

10 • Alternative reproductive tactics in fish

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CHAPTER SUMMARY

Among vertebrates, fish show by far the greatest variability of alternative reproductive tactics (ARTs). Usually, males attempting to monopolize access to females or fertilizations are parasitized by conspecific male competitors (Taborsky 1997). This is so common in fish (Mank and Avise 2006) that it appears to be the rule rather than the exception: in fish with external fertilization, 170 species belonging to 32 families have been described to show ARTs (Table 10.1). Apart from being common, ARTs in fish are also exceptionally variable. Parasitic males exploiting the effort of conspecific competitors may do so by surreptitious participation in spawning; they may mimic females in appearance and behavior to reach their goal; intercept approaching mates or steal eggs from neighbors to attract mates to their nest; force copulations in viviparous species; gain access to mates by cooperating with their competitors; or oust a territory owner aggressively to spawn in his nest before letting him care for their brood. Sometimes, three or more alternative tactics may exist within a species (Taborsky 1994, 2001, Avise *et al.* 2002). Our understanding of sexual selection mechanisms and the concepts underlying conventional classifications of mating patterns largely ignore the existence and importance of ARTs (Emlen and Oring 1977, Wittenberger 1979, Davies 1991, Andersson 1994, 2005). One could argue that the way reproductive behaviour in animals is viewed and categorized today would be different if it had been developed on the basis of fish reproduction instead of bird mating systems. The existence and form of ARTs in fish is important also for population ecology, conservation, and speciation (the latter because of hybridization events caused by ARTs: Taborsky 1994, Wirtz 1999). In this chapter, I discuss why alternative reproductive behaviors are so frequent in fish compared to other taxa; how this relates to sperm competition and how males of different types cope with it; to what extent ARTs

result from phenotypic plasticity or fixed life-history patterns; our understanding of the origin of alternative reproductive phenotypes and the importance of genes and environment; how alternative mating patterns in fish may be maintained in a population and why cooperation between reproductive competitors may be involved; what role females play for male alternative behaviors; and what forms of ARTs we find in female fish. Finally, I shall discuss important areas for future research of alternative reproductive phenotypes in fish.

10.1 WHY ARE ARTs SO PROMINENT IN FISH?

There are four potential reasons why alternative reproductive tactics (ARTs) are more frequent and more variable in male fish than in males of other vertebrate taxa (see Table 10.1).

- (1) *Fertilization mechanism.* The vast majority of fish taxa show external fertilization of eggs (Breder and Rosen 1966). This has two important consequences. First, it is difficult for males to monopolize access to partners or fertilizable eggs. Mate guarding is not really an option when eggs are fertilized outside of the female body and potential competitors can access these eggs in a three-dimensional space. Second, external fertilization selects for large numbers of sperm, which in turn is a precondition for a successful role in sperm competition. In contrast, males fertilizing eggs inside the female will be selected to economize in gametic expenditure (Parker 1984).

The variability of ARTs in fish also relates to their diverse spawning patterns. In fish with external fertilization eggs may be released in the water column (pelagic spawning), on the ground, or on/in a substrate (demersal or benthic spawning). With pelagic spawning,