Learning from Our Study Organisms about Sexual Selection: Lessons from the Ocellated Wrasse*

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ABSTRACT: Sexual selection is a powerful force shaping not only the details but also the breadth of what we see in nature. Yet so much unexplained variation remains. Organisms often solve the "problem" of how to pass on their genes in ways that do not fit our current expectations. I argue here that integrating empirical surprises will push our understanding of sexual selection forward. Such "nonmodel" organisms (i.e., species that do not do what we think they should do) challenge us to think deeply, integrate puzzling results, question our assumptions, and consider the new (and arguably better) questions these unexpected patterns pose. In this article, I share how puzzling observations from my long-term research on the ocellated wrasse (*Symphodus ocellatus*) have shaped my understanding of sexual selection and suggested new questions about the interplay among sexual selection, plasticity, and social interactions. My general premise, however, is not that others should study these questions. Instead, I argue for a change in the culture of our field—to consider unexpected results a welcome opportunity to generate new questions and learn new things about sexual selection. Those of us in positions of power (e.g., as editors, reviewers, and authors) need to lead the way.

Keywords: sexual selection, sperm competition, mate choice, plasticity, social interactions.

Introduction: The Power and Puzzle of Sexual Selection

The thing that first drew me to the study of sexual selection is the way it can explain a trait or pattern that would otherwise seem completely counterintuitive. For example, many of the bizarre and beautiful courtship displays we see in the natural world seem designed to decrease survival and waste energy. Yet these bizarre and beautiful traits are often easily explained by the advantage they provide in the context of mating and competition for fertilization (e.g., reviewed in Andersson 1994; Macedo and Machado 2014; Servedio and Boughmann 2017; Rosenthal 2017; Ryan 2019). In addition, many of the reproductive traits and patterns that we see in nature only make sense in light of interactions between individuals; what is predicted to evolve is the best response to an ever-changing social landscape, which often is not the highest fitness solution in an absolute sense (e.g., Maynard Smith 1982; Eberhard 1996; Arnqvist and Rowe 2005; Alonzo 2010; Taborsky and Oliveira 2012). How else could we explain why both parents sometimes desert offspring that require care for survival or the existence of traits that harm a mate's ability to produce offspring? My fascination with sexual selection continues because we keep learning new things about the diverse, impressive, and often surprising ways in which different individuals and species solve the common "problem" of passing their genes on through reproduction and navigating these complex yet essential interactions.

Before embarking on a article focused on sexual selection, it is worth pausing to acknowledge that a single consensus definition of sexual selection does not exist (e.g., Clutton-Brock 2007; Shuker 2010; Alonzo and Servedio 2019, 2021; Shuker and Kvarnemo 2021). Controversy exists regarding what does and what does not count as sexual selection (e.g., Shuker 2010; Alonzo and Servedio 2019, 2021). For this article, I will adopt the definition recently put forward by Shuker and Kvarnemo (2021, p. 781): "Sexual selection is any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization." I also acknowledge that there are important nuances and gray zones of sexual selection, beyond the scope of this article, that this definition does not fully address (Alonzo and Servedio 2019, 2021). Here, I focus on selection arising from competition for access to gametes for fertilization, which includes competition for mates or resources that allow access to gametes for fertilization and considers variation in both gamete quality and gamete quantity.

Although the idea of sexual selection was controversial from the beginning (reviewed in Gayon 2010; Richards 2017), there is now abundant evidence that sexual selection is a powerful concept and fundamental force shaping biodiversity (e.g., Andersson 1994; Servedio and Boughmann 2017; Rosenthal 2017; Ryan 2019). Furthermore, our understanding of and the evidence for sexual selection have increased immensely over the past decades. As a field, there is much to be proud of and excited about. Yet extensive unexplained variation remains. Given all of that, how do we as a field move forward and increase our ability to predict and understand empirical patterns? There are many ways to answer this question. One limitation I see is a tendency to focus on a small subset of common questions and traits. These questions and traits are certainly worth studying and exploring; we have made immense progress as a field in the past few decades through this focus. Yet if we want to not only refine our answers to these common questions but also expand our knowledge of how and what shapes the patterns we see in nature, we also need to be constantly expanding the questions we ask. One way to do this is to ask, What questions are we missing? Put another way, what about sexual selection remains untapped that could help us explain and predict empirical patterns? Greater understanding will require not only more data but also expanding the questions we ask. The articles included in this special section titled "The Power of Sexual Selection" were selected because they illustrate how asking new questions can increase our understanding of the power of sexual selection to shape what we see in nature (Bacon et al. 2023; Harrison et al. 2023; Lipshutz et al. 2023; McGinley et al. 2023; Pinzoni et al. 2023).

