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 conspecific, 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

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Box 1.1 Examples of ARTs in animals

Reference to literature on ARTs in taxa mentioned here is given in the text of this chapter and in other chapters of this book.

Molluscs	Phallic and aphallic 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 noncalling 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
	Dominant breeders with helpers that share in reproduction in scrubwrens, *Campylorhynchus* wrens, and dunnocks
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)

Cambridge University Press
978-0-521-54006-3 - Alternative Reproductive Tactics: An Integrative Approach
Edited by Rui F. Oliveira, Michael Taborsky and H. Jane Brockmann
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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[1] 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

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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.

Investment in the privileged access to mates or fertilizable gametes bears costs (Taborsky *et al.* 1987, Simmons *et al.* 1992, Bailey *et al.* 1993, Lens *et al.* 1994, Prestwich 1994, Cordts and Partridge 1996, Grafe 1996, Hoback and Wagner 1997, Reinhold *et al.* 1998, Grafe and Thein 2001, Thomas 2002, Yoccoz *et al.* 2002, Basolo and Alcaraz 2003, Ward *et al.* 2003, Barboza *et al.* 2004, Pruden and Uetz 2004, Wagner 2005; but see Hack 1998, Kotiaho and Simmons 2003). It may involve (1) the production of conspicuous signals that may not only attract mates but also predators and competitors (Andersson 1994); (2) the construction of energetically demanding structures for mate attraction and brood care (Hansell 1984, 2005); or (3) parental investment to protect, provision, and raise offspring (Clutton-Brock 1991). Individuals using parasitic tactics may omit these costs and exploit their competitors' investment to gain access to mates or fertilizable gametes (Wirtz 1982, Miller 1984, Taborsky *et al.* 1987, Tomkins and Simmons 2000; see Taborsky 1994 for review). Often they use secretive "sneaking" tactics or fast "streaking" that cannot be easily overcome by the exploited bourgeois males (Warner and Hoffman 1980, Gross 1982, Westneat 1993, Kempenaers *et al.* 1995, 2001, Hall and Hanlon 2002, Correa *et al.* 2003, Sato *et al.* 2004; see Taborsky 1994, Westneat and Stewart 2003 for review). Alternatively, males using parasitic tactics may receive resources required for mating, or brood care for their offspring from bourgeois males also by force (van den Berghe 1988, Sinervo and Lively 1996, Mboko and Kohda 1999).

Cooperative behavior may be applied as an alternative to a purely parasitic tactic when individuals attempt to benefit from the effort of bourgeois competitors (Taborsky *et al.* 1987, Martin and Taborsky 1997, Dierkes *et al.* 1999, Taborsky 2001, Oliveira *et al.* 2002). Competing individuals may cooperate or "trade" with resource holders by paying for access to reproductive options by mutualism or reciprocity (Reyer 1984, 1986, Taborsky 1984, 1985, Lejeune 1985, Taborsky *et al.* 1987, Hatchwell and Davies 1992, Hartley *et al.* 1995, Davies *et al.* 1996, Magrath and Whittingham 1997, Martin and Taborsky 1997, Whittingham *et al.* 1997, Balshine-Earn *et al.* 1998, Johnstone and Cant 1999, Clutton-Brock *et al.* 2002, Oliveira *et al.* 2002, Richardson *et al.* 2002, Double and Cockburn 2003, Dickinson 2004, Huck *et al.* 2004, Webster *et al.* 2004, Bergmüller and Taborsky 2005). The relationships between such cooperating competitors are usually asymmetric, particularly in their resource-holding potential. The mechanisms regulating and stabilizing such cooperative relationships between reproductive competitors have been the target of much recent research (Vehrencamp 1983, Keller and Reeve 1994, Magrath and Whittingham 1997, Balshine-Earn *et al.* 1998, Johnstone and Cant 1999, Johnstone 2000, Kokko *et al.* 2002, Kokko 2003, Skubic *et al.* 2004, Bergmüller and Taborsky 2005, Bergmüller *et al.* 2005, Stiver *et al.* 2005), but there is still a great need for further integration of theory and empirical data.

