1 · The evolution of alternative reproductive tactics: concepts and questions

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CHAPTER SUMMARY

Here we outline the meaning of the term alternative reproductive tactics, or ARTs, and discuss why the existence of ARTs is so widespread in animals. We ask what we need to know to understand the evolution of ARTs and the importance of general principles such as frequency dependence, density dependence, and condition dependence, and what we need to know about proximate mechanisms involved in the regulation of ARTs to comprehend evolutionary patterns. We discuss current issues in the study of ARTs and list 12 questions that we think need particular attention. Throughout we shall provide representative examples of ARTs in animals to illustrate the ubiquitous nature of this phenomenon.

1.1 WHAT IS THE MEANING OF ALTERNATIVE REPRODUCTIVE TACTIC?

1.1.1 Alternative

The concept of ARTs refers to alternative ways to obtain fertilizations in both males and females. In its most common use, this term refers to traits selected to maximize fitness in two or more alternative ways in the context of intraspecific and intrasexual reproductive competition. In general, alternative phenotypes are characterized by a discontinuous distribution of traits evolved towards the same functional end. Examples include size dimorphism, color polymorphism, dimorphic morphological structures involved in the monopolization of resources or mates, and various behavioral alternatives such as territoriality vs. floating, monopolization vs. scramble competition, or investment in primary access to a resource vs. social parasitism. Individuals allocate resources to either one or the other (mutually exclusive) way of achieving the same functional end using evolved decision-making rules (Brockmann 2001).

It is important to note here that in the study of allocation decisions in general, and ARTs in particular, any expression of continuous variation of traits is not regarded as alternative tactics. Discontinuity in morphological and physiological traits is often difficult to determine (Eberhard and Gutiérrez 1991, Emlen 1996, Kotiaho and Tomkins 2001). In behavioral traits, in contrast, discontinuities may seem easier to measure because of their visibility to observers. For example, there may be overlap between male types of dung beetles in their expression of horns and body sizes, but it is very clear-cut whether these male types fight for access to females or copulate without investing in primary access to mates (Kotiaho and Tomkins 2001; see also Hunt and Simmons 2000). However, subtle discontinuities might exist in any phenotype, including behavior (e.g., when the performance of alternative tactics depends on condition or situation: Brockmann and Penn 1992, Brockmann 2002). In a nutshell, in the context of ARTs, alternative refers to traits that show a discontinuous distribution.

1.1.2 Reproductive

We speak of alternative reproductive tactics when con specific, intrasexual competitors find different solutions to reproductive competition. It is irrelevant whether the observed variation happens within or between individuals, but reproductive discontinuity within one population at the same time is of essence. In a general sense the concerned traits are alternative responses to competition from members of the same sex. Examples are males either courting females or forcing copulations, as in guppies and other poeciliid fishes (Bisazza 1993, Bisazza and Pilastro 1997), or females either digging burrows for their eggs or usurping those dug by others, as in digger wasps (Brockmann and Dawkins 1979, Brockmann et al. 1979). It is irrelevant whether adaptations to reproductive competition are mainly
<table>
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<th>Box 1.1 Examples of ARTs in animals</th>
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<td>Reference to literature on ARTs in taxa mentioned here is given in the text of this chapter and in other chapters of this book.</td>
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**Molluscs**

- Phallic and aphasis males

**Horseshoe crabs**

- Males attached to females and satellites

**Mites**

- Fighter and scrambler males

**Crustacea**

- Mate guarding vs. searching in amphipods
- Three alternative male mating types in isopods

**Insects**

- Calling and non-calling males in crickets
- Winged and wingless male morphs in bladder grasshoppers
- Single- and joint-nest foundresses in social wasps
- Color and horn polymorphisms in male damselflies and beetles
- Territorial vs. roaming males in dragonflies

**Fishes**

- Bourgeois males and reproductive parasites in sunfish, salmonids, wrasses, cichlids, blennies, and gobies
- Bourgeois males and helpers or satellites in ocellated wrasse, cooperative cichlids, and anabantoids
- Courting and coercive males in poeciliids

**Amphibians**

- Calling males and silent interlopers in frogs and toads

**Reptiles**

- Differently colored males with different mating tactics in lizards

**Birds**

- Courting males and satellites in lekking birds such as ruffs
- Pair and extra-pair matings in many monogamous species (e.g., red-winged blackbirds, blue tits)
- Single vs. joint courtship in manakins
- Nesting oneself or dumping eggs elsewhere (i.e., intraspecific brood parasitism) in many anatids

**Mammals**

- Bourgeois males and satellites in ungulates such as waterbuck and kob
- Displaying/defending males and harassing interlopers in fallow deer
- Harem owners and opportunistic, submissive group males in many primates
- Flanged and unflanged males in orang-utans

What is not an ART?