Here, I argue that one powerful way to find new questions is to let the organisms we study guide us. There is, of course, a need for objectivity, rigor, and generality. Yet there is also a common (and very human) tendency to bias the questions we ask and the way we interpret our results through the lens of existing expectations (e.g., Tavris and Aronson 2020; May 2021). While a common method for dealing with human cognitive bias is blind analysis (e.g., MacCoun and Perlmutter 2015), well-established alternatives do exist (e.g., Glaser and Strauss 1967, 1999; Gilgun 2019). In this article, I suggest that we can find new questions and deeper understanding when we work to integrate and remain open to puzzling results or a study species' "failure" to do what we expect. I propose that our field will benefit from adopting a different way of responding to puzzling and surprising results.

One way to make my argument would be to synthesize existing evidence in the literature. There are numerous examples of initially puzzling observations that activated new research questions and insights. Here, I take a different, and admittedly more personal, approach. This is not intended to be a typical research article or review. Instead, in this article I share some things I have learned about sexual selection from my main study species, a marine fish called the ocellated wrasse (*Symphodus ocellatus*; fig. 1). In my research group, we jokingly call this species the "nonmodel organism" because it seems more likely to do the unexpected than the expected thing. In fact, a well-intentioned colleague once suggested that I should change study species (for the sake of my career) after a talk in which I described how the wrasses had, once again, defied our field's expectations. It has not been an easy career path to continue studying a species that does not do what theory predicts it should and keep finding puzzling results that are difficult to explain and publish. In my experience, however, it has been a successful and fulfilling strategy for doing science. These surprising results have consistently suggested exciting new questions and research directions. My current understanding of sexual selection has been shaped by the ongoing challenge of trying to figure out why and how these animals do what they do and by working to fit different pieces of information into an integrated understanding of how sexual selection has shaped the suite of behaviors, traits, interactions, and reproductive patterns we observe. Working to understand this species more deeply has been one of the greatest challenges and delights of my career.

It is not my intention to argue that this approach (i.e., working to generate an integrated understanding of one study species even when it fails to do what our field expects it to do) is the only or even the best way of doing research. I simply argue that it provides one powerful way of generating new insights and finding new questions that push our ability to explain the diversity of what we see in nature forward. Yet embracing our organisms' failures to do what our current theories and understanding predict will require a mental and cultural shift within ourselves and as a field. Can you imagine a world in which we delight in learning that our data do not fit our field's general expectations because we know that this will push our understanding forward in ways that empirical support for our current ideas never could? This may be hard to imagine; it may even upset or offend some. But I argue that it is an essential step if we wish to increase our ability to explain what we see in nature.

