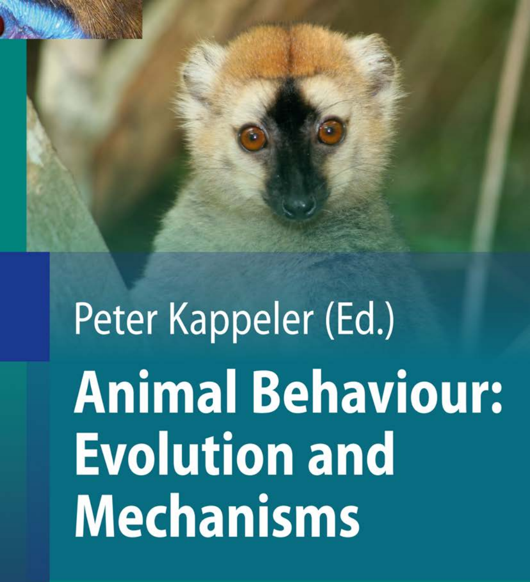

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Chapter 18

Alternative reproductive tactics and life history phenotypes

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ABSTRACT

Alternative reproductive tactics (ARTs) coexisting within a population are found in many organisms. Their existence has been an enduring puzzle in evolutionary biology. Why should selection produce distinctly different alternatives to reach the same goal? How can such alternative solutions coexist in a population? What determines their evolutionary stability? Here we outline ultimate and proximate mechanisms responsible for the origin, coexistence and stability of ARTs. We argue that behavioural and reproductive polymorphisms often reflect different allocation decisions in response to trade-offs in reproduction or life-history optima that may involve heritable threshold responses to environmental variation. Alternative tactics may either be fixed for life or plastic, with simultaneous or sequential switches between tactics. General principles include disruptive selection, negative frequency dependence, density dependence, and an interaction between genetic and environmental components to generate alternative tactics. ARTs are found often where individuals invest heavily in reproduction in a way that can be circumvented and exploited by competitors, which reflects disruptive selection on reproductive investment. This often coincides with consistent size variation between individuals pursuing bourgeois and parasitic tactics.

18.1 Introduction

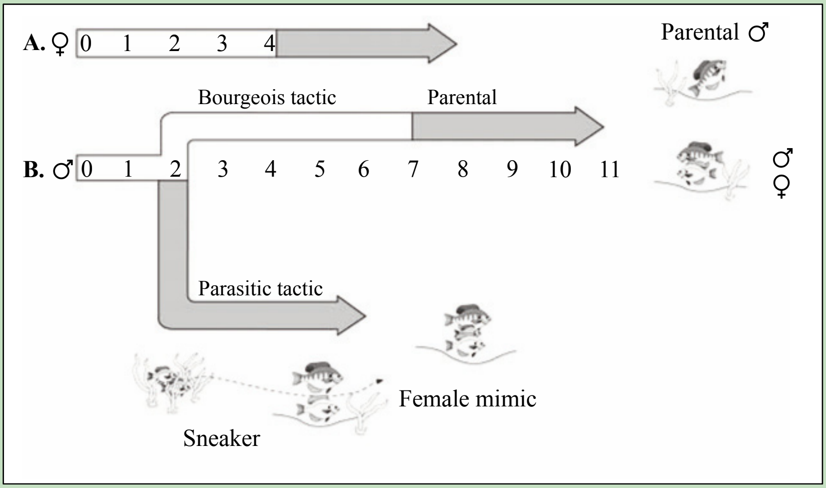
Alternative reproductive tactics refer to alternative ways to obtain fertilisations or, more generally, to reproduce (Taborsky et al. 2008). They are part of a much broader category of alternative phenotypes that include alternative life-history tactics, sex allocation, mimicry, polyphenism, polyethism and social insect castes, all of which are characterised by bimodal or multimodal trait distributions (Lloyd 1987, Brockmann 2001, Brockmann and Taborsky 2008). ARTs are characterised by a discontinuous distribution of reproductive traits between individuals of the same sex. These distinct traits may include behavioural, morphological and physiological differences that form a stable and regular pattern within a population. For example, within a population of bluegill sunfish, *Lepomis macrochirus*, there are three kinds of males, 'bourgeois' males that construct and guard nests, and two types of 'parasitic' males that do not guard but exploit the effort of others (Gross 1982; BOX 18.1). In some scarab beetles (*Onthophagus* sp.), large males develop horns and guard the entrance to a tunnel containing a female, while small, hornless males sneak towards the guarded female for mating by digging a side tunnel (Emlen 1997). Female Sphecid digger wasps may either build a nest or usurp a nest of a conspecific female to deposit and raise their brood (Brockmann and Dawkins 1979). Males of some damselflies, katydids, wasps and bees, swordtails and guppies, frogs and toads, lizards, ruffs, ungulates and pinnipeds may either court females or intercept them on the mating ground to obtain copulations (see reviews in Oliveira et al. 2008a). Such variation within populations is a puzzle that demands an evolutionary explanation. What are the selective pressures that maintain such a pattern at stable frequencies across generations? Such variation is also puzzling from a developmental and physiological point of view. What, for example, are the hormonal, neural and metabolic mechanisms that can cause males to follow one of two different life-history trajectories? In this chapter we address the maintenance of variation from both, a proximate and an ultimate perspective through the study of ARTs.

ARTs are particularly common when there is investment to be exploited by same-sex competitors (Brockmann and Dawkins 1979, Dominey 1984, Waltz and Wolf 1984, Taborsky 1994, 2001, Tallamy 2005). In principle, this is possible in both sexes, but because of the higher investment of females (the burden of anisogamy), ARTs evolve more often in the male sex.

According to our current understanding, ARTs evolve most commonly when there is fitness to be gained by pursuing different reproductive tactics and when the intermediate expressions of a reproductive trait are selected against. In the bluegill sunfish, for example (BOX 18.1), males of intermediate size are selected against (disruptive selection) because they are too small to compete with the large, bourgeois and territorial male tactic and too large to gain access to females through the surreptitious, parasitic tactic (Gross 1982), which is a general pattern in fishes and other taxa (Taborsky 1997, 2008, Wolff 2008). In this case the frequency of each morph is thought to be set by frequency-dependent selection. ARTs also evolve

BOX 18.1

Bluegill sunfish: ARTs fixed for life and sequential ARTs



Schematic representation of life histories and reproductive behaviour of females and alternative types of males in bluegill sunfish. Numbers denote age in years, shaded arrows indicate maturity (Picture by Brian Neff with permission).

In the bluegill sunfish, *Lepomis macrochirus*, males develop into either a bourgeois or parasitic morph. These tactics are fixed for life. Males pursuing the parasitic pathway mature sexually when still small, at about 2 years of age, and remain parasitic throughout life (Gross 1982). In one population, they grow much slower than males pursuing the bourgeois pathway during the years 2-4 of their lives (Taborsky 1994). Burgeois males mature only at an age of about 7 years, when they start to construct nests in densely packed colonies, and court and spawn sequentially with multiple females. They care for the developing eggs and fry in their nests; hence, they have been termed ‘parentals’ (Gross 1982). Parasitic males start with a sneaking tactic at an age of 2-3 years, hiding near nests of parentals from where they dart into the nest to steal fertilisations during female spawning. Once parasitic males reach the size of mature females at an age of 4-5 years, they mimic females to mislead the nest owner and participate when a female is spawning in his nest (Gross 1982, Neff and Gross 2001). At another population, both, satellites behaving as female mimics and bourgeois males reproduce at an average age of 6 years (Dominey 1980), underscoring the fact that parasitic and bourgeois phenotypes reflect fixed lifetime tactics. In contrast, sneaker behaviour is performed as a transient tactic early in the reproductive lives of satellite males. Offspring from parasitic males grow quicker (Neff 2004), but it is yet unknown whether and to what extent the bourgeois and parasitic tactics are heritable (Neff 2008). An ontogenetic switch mechanism involving a size threshold reaction norm seems likely.

when there are different reproductive niches that favour divergent tactics and specialisation for exploiting each niche. Such alternative tactics might be created in males, for example, if there were a polymorphism in female preference traits (Henson and Warner 1997, Alonzo and Warner 2000, Alonzo and Sinervo 2001, Morris et al. 2003, Neff 2008) or if some males exploited females at aggregated emergence sites whereas other males exploited widely dispersed females (Brockmann 2008). Disruptive selection would operate in these cases as well because intermediate phenotypes would not be as effective as specialised ones when exploiting the available options (Skúlason and Smith 1995, Smith and Skúlason 1996, Shuster and Wade 2003, Brockmann and Taborsky 2008). Here the frequency of morphs depends on the reproductive potential in each niche (Zera and Rankin 1989, Denno 1994, Langellotto and Denno 2001). Many species show continuous variation in size or sexually selected traits but ARTs evolve only when disruptive selection favours discrete phenotypes by selection against intermediates (Danforth and Desjardins 1999).

