

Correlated Evolution of Sex Allocation and Mating System in Wrasses and Parrotfishes

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ABSTRACT: In accordance with predictions of the size-advantage model, comparative evidence confirms that protogynous sex change is lost when mating behavior is characterized by weak size advantage. However, we lack comparative evidence supporting the adaptive significance of sex change. Specifically, it remains unclear whether increasing male size advantage induces transitions to protogynous sex change across species, as it can within species. We show that in wrasses and parrotfishes (Labridae) the evolution of protogynous sex change is correlated with polygynous mating, and that the degree of male size advantage expressed by polygynous species influences transitions between different types of protogynous sex change. Phylogenetic reconstructions reveal strikingly similar patterns of sex allocation and mating system evolution with comparable lability. Despite the plasticity of sex-determination mechanisms in labrids, transitions trend toward monandry (all males derived from sex-changed females), with all observed losses of protogyny accounted for by shifts in the timing of sex change to prematuration. Likewise, transitions in mating system trend from the ancestral condition of lek-like polygyny toward greater male size advantage, characteristic of harem polygyny. The results of our comparative analyses are among the first to confirm the adaptive significance of sex change as described by the size-advantage model.

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Keywords: Labridae, polygynous mating, phylogenetic comparative method, protogynous hermaphroditism, size-advantage model, Teleostei.

Introduction

Sequential hermaphroditism is a reproductive strategy with multiple evolutionary origins distributed sporadically across the tree of life (Policansky 1982; Sadovy de Mitcheson and Liu 2008). It is characterized by a change in the functional expression of sex, from one to the other. Among vertebrates,

sequential hermaphroditism is known only in teleosts (Todd et al. 2016), where sex change can be male to female (protandry), female to male (protogyny), or serial bidirectional. Each form of sequential hermaphroditism has evolved multiple times within teleosts, demonstrating the lability of fish sex-determination mechanisms (Smith 1975; Charnov 1982; Policansky 1982; Mank et al. 2006).

The dominant theory describing the adaptive significance of sequential hermaphroditism is the size-advantage model (SAM; Ghiselin 1969; Warner 1975; Leigh et al. 1976; Charnov 1982). The model contends that sex change is favored when the rate of increase in reproductive value with size and age differs between the sexes. Correspondingly, gonochorism (the existence of separate, fixed sexes) is predicted when size-specific male and female reproductive outcomes do not differ (Warner 1975; Muñoz and Warner 2003, 2004). A range of complex, interacting factors capable of contributing to differences in reproductive value between the sexes, including aspects of population demography, life history, social system, and the local environment, have been integrated into the SAM (Charnov 1982; Warner 1988; reviewed in Avise and Mank 2009). Of these, mating behavior has emerged as an important determinant of size-related differential reproductive outcomes (Shapiro 1987; Ross 1990; Munday et al. 2006a). This is because certain mating systems are also contingent on male size advantage.

For example, protogyny, the most prevalent form of sequential hermaphroditism in fishes (Sadovy de Mitcheson and Liu 2008; Todd et al. 2016), is predicted to be adaptive when reproductive value increases with size faster in males than in females (Warner 1975; Leigh et al. 1976). Protogynous species can be either monandric, in which case all males are derived from sex-changed females, or diandric, in which case males are either born into the population or derived from sex-changed females (see fig. 1 for definitions). Sex-based size asymmetry is also characteristic of polygynous mating, where males use their size advantage to monopolize access to females by guarding them or the resources

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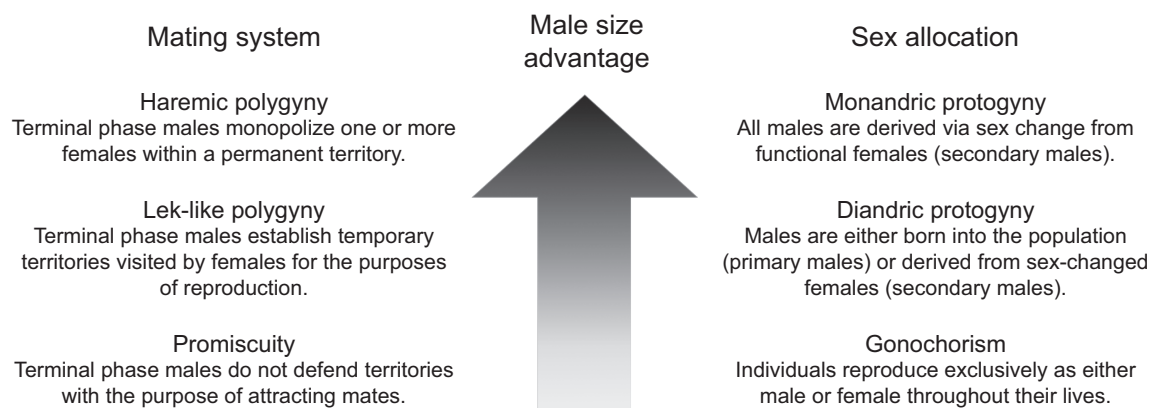


Figure 1: Types of mating and sex allocation systems expressed by labrid fishes, their definitions, and predicted associations with the degree of male size advantage. As male size advantage increases from promiscuous mating to lek-like polygyny, selection is predicted to favor transition from gonochorism to diandric protogyny. Likewise, as male size advantage increases from lek-like to haremic polygyny, selection should favor transitions from diandric to monandric protogyny. Definitions are from Warner and Robertson (1978), Colin and Bell (1991), and Sadovy de Mitcheson and Liu (2008).

on which they depend (Ghiselin 1969; Taborsky 1998). This behavior results in large males having a reproductive advantage over females and small males, thereby enabling selection for protogynous sex change (Warner 1975, 1984, 1988). Polygynous mating can include haremic systems, where a single male monopolizes and mates with one (Pitcher 1993) or more females within a defined permanent territory, and lek-like systems, where males establish temporary territories that are visited by females for the purpose of reproduction. As mating becomes more promiscuous, sperm competition increases, and the reproductive advantage of large males decreases because of the dilution of gametes by other males, consequently reducing selection for protogyny (Warner 1975).