Females may benefit from exploiting the nests built by other females (e.g., in digger wasps: Brockmann and Dawkins 1979, Brockmann *et al.* 1979, Field 1992, 1994) or by dumping eggs in another female's nest (or mouth) that will be cared for by the owner (i.e., intraspecific brood parasitism in insects: Eickwort 1975, Tallamy 1985, 2005, Müller *et al.* 1990, Brockmann 1993, Zink 2003; fish: Ribbink 1977, Yanagisawa 1985, Kellog *et al.* 1998; and birds: Yom-Tov 1980, 2001, Rohwer and Freeman 1989, Petrie and Møller 1991, Eadie and Fryxell 1992, Lyon 2003, Griffith *et al.* 2004). In this way, preparation of breeding sites and brood care can be spared by applying parasitic tactics (Sandell and Diemer 1999), or productivity can be increased (Tallamy and Horton 1990, Brown and Brown 1997, Ahlund and Andersson 2002, Zink 2003).

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

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function of alternative tactics, these terms are preferable to the more descriptive terms often used in particular case studies (e.g., bourgeois males have been named guarders, territorials, primary males, parentals, nest males, type 1 males, or cuckolds, while parasitic males have been referred to as sneakers, streakers, satellites, hiders, pseudo-females, type 2 males, or cuckolders). For a discussion of reasons to use "bourgeois" and "parasitic" as collective, functional terms for ARTs see Taborsky (1997).

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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*. 2001a, 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,

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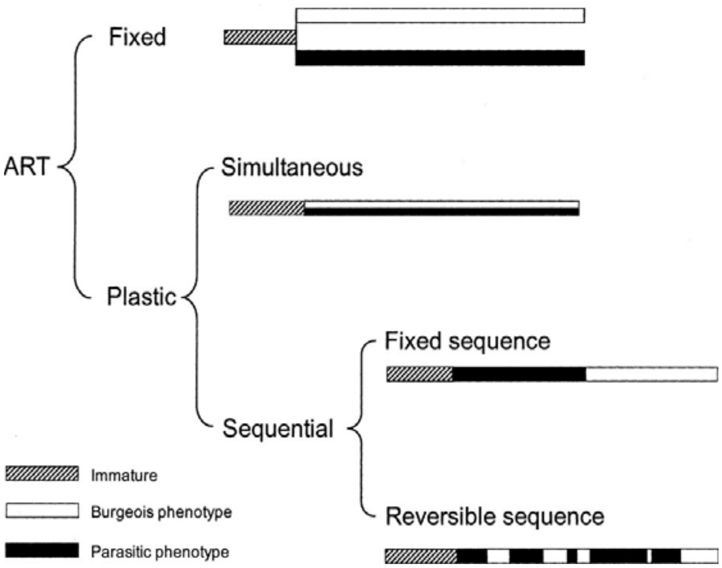

Figure 1.1 Alternative reproductive tactics can be fixed over a lifetime or plastic. In the latter case, they may be performed at the same time interval (simultaneous ARTs) or in a fixed or reversible sequence (sequential ARTs). See text for examples.

and gonochorism: Charnov 1982). Simultaneous and sequential ARTs are the product of a flexible or plastic response to conditions. A flexible response (i.e., phenotypic plasticity) may be beneficial if conditions vary either with regard to the physical or social environment of an animal, or its own physical condition (West-Eberhard 2003). If momentary conditions are highly unpredictable (e.g., number of potential partners, quality and number of current competitors in the neighborhood, tactic-dependent risk), there is selection for simultaneous ARTs as found, for example, in many fishes (Keenleyside 1972, Rowland 1979, Jennings and Philipp 1992; reviewed in Taborsky 1994), anurans (Perrill *et al.* 1982, Fukuyama 1991, Lucas *et al.* 1996, Byrne and Roberts 2004; reviewed in Halliday and Tejedo 1995), and birds (Westneat 1993, Kempenaers *et al.* 1995, 2001; reviewed in Westneat 2003). If conditions change with ontogeny, which applies in particular for organisms with indeterminate growth, sequential ARTs may be the optimal response (e.g., Warner *et al.* 1975, Magnhagen 1992, de Fraipont *et al.* 1993, Dierkes *et al.* 1999, Alonzo *et al.* 2000, Utami *et al.* 2002). If conditions either change rarely during the lifetime of an individual or change is unpredictable, fixed ARTs may be selected for (Shuster and Wade 2003). Additional factors influencing the existence (and coexistence) of fixed and flexible ARTs are differences in success between tactics and the costs of plasticity (Plaistow *et al.* 2004).