Investment in gaining privileged access to mates or fertilisable gametes usually bears costs (e.g. Taborsky et al. 1987, Simmons et al. 1992, Plaistow and Tsubaki 2000, Wagner 2005). These costs may involve (i) the production and display of conspicuous signals suited to attract mates and repel rivals, which may also lure predators and competitors (Andersson 1994); (ii) the construction of costly structures for mate attraction, defence, or brood care (Hansell 2005, Schädelin and Taborsky 2009); or (iii) parental investment to protect, provision, and raise offspring (Clutton-Brock 1991). Individuals using surreptitious and parasitic tactics can omit these costs and in many cases exploit the investment of bourgeois conspecifics to gain access to mates or fertilisable gametes (reviewed in Taborsky 1994, Oliveira et al. 2008a). Often they use secretive or quick behavioural tactics that cannot be easily overcome by the exploited bourgeois individuals (Gross 1982, Correa et al. 2003; reviewed by Taborsky 1994, 2008 for fish and Westneat and Stewart 2003 for birds). Alternatively, individuals using exploitive reproductive tactics may take by force the resources needed for mating or brood care from bourgeois individuals (van den Berghe 1988, Sinervo and Lively 1996, Mboko and Kohda 1999). In a few species, competitive individuals defend areas that females frequent, such as leks, which otherwise lack obvious resources; other males intercept females as they arrive at the breeding ground (Thornhill and Alcock 1983, Zamudio and Chan 2008). Also, when some females are widely dispersed and others are clumped, there are opportunities for some males to gain fitness by searching and others by staying near the aggregation and fighting over females (Brockmann 2008). In principle, when acquiring mates is costly, limited resources are allocated using evolved decision rules that maximise reproductive success in the face of inevitable trade-offs. ARTs evolve when those allocation rules involve mutually exclusive adaptations.

Among females, individuals pursuing parasitic tactics often benefit from exploiting the maternal effort of conspecifics, for example by using nests built by other females (e.g. in digger wasps, *Sphex ichneumoneus*: Brockmann and Dawkins 1979, Brockmann et al. 1979, Field 1994) or by dumping eggs in a host female's nest (or mouth) that will be cared for by the host (i.e. intraspecific brood parasitism in insects: Brockmann 1993, Zink 2003, Tallamy 2005; fish: Ribbink 1977, Yanagisawa 1985, Kellog et al. 1998; birds: Yom-Tov 1980, 2001, Petrie and Møller 1991). Thereby parasitic females save the effort required to prepare breeding sites and care for their brood (Sandell and Diemer 1999), or they can raise their productivity at the expense of their competitors (Tallamy and Horton 1990, Ahlund and Andersson 2001, Zink 2003). Female ARTs may also arise as a way to avoid sexual conflict (Alonzo 2008). In *Ischnura ramburi* and some other damselflies, females avoid long and costly mating interactions with males either by mimicking males or by avoiding males through cryptic appearance and behaviour (Sirot et al. 2003). As with male ARTs, distinct alternative tactics in females involve trade-offs and disruptive selection against the intermediates.

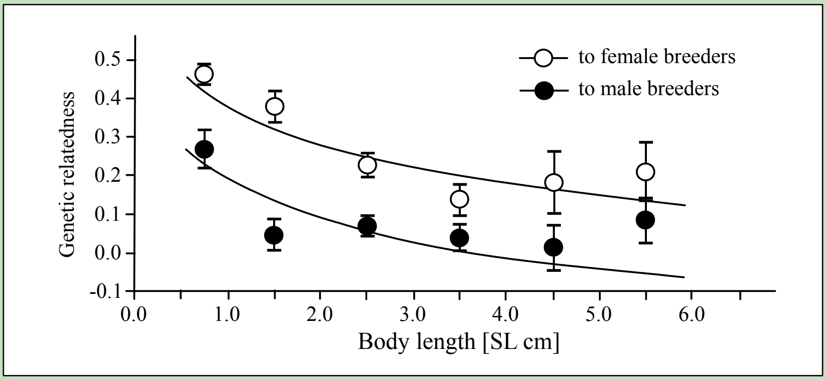
ARTs are usually thought of as competitive but they may involve cooperative behaviour between competitors (Packer 1977, Harcourt and de Waal 1992, Taborsky 1994, 2001, Watts 1998, Feh 1999, Connor et al. 2000, Awata et al. 2005). Competing individuals may cooperate or 'trade' with resource holders by paying for access to reproductive options by mutualism or reciprocity (Taborsky 1985, Taborsky et al. 1987, Martin and Taborsky 1997, Oliveira et al. 2002, Dickinson 2004, Heg et al. 2009; BOX 18.2). These relationships are usually characterised by asymmetries in the resource-holding potential of individuals pursuing alternative tactics. The mechanisms regulating and stabilising such cooperative associations between reproductive competitors are a challenge for evolutionary theory and require experimental scrutiny (Vehrencamp 1983, Keller and Reeve 1994, Johnstone 2000, Skubic et al. 2004, Bergmüller et al. 2005, Stiver et al. 2005, Taborsky 2009).

The evolution of ARTs is influenced by interactions between the sexes as well as competitive interactions within a sex (Alonzo 2008). For example, parasitic tactics often appear to circumvent not only the attacks of territorial males but also female choice (Taborsky 1994). When this is the case, females and bourgeois males have similar interests in preventing extra-pair mating whereas females and sneaker males have conflicting interests (Neff 2008). On the other hand, multiple mating may be advantageous to females, such as when the presence of sneaker males ensures that

BOX 18.2

Cooperation between reproductive competitors – a case of trading care with a share in reproduction

In the cooperatively breeding cichlid *Neolamprologus pulcher*, both male and female subordinates help to raise the broods of dominant breeders of a group. They jointly defend a territory, where they dig out and maintain shelters to hide and breed (Taborsky and Limberger 1981, Taborsky 1984). Mature helpers may attempt to participate in reproduction (Taborsky 1985, Dierkes et al. 1999, Heg et al. 2006, 2008), but the reproductive tactics are sex-specific. Male subordinates attempt to steal fertilisations by instantaneous darts into the breeding shelter during spawning (Dierkes et al. 1999, Mitchell et al. 2009a). In contrast, subordinate females may produce clutches when they have separate shelters available in the territory (Heg and Hamilton 2008, Heg et al. 2009), posing differential costs for male and female dominant breeders (Taborsky 1985). Male breeders and helpers compete for fertilisations, i.e., each egg fertilised by a male subordinate is lost for the dominant male breeder, because male breeders and large helpers are rarely related to each other (Dierkes et al. 2005; Figure below). In contrast, a female breeder is not loosing offspring when a subordinate female produces an own clutch within the territory (Heg et al. 2008), although there may be competition between females and their offspring for resources and consequently mutual egg cannibalism (Heg and Hamilton 2008), which raises the conflict between male and female dominants (Mitchell et al. 2009a). Both, male and female dominants profit from the presence and effort of subordinates in the group by increased productivity (Taborsky 1984) and offspring survival (Brouwer et al. 2005).



Relatedness of subordinate members of *N. pulcher* groups to male and female dominant breeders (means ± SEM and regression lines from a GLMM), as a function of the subordinate's body size; reproductive maturity is reached at about 3.5 cm. Subordinates are hardly related to dominant male breeders, due to the high natural exchange rate of the latter (Dierkes et al. 2005).

Experiments revealed that helpers pay to stay in the territory of dominant breeders (Taborsky 1985, Balshine-Earn et al. 1998, Bergmüller and Taborsky 2005, Bergmüller et al. 2005, Bruintjes and Taborsky 2008), which serves to increase their survival chances due to the protection they get (Taborsky 1984, Heg et al. 2004a), but is also a reproductive tactic (Taborsky 1985, Dierkes et al. 1999, 2008, Skubic et al. 2004, Heg et al. 2009). Especially male subordinates gain from producing offspring in the dominant's territory (Dierkes et al. 1999), and they are more successful if other male helpers are present (Heg et al. 2008). However, apparently due to the costs this entails for male breeders, the latter suppress the growth of large male helpers (Heg et al. 2004b), and to some degree also their gonadal development (Fitzpatrick et al. 2006). This is not the case for females, where subordinates do not entail noticeable fitness costs to dominants and where growth is not suppressed (Hamilton and Heg 2008, Heg et al. 2008). Hence in this species, reproductive competitors join forces to raise offspring, but they rival for their production, especially in the male sex. Careful examination of empirical evidence revealed that conventional reproductive skew models cannot account for the complexity of evolutionary mechanisms involved in reproductive participation among group members of this species (Taborsky 2009). Instead, a dynamic programming approach using body size as a state variable might provide a better model for the decisions of male subordinates to reproduce in the group or not (Skubic et al. 2004).

