

2 • Alternative reproductive tactics and the evolution of alternative allocation phenotypes

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CHAPTER SUMMARY

Alternative reproductive tactics (ARTs) are part of a much larger class of alternative phenotypes that include sex allocation and alternative life histories. We examine the evolution of ARTs by drawing on the much larger base of theory from sex-allocation and life-history evolution. Insights into how alternative tactics evolve (their maintenance in populations, the evolution of their underlying mechanisms and flexibility, the evolution of morph differences and morph frequencies) are derived from principles developed for understanding the evolution of sex, sex determination, hermaphroditism, sexual dimorphism, and sex ratios.

2.1 INTRODUCTION

Darwin (1871) was fascinated by variation. In part this was because so many scholars at the time emphasized typological thinking and ignored the biological variation around them. But more importantly Darwin realized that heritable variation was at the heart of his theory. If variants showed differential survival and if those characteristics were passed on to their offspring, then evolution occurred. He understood that if one form were just a little more successful than the other, then the variant with the higher success would prevail. This understanding led him to worry about cases in which discrete variation was maintained at a stable frequency in one population. These worries included social insect castes, sexual dimorphism, and alternative forms of one sex (Shuster and Wade 2003).

Variation within one population is usually continuous but under some circumstances, discrete, discontinuous patterns of variation evolve and are maintained. Sexual dimorphism is the most obvious case. Sons and daughters are alternative, parental allocation tactics for achieving the same functional end, reproduction (Charnov 1982) (Box 2.1). Alternative, discrete forms can also be found in

life-history patterns where two forms differ in their schedules of age-specific maturation, dispersal, and reproduction. For example, male bluegill sunfish show two life-history trajectories that are maintained in populations over generations (Gross 1984, 1991a) (see Figure 2.2). Some males mature quickly and begin to breed at a young age and small size (parasitic tactic). Other males take longer to mature and begin breeding at a later age and larger size (bourgeois tactic). Once mature, the larger males invest in guarding nests, attracting females, and providing brood care, whereas the smaller males obtain fertilizations by joining spawning pairs. When quite small they release sperm by sneaking into nests (Philipp and Gross 1994) or, when older and similar in size to females, by mimicking female behavior (Dominey 1980). As adults the two male forms are ARTs, but during development they represent alternative life-history pathways.

Sex allocation, alternative life histories, and ARTs are part of a much larger set of alternative allocation phenotypes (Waltz and Wolf 1984, Lloyd 1987, Brockmann 2001). They include mimicry, color, and other protective polymorphisms (Turner 1977, Brönmark and Miner 1992, Sword 1999, Gonçalves *et al.* 2004), trophic polymorphism (Collins and Cheek 1983, Pfennig 1992, Skúlason and Smith 1995), partial migration (Kaitala *et al.* 1993), seasonal and phase polyphenism (Greene 1989, 1999, Moran 1992, Sword 1999, Sword *et al.* 2000), predator-induced reaction norms (Dodson 1989), alternative germination strategies in plants (Mathias and Kisdí 2002), caste polymorphism and polyethism in social insects (Wheeler 1991), and producer-scrounger systems (Barnard and Sibly 1981, Barnard 1984, Giraldeau and Livoreil 1998, Giraldeau and Caraco 2000). Although very diverse, alternative allocation phenotypes share important features. First, like all forms of phenotypic plasticity, alternative allocation phenotypes occur in one of three general patterns (Barnard and Sibly 1981, Gross 1984,