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

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 (*Sancassa-Sancassania, Rhizoglyphus, Schwiebia: 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).*

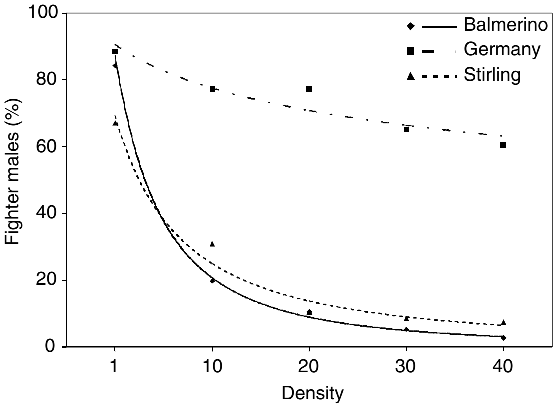

Figure 1.2 The proportion of fighter males emerging in laboratory populations of the acarid mite *Sancassania berlesei* depends on density. In an experiment, larvae originating from three different field populations were introduced into vials either alone or in groups of 10–40 individuals. While the majority of lone males turned into the fighter morph, the proportions of fighter males declined with increasing density, especially strongly in mites coming from two out of three natural populations. (After Tomkins *et al.* 2004.)

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).

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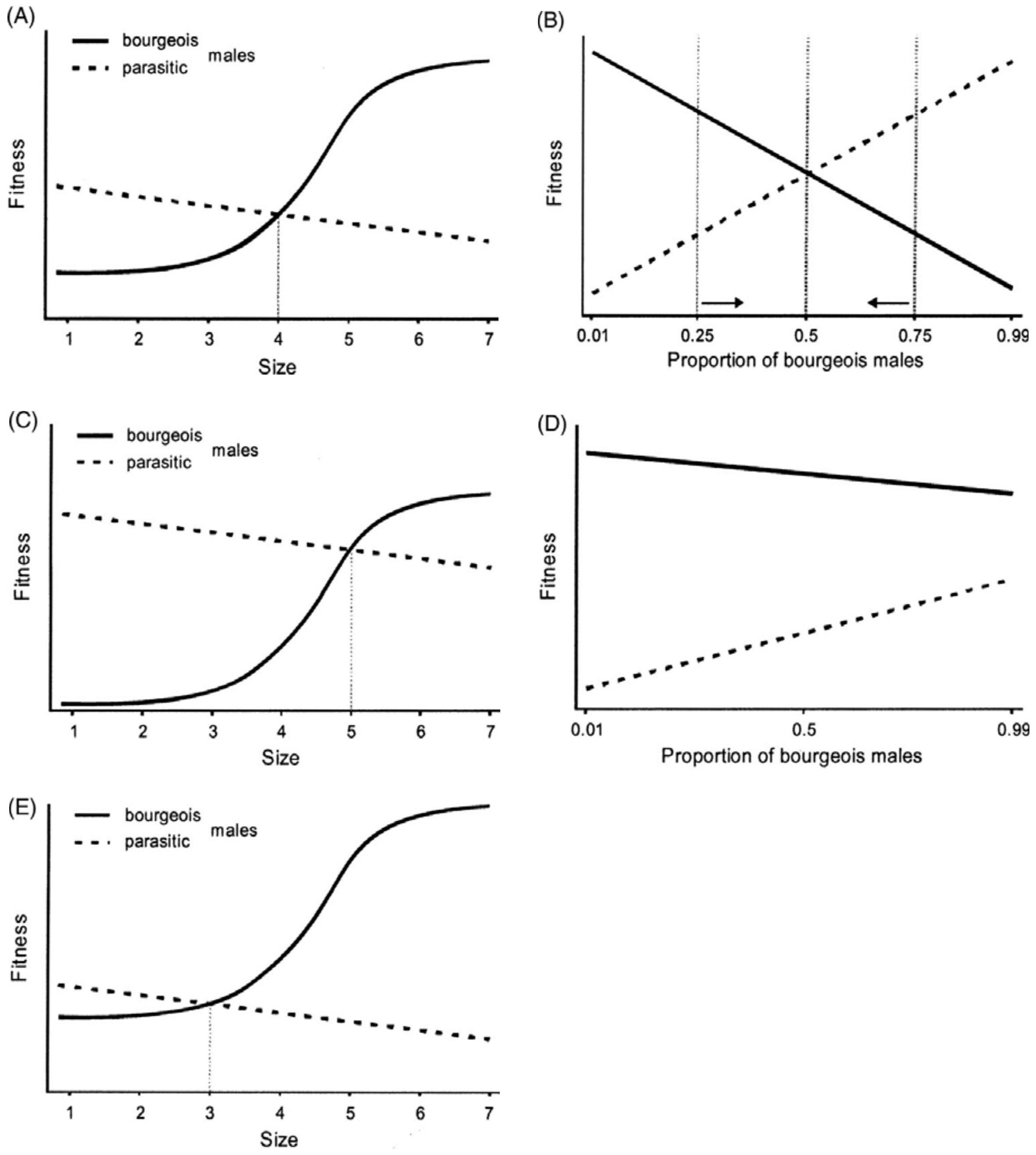