- Cooperative breeding, if helpers do not share in reproduction (*reproduction* is a necessary component of an alternative reproductive tactic)
- Interspecific brood parasitism, as heterospecifics are not reproductive competitors
- Sex change, even though in species with alternative tactics within one sex bourgeois and parasitic options in this phase may determine the threshold for the optimal timing of sex change (e.g., in wrasses with two or more male reproductive tactics: Munoz and Warner 2003)
- Simultaneous hermaphroditism, as shedding sperm is not an alternative to shedding eggs among competitors for fertilizations
- Infanticide, because it is not a *reproductive* tactic (i.e., to obtain fertilizations or produce offspring, even though it may indirectly contribute to this end)
- Pure scramble competition for reproduction without discontinuous phenotypic variation

Alternative phenotypes in nonreproductive contexts (e.g., foraging or trophic polymorphisms such as left- and right-jawed fish, castes, and age polyethism in social insects when the different morphs do not engage in reproductive competition; polymorphisms that involve both males and females such as winged and wingless forms in some insects, alternative migratory patterns and diapause patterns; seasonal polyphenism that does not involve reproductive characters or individuals; and color polymorphisms caused by apostatic prey selection or other anti-predator strategies)
or partly resulting from intrasexual, intersexual, or natural selection mechanisms. For example, the evolution of courting and sneaking tactics in a species may be subject to intrasexual rivalry, but it may also be influenced by mate choice (intersexual selection) and by the tactic-specific potential to evade predation (natural selection). Alternatively, there may be specialization of same-sex conspecifics in exploiting different reproductive niches. Irrespective of the underlying selection mechanisms, ultimately the existence of the two alternative tactics will be the expression of different solutions to reproductive competition. Interspecific brood parasitism, for example, is not an ART, because it is not the result of reproductive competition; neither are phenomena like infanticide, sex change, or age polyethism in social insects (see Box 1.1).

### 1.1.3 Tactic

In a general sense *tactic* refers to a trait or set of traits serving a particular function. In the context of ARTs, tactics usually involve behavioral traits, but the term is by no means restricted to behavioral phenotypes. For instance, various types of horns in a male population of horned beetles may be expressions of alternative reproductive tactics (Emlen 1997, Emlen and Nijhout 2000, Moczek and Emlen 2000); so are color morphs of some lizards (Sinervo and Lively 1996) and male genitalia in certain snails (Doums et al. 1998; see Box 1.1). Often, suites of behavioral, morphological, and physiological traits are associated in creating alternative phenotypes within a species (e.g., in plainfin midshipman fish: Bass and Andersen 1991, Bass 1992, 1996, Brantley et al. 1993, Brantley and Bass 1994).

We do not think that a distinction between “tactic” and “strategy” is useful here, because these two terms relate to the same issue, but at different levels. A distinction is often made in evolutionary game theory models (Maynard Smith 1982) where strategy relates to a particular life-history pattern or “genetically based program” (Gross 1996), and tactic classifies the application of rules that are part of a strategy (i.e., the phenotype: Shuster and Wade 2003). When analyzing empirical data, usually our potential for inference is limited to the level of phenotype, even if we are ultimately interested in the *evolution* of traits and hence in the effect on genotype frequencies. However, most often we lack information about underlying genotypes. For instance, we do not know whether different genotypes are involved at all or whether phenotypic traits are the expression of conditional variation produced by *exactly the same* genotype (Shuster and Wade 2003). This may not be so bad in the end (see Grafen’s [1991] discussion on “the phenotypic gambit”). The difference made between phenotypic traits produced by same or different genotypes has heuristic importance for (game theory) evolutionary models, but it ignores the fact that virtually all phenotypic traits are the product of genotypic and environmental influence (West-Eberhard 1989, 2003, Scheiner 1993). Hence, in reality the borders between the terms “strategy” and “tactic” are vague and flexible. The underlying mechanisms are usually unknown (i.e., to which extent patterns are genetically determined) at a point when we have not yet studied a phenomenon extensively but nonetheless wish to communicate about it. Therefore, we prefer an operational use of terms here instead of one encumbered with functional implications, just as in the sex-allocation literature (Charnov 1982; see Brockmann 2001). In short, we regard “tactic” and “strategy” as synonymous but prefer the use of “tactic” because we mainly deal with phenotypes and because of the connotations of the term strategy.