Males of *N. pulcher* show sequential ARTs. They start to reproduce early, usually when still staying in their natal group (Stiver et al. 2004). However, their reproductive effort in testes and behaviour is much lower than when they have obtained a dominant breeding position later in life (Fitzpatrick et al. 2006, Mitchell et al. 2009b). Their early reproductive activity reflects an opportunistic tactic while growing up in a safe territory, in dependence of the costs of expulsion they risk by their participation in reproduction. Once they manage to take over a territory as dominant breeder, they will do so (Balshine-Earn et al. 1998, Stiver et al. 2006) and raise their reproductive effort accordingly (Fitzpatrick et al. 2006).

all the female's eggs will be fertilised (Jennions and Petrie 2000). If this is the case then selection will favour collaboration between females and sneakers and conflict with bourgeois males (Reichard et al. 2007). In general, female behaviour alters the benefits and costs of male phenotypes and in this way shapes the evolution of male ARTs (Henson and Warner 1997, Alonzo 2008).

Alternative tactics may be performed by individuals either simultaneously (the choice of tactic depending on circumstances), in succession during different life stages (sequential tactics), or ARTs may be fixed for the entire life of an animal (Taborsky 1998, Brockmann 2001, Taborsky et al. 2008; Fig. 18.1). Simultaneous and sequential ARTs result from flexible or

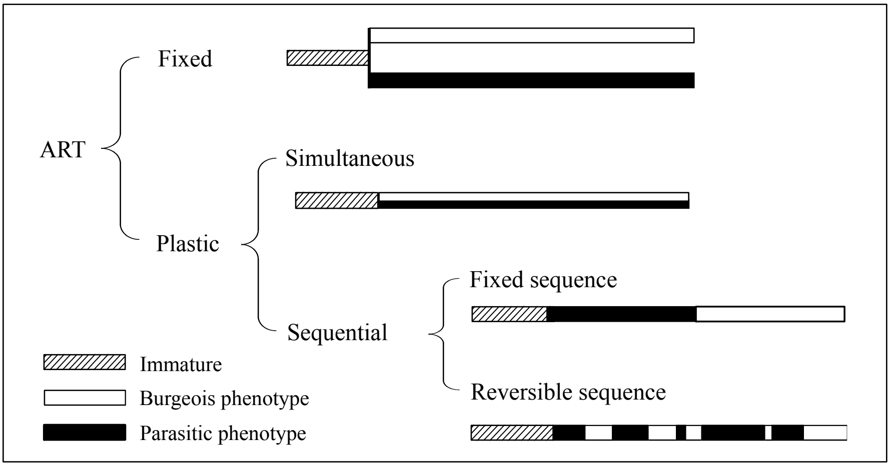


Fig. 18.1 Alternative reproductive tactics can be fixed over the lifetime of an animal or plastic. Plastic tactics may be performed at the same time interval (simultaneous ARTs) or in a fixed or reversible sequence (sequential ARTs). Examples are given in the text. (From Taborsky et al. 2008)

plastic responses to conditions (BOX 18.3). Such phenotypic plasticity is favoured if individual fitness is correlated with conditions varying either with regard to the physical or social environment of an animal, or its own physical condition (West-Eberhard 2003). If conditions change predictably with ontogeny or with size, which applies in particular to organisms with indeterminate growth, a sequential expression of tactics may be favoured (Warner et al. 1975, Magnhagen 1992, Dierkes et al. 1999, Alonzo et al. 2000, Utami et al. 2002). If conditions change either rarely during a lifetime or if the change occurs unpredictably, then fixed tactics may result (Shuster and Wade 2003). Highly unpredictable conditions, for example regarding partner availability, competition and tactic-specific risk, may favour also simultaneous ARTs, which are common in fishes (Taborsky 1994), anurans (Zamudio and Chan 2008), and birds (Westneat and Stewart 2003). The existence (and coexistence) of fixed and flexible tactics is also influenced by tactic specific success and the costs of plasticity (Brockmann 2001, Plaistow et al. 2004).

BOX 18.3

Definitions of terms

‘Tactic’ vs. ‘Strategy’:
In evolutionary game theory models (Maynard Smith 1982), ‘strategy’ denotes 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). However, with empirical data our potential for inference is usually limited to the phenotype level. Information about underlying genotypes is virtually always missing. Moreover, the difference made between phenotypic traits produced by same or different genotypes ignores the fact that virtually all phenotypic traits are the product of genotypic *and* environmental influence (Scheiner 1993). Hence, in reality the borders between the concepts underlying the terms ‘strategy’ and ‘tactic’ are vague and flexible, and the underlying mechanisms are usually unknown. Therefore, an operational use of terms is preferable to one encumbered with functional implications: ‘tactic’ and ‘strategy’ are synonymous terms, but in the context of ARTs ‘tactic’ is a less equivocal expression because researchers mainly deal with phenotypes, and because of the connotations of the term strategy as outlined.

‘Fixed’ vs. ‘Plastic’ vs. ‘Conditional’ Tactics:
‘Fixed tactics’ refer to cases where individuals retain a specific phenotype throughout life. In contrast, ‘plastic tactics’ allow for a flexible response to the environment (Fig. 18.1). If alternative phenotypes can be expressed at the same time, the choice of tactic is conditional on instantaneous circumstances – hence the term ‘conditional tactics’. If tactic expression is sequential, it does usually not depend on present conditions, but on conditions during earlier stages of life, or on the passing of a criterion (e.g., a threshold body size). Therefore, these tactics are not ‘conditional’ in the strict sense of the term, even though the switch points may be influenced by conditions (especially when the sequence is reversible). If these tactics are denoted ‘conditional’, fixed tactics should also be thus termed, at least sometimes, as tactic choice may also depend on some threshold criterion relating to conditions early in ontogeny. Therefore, the term ‘conditional tactic’ is somewhat equivocal, because in the broad sense of the term it refers to virtually all cases of ARTs, whereas in the strict sense it is reserved for cases where different phenotypes can be expressed by an individual at a time, i.e., to plastic ARTs with *simultaneous* tactic flexibility (see Fig. 18.1).

‘Bourgeois’ vs. ‘Parasitic’ Tactics:
The term ‘bourgeois’ tactic refers to individuals investing in privileged access to mates, by behavioural (e.g., defence, courtship, nest building, brood care), physiological (e.g., pheromones), or morphological means (e.g., secondary sexual characters). In contrast, ‘parasitic’ tactic denotes individuals exploiting the investment of bourgeois conspecifics. In general discussions

of the function of alternative tactics, these terms are preferable to the more descriptive terms often used in particular case studies (e.g., guarders, primary males, parentals, or sneakers, streakers, satellites, and cuckolders; Taborsky 1997). It is important to note, however, that not all alternative reproductive tactics fall into this dichotomy of bourgeois ‘investor’ and parasitic ‘exploiter’, as mutualistic or reciprocal relationships between reproductive competitors are also possible (cf. BOX 18.2).

18.2 Evolutionary mechanisms

18.2.1 Threshold responses and selection on switch points

Above we argued that alternative phenotypes reflect different allocation decisions in response to trade-offs in reproduction or life-history optima. Different decisions often involve threshold responses to environmental variation that show heritable variation and are the product of selection like other heritable traits (Roff 1996, Tomkins and Brown 2004). Alternative phenotypes may result from threshold responses of one genotype to environmental changes (reaction norm), two or more genotypes reacting differently to an environmental threshold value (genetic polymorphism), or from a genotype expressing different trait values or tactics depending on their own phenotypic transitions during a lifetime (condition-dependent or status-dependent switch, such as when tactics change with size or age; Dempster and Lerner 1950, Falconer and Mackay 1996, Shuster 2008). A polygenic model that assumes genetic variation in reaction norm switch points (and the switch points are defined by the environment at which a phenotype switches from one alternative to another) reveals that the evolutionary outcome depends primarily on two parameters: (i) the probability density function of the environmental variation acting on the switch points that are responsible for the production of the alternative phenotypes, and (ii) the magnitude of the fitness trade-offs of the phenotypes across this environmental variation (Hazel et al. 1990). Other factors may also influence the evolution of alternative phenotypes, including the effects of other switch points (more than one threshold mechanism may be involved in the production of phenotypic polymorphisms; Rowland and Emlen 2009) and genetic, developmental and physiological trade-offs or coupling that cause selection on one morph to act also on the other (Tomkins et al. 2005, Tomkins and Moczek 2009; cf. Falconer 1952). As with sexual dimorphism, the action of selection on one alternative phenotype (male) can affect the phenotype of the other (female) because of genetic correlations (antagonistic pleiotropy) or linkage disequilibrium (Roff 1990). This will favour the evolution of mechanisms that break up the genetic correlations between alternative phenotypes and favour phenotype-limited traits (Via and Lande 1985). Once this has occurred, unique adaptations for each of the alternative phenotypes can evolve (Crnokrak and Roff 1998, Brockmann and Taborsky 2008).