An Introduction to the Ocellated Wrasse

The ocellated wrasse is a marine fish found in coastal waters throughout the Mediterranean. This species first fascinated me because it exhibits three alternative male (i.e., sperm producer) phenotypes (see fig. 1; Lejeune 1985; Taborsky et al. 1987). Nesting males build nests out of algae, court females (i.e., egg producers), defend their nest against competitors, and care for the developing eggs until hatching. Sneaker males do not defend nests, court females, or provide
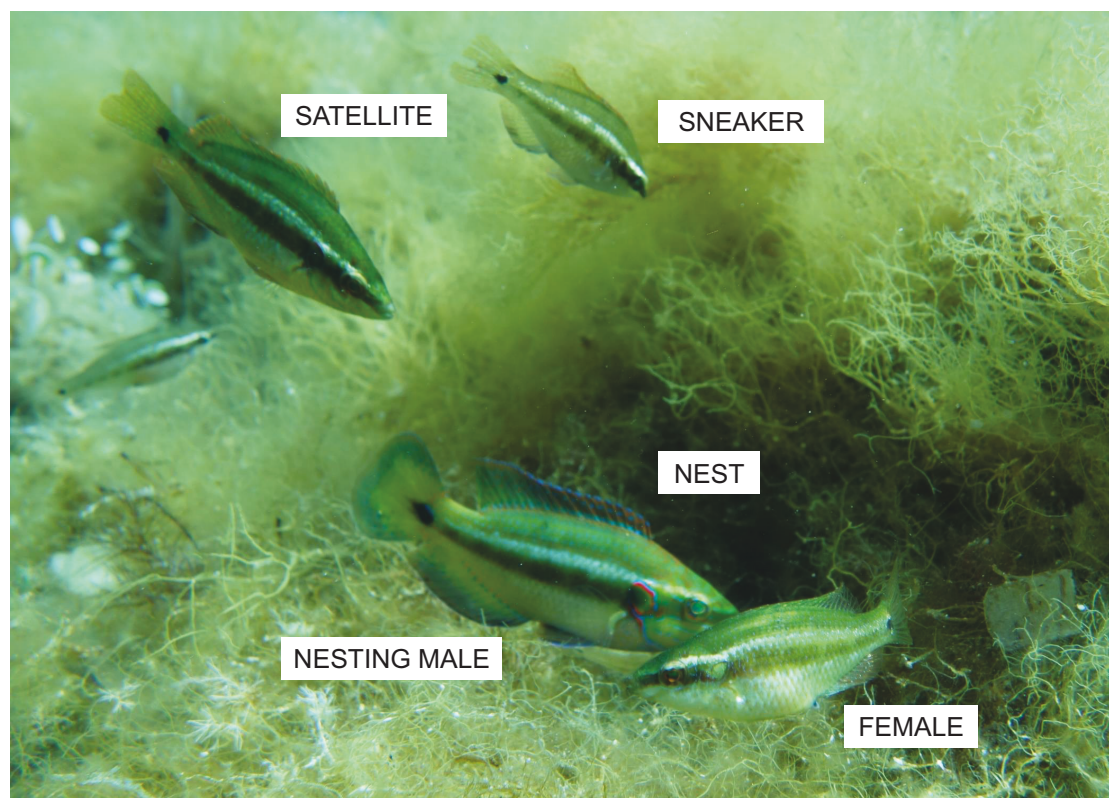
Figure 1: Alternative phenotypes in the ocellated wrasse (*Symphodus ocellatus*). The larger and more colorful nesting male is shown in front of his nest, which is made of algae. A female is visiting the nest and interacting with the nesting male while the sneaker and satellite males hover nearby, waiting for opportunities to sneak spawn. Photo credit: Susan Marsh-Rollo.

care. Instead, they sneak into the nest and release sperm just after a female has spawned with a nesting male. Fertilization is external in this species. The third phenotype, called satellite males, are intermediate in body size and coloration relative to the larger and more brightly colored nesting males and the smaller, relatively cryptic sneaker males. Satellite males do not build nests or provide care. Instead, they partner with a nesting male (although these partnerships last only a few days) and attempt to attract females to the nest defended by their nesting male "partner" (Taborsky et al. 1987). Satellite males chase away sneaker males, and their presence at the nest reduces the risk of sperm competition (Stiver and Alonzo 2013). Males can switch types between reproductive seasons, but they remain one type within a season (Lejeune 1985; Taborsky et al. 1987; Alonzo et al. 2000). Males that grow less as juveniles are likely to reproduce as sneakers in their first year and become satellite males if they survive to reproduce in a second season (Alonzo et al. 2000). Males that grow more as juveniles tend to reproduce as satellite males in their first year and become nesting males if they survive to a second season (Alonzo et al. 2000). We therefore know that the three male types do not arise as a result of a simple genetic polymorphism. To date, we have no evidence of genetic differences between these two trajectories, although further research is needed to rule out this possibility.

The ocellated wrasse is part of a group of 10 closely related species that radiated rapidly from a single ancestral species, most likely soon after that common ancestor entered the Mediterranean from the Atlantic (Hanel et al. 2002; Kazancıoğlu et al. 2009; Fark et al. 2022). These species all breed in the same basic habitat and occupy similar ecological niches, yet they differ strikingly in their reproductive and social systems (Michel et al. 1987). Some species have no parental care, others have relatively simple and facultative care, and others—like the ocellated wrasse—have relatively complex nests and parental care behaviors (Michel et al. 1987; Hanel et al. 2002). In a few species, both sexes provide care, although male-only care is most common. Sexual dimorphism ranges from minimal to striking (Michel et al. 1987), and four of the species exhibit alternative male reproductive types and have complex social systems while the rest do not (Michel et al. 1987). This variation is not only fascinating in itself but raises the question of how and why the ocellated wrasse evolved to be

the way that it is, given that other "solutions" clearly exist in these close relatives that have very similar evolutionary histories and ecology.