When large males have strong social control over females (i.e., male size reflects dominance or social status), as in haremic systems, monandric protogyny is predicted (Robertson and Choat 1974; Robertson and Warner 1978; Warner and Robertson 1978; Warner 1984; Nemtsov 1985). In lek-like systems where the social control of large males is reduced, primary males are able to realize reproductive success, and selection should favor diandric protogyny (Robertson and Choat 1974; Emlen and Oring 1977; Robertson and Warner 1978; Warner and Robertson 1978). Correspondingly, gonochorism is predicted when males lose social control, as in promiscuous mating behaviors such as group spawning (Robertson and Warner 1978; Warner 1984; Hoffman 1985). Qualitative assessments of mating behavior support its role as a primary determinant of the degree of size advantage and, consequently, of the incidence and direction of sequential hermaphroditism in fishes (Warner 1984; Ross 1990; Munday et al. 2006a; Erisman et al. 2013).

Population demographic studies and observations of mating dynamics within species provide empirical support for the influence of mating behavior on sex allocation as predicted by the SAM (Robertson 1972; Warner and Robertson 1978; Warner and Hoffman 1980a; Fukuda et al. 2017). Phylogenetic comparative studies have shown that the loss of protogyny is contingent on weak size advantage (Kazancıoğlu and Alonzo 2010) and group spawning (Erisman et al. 2009). However, no comparative studies have supported predictions about the adaptive significance of protogynous sex change. Specifically, we lack comparative evidence showing that as size advantage increases, and large males have greater opportunity to monopolize mating, protogynous sex change evolves. Many aspects of an organism's biology, demography, and ecology have the potential to affect the expression of complex traits such as mating system and sex allocation. Moreover, behavioral traits tend to be more evolutionarily labile than life-history traits (Blomberg et al. 2003). It remains unknown whether variation in the degree of male size-advantage characteristic of specific types of polygynous mating induces evolutionary transitions to and within types of protogynous sex change in the context of other influential factors. Do the effects of mating behavior on sex allocation observed within species scale up to macroevolutionary patterns?

The wrasses and parrotfishes, along with cales and weed-whittings (Labridae) provide an ideal opportunity to evaluate the evolutionary synergy between sex allocation and mating behavior along a spectrum of male size advantage (fig. 1). The Labridae form a monophyletic assemblage (Westneat and Alfaro 2005) comprising one of the largest families of marine fishes, with a global distribution spanning

tropical and temperate waters. Extensive scientific interest in labrid mating and sex systems has produced some of the most influential insights into the adaptive significance of sequential hermaphroditism (Darwin 1871; Ghiselin 1969; Robertson 1972; Robertson and Choat 1974; Warner 1975; Warner et al. 1975; Leigh et al. 1976; Muñoz and Warner 2004), as well as many observations that both support and contradict predictions of the SAM (Robertson and Warner 1978; Warner 1984; Nemtsov 1985; Warner and Lejeune 1985; Cowen 1990; Morrey et al. 2002; Adreani et al. 2004; McBride and Johnson 2007). The most comprehensive comparative analysis to date of the SAM focused on labrids, whereby the authors combined mating behavior with other phenotypic traits, including color, to quantify male size advantage as either strong or weak (Kazancıoğlu and Alonzo 2010). They found that protogyny is less likely to be lost under strong size advantage but did not find evidence that strong size advantage induces transitions from gonochorism to protogyny. Incorporating variation within polygyny and protogyny will provide more detail about the evolutionary dynamics between mating behavior and sex allocation and allow us to assess the effects of each trait regime on the adaptive evolution of the other.

As a result of considerable past research efforts, labrid mating and sex systems are comparatively well quantified. Protogynous sex change is pervasive among labrids and has been reconstructed as the ancestral condition (Sadovy de Mitcheson and Liu 2008; Kazancıoğlu and Alonzo 2010; Erisman et al. 2013). Labrid species express both types of protogyny—monandry and diandry—the origins of which have yet to be inferred in the context of a time-calibrated phylogeny. The family also includes some gonochoristic species. Mating systems are equally as diverse; some species maintain harems, other species exhibit lek-like polygyny, and other species mate promiscuously with no territory defense by males for the purpose of attracting mates. Finally, robust phylogenetic hypotheses exist that include more than half of the nominal labrid species, with opportunities to expand the taxonomic representation of species arising frequently.

We are now in a position to explore the evolutionary history of and synergy between mating behavior and sex allocation in wrasses and parrotfishes along a continuum of male size advantage. We use Bayesian methods to reconstruct the evolutionary history of each trait in the context of a new, taxonomically expanded phylogeny, and apply discrete trait comparative methods to test predicted associations between specific types of protogynous sex change and polygynous mating with distinct degrees of male size advantage. In doing so, this work broadens our understanding of the interplay between reproductive and social systems on a macroevolutionary scale.

Material and Methods

Phylogenetic Inference and Divergence Time Estimation

To account for evolutionary relatedness among labrid species, we reconstructed their phylogenetic relationships using a molecular data set consisting of four mitochondrial (12S, 16S, COI, and CytB) and three nuclear loci (RAG2, TMO4c4, and S7), with a total of 4,578 base pairs. Sequence data were compiled from GenBank for all available nominal species—at the time of sampling this included 403 species from 74 genera, and two outgroup taxa (see table S1 for accession numbers and table S2 for information on molecular sampling; tables S1–S7 are available online). Methods used in tree construction and divergence time estimation are presented in section 1 of the supplemental PDF, along with the results and discussion.

Trait Data Compilation

We compiled data on species-specific mating systems and sex allocation pathways from the primary literature (fig. 1; table S5; deposited in the Dryad Digital Repository: <https://doi.org/10.25338/B8GC91>; Hodge et al. 2020). Mating system classifications focused only on terminal-phase males and did not consider the mating strategies of initial-phase males—although it is known that the reproductive output of initial-phase males can outweigh that of terminal-phase males for some species dependent on location-specific population dynamics (Warner and Hoffman 1980a, 1980b; Warner 1982). We applied the consensus classification of the predominant mating system (i.e., supported by multiple authors) whenever possible and otherwise relied on the most recent observations. We restricted sexual ontogeny data to accounts of protogyny that were distinguishable as either monandric or diandric based on gonad histology or population demographics, or both. Cases where males are derived from females that have not passed through a functional stage were categorized as functionally gonochoristic following previous work (Sadovy and Shapiro 1987; Sadovy de Mitcheson and Liu 2008; Kazancıoğlu and Alonzo 2010; Erisman et al. 2013). Mating system and sex-change data were available for 89 labrid species (table S5).

