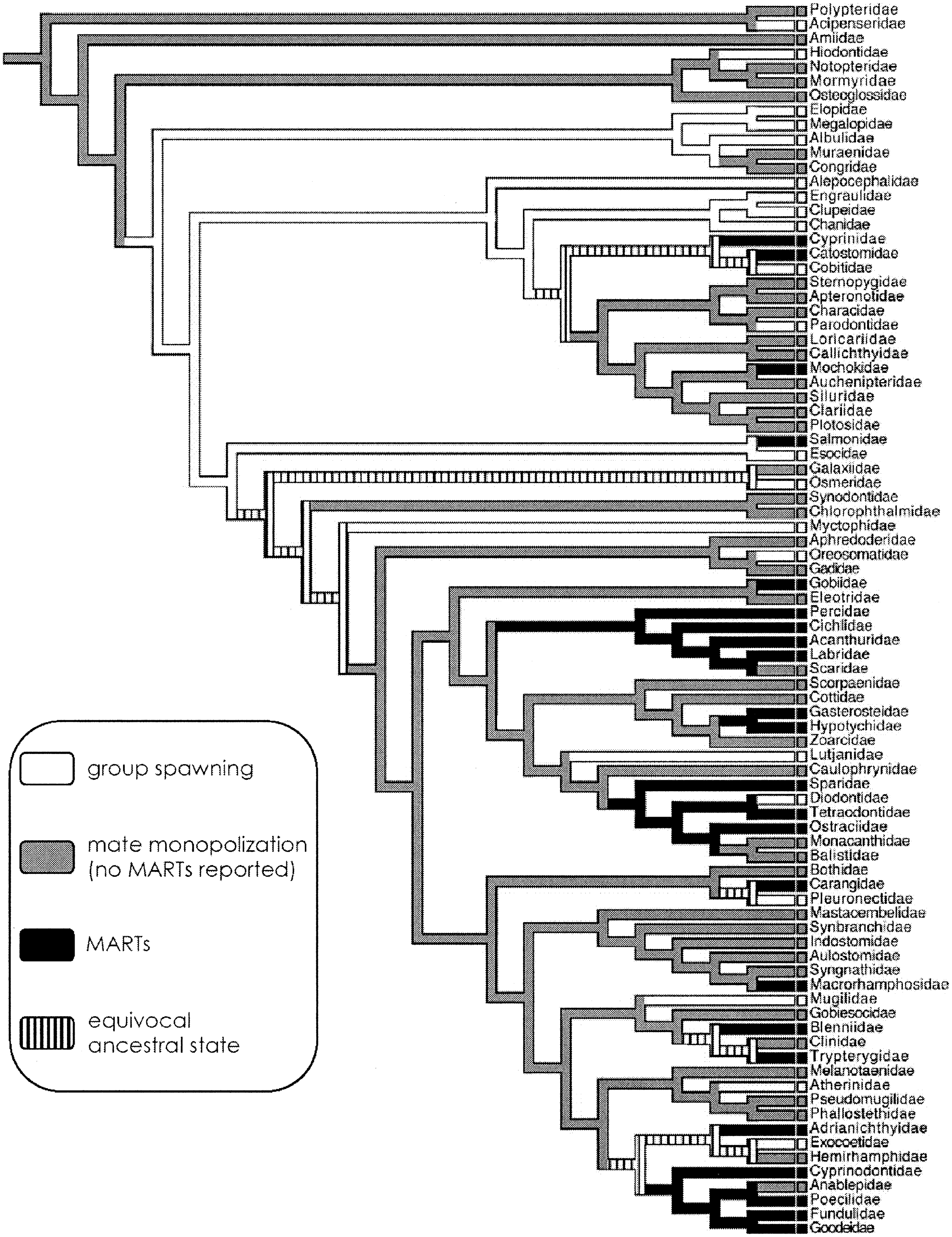

FIG. 1. Phylogenetic patterns of male alternative reproductive tactics (MARTs) in ray-finned fishes. Mapped onto the supertree phylogeny (Mank et al. 2005) are MART observations in extant species and ancestral state reconstructions by maximum parsimony criteria. For simplicity of presentation, the MART condition displayed here (as solid black branches) is any behavior in an aggregate of sneaking, piracy, female mimicry, or satellite activity. Also shown are lineages that exhibit either group spawning or some degree of mate monopolization.