In essence, “alternative reproductive tactics” refers to discontinuous behavioral and other traits selected to maximize fitness in two or more alternative ways in the context of intraspecific and intrasexual reproductive competition. Individuals allocate resources to either one or the other (mutually exclusive) way of achieving the same functional end using evolved decision-making rules. This concept may apply to any major taxon, but we shall confine our discussion to the animal kingdom.

### 1.2 WHERE, WHEN, AND WHY DO WE EXPECT TO FIND ARTs?

We expect to find ARTs whenever there is fitness to be gained by pursuing different reproductive tactics and when intermediate expressions of a reproductive trait are either not possible (e.g., there is nothing in between nesting oneself and dumping eggs in conspecifics’ nests: Yom-Tov 1980, 2001) or selected against by disruptive selection (e.g., benefits of large size for bourgeois tactics and of small size for parasitic tactics: Taborsky 1999). Most often we find

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1 The term “bourgeois” tactic refers to individuals investing in privileged access to mates, by behavioral (e.g., defense, courtship), physiological (e.g., pheromones), or morphological means (e.g., secondary sexual characters). The “parasitic” tactic, in contrast, is performed by individuals exploiting the investment of bourgeois conspecifics. In general discussions of the
ARTs when there is investment to be exploited by same-sex competitors (Brockmann and Dawkins 1979, Wirtz 1982, Field 1992, 1994, Andersson 1994, Taborsky 1994, 1998, 2001, Villalobos and Shelly 1996, Hogg and Forbes 1997, Tallamy 2005). In principle, this is possible in both sexes, but because of the unavoidable higher investment of females (even parasitic females assume the costs of egg production), ARTs are expected to evolve more often in the male sex. It is worth emphasizing that anisogamy biases not only the intensity of sexual selection between the sexes, but consequently also the evolution of ARTs.


We may find ARTs also when animals use different niches for reproduction (such as temporally varying habitats). Selection may then favor multiple phenotypes that are specialized to exploit reproductive opportunities in each niche. Intermediate phenotypes will not be as effective as specialized ones when using the available options (Shuster...
and Wade 2003). In this case, the frequency of morphs will depend on the reproductive potential in each niche (Zera and Rankin 1989, Mole and Zera 1993, Denno 1994, Langellotto et al. 2000, Langellotto and Denno 2001; see also Chapter 2 of this book).

1.3 WHICH EVOLUTIONARY PROCESSES ARE CAUSING THE PATTERNS WE FIND IN ARTs?

A major objective in evolutionary biology is to understand processes by which alternative phenotypes are created and maintained within populations (West-Eberhard 1986, Skúlason and Smith 1995, Smith and Skúlason 1996). This includes the question for the existence of two sexes (Parker et al. 1972), polymorphisms for the use of food and habitat (Sage and Selander 1975, Snorrason et al. 1994, Skúlason and Smith 1995, Robinson and Wilson 1996, Smith and Skúlason 1996), laterality (Hori 1993, McGrew and Marchant 1997, Nakajima et al. 2004), locomotion and migration patterns (Berthold and Querner 1982, Verspoor and Cole 1989, Berthold et al. 1990, Hindar and Jonsson 1993, Kaitala et al. 1993, Biro and Ridgway 1995, Smith and Skúlason 1996), predator evasion (Taborsky et al. 2003, Chipps et al. 2004), and the existence of reproductive “producers” and “scroungers” in same-sex conspecifics (Taborsky 1994, 2001, Gross 1996, Brockmann 2001). To understand the discontinuity of reproductive tactics, we should first look at the options of the involved players; that is, we should first know the patterns before disentangling the processes causing them. How do competitors achieve fertilizations? How divergent are the alternative tactics? Do individuals differ consistently in their tactics or are they choosing tactics according to circumstances? To identify underlying processes, we may analyze ARTs at three different levels of classification (Taborsky 1998).