Ancestral State Reconstruction

We reconstructed the evolutionary history of sex allocation and mating system using the MultiState package implemented in BayesTraits version 3.0.1 (Pagel et al. 2004; Pagel and Meade 2006). We fit continuous-time Markov models to each set of discrete character data using a reversible-jump Markov chain Monte Carlo (rjMCMC) analysis to derive posterior distributions of the ancestral state and transition rates. An exponential reversible jump

q3 hyperprior (0 10) was specified for the rate parameter distributions, and the trees were scaled to have a mean branch length of 0.1. Markov chains were run three times across a random sample of 1,000 time-calibrated phylogenies (deposited in the Dryad Digital Repository: <https://doi.org/10.25338/B8GC91>; Hodge et al. 2020) for 4 million iterations, sampling every 4,000 steps, following a burn-in of 1 million iterations. We monitored the average acceptance rates to ensure that the values were between 20% and 40%, indicating that the rjMCMC was mixing well. We examined traces of the likelihood and parameters in Tracer version 1.5 (Rambaut et al. 2009) to ensure convergence and effective sample sizes ($ESS > 200$) across the three independent runs. Parameter summary statistics were calculated from the concatenated estimates of three converged runs.

To visualize the evolutionary history of each trait, we also performed ancestral state reconstructions as described above on the maximum clade credibility (MCC) tree and calculated the average posterior probabilities of each character state at each node in the phylogeny (fig. 2). Transitions in character states were defined as nodes with posterior probability values ≥ 0.50 in support of a transition relative to a preceding node (i.e., a direct ancestor) with posterior probability ≥ 0.50 for a different state and included changes along terminal branches. We summarized the number, location, and nature of these transitions.

Trait Correlations

To test whether increasing male size advantage results in transitions to protogynous sex change, we compared the fit of independent and dependent models of trait evolution using the Discrete package implemented in BayesTraits version 3.0.1 (Pagel et al. 2004; Pagel and Meade 2006). The independent, or null, model of evolution assumes that there is no correlation between two traits and that they evolved independently. The dependent model describes the correlated evolution of two traits such that the rate of change in one trait depends on the state of the other trait. As Discrete accepts only binary trait data, we performed two tests: the first test used the full data set ($n = 89$ species) to assess the correlation between polygyny and protogyny (species coded as either promiscuous or polygynous and gonochorous or protogynous); the second test used a reduced data set that included only species that are both polygynous and protogynous ($n = 70$ species) to assess predicted correlations between the two traits based on different degrees of male size advantage (species coded as either lek-like or harem and diandric or monandric).

Models were fit using the same set of 1,000 trees, number of generations, sampling frequency, burn-in, and hyper-

prior specifications as the MultiState analysis described above. Run diagnostics of the acceptance rates, likelihood, and parameter traces were also performed as above. We determined the most probable evolutionary model by calculating log Bayes factors (BFs) for each pair of models as twice the difference in the log marginal likelihood of the dependent model minus the independent model (Kass and Raftery 1995). Marginal likelihoods were estimated using the stepping-stone sampler (Xie et al. 2011) implemented in BayesTraits version 3.0.1 (Pagel et al. 2004; Pagel and Meade 2006), where each independent run sampled 100 stones, each with 10,000 iterations. Log BFs were averaged across independent runs. The log BF quantifies the weight of evidence against the null hypothesis (the independent model) whereby values > 2 indicate little evidence, values from 2 to 5 indicate positive evidence, and values > 5 indicate strong evidence for the dependent model over the independent model (Raftery 1996). We calculated z -scores for each transition parameter as the proportion of transitions assigned to 0 across the three independent, concatenated runs. The z -score provides an additional descriptor of the likelihood distribution of the transition rate. Low z -scores indicate that transitions were rarely assigned to 0 and are likely to occur, whereas z -scores close to 1 describe transitions that were frequently assigned to 0, indicating that they are unlikely to occur.

Results

Evolutionary History of Sex Change and Mating System

Bayesian analyses indicated that the ancestral labrid mating system was most likely lek-like polygyny (average posterior probability = 0.57, 95% highest posterior density [HPD] interval: 0.3–1) but did not resolve the ancestral sex allocation pathway, as all three possible states had comparable posterior probabilities of ~ 0.33 (fig. 2). Twenty-six transitions were recovered from Bayesian analyses of the MCC tree for both mating system and sex allocation. Nine of the 26 transitions in mating system occurred at the nodes and 17 occurred along terminal branches. Transitions out of lek-like polygyny (61.5%) and to harem polygyny (42.3%) were the most frequent. Ten of the 26 transitions in sex allocation occurred at the nodes and 16 occurred along terminal branches. Transitions out of diandric protogyny (61.5%) and to monandric protogyny (65.4%) were the most frequent.

Transitions in mating system and sex allocation are tightly coupled. The effectively equal number of state-dependent transitions summarized on the MCC tree provide little resolution regarding the predominant effects of one trait regime over the other. Focusing on predicted