Behavioural polymorphisms based on heritable threshold responses have been described in several species. For example in scarab beetles, males with alternative morphologies (large or small horns relative to body size) adopt different mating tactics (Emlen 1997, Moczek and Emlen 2000): large males with large horns guard tunnels dug by females for egg deposition and thereby attempt to monopolise access to the female(s) inside. Males not passing a threshold body size develop only rudimentary horns and do not guard tunnels. Instead, they sneak into the tunnels past guarding males or dig side tunnels to bypass them. In the beetle *Onthophagus acuminatus*, the switch point for male dimorphism was found to be heritable by conducting artificial selection experiments. Emlen (1996) bred those males that had the shortest horn lengths relative to their body size for the ‘low’ line and those with the longest horns relative to body size for the ‘high’ line. All males were mated to random females. The result in both lines was a shift in the body size at which the animals switched from developing small horns to large horns (Fig. 18.2). Heritable, size-dependent, life-history switch points have been found also in Atlantic salmon, suggesting discontinuous reaction norms for age and size at maturity (Aubin-Horth and Dodson 2004, Piché et al. 2008). Salmon males either swim to the sea to grow large (1-10 kg) and return to their home stream for breeding, typically at an age of 4-8 years (anadromous males); or they reproduce at an age of 1-4 years at a very small size (10-150 g; parr males), without having left their home stream. On the spawning ground, anadromous males search for, court and fight for mates, whereas parr males sneak under the egg-laying female or dart in to shed sperm, thereby parasitising the effort of bourgeois males. It has been assumed that the success of salmon male tactics is strongly size-dependent, with bourgeois males benefitting from large and parasitic males from small body size (Gross 1984, 1985). However, experimental results revealed that size was not important for the reproductive success of anadromous males within the size range tested, and parr males benefitted from large instead of small size (Thomaz et al. 1997, Jones and Hutchings 2002). This suggests that, although both male types gain from being larger, the slopes of body size effects on fitness differ between the two male morphs (Taborsky 1999; Fig. 18.3).

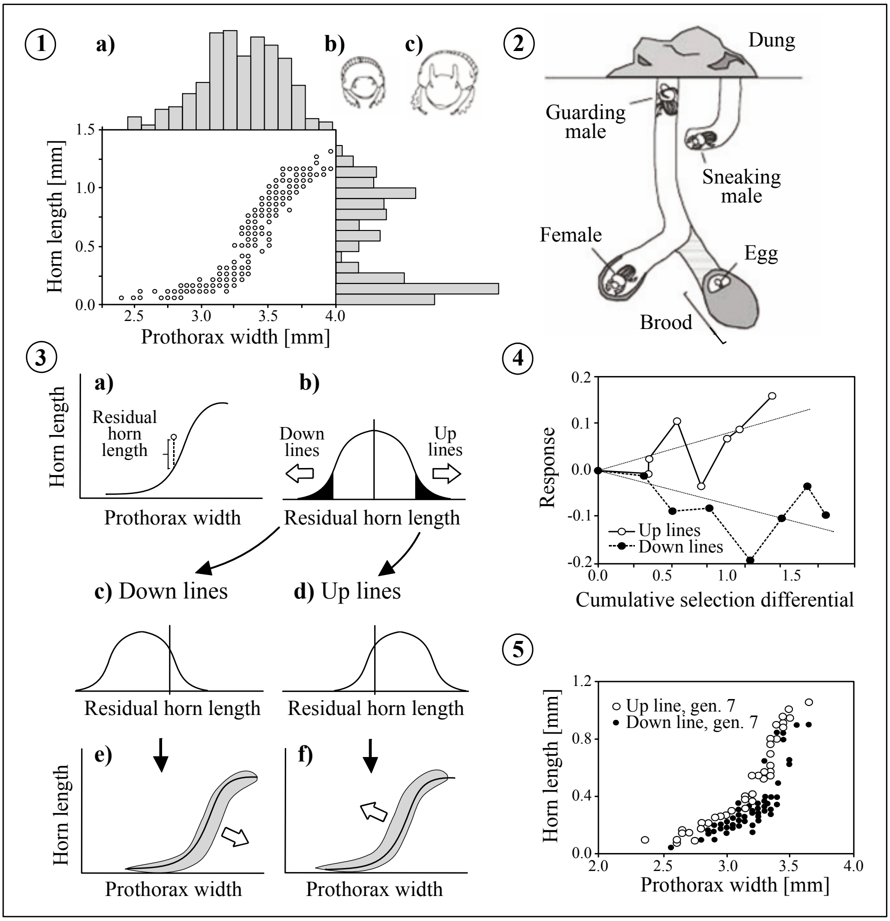


Fig. 18.2 Artificial selection for male ARTs in *Onthophagus acuminatus*. **1**. **a**) Allometric relationship between body size and horn length. The frequency distribution of body sizes is unimodal, whereas horn length representing male ARTs shows a bimodal distribution; **b**) hornless and **c**) horned male phenotypes. **2**. Sketch of male tactics in scarab beetles, with bourgeois males guarding tunnels with females and parasitic males sneaking past them to fertilise females. **3**. Scheme of the artificial selection procedure for alternative body size/horn length phenotypes. **a**) Residual horn lengths were calculated for all males as the difference between their horn length and the horn length expected for their body size; the curve shows the nonlinear regression between body size and horn length. **b**) Males with the largest and smallest residual horn lengths were selected. **c**) – **f**) This resulted in respective shifts in the body size/horn length allometry. **4**) Linear regressions of mean response to selection for residual horn length. **5**) Final horn length/body size distributions for lines selected for long (open circles) and short (closed circles) horns for seven generations. (From Emlen 1996, 2008)

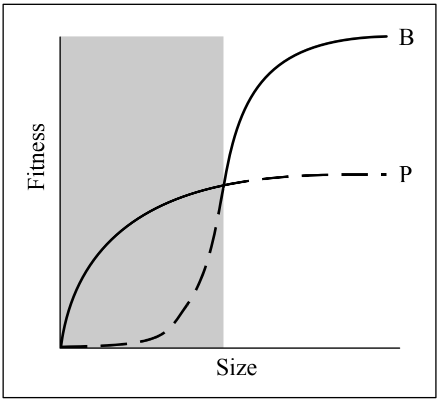


Fig. 18.3 Selection may cause limited size distributions of bourgeois (B) and parasitic (P) males when the slopes of their fitness functions differ. Even if increasing body size affects fitness positively in both, bourgeois and parasitic tactics, selection may favour parasitic reproductive behaviour in small males (size range marked grey) and bourgeois behaviour in large males (to the right of the intersection). This pattern is probably prevalent. (From Taborsky 1999)

Threshold switches between morphs have been proposed also as explanations for many other traits, for instance environmentally sensitive sex determination (Kraak and Pen 2002), wing polymorphisms in crickets (Zera and Huang 1999), seasonal polyphenisms and partial bivoltinism (Dingle and Winchell 1997, Nijhout 1999), the expression of insect castes (Nijhout and Wheeler 1982), and the age polyethism in honeybees (Whitfield et al. 2003).

18.2.2 Discrete phenotypes and conditional tactics

As described above, alternative phenotypes may reflect either life-long individual specialisations or flexible responses to intraspecific competition. The evolutionary mechanisms involved in these alternative scenarios differ substantially. Fixed alternative tactics are characterised by equal average lifetime fitness if they reflect an evolutionarily stable state (Maynard Smith 1982), whereas tactics adopted in response to variation in individual condition, status or environment do not necessarily generate equivalent fitness in the alternative phenotypes (Lively 1986, Repka and Gross 1995, Gross 1996, Tomkins and Hazel 2007). Populations frequently consist of a mixture of conditional and pure tactics (Plaistow et al. 2004). Conditional tactics (cf. BOX 18.3) have been found in a wide range of taxa and in many different functional contexts, being quite likely the most common form of discrete variation within species (West-Eberhard 2003, Oliveira et al. 2008a). Conditional tactics in response to environmental variation, where ‘environment’ also includes competitors and social conditions, have been studied in some acarid mites, where ‘fighter’ and ‘scrambler’ males compete for access to females (Radwan 1993, 1995, Radwan et al. 2002).

Experimental studies revealed considerable heritability of morph expression due to an adaptive response of the threshold reaction norm in *Sancassania berlesei* (Tomkins et al. 2004, Unrug et al. 2004).

Essential preconditions for conditional tactics to be evolutionarily stable are that (i) there is discrete environmental variation, (ii) environmental cues are reliable (i.e., they allow predictions about the environment that are better than random), and (iii) alternative phenotypes must have different fitness optima in different environments (Lively 1986). In the reproductive context such environments might include different opportunities to access partners, such as the size-dependent access options of males in the bee *Centris pallida* (Alcock et al. 1977). Here, large males patrol emergence sites to locate females that they defend aggressively, whereas small males wait for females hovering near emergence sites. As is consistent with our understanding of conditional tactic choice, the hovering tactic pursued by small males provides considerably less fitness rewards than the patrolling and fighting tactic adopted by large males, which Dawkins (1980) referred to as pursuing the ‘best of a bad job’. The polygenic environmental threshold model for the evolution and maintenance of conditional tactics developed by Hazel and collaborators suggests that for the conditional tactic ‘if small hover, if large patrol and fight’ to be maintained, there must be a size-dependent fitness trade-off between these phenotypes, such that there is some body size above which ‘patrolling’ provides higher fitness rewards than ‘hovering’, and below which it is the other way round (Hazel et al. 1990, 2004). For such a trait to evolve, it is important that there is heritable genetic variation for the tactic switch point (i.e., the response to the environmental cue) to be subject to natural selection (Dempster and Lerner 1950, Hazel et al. 1990, Tomkins and Hazel 2007; cf. Shuster and Wade 2003). This example is, however, complicated by the fact that offspring size is set by maternal investment tactics: large males are the product of females providing large amounts of food and small males come from reduced female investment. This means that what is played out as a ‘best of a bad job’ tactic among males may reflect alternative maternal investment tactics (Danforth and Neff 1992, Alonzo 2008, Brockmann 2008).