1.3.1 Selection

Alternative tactics evolve when there is fitness to be gained by pursuing divergent allocation tactics. There are two principal conditions favoring the evolution of ARTs:

(1) Investment may be there to be exploited by conspecific, same-sex competitors, as we have outlined above. In the chosen sex, sexual selection leads to high investment in structures promoting mate acquisition. This includes secondary sexual signals that indicate quality (indirect benefits to mates) and supplying resources and brood care (direct benefits). Sexual selection has two major effects in this context; firstly, it causes variation in the success of the chosen sex (Darwin 1871). If some males are able to obtain several mates, others will end up without success (depending on the operational sex ratio: Shuster and Wade 2003), which selects for the pursuit of alternative tactics. Secondly, exploiting the investment of competitors without paying their costs may result in higher fitness (Fu et al. 2001). Both consequences of strong sexual selection set the stage for the evolution of ARTs. Indeed, a positive relationship between strong sexual selection and the evolution of ARTs has been observed (Gadgil 1972, Gross 1996, Sinervo 2001), although there may be negative feedback mechanisms involved as well (Jones et al. 2000a, b, Reichard et al. 2005).

(2) Different reproductive niches may exist for conspecific, same-sex competitors (see Chapter 2). This may occur when reproductive habitats differ discontinuously (Denno 1994, Langellotto and Denno 2001, Hiebeler 2004) or when competitors differ in some important feature as a result of natural selection (e.g., food niches or predation may select for body-size divergence: Pigeon et al. 1997; Lu and Bernatchez 1999, Jonsson and Jonsson 2001, Trudel et al. 2001, Kurdziel and Knowles 2002, Taborsky et al. 2003, Snorrason and Skúlason 2004). Little is known about the consequences of such polymorphisms on reproductive tactics (but see Kurdziel and Knowles [2002] for a notable exception) or about what is cause and what is effect (e.g., is a particular size dimorphism caused by natural selection favoring divergence, with respective consequence for reproduction, or does it result from ARTs caused by sexual selection as outlined above, with respective consequences regarding other aspects of life such as feeding and predator evasion? See Parker et al. 2001).

1.3.2 Flexibility

On the individual level, alternative tactics may be performed at the same time (simultaneous ARTs), in succession (sequential ARTs), or they may be fixed for life (fixed ARTs: Taborsky 1998) (Figure 1.1). This is a general feature of allocation patterns (Brockmann 2001), as found also in sex allocation (simultaneous and sequential hermaphroditism,
1.3.3 Origin of variation

Discontinuous phenotypic variation may originate from monomorphic or polymorphic genotypes (Austad 1984, Gross 1996, Shuster and Wade 2003). In genetically uniform individuals, the response to reproductive competition may be triggered by current conditions or by developmental switches; individual tactics differ due to diverging conditions, despite the same underlying genetic architecture. For example, individuals finding themselves in an unfavorable condition may do best by adopting an alternative tactic to the monopolization of mates, thereby doing “the best of a bad job” (Dawkins 1980). If resource availability varies strongly during development, the decision to adopt one or the other tactic may depend on the passing of a threshold; an individual passing a size threshold, for example, may do best by continuing to grow to adopt a bourgeois reproductive tactic later, while if this threshold is not passed, it may pay to reproduce early and in a parasitic role (note that in some salmonid fishes, it works the other way round; see below). Size thresholds may be important particularly for short-lived animals in seasonal habitats: early-born individuals have more time to grow in favorable conditions, so they will be larger at the start of reproduction. Such “birthdate effects” (Taborsky 1998) apparently influence the occurrence of ARTs in temperate fish (see Thorpe 1986). Thresholds in
growth rates can also influence the choice of tactic (Hutchings and Myers 1994); fast-growing male salmon may start to reproduce earlier, while slow growers delay reproduction and end up in the bourgeois role as a consequence of prolonged growth (Thorpe and Morgan 1980, Thorpe 1986, Gross 1991). In anadromous salmonids this is linked to highly divergent feeding conditions between reproductive sites (oligotrophic rivers) and productive foraging areas (sea habitats: Healey et al. 2000, Vollestad et al. 2004).