Figure 1.3 (A) When male competitors in a population show either bourgeois or parasitic reproductive behavior depending on condition, e.g., body size, and their fitness functions cross at a given size, males should switch from one to the other tactic at this intersection. (B) The fitness of males may 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).

Wade 1991, Shuster 1992) to fish (Ryan *et al.* 1992), lizards (Sinervo and Lively 1996), and birds (Lank *et al.* 1995, 1999). In this case, genotype frequencies underlying ARTs are believed to be balanced by frequency-dependent selection, leading to equal lifetime fitness expectations of individuals using different tactics (Shuster and Wade 1991, Ryan *et al.* 1992, Repka and Gross 1995; but see Boxes 1.2 and 1.3; see also Chapter 2 of this book).

The relative importance of genetic monomorphism with conditional responses as opposed to genetic polymorphism for the evolution of ARTs has been extensively debated (Pienaar and Greeff 2003; see Gross 1996, Shuster and Wade 2003 for review). The vast majority of described cases of ARTs involves some conditional responses of reproductive competitors (Gross 1996, Lank *et al.* 1999). Because a conditional choice of tactics has been associated with genetic monomorphism, it has been argued that genetic polymorphisms play only a minor role in the causation of ARTs (Gross 1996, Gross and Repka 1998a). This view has been challenged (Shuster and Wade 2003). Why is this debate of general interest? To appreciate the importance of the issue, we need to consider the implications of these two

Caption for Fig. 1.3 (*cont.*) to competition among males of this type, the fitness of parasitic males increases, which means that males should switch to the bourgeois tactic at a larger size (size “5” instead of “4” as depicted in (A)). If in contrast only 25% of the males in the population perform the bourgeois tactic, the fitness of bourgeois males will increase because of low competition while that of parasitic males will drop due to competition of these males when exploiting the relatively small number of bourgeois males in the population (see (E)). Males should switch earlier now from the parasitic to the bourgeois tactic. Note that for simplicity in this graphical model we assume that the relative frequency of both tactics (as shown in (B)) influences the pay-off of males in a similar way over the whole range of sizes, i.e., the intercept of the fitness function changes, but not its shape or slope (cf. panels (C) and (E), and panel (A)). (D) It may be, however, that the fitness functions depending on relative frequencies of both male types do not cross, i.e., bourgeois males may always do better than parasitic males, regardless of the proportions of males in the population performing either tactic (see explanation in text). If this is the case, frequency-dependent selection will not determine tactic choice in the population. Tactic choice and hence tactic frequencies will then depend only on other factors (like male phenotypic quality such as size, which may be determined by developmental constraints).

Cambridge University Press
978-0-521-54006-3 - Alternative Reproductive Tactics: An Integrative Approach
Edited by Rui F. Oliveira, Michael Taborsky and H. Jane Brockmann
Excerpt
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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