In the Mediterranean wrasse *Symphodus ocellatus*, nest-building, gaudy males attract females to spawn in their nests where they fan and guard the eggs until hatching. Smaller, inconspicuous males adopt two alternative tactics, either opportunistically darting into the nest during spawning (sneakers) or joining a bourgeois male to defend the nest against other reproductive parasites while attempting to fertilise eggs from a privileged position (satellites; Taborsky et al. 1987; Fig. 18.4). Analyses of growth patterns revealed that there are three different life-history pathways in

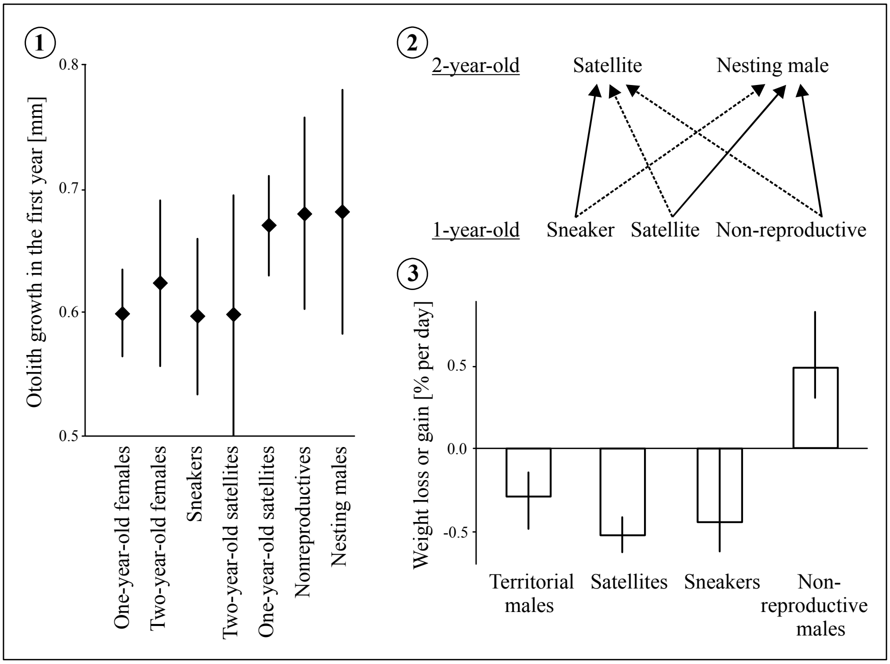


Fig. 18.4 Three different life history pathways in males of the Mediterranean wrasse *Symphodus ocellatus* are revealed by otolith growth patterns. **1**) In the first year of life growth varies significantly between age and behaviour types (means ± SD). Sneaker males and 2-year-old satellites had grown less in their first year than 1-year-old satellites, non-reproductive males and nesting males. **2**) The three male life-history pathways 1- to 2-year-olds are: sneaker – satellite, satellite – nesting male, and non-reproductive – nesting male. **3**) Reproductive males lose on average 0.44% of their body weight per day and ~17% per season due to their behavioural and gonadal effort. Males not participating in reproduction put on weight during the same period, demonstrating a high growth potential during that season. The large and similar reproductive costs of bourgeois and parasitic males can be regarded as an adaptation to sperm competition. (From Taborsky et al. 1987, Taborsky 1998, and Alonzo et al. 2000)

males of this species (Alonzo et al. 2000): one-year-old males may reproduce as sneakers or satellites, or they refrain from reproduction in order to grow (Taborsky 1998; Fig. 18.4); two-year-old males reproduce as satellites (after behaving as sneakers in their first year) or nest males (after behaving as satellites or non-reproductives in their first year). Hence, one life-history pathway includes parasitic and bourgeois behaviour, another one two types of parasitic behaviour and the third one delayed reproduction by the bourgeois tactic. The growth during the first year of life, i.e. before their first reproductive season, apparently determines which trajecotory males adopt (Alonzo et al. 2000). This illustrates the potential importance of the date of birth in a seasonal environment ('birthdate effect', Taborsky 1998); if growth conditions differ strongly between reproductive and non-reproductive seasons, individuals born late in the season will be exposed to favourable growth conditions before their first winter when compared with early born individuals. In the next season, late-born will be much smaller than early-born individuals, which affects their reproductive opportunities and, hence, tactic choice. Birthdate might be an important trigger for tactic expression also in salmonids (Thorpe 1986).

Conditional alternative tactics are not confined to the reproductive context. Other functional conditions in which they have been demonstrated include size-dependent trophic polyphenisms (Frankino and Pfennig 2001), seasonal polyphenism (Shapiro 1976), sex ratio determination (Clutton-Brock et al. 1986, Tomkins et al. 2001), predator induced defence polymorphisms (Lively 1986), and dispersal polymorphism (Zera and Rankin 1989, Denno 1994, Denno et al. 1996, Zhao and Zera 2002). In these cases the cues used to switch conditional tactics include environmental cues, such as food availability, food quality, local population density, rainfall, chemical cues from predators, and day length, or they may involve internal cues about the individual's internal state such as growth rate, size, condition or dominance. Regardless of the proximate cause, these cues are used because they provide individuals with information about the fitness prospects when following different alternative tactics.

18.2.3 Frequency dependence

When individuals exhibit alternative reproductive tactics, their success depends on the frequency with which their own tactic is pursued and on the frequency with which alternative tactics are adopted in the population. The evolutionary mechanism responsible for tactic frequencies in a population is negative frequency dependence: the success of a tactic depends on its proportion in the population. In the simplest case, selection will produce an equilibrium distribution of alternative tactics in the population that is stable over evolutionary time. For this situation game theory models assume that evolutionary stability is reached either by equilibrium proportions of pure behavioural strategies (e.g., 70% bourgeois and 30% parasitic individuals), or by equilibrium proportions of behaviour (e.g., on average 70% bourgeois and 30% parasitic behaviour) shown by all individuals of the population (mixed strategies). Both pure and mixed strategies are referred to as 'evolutionary stable strategies' (ESS) if the condition of a stable frequency distribution is reached by negative frequency-dependent selection (Maynard Smith 1982, Parker 1984). Negative frequency dependence affects the distribution of tactics regardless of whether they are fixed for life or dependent on conditions (Brockmann and Taborsky 2008). However, plastic responses to present conditions allow a much quicker response to deviations from equilibrium (i.e., within a generation), whereas with fixed tactics the population is returned to an equilibrium point by natural selection (i.e., between generations). Due to this retarded dynamic, fixed alternative tactics are expected to occur mainly if crucial environmental conditions change rarely in relation to the average lifetime of organisms, or if change is unpredictable and, hence, information about the best tactic is not available or too costly to obtain (Brockmann 2001, Shuster and Wade 2003). These predictions have not yet been scrutinised, however.

Three fixed alternative tactics are exhibited by male marine isopods (*Paracerceis sculpta*: Shuster 1992), and there is evidence that these tactics have a genetic basis and lead to equal reproductive success (Shuster and Wade 1991, Shuster and Sassaman 1997). In livebearing swordtail fish (*Xiphophorus nigrensis*) two size-dependent male alternative tactics have been described (Zimmerer and Kallman 1989): large males courting females before copulation, and small males reproducing by surreptitious, forced copulations, at least when large competitors are present (Ryan and Causey 1989). Male size classes are genetically based as size and age at maturation are determined by a series of sex-linked alleles, with little growth occurring after maturation (Kallman 1989, Zimmerer and Kallman 1989; maturation may also depend on social status, however; Sohn 1977). The fitness of male swordtails pursuing alternative tactics seems to be balanced due to a higher probability to survive until reproduction for small males and a greater copulation success by large males (Ryan et al. 1992). A somewhat similar balance between a greater reproductive rate of bourgeois males and a longer reproductive lifespan of parasitic males resulting in equivalent lifetime fitness estimates has been observed in the damselfly *Mnais costalis* (Tsubaki et al. 1997).

The lek mating system of ruffs (*Philomachus pugnax*) is characterised by dark, bourgeois males displaying to attract females and light satellite males staying close by, interfering and copulating with females that approach the court (Hogan-Warburg 1966, van Rhijn 1973). A captive rearing study showed that differential morph development is genetically controlled and consistent with a single-locus, two-allele autosomal genetic polymorphism (Lank et al. 1995). Courting males seem to benefit from the presence of satellites due to some female mating preference for male couples (Hugie and Lank 1997, Widemo 1998). Although it has been assumed that the lower reproductive success of satellite males might be compensated by a longer reproductive lifespan like in the damselfly described above (Widemo 1998), it is yet unclear whether morph frequencies are stable over time due to negative frequency dependence. In addition, female mimics appear to be a third, very rare morph reproducing parasitically on leks (Jukema and Piersma 2006).

