

20 • Integrating mechanisms and function: prospects for future research

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CHAPTER SUMMARY

In this chapter we pull together the common threads of the other chapters of this book. In doing this we identify a number of issues that need further research. Rather than repeating what has been said before, we identify the features that stand out because they are unexplained, previously unrecognized or just neglected. We argue that to understand alternative reproductive tactics (ARTs) we must use an approach that integrates the study of mechanisms and evolution.

20.1 WHAT IS NEXT IN THE STUDY OF ARTs?

Continuous variation in reproductive characters (behavior, morphology, physiology) is found in all species but the real puzzle comes in understanding the special cases in which variation is discontinuous and thus constitutes consistent, discretely different ways of achieving reproduction for animals within one population. If one phenotype were just a little less successful than the other, then we would expect it to be eliminated from the population over time by natural selection. It is for this reason that the maintenance of ARTs is an evolutionary puzzle. ARTs are also a puzzle to geneticists, physiologists, and developmental biologists who must explain how one genetic and developmental program can result in two different phenotypic outcomes. Our chief challenge is to draw together the genetic, developmental, behavioral, and physiological views of ARTs to understand the evolution of the mechanisms that we see as alternative phenotypes.

20.1.1 Categories of ARTs

Discontinuities in behavioral, morphological, or physiological traits can be difficult to detect (Eberhard and

Gutiérrez 1991, Emlen 1996, Kotiaho and Tomkins 2001, Rowland and Qualls 2005, Rowland *et al.* 2005, Tomkins *et al.* 2005), but many clear examples are illustrated in the chapters of this book. In some cases authors describe continuous variation by the extremes and this has made it difficult to be sure whether particular cases are true ARTs or not. For example, singing to attract mates in male crickets may be highly variable with some individuals singing much of the night whereas others utter only a chirp or two, a continuous pattern in which the two ends of the continuum may be described as singing and nonsinging male behavior. Certainly the development, mechanisms, and maintenance of such variation is intriguing, but the processes involved are likely to be different from those acting on two (or more) discretely different kinds of males, singers and nonsingers described by a bimodal distribution (e.g., threshold mechanisms, disruptive selection). Often, suites of behavioral, morphological, and physiological traits are correlated with alternative phenotypes and it may be that some of these traits are discontinuous whereas others are continuous, but as long as the reproductive functions are discrete, then they are ARTs.

The study of ARTs has been hampered by typological thinking about mating systems that ignores significant and consistent variation. Parasitic tactics were often considered to be mistakes or desperate maneuvers by animals with no hope of achieving success. The result is that one of the most important unresolved issues for the study of ARTs is that many are poorly or incompletely described. Good descriptions are crucial to our ability to study the phenomenon. For example, some of the best-studied ARTs turn out to have three phenotypes (Chapters 9, 10, and 12), Differences between these phenotypes in social interactions (such as territoriality or aggressiveness), mating, and life-history patterns can result in cyclical dynamics such as rock–paper–scissors (Sinervo and Calsbeek 2006).