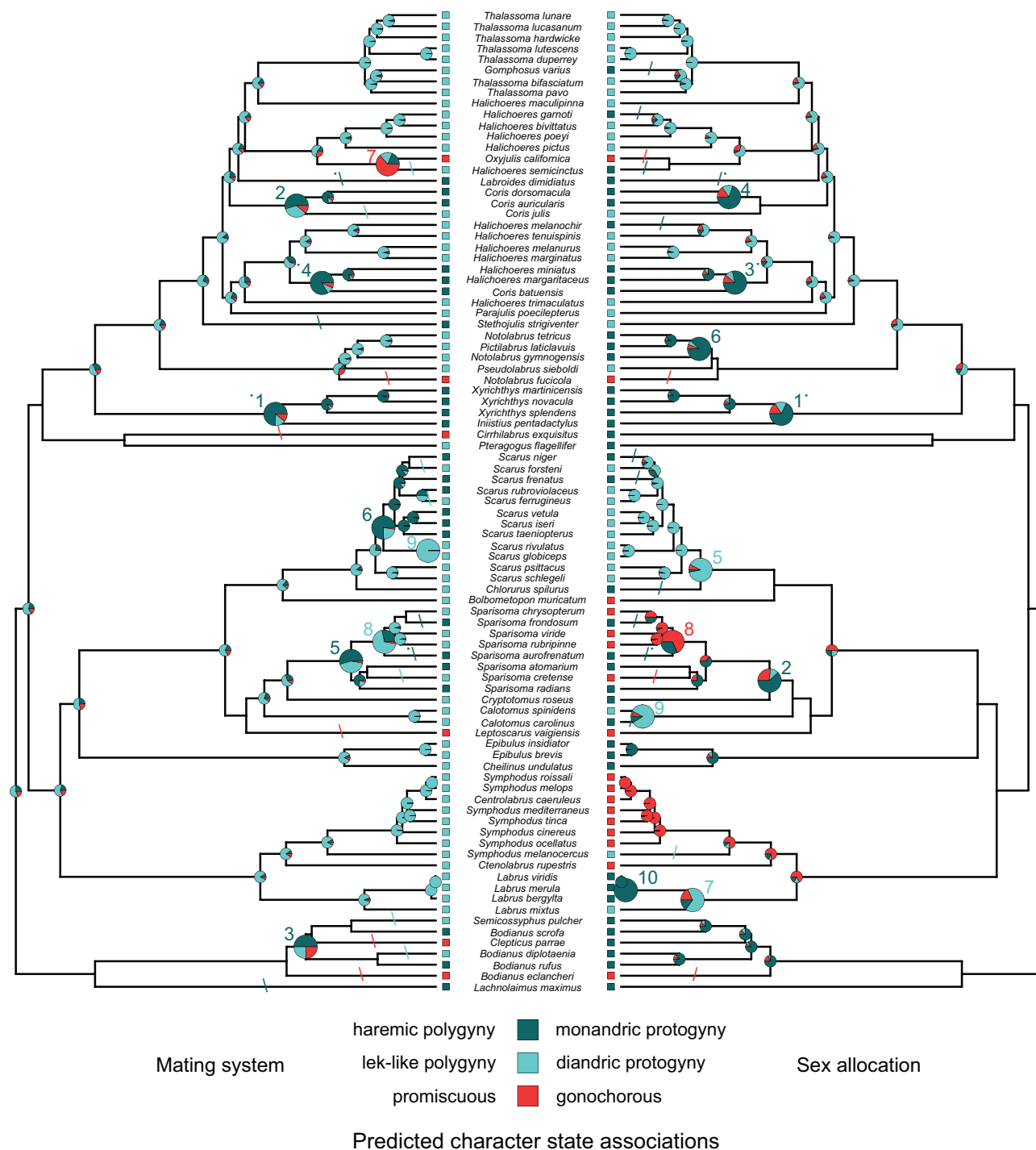


Figure 2: Bayesian reconstructions of the evolutionary history of mating system and sex allocation. Character states that share colors correspond to predicted associations. Pie charts at nodes are only shown for ancestral states resolved with ≥ 0.50 posterior support (i.e., the probability of one of the three-character states is ≥ 0.50 , conditional on the data). Enlarged pie charts indicate evolutionary transitions, defined as nodes with posterior probability values ≥ 0.50 in support of a transition relative to a preceding node with posterior probability ≥ 0.50 for a different state, and are numbered chronologically. Evolutionary transitions along terminal branches are indicated by dashes at the midpoint of the terminal branch. In the interest of visual clarity, these transitions are not numbered. Dots next to numbers and dashes indicate simultaneous transitions to states with predicted associations. Data and tree files have been deposited in the Dryad Digital Repository (<https://doi.org/10.25338/B8GC91>; Hodge et al. 2020).

character-state associations, we recovered seven state-dependent transitions in mating system (i.e., where mating system transitions to the predicted state given the state of sex allocation; nodes 1, 2, and 5; tip transitions 6, 10, 11, and 15) and eight in sex allocation (i.e., where sex allocation transitions to the predicted state given the mating system state; nodes 1, 4, 6, and 10; tip transitions 2, 8, 9, and 14), with another seven simultaneous transitions where mating system and sex allocation transition at the same node or along the same terminal branch (indicated by dots next to numbers and dashes in fig. 2).

From the Bayesian analyses of 1,000 tree topologies, transitions between lek-like and harem polygyny had the highest rates and likelihoods (fig. 3). Promiscuity evolved with a higher rate and likelihood among lineages with harem polygyny, but for harem lineages, transitions to promiscuity were less likely than reversals to lek-like polygyny. For sex allocation, transitions to monandric protogyny had the highest rates and likelihoods (fig. 4). Transition rates between gonochorism and monandric protogyny are high in both directions, while transitions to and from diandric protogyny are unidirectional. Specifically, transitions to diandric protogyny rarely occur among monandric lineages and diandric lineages rarely transition to gonochorism. Transition rates and likelihoods are summarized in figure 5 for both mating system (fig. 5A) and sex allocation (fig. 5B).

Evolutionary Correlations

Bayesian analyses show strong support for the correlated evolution of polygynous mating and protogynous sex change (average log BF = 5.83; fig. 6A; table S7). Protogynous sex change is lost at a lower rate and with lower probability among polygynous lineages than those that are promiscuous (91.6% of posterior samples had lower transition rates under polygynous mating). Polygynous lineages transition to protogynous sex change at a higher rate and with greater probability than those that are promiscuous (51.0% of posterior samples had higher transition rates under polygynous mating). Transitions between promiscuous and polygynous mating showed some dependence on the state of sex allocation—specifically, protogynous lineages transitioned to polygyny at a higher rate than gonochorous lineages, but only 41.2% of posterior samples reflected this state-dependent rate difference.

Specific types of polygynous mating and protogynous sex change are also evolutionarily correlated as predicted by the SAM (average log BF = 3.52; fig. 6B and table S7). Harem lineages transition from monandric to diandric protogyny at a lower rate and with lower probability than those with lek-like polygyny (80.9% of posterior samples had lower transition rates under harem mating). How-

ever, transitions to monandry occurred at similar rates and with similar probability among lineages with either type of polygynous mating (94.8% of posterior samples had similar probabilities under each type of polygynous mating). Finally, the state of sex allocation does have some effect on the rate of transition between different types of polygynous mating, whereby diandric lineages revert to lek-like mating at a higher rate than monandric lineages, but only 42.8% of posterior samples reflect this state-dependent rate difference.