Sometimes selection does not seem to produce an equilibrium distribution of alternative tactics in a population, but morph frequencies oscillate over time. In males of side-blotched lizards (*Uta stansburiana*), for example, there are three genetically determined throat colour morphs (orange, blue and yellow), each of them linked to a different mating tactic. Blue throated males are monogamous and guard their mates, orange males are polygynous, defend large territories and dominate blue neighbours siring some of their females' offspring, and yellow males adopt a surreptitious parasitic tactic, siring offspring of females defended by orange males by secretive copulations (Zamudio and Sinervo 2000). An ESS-model suggested a frequency-dependent cycle of male morphs with an oscillation period of six years, reflecting a rock-paper-scissors dynamic (Sinervo and Lively 1996). Laboratory breeding experiments (Sinervo et al. 2001) and gene mapping (Sinervo et al. 2006) have suggested a single genetic factor of major effect controlling this male polymorphism. Manipulations of tactic frequencies in six populations revealed that the respective common phenotypes lost fitness in comparison to their antagonists (Bleay et al. 2007), which is a crucial prediction of the balancing function of negative frequency dependence. Oscillations of morph frequencies around an equilibrium point by negative frequency dependence are probably widespread also in systems with two alternative morphs, as exemplified in the feeding polymorphism of scale-eating Lake Tanganyika fishes with asymmetrical mouths (*Perissodus microlepis*: Hori 1993, Takahashi and Hori 1994).

Negative frequency dependence will balance morph frequencies whenever fitness lines of alternative tactics cross, with selection pushing frequency deviations back to the point of intersection (Gadgil 1972, Waltz 1982, Brockmann and Taborsky 2008). This will lead to stable equilibrium conditions or oscillations of various phase length and amplitude around the intersection point. Negative frequency dependence is a straightforward and captivating mechanism that has been demonstrated to work by observational and manipulative studies (e.g., Hori 1993, Bleay et al. 2007), but experimental proof that alternative tactics are balanced by negative frequency-dependent selection is still lacking. Dimorphic or polymorphic trait distributions in natural populations do not necessarily imply simple genetic or even Mendelian causation and equilibrium morph frequencies (Pienaar and Greeff 2003). Fitness lines do not always cross, for instance when conditional tactics are employed by individuals diverging in quality due to variation in developmental constraints (Schlichting and Pigliucci 1998), which may result in morph frequencies that are not balanced by negative frequency-dependent selection (Taborsky et al. 2008).

18.2.4 Density dependence

When same or different phenotypes are competing for the same resources or mates, then the economic defendability of the resource or mate depends on the density of competitors in a population (Emlen and Oring 1977). This affects the occurrence, coexistence and frequency of alternative reproductive tactics. At high densities the bourgeois (i.e. investing) tactic may become much less rewarding due to more intense resource competition. Dragonfly (*Nannophya pygmaea*) males, for example, are more likely to switch from a territorial to a satellite tactic at high population densities (Tsubaki and Ono 1986). Male field crickets (*Gryllus integer*) switch from calling to searching at high densities (Cade and Cade 1992), whereas male white-footed mice (*Peromyscus leucopus*) change from territoriality to wandering at low female densities (Wolff and Cicirello 1990). Similarly, in fallow deer (*Dama dama*), male reproductive tactics vary mainly with male and female densities (Langbein and Thirgood 1989). Density dependence often interacts with frequency dependence in the evolution of alternative phenotypes (Bleay et al. 2007), especially as frequency dependence may be much stronger at high than at low densities (Eadie and Fryxell 1992, Lucas and Howard 1995, 2008). In addition to population density, operational sex ratio may also influence tactic choice (Forchhammer and Boomsma 1998, Zamudio and Chan 2008) and the response to frequency-dependent selection (Andrés et al. 2002). The interaction between density dependence and frequency dependence may be influenced by other ecological factors such as predation or parasitism risk (Walker and Cade 2003) and female choice (Rios-Cardenas et al. 2007).

If alternative phenotypes are using different resources or habitats (Halama and Reznick 2001), density within phenotypes but not frequency dependence between them will affect their occurrence. For example when animals dwell in a patchwork of interspersed niches (or temporally varying habitats), selection may favour multiple phenotypes that are specialised for exploiting resources in each niche (Brockmann and Taborsky 2008). Intermediate phenotypes will not be as effective as specialists in exploiting the resource or at finding mates, resulting in disruptive selection for morphs specialised for each habitat. In this situation, the success of one phenotype does not depend on the other, as each morph simply exploits the habitat to which it is adapted. The two morphs should occur at frequencies that match the resource availability in the different niches (Seger and Brockmann 1987), i.e., the success of alternative phenotypes is density dependent (Denno et al. 1985) but not frequency dependent. Similarly, alternative reproductive phenotypes in one sex may be favoured by a polymorphism in preference traits of the other sex (Henson and Warner 1997, Alonzo and Sinervo 2001, Morris et al. 2003), which would mean that members of a phenotype compete with one another but not with members of the other phenotype and would be subject to density but not frequency dependence. It should be considered also that density effects may cause frequency oscillations between alternative phenotypes in ways that are similar to negative frequency dependence, although it may need additional frequency dependence effects to reach equilibrium conditions (Sinervo et al. 2000).

Population density and resource abundance may influence morph frequencies of males also through maternal allocation decisions, as occurs for example in Dawson's burrowing bees (*Amegilla dawsoni*), where females invest in either large or small males that then pursue alternative mating tactics based on their size (Alcock 1999, Tomkins et al. 2001). In this situation, an understanding of the factors responsible for male morph frequencies requires information about the factors influencing maternal allocation tactics and not just the relative success of male tactics (Brockmann 2008). Density effects may vary between populations with different selection histories, as demonstrated by responses to experimental variation of population size on distinct male morphs in acarid mites (Tomkins et al. 2004). In *Sancassania berlesei* the decision of males to turn into fighters or non-fighters depends on social conditions and food during development (Radwan 1995, Radwan et al. 2002). Small and low density populations contain larger proportions of the fighting male morph. In a captive breeding experiment, most males originating from three natural populations could be manipulated to become fighters when kept alone, but a pronounced response to increasing density by emergence of a much smaller number of fighters was only shown by two of the three populations (Tomkins et al. 2004). When disruptive selection occurs and different traits are favoured under different conditions, selection favours the evolution of a threshold switching mechanism between alternatives (Nijhout 2003).

18.3 Proximate mechanisms

18.3.1 Genetic and environmental components

As with any other biological trait, ARTs are a product of genes and the environment and of interactions between these causal factors; it would be naïve to assume that ARTs are either 'genetically' or 'environmentally' determined (Caro and Bateson 1986). Dimorphic traits usually 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). This has been demonstrated for the expression of different male morphs in mites, in which the threshold reaction norm was shifted in artificial selection experiments (Unrug et al. 2004). Threshold traits frequently operate during development, and alternative pathways may change abruptly, e.g. at a particular body size, producing different phenotypes on either side of the threshold (Emlen and Nijhout 2000, Nijhout 2003, Lee 2005). As developmental thresholds have a genetic basis, trait expression is both conditional and heritable, allowing alternative phenotypes to evolve largely independently from one another. This greatly increases the scope for the evolution of alternative tactics (West-Eberhard 1989, 2003). Since thresholds or developmental switch points involved in the determination of tactics have a genetic basis they will be subject to selection and adaptive evolution (Tomkins et al. 2004). It is important to bear in mind that even if divergent conditional responses have different genetic bases and result in different fitness outcomes for alternative tactics they may still persist in a population (Hazel et al. 1990; see Sect. 18.2.2).

18.3.1.1 Plastic tactics

When alternative phenotype expression remains flexible throughout life, the decision to choose one or the other option depends on cues specific to the current situation. Stickleback males, for example, display bright nuptial colours, defend territories, build nests and attract females, but if their nest is already full of eggs and a female spawns nearby in a neighbour's nest, this male turns drab mimicking a female-like colour pattern and sneaks into the neighbor's nest to steal fertilisations (van den Assem 1967, Rowland 1979). Stickleback males in general seem to switch between tactics instantaneously, adjusting to the respective situation in response to a number of factors that include the state of their own brood, the distance to neighbours and their courtship success, among others. Similar opportunistic reactions to present conditions are shown, for example, in male frogs and toads that switch from calling to satellite behaviour in response to their neighbourhood on the pond (Perrill et al. 1982, Arak 1988; reviewed in Zamudio and Chan 2008), and in birds switching between bourgeois and parasitic mating tactics in response to their social environment (Birkhead and Møller 1992, Westneat and Stewart 2003).