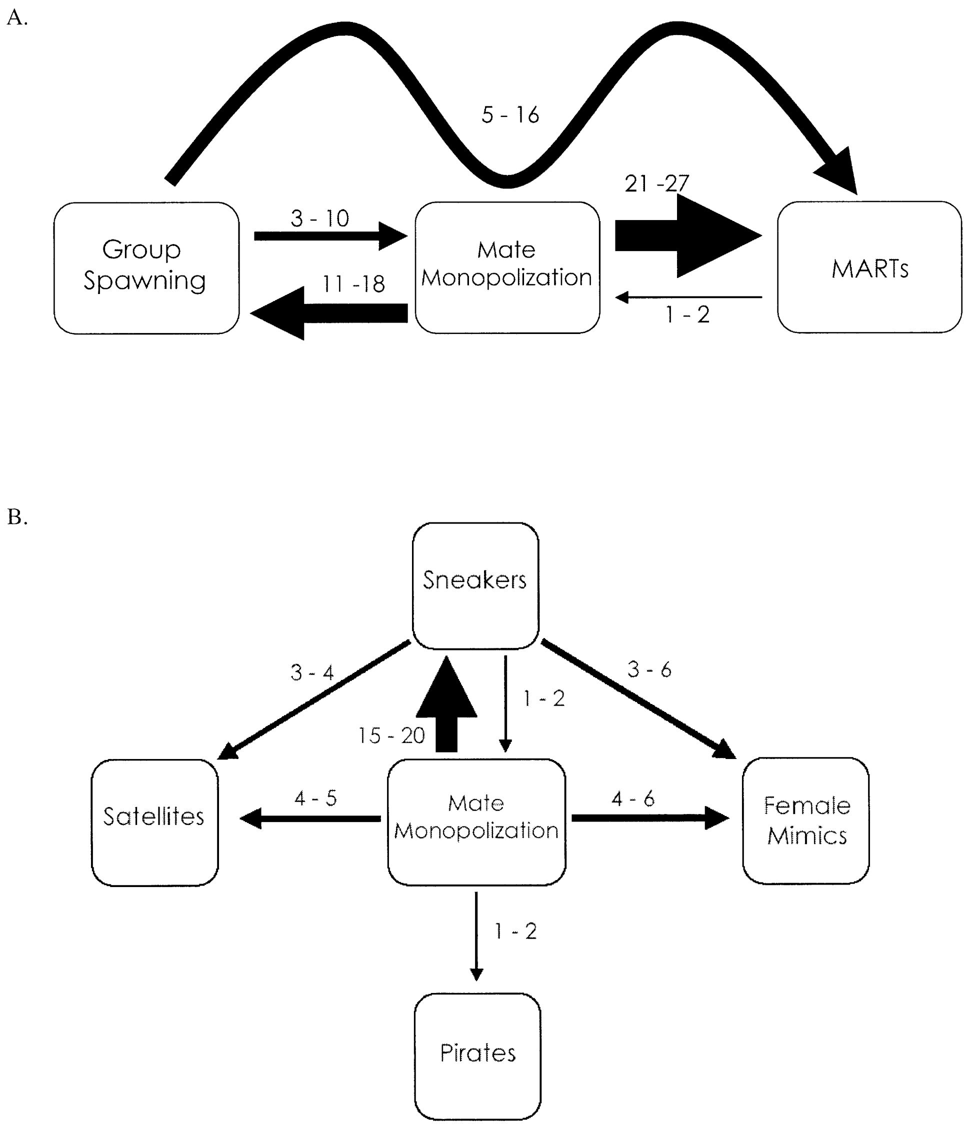

FIG. 2. Numbers of independent evolutionary transitions (as inferred from maximum parsimony criteria) among reproductive tactics in ray-finned fishes. Arrow sizes correspond to mean numbers of transitions among states; numbers beside arrows indicate minimum and maximum estimates. (A) Evolutionary transitions from group spawning to alternative MARTs in ray-finned fishes. The transition from group spawning directly to MARTs may represent transitions that went through a mate-monopolization intermediate, but were not presently detected under maximum parsimony (see text). (B) Evolutionary transitions among alternative MART character states, assuming that mate monopolization is normally the ancestral state. For clarity, only significant transitions (those in which the minimum estimate >0) are shown.

MARTs and two other reproductive traits. The presence of male parental care was not statistically associated with MART evolution (likelihood ratio = 3.44, ns.), but a significant evolutionary correlation did prove to exist between presence of male sexually selected traits and the evolutionary appearance of MARTs (likelihood ratio = 8.91, $P = 0.001$).