Discussion

Evolutionary patterns of mating behavior and sex allocation across species of wrasses and parrotfishes are consistent with intraspecific patterns (Robertson 1972; Warner and Robertson 1978; Warner and Hoffman 1980a; Fukuda et al. 2017) and predictions of the SAM (Robertson and Choat 1974; Robertson and Warner 1978; Warner and Robertson 1978; Warner 1984). Our results confirm that protogynous sex change is less likely to be lost under polygynous mating where male size advantage is stronger (Erisman et al. 2009, 2013; Kazancıoğlu and Alonzo 2010) and provide some of the first comparative evidence to support the adaptive evolution of protogynous sex change with increasing male size advantage. As male control over reproductive access to females increases from promiscuous to polygynous mating, so too does the size-dependent reproductive output of males relative to females, resulting in transitions from gonochorism to protogyny (fig. 6A). We also find that specific types of polygynous mating and protogynous sex change have coevolved (fig. 6B), following predictions of the SAM (Robertson and Choat 1974; Robertson and Warner 1978; Warner and Robertson 1978; Warner 1984). Our results support mating behavior as an important driver of transitions in sex allocation, with limited support for effects of sex allocation on mating behavior. The tight evolutionary coupling of the two trait regimes is likely facilitated by the labile nature of sex determination in fishes, allowing it to be less phylogenetically patterned than other life-history or physiological traits (Blomberg et al. 2003). Despite the lability of sex allocation, we found that monandric lineages rarely transition directly to diandric protogyny, instead transitioning through functional gonochorism on the pathway from monandry to diandry. The overarching evolutionary trend in labrid fishes is toward monandric protogyny and harem polygyny.

Lek-like polygyny can be traced back to the origin of the Labridae—as the estimated ancestral state with a high rate of reversal (figs. 2, 3, 5), it appears to be evolutionarily stable with the potential to affect detectable change in related traits. Early labrid lineages transitioned predominantly

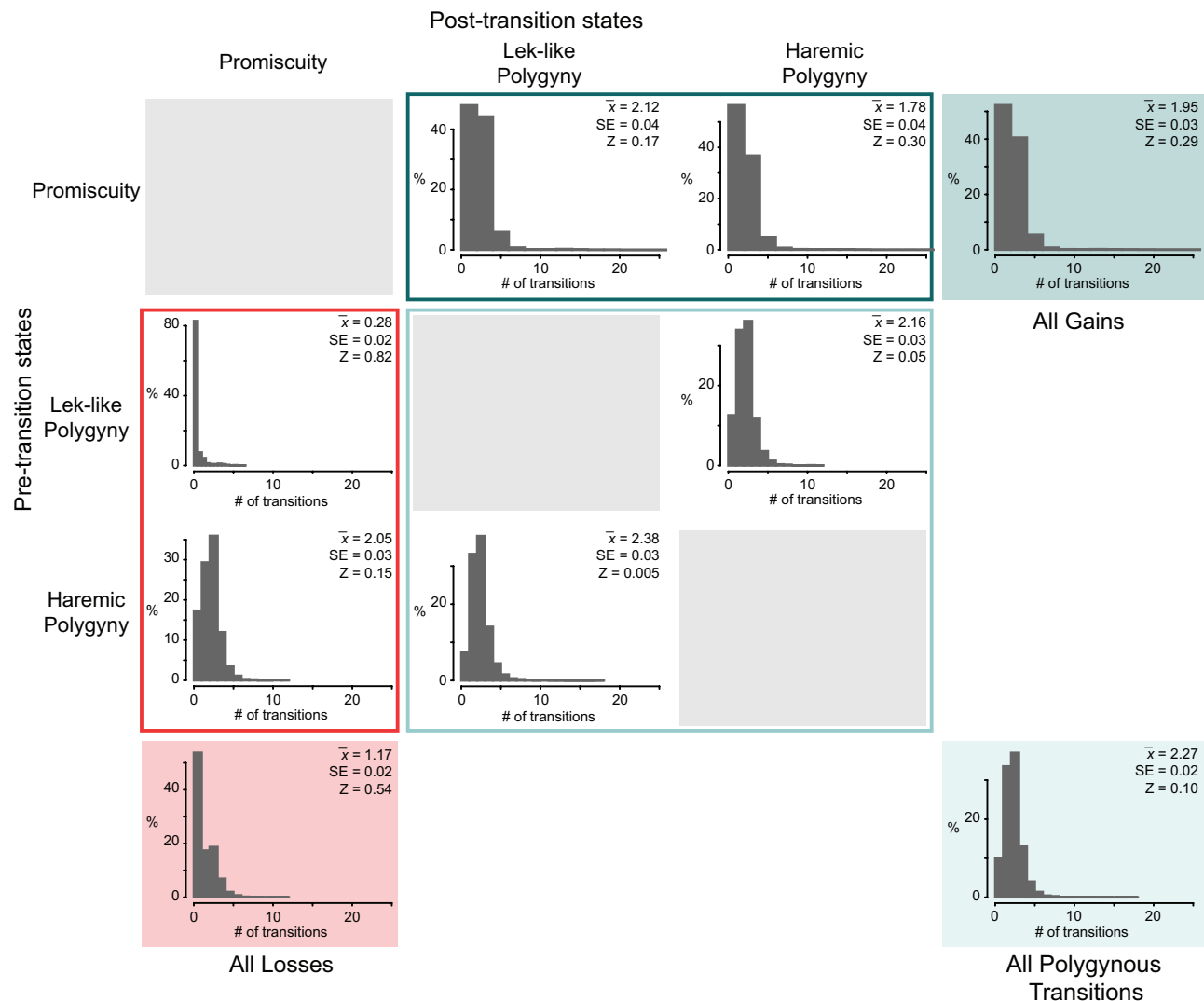


Figure 3: Probability distributions of rate coefficients conditional on the data (posterior probability distributions) characterizing transitions in mating system, estimated from 1,000 trees sampled from the Bayesian posterior distribution of trees. Sample means (\bar{x}), standard errors (SE), and z-scores are provided for each type of transition. All transitions to polygynous mating are summarized in All Gains (dark green boxes), all transitions to promiscuity are summarized in All Losses (red boxes), and all transitions between lek-like and haremic polygyny are summarized in All Polygynous Transitions (light green boxes).

to haremic polygyny, which is estimated to have arisen as early as 45.7 Ma (95% HPD: 55.5–38.6) along the lineage leading to the most recent common ancestor of the Novaculini (earlier transitions are also possible, specifically after the initial split of the Hypsigenyini [56.3 Ma; 95% HPD: 55.5–38.6] along the branch leading to *Lachnolaimus maximus*). In contrast, most transitions to promiscuous mating occur along much shallower, terminal branches, suggesting that for labrids this type of mating system may be less evolutionarily stable. Furthermore, Bayesian analyses show that promiscuous mating is more likely to arise from haremic polygyny than from lek-like polygyny (figs. 3, 5A), suggesting

that promiscuity is a secondarily derived state. However, lineages that exhibit haremic polygyny are more likely to revert back to lek-like polygyny than they are to transition to promiscuity. This is concurrent with the expectation that differential dominance relationships between males will form when access to females cannot be controlled (Emlen and Oring 1977).