When tactic expression is sequential, such as in numerous fish species where males exhibit parasitic tactics when small, but turn into bourgeois males when large (Taborsky 1994, 2008), the decision to behave in one or the other way will again depend on momentary conditions, which includes the individual's relative resource holding potential as a function of body size. This ontogenetic switch has a strong causal relationship to indeterminate growth as exhibited by most fishes (Taborsky 1999), which generates age-related size variation among reproductive competitors. Similar patterns have been observed for example in frogs (Howard 1984, Forester and Lykens 1986) and marine iguanas (Wikelski et al. 1996). A similar mechanism of size-dependent tactic choice can be observed in species with ontogenetic sex change. Here, the switch is not from one to another reproductive tactic within a sex, but from one sex to another (Warner et al. 1975, Shapiro 1987, Ross 1990). The direction of switch depends on environmental conditions determining which sex benefits more from large size or dominant status (Warner et al. 1975, Muñoz and Warner 2004). In contrast, in sequential intrasexual choice of alternative reproductive tactics the direction of change is always from parasitic to bourgeois, because the latter tactic inevitably benefits more from large size. A sequential choice of tactics is not confined to species with indeterminate growth, however, even though size and age dependence may still be important in species halting growth at maturity (livebearing fishes: Constantz 1975, Farr 1980; mammals: Le Boeuf 1974, Wirtz 1982, Gosling and Petrie 1990, Pemberton et al. 2004). In horseshoe crabs for example age-related condition and not size affects tactic switches (Brockmann and Penn 1992, Brockmann 2003). The important point is that selection favours mechanisms (such as status dependence of sex change; Rodgers et al. 2007) that switch the individual from one tactic to another at the point that maximises lifetime fitness.

18.3.1.2 Fixed tactics: genotype polymorphism

When the expression of ARTs is fixed for life, alternative tactics may be determined either by polymorphic genotypes originating from major gene or polygenic effects, or by some developmental mechanism. Genetic polymorphisms responsible for the expression of fixed alternative reproductive tactics have been described for the marine isopod *Paracerceis sculpta*, where male tactics are apparently controlled mainly by the Mendelian segregation of three alleles at one autosomal locus of major effect (Shuster and Wade 1991, Shuster and Sassaman 1997). The involved alleles show directional dominance and interact with alleles at other loci, setting off developmental cascades that determine the three alternative morphological and behavioural phenotypes. Interactions between alleles of this and another autosomal locus, primary sex-determining factors and possibly unknown extrachromosomal factors, affect sex determination in this species, which can distort sex ratios within groups and influence male tactic frequencies (Shuster et al. 2001). In plumage polymorphic male ruffs that show either a bourgeois courtship tactic or parasitic satellite behaviour, offspring phenotype is strongly influenced by paternal inheritance. Common garden breeding experiments provided evidence for a single locus, two-allele autosomal genetic polymorphism, with the best fit to the pedigree data obtained with a satellite allele dominance model (Lank et al. 1995). Variance in environmental factors was minimised in this experiment, so a potential modifying effect by environmental or social conditions may occur. Similarly, males of the damselfly *Mnais costalis* differing in wing colouration pursue either a bourgeois tactic by defending potential oviposition sites or a parasitic tactic where females are opportunistically pursued, which is most successful when accomplished on bourgeois male territories (Tsubaki et al. 1997). A captive rearing experiment suggested that this male polymorphism is genetically controlled by a single-locus, two-allele autosomal polymorphism (Tsubaki 2003).

In males of the swordtail *Xiphophorus nigrensis* that show determinate growth, a simple Mendelian polymorphism linked to the male sex chromosome is largely responsible for different body sizes (Kallman 1984, 1989). A locus ('pituitary locus') with three alleles triggers the timing of activation of the hypothalamic-pituitary-gonadal axis during ontogeny and hence the secretion of androgens, resulting in three male size classes, and body size heritabilities > 90% (Ryan and Wagner 1987, Kallman 1989). The males of the smallest size class perform primarily forced copulations, which is different from the courtship based mating tactic preferably used by large males (Ryan and Causey 1989). Intermediate males perform either one or the other tactic, depending on their size. Tactic choice was shown to be genetically determined also independently of body size effects (Zimmerer and Kallman 1989; this study apparently used the sister species, *X. multilineatus*; cf. Ryan et al. 1992). Hence, in this system genotype affects the choice of mating tactic through body size and through size-independent effects. It should be noted, though, that there is overlap both in body size and mating behaviour between the three male types (Ryan and Causey 1989, Zimmerer and Kallman 1989), suggesting more complex genetic and environmental causation of male mating behaviour than is hitherto understood. In another male-polymorphic poeciliid fish, *Limia perugiae*, also three male size morphs have been described, which coincides with similar specialisation between courting and forced copulation tactics as observed in *Xiphophorus* males. Here, breeding experiments suggested that male morphs are determined by Y-chromosome linked genes for small and large size interacting with an autosomal recessive repressor responsible for the development of intermediate males (Erbelding-Denk et al. 1994). The dominant allele of the recessive repressor might activate the Y-genes for large or small size, respectively, resulting in males that only attempt forced copulations (small males) or both, forced matings and copulations induced by courtship (intermediate and large males).

18.3.1.3 Fixed tactics: developmental threshold mechanisms

Tactics that are fixed for the adult life of organisms are often generated by developmental mechanisms where the decision on which life-history trajectory to follow depends on environmental or social conditions. For example in a number of species including salmon (Thorpe and Morgan 1980, Thorpe et al. 1998, Hutchings and Jones 1998), the rate of growth during the first year results in a permanent condition-dependent developmental switch to the parasitic tactic. The switch may also depend on passing a threshold size by a particular life stage, such as the end of the larval period (Emlen 1994, Moczek and Nijhout 2002, Thériault and Dodson 2003). Such threshold-dependent switch mechanisms are probably a much more widespread phenomenon than the rather rigidly determined polymorphisms just described (Brockmann 2001; reviewed in Emlen 2008). In seasonal environments, condition-dependent switches may be influenced by the time of birth of an individual in relation to environmental oscillations (the ‘birthdate effect’, Taborsky 1998; see above). In temperate marine fishes, for example, the time available to grow before the first winter may determine the choice of reproductive tactic in the subsequent reproductive season, because late-born males may be too small to compete with early born or older rivals on equal terms (Alonzo et al. 2000, Oliveira et al. 2001, 2002). Gene-environment interactions are of prime importance for the expression of alternative tactics, as illustrated by reproductive patterns of male salmon (Heath et al. 1994, Aubin-Horth et al. 2005a). Size thresholds responsible for tactic expression may differ between individuals within or between populations so that accelerated early development does not influence the choice of tactic uniformly across all genotypes, and the thresholds can be affected by environmental conditions and are subject to selection (Heath et al. 1994, Aubin-Horth and Dodson 2004, Baum et al. 2004, Piché et al. 2008). Potential cues other than size or growth rate during development that may affect phenotype expression include temperature, humidity, photoperiod, light conditions, food components and population density; in effect any external or internal cue that provides information to the individual about potential fitness effects of choosing one or another phenotype expression or life history trajectory (Dunbar 1982; reviewed in Levins 1968, Moran 1992, West-Eberhard 2003, Emlen 2008).

18.3.2 Physiological regulation

Neural circuits may strongly differ between individuals showing alternative behaviours, or biochemical switching of existing circuits may be caused by neuromodulators. These neural mechanisms interact closely with hormonal mechanisms, as neurons synthesise peptides regulating hormone production and, in turn, structural organisation of neural circuits can be influenced by organisational effects of hormones. Biochemical switches, in contrast, can be driven by activational effects of hormones on regulatory pathways of behaviour. Structural reorganisation and biochemical switching are the major mechanism underlying behavioural plasticity (Zupanc and Lamprecht 2000). It has been argued that these regulatory processes might differ systematically between fixed and flexible alternative tactics. Flexible tactics requiring rapid and transient changes in neural activity are mediated by biochemical switches involving activational effects of hormones, whereas fixed and sequential tactics are mediated by structural (re)organisation of neural networks (Oliveira et al. 2008b). Threshold responses are usually associated with hormonal differences (e.g., differences in rates of synthesis or degradation of hormones, timing of secretion or receptor expression, changes in binding affinities or in the number of receptors expressed; Emlen 2008) and they have been found to be associated with changes in gene expression in the brain that affect behaviour (Whitfield et al. 2003).