DISCUSSION

Our comparative phylogenetic analyses indicate that similar MARTs have arisen on numerous separate occasions during the evolution of actinopterygiian fishes. Although our current tallies of the number of evolutionary transitions will likely need revision as more published data become available to further resolve the actinopterygiian supertree, the large number of changes already inferred between MARTs clearly paints an overall picture of rapid evolutionary switches among these alternative reproductive behaviors.

How might these presumably complex behavioral pathways, some of which are genetically embedded and therefore heritable (Dominey 1980; Ryan and Causey 1989; Zimmerer and Kallman 1989; Ryan et al. 1992; Heath et al. 2002; Garant et al. 2003), have arisen so many times over the course of actinopterygiian evolution? A proximate or mechanistic answer may lie partly in the hormonal components of reproductive behavior. In a wide variety of fishes, conditional male reproductive strategies, as well as their associated morphotypes, repeatedly have been shown to be due to differential expression of the same sets of sex hormones. Endocrine analyses have identified arginine vasotocin (Foran and Bass 1998, 1999; Carneiro et al. 2003), gonadotropin-releasing hormone (Foran and Bass 1999; Bass and Grober 2001), and 11-ketotestosterone (Brantley et al. 1993; Borg 1994; Ros et al. 2004) as important hormonal controls affecting MART expression in species throughout the Actinopterygii.

Increasing evidence from comparative endocrinology also suggests that the sexual evolutionary plasticity we describe here may be due to convergent selection on these hormones (or their receptor proteins) across the clade (Knapp 2004; Fitzpatrick et al. 2005). Although definitive genetic links between differential hormonal expression and MARTs are not yet firmly established, a working hypothesis is that similar MARTs in different species may share proximate elements of endocrine expression that ultimately have evolved convergently under selection pressures for or against particular reproductive tactics, depending upon ecological circumstances (Mank and Avise 2006).

Our phylogenetic analysis, in conjunction with behavioral reasoning, also suggests that particular evolutionary pathways for MART progression predominate. As summarized in Figure 2, mate monopolization usually precedes the evolution of sneaking behavior, which in turn may often be a precursor to female mimicry and cooperative male satellite tactics. These progressions make sense, as sneaking is often a conditional strategy based on body size (Gross and Charnov 1980; Mazzoldi and Rasotto 2002; Aubin-Horth and Dodson 2004; Leiser and Itzkowitz 2004) and may require few specialized adaptations. In contrast, female mimicry (which requires that female behaviors and phenotype are decoupled from gonadal development and gamete production) and male satellite behavior (which requires the evolution of cooperation between satellites and bourgeois males) are more complex and may therefore be secondary adaptive add-ons. Because sneaking can be a purely body-size-dependent tactic and thus potentially devoid (at least initially) of a heritable genetic trigger, it may well precede the evolution of heritable mechanisms for sneaking, as well as genetic mechanisms for secondary MARTs involving female mimicry and satellite behaviors.

Interestingly, our phylogenetic analysis suggests that piracy is not a part of this progression. A combination of factors may explain this outcome. Piracy is much less common than sneaking and, being a tactic conditioned primarily on large body-size, is likely to be exhibited only late in a fish's life cycle (most actinopterygiian fish have more or less indeterminate growth in which body size continues to increase with age). The combination of rarity and late onset may reduce the effects of selection on this MART, and prevent it from being readily incorporated into the normal evolutionary pathways of MART progression. However, accounts of piracy are sparse in the scientific literature, so we cannot refute an alternative possibility that our phylogenetic analysis simply lacked the power to accurately place this MART in a clear evolutionary pathway.

Finally, the phylogenetic correlation tests revealed a statistically significant relationship between the presence of sexual selection and the presence of MARTs across evolutionary lineages. This is hardly unexpected, because the same factors that foster the evolution of sexually selected traits (namely, mate monopolization through the differential reproductive success of bourgeois males; Emlen and Oring 1977) may also promote the evolution of alternative reproductive tactics by other males to circumvent such monopolization. It is therefore surprising that we did not also observe a phylogenetic correlation between MARTs and male parental care. In a previous analysis of this clade (Mank et al. 2005), we uncovered a significant relationship between male care of offspring and the same sexually selected traits examined here, initially suggesting to us that sexual selection, MARTs, and paternal care are all intertwined forces in the evolution of fish mating systems. Our current analysis may clarify this relationship by suggesting, more basically, that MARTs are evolutionary avoidance responses to the costly investments by bourgeois males in mate monopolization (rather than an avoidance of male brood care per se). Such costs of mate monopolization may often include the maintenance of sexually selected traits, defense of territories, and attraction of females.

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