Protogyny was previously reported as ancestral among labrids (Sadovy de Mitcheson and Liu 2008; Kazancıoğlu and Alonzo 2010; Erisman et al. 2013). Here we distinguished between the different types of protogyny (monandric and diandric) but were not able to resolve the ancestral

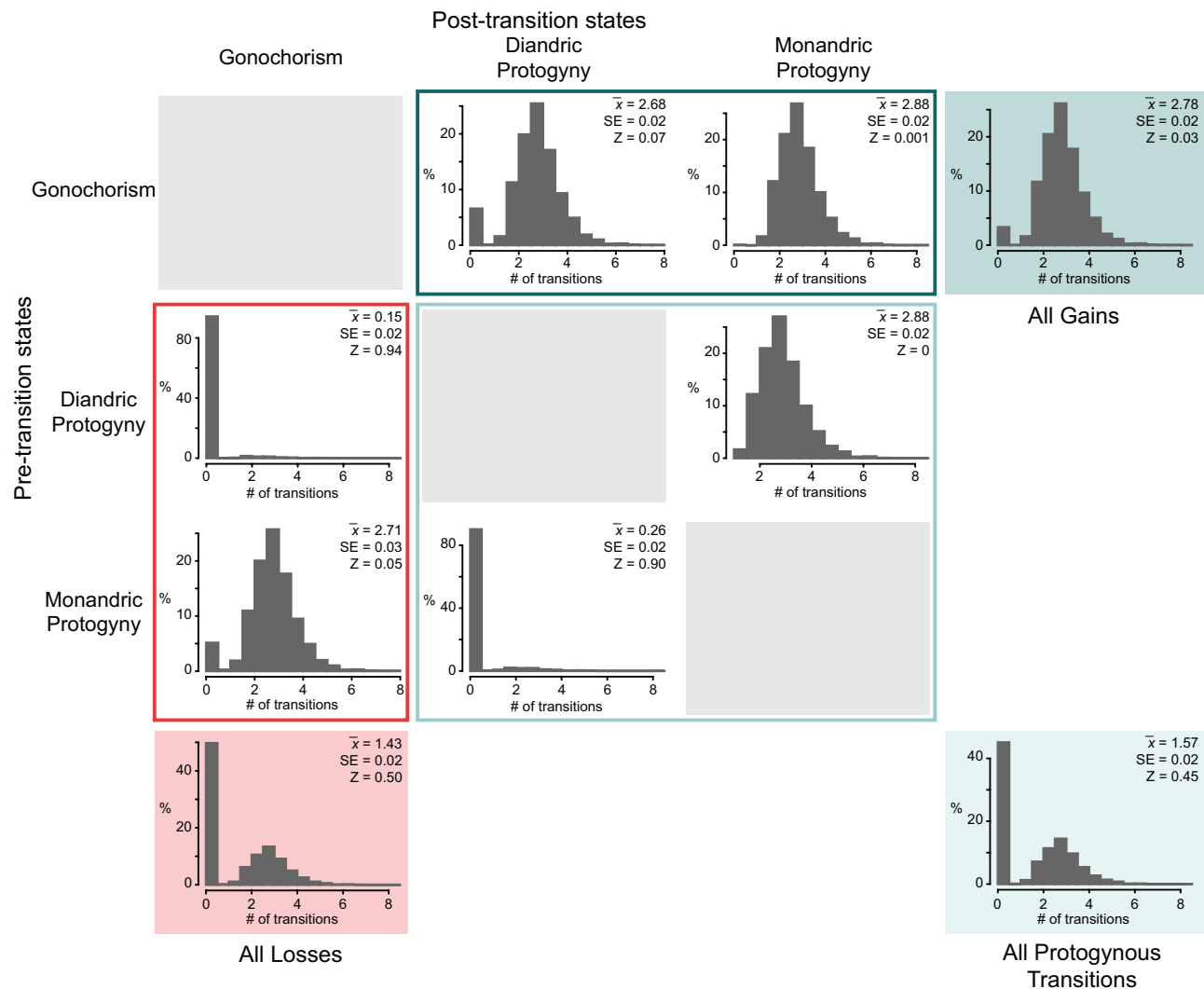


Figure 4: Probability distributions of rate coefficients conditional on the data (posterior probability distributions) characterizing transitions in sex allocation, estimated from 1,000 trees sampled from the Bayesian posterior distribution of trees. Sample means (\bar{x}), standard errors (SE), and z-scores are provided for each type of transition. All transitions to protogynous sex change are summarized in All Gains (dark green boxes), all transitions to gonochorism are summarized in All Losses (red boxes), and all transitions between diandric and monandric protogyny are summarized in All Protogynous Transitions (light green boxes).

condition. Our result is based on the limited number of species for which sex allocation pathways are known; as this number increases, so too may our ability to resolve the ancestral condition. The Novaculini and Julidini shared a diandric common ancestor ~ 45.7 Ma (95% HPD: 55.5–38.6)—the earliest sex-allocation pathway reconstructed with confidence (fig. 2). Gonochoristic ancestors were reconstructed for other major clades including the Scarini and the Labrini (respective divergence time estimates: 28.3 Ma; 95% HPD: 35.0–23.2 and 23.5 Ma; 95% HPD: 30.0–18.8), while monandric protogyny emerged later in the evolutionary history of labrids, constituting the earliest reconstructed

transitions (fig. 2). More broadly, transitions to monandric protogyny occurred with the highest overall rates (fig. 4).