While I have certainly learned a lot about sexual selection from the abundant research on the topic, my understanding of sexual selection and the evolution of traits has been shaped just as much by observing this species closely, spending a ridiculous amount of time wondering why they do what they do, designing studies that let me ask them questions, and often being surprised by the answers they provide. The more we know about this species, the more I have been forced to expand my thinking about how sexual selection works and develop a more nuanced understanding of how sexual selection and natural selection interact to shape observed traits and behavioral interactions. I am not arguing that studying one species closely is superior to other approaches one can take. I argue (and aim to demonstrate below) that the careful study of a single species over an extended period can challenge our assumptions and get us to ask questions in a different way. As a result, this is one very powerful way to gain a deeper understanding of sexual selection (and likely many other topics in biology).

Puzzling Results and Their Lessons about Sexual Selection

In the sections below, I first review a generally predicted pattern we might expect to see in nature. I then describe the unexpected results we actually observed in the ocellated wrasse that differed from these general expectations. Next, I explain how these initially puzzling results can be understood when we shift or expand our thinking. Finally, I describe some new questions that these unexpected but now understandable results raise and explore the general insights they provide about sexual selection. My intent is not to argue that these classic general expectations are universally true or that I am the first to observe other patterns. Instead, I use them as a baseline against which to explore and learn from the genuinely surprising patterns we observe in the ocellated wrasse. I hope to illustrate, with a few examples from my own research, how initially puzzling results can suggest new questions and research directions if we are willing to shift and/or expand our thinking. The larger goal of finding new questions and perspectives is to increase our understanding of sexual selection and therefore help us explain and predict more of what we see in nature than is currently possible.

Females Choose among Social Environments, Not among Courting Males or Territories

Expected Patterns. The classic view of mate choice focuses on females choosing among males on the basis of male

traits or resources (reviewed in Anderson 1994). These preferences may confer direct fitness benefits, direct or indirect genetic benefits, and/or arise from sensory bias (Anderson 1994; Rosenthal 2017; Ryan 2019). Initially, the ocellated wrasse seems like a classic sexually selected species. Larger, older, and more colorful males defend territories, where they build nests out of algae and actively court females (Lejeune 1985; Wernerus et al. 1989; Alonzo and Warner 2000*b*; Alonzo 2004). Females visit multiple nests and deposit eggs in only some of the nests they visit (Stiver et al. 2018). This leads to a distribution of mating success among males and among nests that is skewed and consistent with nonrandom mating (Alonzo and Warner 2000*b*; Alonzo and Heckman 2010; i.e., the opportunity for sexual selection is high). Females also prefer nesting males over sneaker or satellite males (Alonzo and Warner 2000*b*; Alonzo 2008; Alonzo and Heckman 2010). Given this, we would expect that some of the traits associated with the nesting male phenotype (e.g., larger body size, color pattern, and/or courtship behaviors) or his nest and nest site will explain variation in mating success among nests and nesting males.

Unexpected Results. Despite extensive research, we have found no evidence that traits of the nesting male or his nest site explain any significant among-nest variation in mating success (Wernerus et al. 1989; Alonzo 2008; Alonzo and Heckman 2010). Of course, there is always the possibility that we have not identified the characteristics of the male, his nest, or the nest site that females prefer. However, by tracking individually marked nesting males over time, we showed that nesting male identity does not explain any of the variation in mating success among nests (Alonzo and Heckman 2010), and previous research found no evidence that nest location explains variation in mating success (Wernerus et al. 1989); the same nest and/or nest site can change between being very successful one day and unsuccessful the next. In addition, we found no significant change in female visitation or spawning rate when nesting males are replaced by a previously unsuccessful neighboring male either experimentally or naturally (Alonzo 2004). This means that if there is a trait of the male or his nest site that can explain a significant amount of the observed patterns of success, it would have to be something that changes rapidly (i.e., within a day or between days).

In contrast, there is extensive evidence that females choose among nests on the basis of the social environment at the nest (Alonzo and Warner 2000*b*; Alonzo 2008; Alonzo and Heckman 2010). Females prefer nests with high recent mating success, other females present and actively spawning, and fewer sneaker males (van den Berghe et al. 1989; Alonzo and Warner 1999, 2000*b*; Alonzo 2008). While females generally spawn only when a nesting male is present (i.e.,

they strongly prefer nesting males), the only variables that explain the skewed distribution of mating success among nests are the social conditions at the nest (which include the presence of but not the identity of the nesting male). While at first this might seem puzzling, this choice by females is likely very adaptive, as we found that nesting males that are more successful (whether naturally and experimentally) in the current nest cycle are also more likely to defend their nest against predators and provide paternal care (Alonzo 2008; Alonzo and Heckman 2010). A skewed distribution of mating success increases the probability that a female's offspring will receive care (Alonzo 2008; Alonzo and Heckman 2010), but it also leads to a skewed distribution of sneakers among nests, with some nesting males experiencing very high mating success but also high sperm competition (Alonzo and Warner 2000*a*, 2000*b*).