Discontinuous alternative reproductive tactics may result also from polymorphic genotypes, regardless of whether variation is due to major gene effects or polygenic origin. Examples are known from a wide taxonomic range – from mites (Radwan 1995, 2003) and isopods (Shuster and

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**Box 1.2 The origin of male polymorphisms in acarid mites**

“Fighter” and “scrambler” males occur in a number of acarid mites belonging to at least three genera (*Sancassania, Sancassania, Rhizoglypus, Schiewia*: Woodring 1969, Radwan 1995, 2001). Fighter males can kill competitors by puncturing their cuticle with a modified third pair of legs. Fighters may outcompete scramblers in low-density situations, but not at high densities, where they suffer from frequent and costly fights (Radwan 1993). Both a genetic polymorphism and a conditional expression of tactics with strong environmental influence during development have been found in different species of this group. In *Rhizoglyphus robini*, fighters sire higher proportions of fighters and the heritability of the male morphs is high; however the genetic mechanism underlying this polyphenism is not yet understood (Radwan 1995, 2003). Colony size and density have no effect on morph frequency, but diet provided during development does, with fewer fighters emerging under poor conditions (Radwan 1995). In this species, fighters survive longer, independently of colony density and morph ratio in the population (Radwan and Bogacz 2000, Radwan and Klimas 2001). Surprisingly, morph fitness was not found to be negatively frequency dependent, as would be expected if a genetic polymorphism is stabilized at an evolutionarily stable state (ESS) condition (Radwan and Klimas 2001).

In *R. echinopus*, no significant heritability of male morph was found, but the probability of males turning into fighters depended on chemical signals associated with colony density (Radwan 2001). In *Sancassania berlesei*, the decision by males to turn into fighters or scramblers strongly depends on social and food conditions during development (Timms et al. 1980, 1982, Radwan 1993, 1995, Radwan et al. 2002, Tomkins et al. 2004). In small or low density populations the proportion of fighter males is higher (Figure 1.2). Chemical (pheromonal) signals are used to determine tactic choice (Timms et al. 1980, Radwan et al. 2002), but the final-instar nymph weight is also important with heavier nymphs being more likely to become fighters, albeit at some costs: same-weight final-instar nymphs produced smaller fighters than scramblers (Radwan et al. 2002). Even though there is no indication of single-locus inheritance of morphs in this species, there is evidence for genetic covariance between sire status and offspring morph and considerable heritability of morph expression due to an adaptive response of the threshold reaction norm (Tomkins et al. 2004, Unrug et al. 2004). Data from this species are compatible with the status-dependent ESS model (Gross 1996), but a critical test showing that fitness functions of the alternative tactics cross at the phenotypic switch point is still missing (Tomkins et al. 2004).
Figure 1.3 (A) When male competitors in a population show either bourgeois or parasitic reproductive behavior depending on condition, e.g., body size, and their fitness functions cross at a given size, males should switch from one to the other tactic at this intersection. (B) The fitness of males may depend also on the relative numbers of both types of males. If the fitness functions depending on relative frequencies of both male types cross, tactic frequencies in the population should converge towards the point of intersection. How does this relate to size-dependent tactic choice? We assume here that the fitness lines cross at a bourgeois male proportion of 0.5; if the population comprises 75% bourgeois males at some point, the average fitness of individuals performing the parasitic tactic would increase relative to that of bourgeois males. (C) The effect of this situation on optimal size-dependent tactic choice: while the fitness of bourgeois males drops due...
Box 1.3 Do fitness curves always cross?