High transition rates between gonochorism and monandry (figs. 4, 5B) lend more support to the ephemeral or nonexistent nature of intermediate states in such transitions (Erisman et al. 2013) and show that diandry is not a necessary intermediate. Interestingly, transitions between gonochorism and monandry were largely restricted to one clade, the Sparisomatinae (fig. 2). All of the lineages that experienced such transitions (with the exception of the lineage preceding *Leptoscarus vaigiensis*) gave rise to extant species that are purportedly functionally

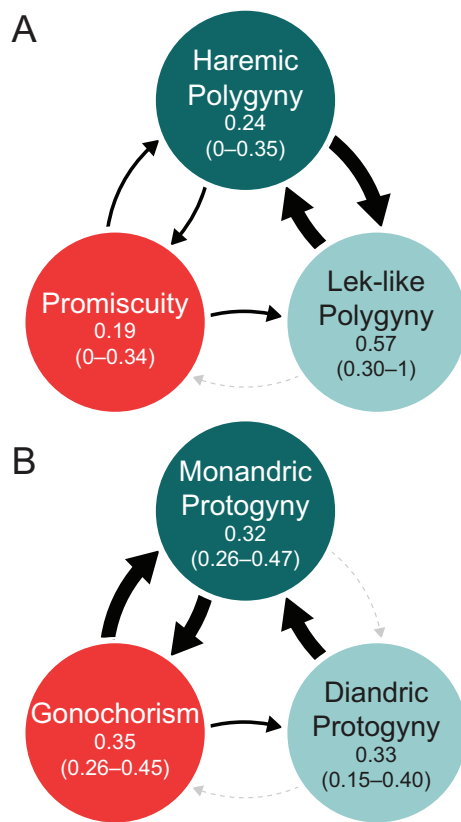


Figure 5: The likelihood of transitions between mating system (A) and sex allocation (B) character states, summarizing the data presented in figures 3 and 4. Relative transition probabilities, calculated as the proportion of iterations with a transition rate of 0 (z -score), are indicated by line weight, where thick solid lines represent z -scores ≤ 0.05 , thin solid lines represent $0.49 > z > 0.06$, and dashed lines represent z -scores ≥ 0.5 . Line color indicates the rate class to which rate coefficients were assigned most frequently. Similar rate coefficients are assigned to the same rate class (integers beginning with 0), where z indicates a rate coefficient assigned to 0. Rates assigned to z are shown in gray, and rates assigned to 0 are shown in black. Below each character state, the posterior probability of reconstructing that state as ancestral is shown (average and 95% highest posterior density interval).

gonochoristic, whereby males are derived from females that have not passed through a functional stage (Sadovy and Shapiro 1987; Sadovy de Mitcheson and Liu 2008). We note that simply because individuals are capable of prematurational sex change does not necessitate that all males be derived in this way. Some individuals could undergo postmaturational sex change, and the overall interval for sexual differentiation may span pre- and post-maturation (Kazancıoğlu and Alonzo 2010). In this case, sex allocation would be more akin to diandric protogyny (Robertson et al. 1982; Munday et al. 2006b). Two observations support the existence of diandry in several of these

species: smaller testes size of terminal-phase males relative to initial-phase males (Robertson and Warner 1978)—a common characteristic of other diandric species (Molloy et al. 2007)—and polygynous lek-like mating.

Regardless of the nature of these transitions, our results show that once lineages evolve the ability of some or all individuals to function first as females and later as males, they rarely lose it. Transitions trend away from diandry toward monandric protogyny (fig. 5B), suggesting that when sustainable, labrids likely incur considerable fitness benefits by functioning first as females (or considerable fitness costs by not doing so). Labrids, like most other teleost fishes exhibit remarkably labile sex-determination mechanisms (Munday et al. 2006a; Kuwamura et al. 2007; Kiewek-Martínez et al. 2010; Avise 2011), where the timing of sexual differentiation is an important driver of variation (Warner 1984; Kazancıoğlu and Alonzo 2010). Despite this flexibility in sex determination and the existence of opportunities throughout their evolutionary history to exercise it, labrids hardly do so in favor of pathways alternative to sex-changed males.

Results of the evolutionary correlation analyses show a greater effect of mating system on sex allocation than the reverse (i.e., 3/4 transition rates and/or probabilities are dependent on mating system, and 2/4 are dependent on sex allocation; fig. 6). The SAM predicts that strong social control over females will provide males with the greatest size advantage, thus enabling the strongest selection for protogyny (Robertson and Choat 1974; Warner 1975, 1984; Emlen and Oring 1977; Robertson and Warner 1978; Warner and Robertson 1978). In harem polygyny, dominant males are able to control the mating and sex change of subordinate females (Robertson and Choat 1974; Nemtsov 1985; Lutnesky 1994; Morrey et al. 2002). Because of this strict social control, nondominant primary males are evolutionarily unfit—they are unable to gain access to females for reproduction—and harem species are predicted to exhibit monandric protogyny (Robertson and Choat 1974). This line of reasoning explains how the expression of harem polygyny can induce change in sex allocation to monandric protogyny.

Indeed, we recovered this pattern of character change for the clade containing *Coris julis* and its close congeneric relatives (fig. 2; see node 2 on the mating system character map and node 4 on the sex-allocation character map). In contrast, at the base of the *Sparisoma* clade it appears that monandry was in place prior to transitions to harem polygyny (fig. 2; see node 2 on the sex allocation character map and node 5 on the mating system character map). Furthermore, Bayesian analyses show that the rate and probability of transitions to monandry are not dependent on the type of polygynous mating (fig. 6B). This suggests that monandric protogyny may also be a sustainable

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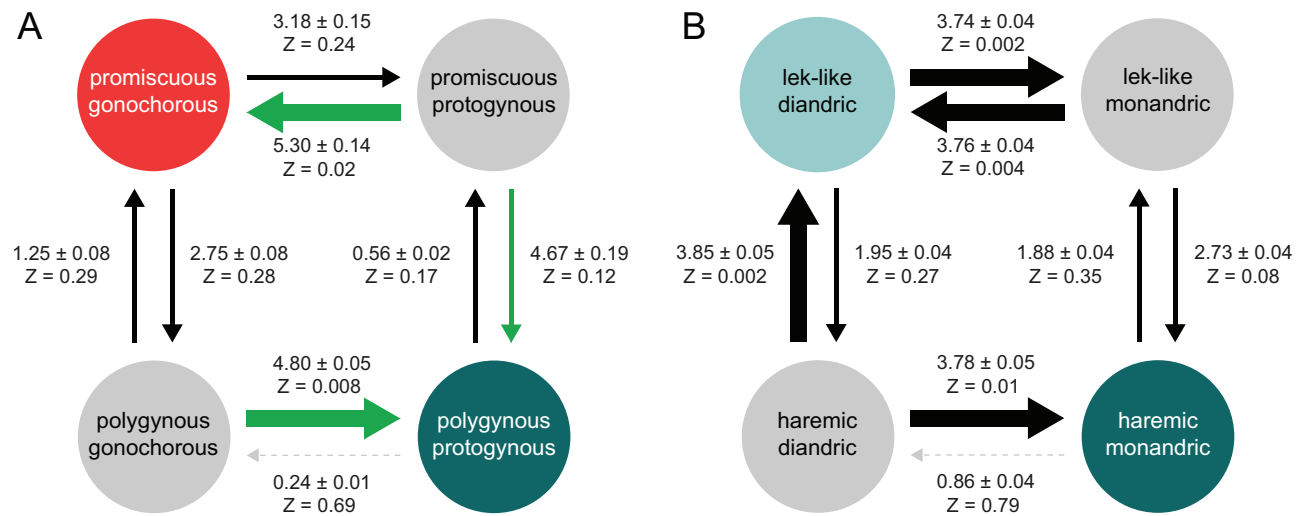