New Questions and Insights. These results have shifted and expanded my perspective on sexual selection and how male traits interact with female choice. As a result of failing to find the nesting male trait that would explain the striking variation in mating success among nests, we started to ask new questions. For example, we flipped our thinking from "What physical or behavioral traits of the male are preferred by females because they predict (i.e., 'indicate') paternal effort?" and instead starting asking, "How do social interactions affect the strength and direction of sexual selection?" and "Can female choice cause males to provide care?" (Alonzo 2010, 2012; Alonzo et al. 2021; Azad et al. 2021). We also started to ask how behavioral plasticity in response to social interactions affects the coevolutionary dynamics of male and female traits (e.g., Alonzo 2010; Kazancıoğlu et al. 2012; Royle et al. 2016). In general, the wrasses taught me that social interactions can drive sexual selection in ways our current theories do not capture. For example, when sexual selection favors an emergent social environment rather than individual heritable traits, the dynamics of sexual selection and the traits they shape change in ways we are just beginning to understand. For example, the distribution of mating success among nesting males is more consistent with a mixture of good luck and social competence than classic sexually selected traits like courtship or color patterns in this (and likely other) species. Sexual selection is therefore likely shaping traits related to social cognition and social decision-making, a theme I explore more below.

Paternal Care Is More Likely When Sperm Competition Has Been High

Expected Patterns. In species with paternal care, higher paternity (i.e., having fathered a greater proportion of the offspring for which they are caring) is generally expected to favor greater paternal effort (Queller 1997). The presence and strength of this pattern, however, varies significantly among species (Griffin et al. 2013). In the ocellated wrasse, paternal care is obligate (i.e., is required for offspring survival), yet roughly one-third of all nesting males desert their nests without providing care (Lejeune 1985; Taborsky et al. 1987; Alonzo 2004). In this species, sperm competition from sneaker and satellite males is high, and the presence of sneakers at the nest serves as a reliable indicator of the current risk and intensity of sperm competition (Alonzo and Warner 2000*a*). Based on the above, we would expect nesting males to be more likely to desert nests when their expected paternity is low because of high sperm competition from other males (i.e., desert nests at which the presence of sneaker males has been high).

Unexpected Results. In fact, we found the opposite pattern—nesting males were more likely to remain and provide parental care when the presence of sneakers at the nest had been high (Alonzo and Heckman 2010). This was the first study, to my knowledge, to show that males are more likely to provide care when sperm competition has been high (although in many species male parental effort does not change with sperm competition or paternity cues; Griffin et al. 2013). Why would males provide more parental effort when more sneakers have been present at their nests? As described above, females prefer nests where other females have recently or are currently spawning. Despite females preferring to mate with nesting males, the stronger female preference for successful nests leads to a skewed distribution of not only mating success but also sneaker presence; the most successful nests also experience the highest sperm competition and shared paternity with sneaker and satellite males. Females also further favor nesting male paternity through cryptic female choice mediated by ovarian fluid (Alonzo et al. 2016). Nesting males that have experienced high sperm competition are therefore also the most likely to provide paternal care because they have sired more total offspring in their current nest (even though they are also caring for the offspring of satellite and sneaker males at the same time; Alonzo and Heckman 2010).

New Questions and Insights. A fascinating implication of these results is that while male paternal care is a key trait driving female choice and therefore sexual selection on males, there is no fixed nesting male trait or behavior that predicts either a male's mating success or whether the male will care for a female's offspring. As noted above, females choosing on the basis of the social environment rather than fixed traits changes the dynamics of sexual selection in ways we do not yet understand. In the ocellated wrasse, female-female interactions (i.e., that females copy the nest choice of other females) generate sexual selection that favors paternal