When condition-dependent fitness functions differ between bourgeois and parasitic males and the lines cross, tactic frequencies should depend on this point of intersection (Gross 1982, 1996) (Figure 1.3A). In addition, the fitness of each type of male may depend on the proportions of both male types in the population, resulting in frequency-dependent selection: the more parasitic males compete amongst each other, the less it may pay to choose this tactic (Figure 1.3B), which feeds back on condition-dependent tactic choice (Figure 1.3C and 1.3E). However, cases in which individuals differ in quality demonstrate that frequency dependence is not necessarily involved in the evolution of ARTs. Take a species with early- and late-born males in a seasonal environment that have very different lengths of growth periods before the first winter. In a short-lived species, reproduction may occur only within one reproductive season, i.e., after the first winter. Early- and late-born males will differ in size because they encountered good growth conditions in their first year during time periods of different period lengths (e.g., Mediterranean wrasses: Alonzo et al. 2000). Large males may do best by monopolizing resources and access to females; small males may do best by parasitizing the reproductive effort of large males because they are not able to compete with their larger conspecifics when performing a bourgeois tactic. The average reproductive success of the small males may never reach the same level as the average success of the higher-quality (large) males, even if they are rare in the population, because their small size may act as a constraint on getting access to fertilizable gametes. The result will be ARTs that are not stabilized by frequency-dependent selection (Figure 1.3D). Parasitic males will still persist in the population because males differ in quality due to differing growth conditions, as outlined above. Quality differences between individuals due to developmental constraints are very widespread (Schlichting and Pigliucci 1998), but hitherto, they have not been dealt with in this context in much detail. In theoretical models Mart Gross and Joe Repka (Repka and Gross 1995, Gross and Repka 1998a, b) showed that equilibria between alternative tactics causing unequal fitnesses may be evolutionarily stable; this approach has been criticized, however, because of unrealistic assumptions (Shuster and Wade 2003).

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potential mechanisms. When animals act according to conditions without any genetic component responsible for the type of response (i.e., tactic performance is not heritable), (a) the form and frequency of this response is not subject to selection (Shuster and Wade 2003), which precludes adaptive evolution, (b) different tactics may result in unequal fitness (Repka and Gross 1995, Gross and Repka 1998b), and (c) the frequencies of tactics may be independent of each other and of their relative success (see Box 1.3). When tactic choice is under genetic control and heritable, frequency-dependent selection will lead to (a) a fitness equilibrium associated with alternative tactics and (b) stable frequencies of ARTs in the population (Ryan et al. 1992), or (c) oscillations of tactics if no stable equilibrium can be reached (particularly if more than two ARTs exist in a population: Shuster 1989, Shuster and Wade 1991, Sinervo and Lively 1996). According to the “status-dependent selection model” (Gross 1996), the assumption of conditional tactics based on genetic monomorphism coincides with unequal fitnesses of players, except at the switch point where an individual is expected to change from one tactic to another. On the contrary, a genetic polymorphism can only persist if the lifetime fitnesses of players are equal or oscillating (Slatkin 1978, 1979, Shuster and Wade 1991, 2003).

It would be naïve to assume that ARTs will be either “genetically” or “environmentally” determined (Caro and Bateson 1986). In reality, many if not most dimorphic traits seem to be threshold traits (Roff 1996) influenced by quantitative trait loci: morph expression depends on whether a “liability” value is above or below a threshold (Falconer and Mackay 1996). In the context of ARTs this was shown for the expression of different male morphs in mites with the help of selection experiments, by which the threshold reaction norm was shifted (Unrug et al. 2004) (see Box 1.2). In this scenario, developmental pathways may change abruptly, e.g., at a particular size, producing different phenotypes on either side of the threshold (Emlen and Nijhout 2000, Nijhout 2003, Lee 2005). The operation of genetically based developmental thresholds means that trait expression is both conditional and heritable. It allows alternative phenotypes to evolve largely independently from each other, which greatly increases the scope for the evolution of alternative tactics (West-Eberhard 1989, 2003; see also Tomkins et al. 2005).

If adaptive evolution is not underlying conditional ARTs (as argued by Shuster and Wade 2003), why do they exist in the first place, why are conditional decisions apparently the rule rather than the exception, and why do genetic polymorphisms associated with ARTs appear to be rare? One may ponder whether these concepts are sufficient to explain the evolution of ARTs. The problem is that in this discussion, conditional response and the genetic basis of tactics apparently have been separated from each other. More realistically, the thresholds or developmental switch points involved in tactic choice have a genetic basis and will therefore be subject to selection and adaptive evolution (Tomkins et al. 2004). In other words, phenotypic plasticity is heritable, and genetically based plastic traits vary among individuals of a population (see Chapter 5 of this book). Conditional responses may have a genetic basis but still lead to different lifetime reproductive successes of tactics (Hazel et al. 1990). This issue needs further theoretical treatment (see Shuster and Wade 2003).

