Alternative reproductive tactics and sexual selection

Alternative reproductive tactics within the sexes are common in nature and often involve a territorial, courting tactic and a nonterritorial, sneaking tactic. The evolution of such tactics is generally thought to increase the variance in reproductive success and thus increase the opportunity for sexual selection. Therefore, mating systems with alternative reproductive tactics should have an associated exaggeration of sexually selected characters, such as body size (e.g. as measured by sexual dimorphism), the development of weapons (e.g. horns) or costly ornaments (e.g. colourful, conspicuous badges). This paradigm has become an integral part of sexual selection theory, and has received widespread support, particularly from results of avian studies. For example, in many bird species, the frequency of sneaking (or extra-pair fertilizations) is positively correlated with the development or exaggeration of sexually selected traits in males, such as plumage brightness, ornament and body size. However, a new model and empirical data[1] from a fish suggest that such a straightforward link between the presence of alternative reproductive tactics and an increase in the opportunity for sexual selection might be unfounded.

Adam Jones *et al.*[1] have recently developed a mathematical model that incorporates not only the frequency of territorial (nesting) and sneaking behaviours, but also allows for individuals to utilize each tactic to a varying degree. They show that when most individuals employ one tactic, for example a nesting tactic, whilst a few individuals successfully employ both tactics (e.g. nesting and sneaking), the opportunity for sexual selection increases. This result is consistent with the many avian studies conducted on species that are usually socially monogamous, but where some nesting males successfully steal fertilizations from neighbouring nesting males through a 'sneaking' tactic. Alternatively, Jones *et al.*[1] show that when there is a discrete reproductive polymorphism, for example when some individuals employ only the nesting tactic, whilst others employ only the sneaking tactic, sneaking can, in many cases, decrease the opportunity for sexual selection (as compared to a mating system in which the sneaking tactic has not evolved). Jones *et al.*[1] use a genetic analysis of paternity to track the relative frequency and success of sneaking and nesting tactics in sand gobies *Pomatoschistus minutus* and show that, based on their model, sneaking has in fact reduced the opportunity for sexual selection.

Of paramount importance will be demonstrating that the evolution of an alternative reproductive tactic, such as sneaking, has reduced the opportunity for sexual selection in a population as measured by the response in sexually selected characters. This could be accomplished by examining the appropriate characters across multiple populations that differ in the proportion of individuals utilizing the sneaking tactic in a species characterized by a discrete reproductive polymorphism. Populations with a greater proportion of specialized sneaker individuals should have less exaggerated sexually selected characters. For example, if nesting males had a secondary sexual trait, such as a colourful badge, then the size or intensity of this badge should be inversely related to the frequency of sneaker individuals. Interestingly, although discrete reproductive polymorphisms generally decrease the opportunity for sexual selection, intense sexual selection might infact be a precursor for the evolution of these polymorphisms.

1 Jones, A.G. *et al.* (2001) How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proc. Natl. Acad. Sci. U. S. A.* 98, 9151–9156

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Straining for a net profit

Pelagic tunicates (salps, appendicularians, pyrosomas and doliolids) are gelatinous marine zooplankton that are common in most of the oceans of the world. These animals are extremely successful, having colonized the nutritionally poor oceanic 'blue water' areas and abyssal depths, and are capable of producing dense populations that mediate massive fluxes of fecal material from the surface to the deep sea. This transformation of planktonic carbon into 'marine snow' is an important part of the role of oceans as an atmospheric carbon sink. However, in spite of their ecological importance, relatively little is known about these animals. Perhaps most intriguing are their relatively large, transparent gelatinous bodies. In a new paper, José Luis Acuña[1] has shown that the strange, gelatinous bodies of these pelagic tunicates are essential to their ability to thrive in nutritionally poor habitats.

Although they have energy requirements that are similar to other zooplankton with the same carbon content, pelagic tunicates are able to maintain normal feeding and swimming behaviours in ultraoligotrophic areas, and during seasonal periods of food scarcity in temperate seas, without resorting to dormant stages or diapausing eggs. Acuña links a previous suggestion, that gelatinous zooplankton can develop large and delicate feeding structures because of the reduced gravitational and turbulent sheer stresses in their natural environment, with filtration theory to provide an answer to the success of these tunicates. By combining theory and empirical data on their physiology, Acuña shows that these zooplankton use physiologically inert gelatinous bodies to reduce the amount of their tissue that is metabolically active, whilst simultaneously retaining the physically large bodies needed to house their filtration apparatus. His calculations suggest that a scaled-down salp with the same amount of body carbon, but normal water content (i.e. not gelatinous), would starve to death in a large fraction of the oceans. It thus seems likely that pelagic tunicates use large, gelatinous, but relatively inert bodies to make filter feeding in the open oceans a practical option. As Acuña suggests, we should view these strange creatures as normal animals with the bodies of giants.

1 Acuña, J.L. (2001) Pelagic tunicates: why gelatinous? *Am. Nat.* 158, 100–107

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