care but without selecting on any specific indicator trait of the male or his nest. In essence, in this species females do not choose good fathers, they create them. This has changed the way I think about interactions between the sexes and how they affect the evolution of paternal care. For example, theory on the evolution of care has shown that predicted patterns of male and female care depend on whether you assume parents are fixed in their parental effort or can negotiate (i.e., respond to one another behaviorally) with one another and adjust their effort in response to these interactions (McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone et al. 2014; Barbasch et al. 2020). This theory, however, has not yet considered that plasticity and the ability to negotiate with a mate or social partner likely coevolves with parental care. This theory also has not considered that negotiation and behavioral plasticity may come at a fitness cost not only in terms of time and energy but also because being plastic means that one's behavior can be changed, even manipulated, by the behavior of another. This suggests that patterns of care will depend on the details of interactions within and between the sexes in ways our current theory does not capture. More generally, these results underscore that we do not yet understand how behavioral plasticity affects conflict within and between the sexes. I suggest that plasticity has the potential to both increase and decrease conflict between the sexes (over care and in general), and understanding the net effect on intersexual interactions will require considering the evolution and expression of social information, social decision-making, and other forms of social cognition.

Male Reproductive Cooperation and Competition Coexist and Affect Selection

Expected Patterns. Intrasexual competition and intersexual conflict are pervasive and argued to shape the evolution of a wide variety of behavioral and physical traits (e.g., Arnqvist and Rowe 2005; Pfennig and Pfennig 2012). Reproductive cooperation, although less prevalent, is most easily explained by inclusive (kin-selected) fitness benefits (e.g., West et al. 2007; Boomsma 2007; Cornwallis et al. 2010). Reproductive cooperation among unrelated individuals is expected to arise primarily when reproductively suppressed "helpers" experience short-term survival and/or delayed fitness benefits (e.g., Buston and Balshine 2007; Riehl 2013; Díaz-Muñoz et al. 2014). Early observations indicated that satellite males were "tolerated" by the nesting male and allowed closer to the nest (Taborsky et al. 1987). We might hypothesize, on the basis of these general expectations and initial observations, that satellite males are either (*a*) the largest and therefore most dominant of the sneak-spawning males (i.e., a reproductive competitor) or (*b*) reproductively suppressed

"helpers at the nest" that experience short-term survival and/or delayed fitness benefits of helping the nesting male (i.e., a reproductive helper).

Unexpected Results. By experimentally removing satellite males, we found that the presence of a satellite male decreases the risk of sperm competition for the nesting males (i.e., they do help; Stiver and Alonzo 2013). Yet nesting males and satellites breeding at the same nest are not more closely related to one another than they are to the rest of the population (Stiver and Alonzo 2013). Although the satellite's presence helps the nesting male by decreasing sperm competition from sneaker males, another experiment found that satellite males also experience a direct and immediate reproductive benefit of adopting this role. Satellite males actively seek mating success when the nesting male is distracted or busy with other competitors (Stiver and Alonzo 2013) and achieve a greater share of the paternity in the nest than a sneaker male (unpublished data). Furthermore, rather than being reproductively suppressed, satellite males also have the largest absolute gonads of all three male types (Alonzo et al. 2021), actively compete to fertilize eggs, and are sometimes able to spawn with females without the nesting male (Stiver and Alonzo 2013). In an experiment, we found that the presence of a potential competitor (another satellite male) influences satellite male helping behavior (Hellmann et al. 2020). The presence and helping behavior of satellite males also likely affect female mating decisions. By reducing the presence of sneakers at the nest (Stiver and Alonzo 2013), satellite males can make the nest more attractive to females (van den Berghe et al. 1989; Alonzo and Warner 2000*b*; Alonzo and Heckman 2010) and more successful overall (Alonzo 2004; Alonzo and Heckman 2010). Satellite males therefore are simultaneously the nesting male's most significant reproductive competitor at the nest and the nesting male's important cooperative partner.

New Questions and Insights. The ocellated wrasse is one of several species that challenge the classic expectation that unrelated reproductive competitors will not cooperate (reviewed in Riehl 2013; Díaz-Muñoz et al. 2014). What I find striking is that in the wrasses, reproductive competition and cooperation not only occur simultaneously (i.e., the benefits of cooperation to the satellite males are not delayed) but are fundamentally intertwined. This interplay suggests that satellite and nesting males traits are being simultaneously shaped by reproductive competition and cooperation. Which raises the following question: What traits are favored by sexual selection when males need to rapidly and adaptively switch between competition and cooperation? How does the tension between cooperation and competition alter the traits favored by sexual selection? Furthermore, the only reason that both

satellite and nesting males simultaneously benefit from satellite male helping is because females prefer to avoid nests with many sneakers present and at which sperm competition from sneakers is high (as described above). Female choice is therefore likely playing an important role in making reproductive cooperation among males possible in this species. Which raises a further question: Do females choose not only the social environment at the nest but also more effective nesting and satellite male pairs? If so, intersexual selection might play a yet unknown role in the evolution of cooperation among males and the traits favored in these social interactions. Furthermore, while the coexistence of two (typically territorial and sneaking) male types is relatively well understood (Oliveira et al. 2008), the factors leading to stable coexistence of more than two alternative types is less well understood (Sette 2020). Considering the possibility that cooperation and competition can occur simultaneously may help us understand the coexistence of more than two alternative male types in this and likely other species as well. Finally, a general lesson I take away from these results is that we need to examine the interplay among conflict, competition, and cooperation to understand the evolution of mating systems and the traits favored by sexual selection as a result of this interplay.