1.4 INTEGRATING ACROSS LEVELS: PROXIMATE AND ULTIMATE CAUSES OF ARTS

How do the proximate mechanisms underlying the expression of ARTs relate to their evolution? An important aspect in our understanding of ARTs is the degree of divergence between tactics, which may functionally relate to the underlying mechanisms (e.g., pleiotropic effects if genetic determination is involved, or variance in ontogenetic conditions). In this context it is necessary to understand the proximate mechanisms involved to be able to interpret observed patterns. A distinction should be made, for instance, between alternative phenotypes that diverge only in behavioral traits or also in the expression of morphological and anatomical traits. Since behavior is often more labile than morphology and anatomy, the mechanisms underlying the expression of behavioral variation should be more flexible than those underlying morphological and anatomical variation.

Hormonal regulation is usually involved in the expression of alternative reproductive behavior (Brantley et al. 1993, Oliveira et al. 2005). Ketterson and Nolan (1999) proposed that one could distinguish between adaptations and exaptations (sensu Gould and Vrba 1982) in hormone-dependent traits by assessing whether these traits arose either in response to selection on circulating hormone levels or in response to variation in the responsiveness of the target tissues to invariant hormone levels (Figure 1.4). In the former case, selection probably did not act on all correlated
traits and thus the ones that subsequently conferred an advantage to its carriers should be viewed as exaptations. In the latter case, selection probably acted independently on target tissue sensitivity to constant hormone levels, for example by varying density of receptors or the expression of enzymes for particular biosynthetic pathways. ARTs that involve the differential development of androgen-dependent traits within the same phenotype, such as the differentiation of larger testes in parasitic males without displaying secondary sex characters, suggest a compartmentalization of androgen effects on different target tissues that can be achieved by varying the densities of androgen receptors in different targets. Therefore, ARTs that involve the compartmentalization of different endocrine-mediated traits probably evolved as adaptations, whereas ARTs in which there are no compartmentalization effects (e.g., conditional tactics, such as the facultative use of sneaking behavior by nest-holder males in sticklebacks: Morris 1952, Rico et al. 1992) rather represent exaptations. This approach stresses the importance that studies of proximate
mechanisms may have to increasing our understanding of the evolution of alternative reproductive phenotypes.

The neural mechanisms behind alternative reproductive behavior patterns may involve the structural reorganization of neural circuits underlying the expression of reproductive behavior, or alternatively biochemical switching of existing circuits by neuromodulators (Zupanc and Lamprecht 2000). The former mechanisms may involve synaptogenesis, the regulation of apoptosis, and neurogenesis and thus should be associated with a slower, discontinuous but long-lasting expression of phenotypic plasticity. In contrast, the latter mechanisms should be associated with faster, gradual, and transient changes. These potential neural mechanisms underlying phenotypic plasticity may interact with hormonal mechanisms: structural (re)organization of neural circuits can be influenced by organizational effects of hormones during well-defined sensitive periods in the life of an individual, while biochemical switches can be driven by activational effects of hormones on central pathways underlying behavior (for a review on organizational vs. activational effects of hormones in vertebrates see Arnold and Breedlove 1985). Therefore, it is expected that simultaneous or reversible conditional tactics that may require rapid and transient changes in neural activity are mediated by biochemical switches influenced by hormones in an activational fashion (Zupanc and Lamprecht 2000, Hofmann 2003), whereas both fixed tactics involving the organization of the phenotype early in development and sequential tactics with a fixed sequence that involve a post-maturational reorganization of the phenotype are mediated by structural reorganization of neural networks. Concomitantly, the role of hormones in the expression of the different types of tactics would differ, with organizational (or reorganizational) effects predicted to be associated with fixed and fixed-sequence tactics, and activational effects expected in simultaneous or reversible conditional tactics (Moore 1991, Moore et al. 1998, Oliveira 2005).