Figure 6: Mean evolutionary transition rates ($q_{xy} \pm SE$) derived from Bayesian models of discrete character evolution fit to predicted associations between polygynous mating and protogynous sex change (A) and between specific types of polygynous mating and protogynous sex change (B). Below each transition rate, z-scores denote the proportion of transition rates assigned to 0—values ≤ 0.05 are rarely assigned to 0 and are considered probable evolutionary events. Transition probabilities are also indicated by line weight, where thick solid lines represent z-scores ≤ 0.05 , thin solid lines represent $0.49 > z > 0.06$, and dashed lines represent z-scores ≥ 0.5 . Line color indicates the rate class to which rate coefficients were assigned most frequently. Similar rate coefficients are assigned to the same rate class (integers beginning with 0), where z indicates a rate coefficient assigned to 0. Rates assigned to z are shown in gray, rates assigned to 0 are shown in black, and rates assigned to 1 are shown in green.

sex-allocation strategy under lower male size advantage characteristic of lek-like mating. Such a character combination may arise if sex-changed males are able to limit the reproductive success of other males without restricting female movement to the same degree as in harem systems. For example, pronounced visual traits like color pattern or display behavior combined with unyielding female mate choice may reduce to near zero the chances of primary males gaining access to mates.

Changes in the distribution of resources or other environmental factors can limit the ability of males to monopolize females, resulting in the breakdown of harem polygyny and the formation of differential male dominance characteristic of lek-like polygyny (Emlen and Oring 1977). Transitions of this nature should create the potential for primary males to gain reproductive access to mates and establish evolutionary fitness, thereby facilitating transitions to diandric protogyny (Robertson and Choat 1974; Emlen and Oring 1977; Robertson and Warner 1978; Warner and Robertson 1978). Several clades show this pattern where lineages that first expressed lek-like polygyny transition to diandric protogyny (fig. 2; see nodes 5, 7, and 9 of the sex-allocation character map). However, other species exhibit the opposite order of character change, namely, *Scarus rivulatus*, *S. globiceps*, *S. ferrugineus*, and *S. forsteni* (fig. 2). Bayesian analyses show that transitions to diandry are highly

dependent on whether lineages express lek-like or harem mating, such that they rarely occur if mating is harem (low rate coefficient and high z-score; fig. 6B). Taken together, our results suggest that once evolved, the extent to which protogynous sex change is expressed is highly adaptable, except when mating behavior permits strong male size advantage, in which case labrids rarely decrease their expression of protogyny.

Gonochorism is predicted to evolve when males and females have similar size-specific reproductive expectations (Warner 1975). This can occur if local population growth increases the density of males, thereby increasing the ability of small males to gain reproductive access to females and reducing the reproductive advantage of large males through the dilution of gametes (Warner 1984; Muñoz and Warner 2003, 2004). As mating becomes more promiscuous, selection for protogyny should decrease (Robertson and Warner 1978; Warner 1984; Hoffman 1985). Loss of protogyny has been associated with transitions to promiscuous mating in several groups of teleost fishes, including labrids (Erismann et al. 2009, 2013). Our results also support this pattern of character change and show that for this combination of traits, transitions to gonochorism have the highest dependence on whether lineages express promiscuity (fig. 6A). More notably, we show that transitions to protogynous sex change are also dependent on whether

mating is promiscuous or polygynous, with higher rates and likelihood of transitions to protogyny for lineages with polygynous mating.

Collectively, our results demonstrate that mating behavior with varying degrees of male size advantage can induce evolutionary change in a complex life-history trait. Labrids have long been a model system for studying the adaptive significance of sequential hermaphroditism (Darwin 1871; Ghiselin 1969; Robertson 1972; Robertson and Choat 1974; Warner 1975, 1984; Warner et al. 1975; Leigh et al. 1976; Warner and Robertson 1978; Muñoz and Warner 2004). Our description of the nature and timing of transitions in mating system and sex allocation builds upon considerable past research efforts but remains dependent on the taxa included. Some of the patterns we recovered are consistent with previous ideas about the drivers of change in these complex traits, and our results provide some of the first quantitative evidence showing that specific types of polygynous mating and protogynous sex change have evolved synergistically following predictions of the SAM. However, for many animal clades, the behavioral, ecological, and evolutionary underpinnings of sequential hermaphroditism have yet to be described. The restricted expression of sequential hermaphroditism among vertebrates suggests that plastic sex-determination mechanisms that are not strictly genetically predetermined may be a necessary precondition for mating and social systems to alter the strength of selection in favor of sex change. The development of teleost gonads from a single type of tissue, the peritoneal epithelium, rather than from two germinal layers (the medulla and cortex) as in most other vertebrates (Devlin and Nagahama 2002), likely allows for evolutionarily labile traits like mating behavior to alter the strength of selection and affect transitions in sex allocation. Therefore, we predict similar evolutionary dynamics between mating and sex systems in animal clades with similarly plastic sex determination. It is our hope that this work will spark new research and discussion about the evolutionary interplay between reproductive and social systems.

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Statement of Authorship

J.R.H. and P.C.W. conceived the study; J.R.H. and F.S. compiled the molecular data; J.R.H. collected the remaining data, performed the analyses and interpretation, and wrote the paper with contributions from F.S. and P.C.W.

Data and Code Availability

All molecular data are available from GenBank, accession numbers provided in table S1. Mating system and sex-allocation data are provided in table S5. All tree files and data files have been deposited in the Dryad Digital Repository (<https://doi.org/10.25338/B8GC91>; Hodge et al. 2020).

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