Sexual Selection Shapes the Brains, Bodies, and Behavior of Alternative Male Types

Expected Patterns. I chose the ocellated wrasse as a study species initially because I wanted to ask how interactions between the sexes affect the evolution of alternative male reproductive types (Henson and Warner 1997; Alonzo and Warner 2000c). As described above, we now know that females prefer nesting males over satellite and sneaker males and that interactions between the sexes affect competition among males and the relative reproductive success of the alternative male types (Alonzo and Warner 2000b; Alonzo 2008; Alonzo and Heckman 2010). During this research, we also documented many ways in which these alternative male types differ in behavior, size, age, morphology, and physiology (e.g., Alonzo and Warner 2000a; Alonzo et al. 2000, 2021; Stiver et al. 2015; Nugent et al. 2016, 2019). Specific results of this work have surprised us in various ways. Here, I focus on highlighting results that have raised new questions about how evolutionary and mechanistic processes are connected in ways that are important for our understanding of sexual selection and plasticity. This is a research direction for which clear a priori predictions and expectations do not exist because evolutionary theory on sexual selection and plasticity has yet to consider how the mechanisms underlying both processes influence and are shaped by evolutionary dynamics.

Unexpected Results. As noted above, individual males switch types between breeding seasons. This means that not only can the same genome lead to these very different behavioral and physical male types but when individual males switch between alternative reproductive types, they change not only their behavior (Warner and Lejeune 1985; Taborsky et al. 1987; Alonzo and Warner 2000b) but likely also their brains, gonads, and many other aspects of their bodies. This impressive plasticity inspired us to begin studying the underlying neural, hormonal, cognitive, and other physiological differences among and within male types using a combination of observational studies (e.g., Stiver et al. 2015; Nugent et al. 2016; Dean et al. 2017; Alonzo et al. 2021) and phenotypic engineering experiments (sensu Ketterson et al. 1996) conducted under natural conditions in the wild (Nugent et al. 2019; Stiver et al. 2019; Nugent et al. 2021). These studies asked what mechanisms underlie observed differences in behavior, gene expression, and physiology and how variation at this mechanistic level affects behavior and fitness. We found significant differences between the sexes and among the alternative male types in gene expression in the brain (Stiver et al. 2015; Nugent et al. 2016). Surprisingly, for example, females and satellite males had more similar whole-brain gene expression patterns than sneakers and nesting males despite satellites behaviorally and visually appearing more similar to sneaker males (Stiver et al. 2015), and brain region–specific expression was more similar in nesting males and satellites and quite different in sneakers and females (Nugent et al. 2016). We also measured cognitive-behavioral differences within and between the sexes (using standard assays in the lab) and found that the three discrete alternative male reproductive types found in this species exhibit far greater differences than is found between the sexes (Cummings et al. 2022). These cognitive-behavioral differences are particularly striking because at least some of these differences arise from plasticity during the lifetime of an individual male. These fish literally change their brains along with the rest of their bodies and behavior when changing reproductive types between mating seasons.

New Questions and Insights. Based on the patterns described above, we are now conducting research that asks about the causes and consequences of this impressive plasticity within and between alternative male reproductive types. We have also started asking more questions about how sexual selection has shaped differences in social learning, cognition, and decision-making in the ocellated wrasse and whether alternative male types differ in their ability and motivation to respond to social cues. More generally, these results suggest that we still have a lot to learn about the role that sexual selection plays in shaping traits that are less obviously reproductive and

the mechanisms underlying these traits (e.g., cognition, growth, and development).