Knowledge of the proximate mechanisms underlying the expression of ARTs may help to understand their evolution. Ketterson and co-workers (Ketterson et al. 1996, Ketterson and Nolan 1999) have proposed the use of phenotypic engineering to investigate the evolution of endocrine-mediated traits. This approach is based on the exogenous administration of hormones to study ecological consequences of the development of hormone-dependent traits. This approach can help to identify the costs and benefits associated with particular traits specific to each tactic as well as the evolutionary scenario in which ARTs evolved. A cost–benefit analysis of ARTs in teleosts, for instance, would help to identify costs associated with specific tactics imposed by their underlying physiological mechanisms, which may act as constraints for the evolution of ARTs. For example, bourgeois males usually display a set of androgen-dependent behavioral traits that help them to compete with other males for resources or females (e.g., through territoriality), which suggests that costs associated with maintaining high androgen levels should be associated with the bourgeois tactic (e.g., increased energy consumption, effects on immunocompetence, increased risk of predation, and a higher incidence of injuries from agonistic interactions: e.g., Wingfield et al. 1999, 2001, Ros et al. 2006). Therefore, knowledge of the physiological mechanisms underlying the expression of ARTs may shed light on the evolutionary landscapes in which they might have evolved by helping to identify proximate mechanisms that act as mediators of adaptive traits or as potential physiological constraints imposed by pleiotropic-like effects of hormones on the evolution of ARTs.

1.5 CURRENT ISSUES: WHAT ARE THE QUESTIONS WE NEED TO SOLVE?

Based on the above discussion and arguments we should like to emphasize 12 important questions regarding the evolution of ARTs.

(1) To what extent are thresholds and developmental switches responsible for the evolution of decision rules? In other words, is there genetic variance involved in the conditional response?

(2) If there is sufficient genetic variance among individuals of a population, to what degree are thresholds and developmental switch points subject to selection? An experimental approach would be desirable here.

(3) The occurrence of ARTs is apparently related to the intensity of sexual selection and to the existence of an opportunity to exploit the investment of same-sex conspecific competitors to acquire mates or fertilizations. These potential causes of the evolution of ARTs are not independent; however, they may independently influence the evolution of decision rules. Is one or the other of these factors more important (or of sole importance), or are additional factors involved?
(4) Is the observed intrasexual variation in reproductive phenotypes necessarily adaptive, or are there sometimes constraints (e.g., because a certain part of the population faces inferior conditions during ontogeny, causing significant intrasexual size variation; see Box 1.3) that may produce ARTs?

(5) Are there particular environmental circumstances (both physical and social) that favor either a combination between genetic monomorphism and conditional response or a genetic polymorphism underlying ARTs, either with or without conditional response components?

(6) The expression of ARTs may be fixed for an individual or flexible over a lifetime (Figure 1.1): on the proximate level, to what extent are they caused by structural (re)organization of neural networks, and what organizational and activational hormonal effects regulate fixed vs. plastic alternative phenotypes?

(7) What are the selective regimes favoring the evolution of fixed vs. plastic, simultaneous, or sequential ARTs? That is, which environmental conditions and intrinsic factors (i.e., constraints and life-history patterns) may take effect? Are fixed phenotypes associated with genetic polymorphisms and flexible ones with genetic monomorphism?

(8) How does discontinuous phenotypic variation among competitors that evolved in other functional contexts (e.g., by food niches or predation scenarios) affect the evolution of ARTs?

(9) What causes intermediate types to be less successful than “pure” alternatives? That is, why is selection disruptive?

(10) What controls tactic frequencies? Is frequency-dependent (Repka and Gross 1995) and density-dependent (Tomkins and Brown 2004) selection involved if tactics are purely conditional (which may cause unequal average fitnesses)? When do crossing fitness curves predict relative tactic frequencies (see Box 1.3)?

(11) What processes cause tactics to stabilize at an equilibrium frequency or to oscillate?

(12) Why do particular phenotypes take the form they do? Why are particular solutions so frequent across a wide range of taxa (e.g., female mimicry in males)?

Most of these questions have been asked before in various contexts and often with focus on certain examples, and some have been partially answered either on an empirical or theoretical basis. However, for most if not all of them, we lack enough crucial information to be able to give an answer at the level of specific examples and on a more general basis. This is not an exhaustive list. Of course there are other questions and details we need to consider (e.g., see Box 1.2 and other chapters of this book), but we believe that finding answers to these 12 questions will significantly advance our understanding of ARTs.

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