New Questions and Future Research on the Ocellated Wrasse

Although I described the insights gained for each topic separately, the most exciting new research directions are where these separate insights come together. For example, our research on the wrasses suggests that sexual selection shapes not only differences between alternative male reproductive phenotypes but also the short-term behavioral plasticity of individuals and the mechanisms that make such rapid adaptive behavioral change possible. As described above, female mate choice in this species depends on the social environment and interactions at the nest rather than fixed traits of the male or his territory. Similarly, the patterns described above show that the interactions among males at the nest depend on the social environment and social interactions both within and between the sexes. While sexual selection on specific fixed traits certainly exists, the largest driver of mating success for individuals of this species is likely their ability to exhibit adaptive social plasticity in response to these ever-changing social conditions and interactions. For example, nesting males must navigate a cooperative and competitive short-term partnership with satellite males in order to achieve high mating and fertilization success. Similarly, satellite males must cooperate to defend the nest against sneaker males while also deciding when they can get away with spawning and when spawning will lead to aggression and possible ejection by the nesting males. This suggests that this species experiences strong sexual selection on traits that allow individuals to exhibit adaptive social plasticity, including social cognition, learning, individual recognition, and rapid shifts between aggression and prosocial behaviors. At present, we are exploring this idea empirically in the ocellated wrasse. Yet there is no reason to think that sexual selection will only favor adaptive social plasticity (and the mechanisms underlying it) in this species (Oliveira 2009; Taborsky and Oliveira 2012). I suggest that further research is needed on how sexual selection shapes the ability to switch behavior rapidly and adaptively in response to social partners and systems.

New General Questions about Sexual Selection

In the previous section, I describe the new questions we are asking about sexual selection in the ocellated wrasse as a result of our unexpected results. These specific insights also suggest some general questions that I believe we should be asking about sexual selection. I do not claim to be the only or first person to raise these questions. I simply suggest that interesting and important general questions such as these can arise from the long-term study of a single species (as well as studying a diverse range of nonmodel organisms). For example, How do social interactions affect and evolve in response to sexual selection? When will sexual selection favor plasticity and how does the presence of plasticity affect the strength and direction of sexual selection on other traits? To what extent does sexual selection shape an organism's ability to respond adaptively during social interactions and the mechanisms underlying this capacity? How does our understanding of sexual selection change when we consider that multiple traits, which affect interactions within and between the sexes, evolve simultaneously? These are just some examples of questions I am asking because of what I have learned from and been puzzled by during my research on the ocellated wrasse. My argument is not that these question are more important or interesting than others. Instead, I suggest that it is worthwhile to consider the questions our study organisms are raising even if—and perhaps especially when—what we observe does not align with our current theories or expectations.

Conclusions

Although I have been and continue to be fascinated by the ocellated wrasse, I do not think it is an exceptional species. Instead, it is simply a species for which our current understanding of sexual selection is insufficient to predict what we actually observe. This is likely true for many, if not most, species. One could see this fact as discouraging or even as evidence of flaws with our field or the way science is done. But that is not what I suggest. There is a lot we understand about sexual selection and how it explains what we see in nature. At the same time, there is a lot of unexplained or partially understood variation within and among species. My goal is to keep expanding our ability to understand and predict organismal patterns.

Studying one species for so long has certainly influenced my perspective and biased the questions I ask, as any species we work with can. My experience, however, is that this close study of a single species over a sustained period of time has also forced me to connect the many pieces of the puzzle of what we discover into a single coherent perspective. It has forced me to reconcile complex patterns and wonder about counterintuitive observations. And this practice has challenged existing theories and raised new questions. Our understanding of how sexual selection shapes what we see in nature will become more nuanced and more powerful as we work to fit such pieces of the empirical puzzle together. While it can be frustrating, it is also powerful to study nonmodel organisms that

fail to give us simple answers to the classic sexual selection questions. Here, I propose a shift in mindset and culture to embrace the opportunity that arises when species fail to do what our current theories expect them to do. This means valuing both studying a diversity of species and conducting long-term research in a single species. Both approaches will challenge us to expand our questions, challenge our assumptions, and deepen our understanding of sexual selection. I know from my own experiences that having results that do not meet our field's current expectations can be challenging and make publishing our work much harder. A culture shift of this kind must start with those of us in positions of power to review, edit, author, hire, nominate, mentor, and train. Yet as the other articles in this special section illustrate, early-career researchers can also contribute by pursuing the science that excites them and that helps us all understand what we see in nature.

Statement of Authorship

This is a solo-authored contribution. This article was written and edited by the author and contains the ideas and opinions of the author. The ideas contained in this article, however, have been shaped by the research on the ocellated wrasse cited throughout the article and the work done in collaboration with the individuals acknowledged above.

Data and Code Availability

No new data were generated for this contribution.

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