In vertebrates, the forebrain's preoptic area (POA) together with the anterior hypothalamus is a region of the brain that is highly conserved across classes, synthesising a wide range of neuropeptides and concentrating sexual steroids. This region has important control functions of reproductive and social behaviour patterns by its connections to the somatic and visceral motor systems and the pituitary gland. Peptides synthesised by POA neurons (most vertebrates) or axons reaching the pituitary directly (teleosts) trigger the activity of secretory cells in the anterior pituitary that release peptidergic hormones targeting organs throughout the body via the circulatory system. In addition, POA neurons synthesise and release arginine vasotocin- (AVT; in teleosts) or vasopressin- (AVP; in mammals)-like peptides into the posterior pituitary, which again interfaces with the circulatory system throughout the body. Among other functions, AVT/AVP has facilitating effects on courtship behaviour. The POA is also partly responsible for the production of gonadotropin- (GnRH; in teleosts) or luteinising- (LHRH; in mammals)-releasing hormones, that via the anterior pituitary influence gonad development and the production of sexual steroids. In species with ARTs, the number of neuropeptide-containing neurons within the POA vary systematically with developmental trajectories and alternative tactics (Bass and Grober 2001, Rhen and Crews 2002, Bass and Forlano 2008). In male teleosts, for example, GnRH dimorphisms are associated with differences in relative gonad size and reproductive tactics, with the morph with a larger gonad mass/body mass ratio showing larger or more GnRH-releasing POA neurons (Bass and Forlano 2008; see Bass and Grober 2009 for review of neuroendocrine mechanisms of reproductive plasticity in fish).

When aiming to understand the mediating effect of hormones on the expression of alternative reproductive tactics, it is important to distinguish between their activational effects, which are transient and affect individuals throughout life, and organisational effects, which are long-lasting and typically act during a critical period of development early in ontogeny (Arnold and Breedlove 1985). Moore (1991, Moore et al. 1998) proposed that fixed reproductive tactics should be mainly affected by the organisational role of hormones, whereas flexible phenotypes would rather depend on their activational function (the ‘relative plasticity hypothesis’). The two predictions derived from this hypothesis received only limited support, however: (1) In species with ARTs remaining flexible throughout life, the levels of hormones affecting phenotype expression should differ between morphs, whereas in species with fixed ARTs hormone profiles should be similar between alternative morphs. Regarding androgens, this prediction is consistent with roughly 80% of studied cases with ARTs in mammals, but with less then 50% of cases in birds and only 60 to 70% of cases in other vertebrate classes (see Oliveira et al. 2008b for review). The comparative patterns suggests that this hypothesis might reflect hormonal mechanisms of phenotype expression adequately only in connection with genetic sex determination and male heterogamety, where the expression of secondary sexual characters is androgen dependent (i.e., the condition in eutherian mammals). (2) Hormone manipulations during adulthood should hence affect only the expression of flexible ARTs (activational effect), whereas in species with fixed ARTs such manipulations should be effective only when applied during early development (organisational effect). Twelve experimental studies have again produced equivocal results (reviewed in Oliveira et al. 2008b). In tree lizards (*Urosaurus ornatus*), the only species with fixed ARTs tested to date by a manipulation during early ontogeny, castration or hormonal implants in males significantly affected morph expression when applied at hatching (Hews et al. 1994). In contrast, six of eleven studies where hormone levels were manipulated during adulthood did not confirm the second prediction of the relative plasticity hypothesis.

In marine iguanas, Wikelski and collaborators (2005) tested whether bourgeois males may be transformed into the parasitic phenotype when implanting them with an androgen blocker in combination with an aromatase inhibitor to obstruct the effects of testosterone on bourgeois male behaviour. Even though the treated males reduced their territorial behaviour and attracted fewer females they did not switch to parasitic behaviour. Marine iguanas show sequential ARTs with males developing from parasitic towards bourgeois behaviour with increasing age and size, and the described experiments provide no clue that this switch is solely triggered by the action of testosterone. This and other experimental and correlative evidence suggests that the effects of hormones on the expression of ARTs is not as simple as originally assumed. A ‘one-hormone-one-tactic’ relationship seems unrealistic; rather, different hormones modulate neural pathways underlying behaviour patterns in concert, involving interaction effects and feedback from the social environment (Oliveira 2004). A two-way type of interaction between hormones and behaviour is consistent also with the observation that regarding androgens, for example, their influence on morphological differentiation is much greater than on behavioural traits (this applies to intrasexually polymorphic species; Oliveira et al. 2008b). New insight into the regulatory function of factors responsible for the expression of male tactics comes from a study of gene expression in alternative male types of Atlantic salmon using microarray technology (Aubin-Horth et al. 2005b). This study revealed differential expression of 15% of the 2917 genes tested between reproductive parasites and bourgeois (anadromous) males when tested at the same age. Most of the upregulated genes in sneakers are associated with reproduction (e.g., the production of gonadotropins, growth hormone and prolactin), neural plasticity and neural signalling, whereas the upregulated genes of anadromous males are mainly associated with somatic growth and maturation. Interestingly, these results suggest a greater role for neural plasticity in the parasitic males, which was unexpected.

Understanding the threshold mechanisms involved in the development and expression of ARTs is particularly fruitful also for a comprehension of underlying evolutionary patterns. In horned beetles with guarding and sneaking males, experiments revealed that the juvenile hormone provides the important signal. This hormone varies with larval diet, and male larvae with levels above a threshold (which are the *small* animals) generate a pulse of ecdysone that acts as a secondary signal (Emlen and Nijhout 1999, 2001). This signal prevents significant horn growth in females and small males, perhaps by affecting the sensitivity of horn cells to juvenile hormone during a sensitive period. The physiological mechanisms regulating the divergent behaviour of the resulting male morphs, however, are hitherto less well understood. Importantly, genetic changes in downstream regulatory pathways involving hormones and neural mechanisms may cause changes of tactics, in morphology, physiology and behaviour alike, that are expressed more or less independently from the alternative tactics (Emlen 2008). This insight illustrates basic mechanisms how genes can create divergent phenotypes among individuals of the same species and sex relatively independently from each other (West-Eberhard 2003).

18.4 General questions and future prospects

Which patterns emerge when comparing the occurrence of ARTs in different major taxa (BOX 18.4) and which general principles can be uncovered by the study of alternative phenotypes? Research on alternative tactics can help to understand a range of mechanisms and principles that are of general importance in biology. This includes the role of trade-offs for the evolution of allocation decisions, the costs and benefits of flexibility, the origin of complex suites of characters, the action of disruptive selection, the evolution of decision rules, the functionality of threshold mechanisms and developmental switches, the causes and consequences of individual (behavioural, physiological, morphological) variation among conspecifics, the evolution of cooperation as a means to cope with competition, specialisation and adaptations to sperm competition (at gametic, anatomical and behavioural levels), and the coexistence of several evolutionarily stable strategies within a population. ARTs are an important component of biological diversity and may be a source of sympatric speciation (Garcia-Vazquez et al. 2002, West-Eberhard 2003).

All reproductive traits are variable but ARTs are different because the variation is significantly discrete, i.e. bimodal or multimodal, rather than continuous. Most ARTs are characterised by suites of co-varying and co-adapted traits tightly associated with each alternative phenotype. This means that to understand the evolution and expression of ARTs we need to understand how discrete variation comes about and why it is favoured by selection. We have argued that discrete variation usually arises through threshold mechanisms, i.e. the animal switches from one reproductive phenotype to another when specific conditions are reached (Emlen 2008). These threshold mechanisms have been well studied both physiologically and developmentally (Emlen 1996, Roff 1998, Nijhout 1999, Hartfelder and Emlen 2005). There is a growing literature demonstrating the heritability of thresholds and an ability to respond quickly to selection (Emlen 1996, Zera and Zhang 1995, Shuster and Wade 2003). Threshold mechanisms are favoured by selection when individuals possessing intermediate values of a continuously varying trait are selected against, i.e. under disruptive selection (Danforth and Desjardin 1999). Some alternative phenotypes are fixed during development and some are flexible over the life of the animal. Selection favours flexible alternative tactics when information exists (e.g. from the individual, environment) on the relationship between phenotype and fitness (Brockmann 2001, Shuster 2008).

Selection against intermediates occurs because extreme phenotypes have higher fitness (Brockmann 2008, Brockmann and Taborsky 2008). This may be because of trade-offs (physical, behavioural, physiological, developmental or genetic; see Zera and Harshman 2001) or genetic correlations, or because of different reproductive niches for different phenotypes within a population. Selection for extreme phenotypes is particularly common under intense sexual selection when animals pay high costs for specialised structures that enhance performance in male-male competition or female choice. Any male that can gain even a few fertilisations without paying those extreme costs may have higher than average fitness, since under conditions of high variance in fitness most individuals produce no offspring (Shuster and Wade 2003).

While this broad outline for the evolution of ARTs seems clear, we have little ability to predict the patterns, frequency and occurrence of alternative phenotypes. Evolutionary outcomes are very difficult to understand without the aid of models (Brockmann 2001, Wolf et al. 2007). To predict complex interactions between an individual's physiological condition, prevailing environmental conditions, time constraints, and frequency- and density-dependent factors operating within a population demands a modelling approach (Lucas and Howard 2008). Models allow us to examine assumptions and to specify the factors that we think are influencing the evolution of tactics in a particular system. Dynamic models (Lucas et al. 1996, Skubic et al. 2004) or multi-level dynamic games (Alonzo and Warner 2000) and other kinds of models (e.g. Sinervo et al. 2000, Alonzo and Sinervo 2001) provide subtle and sometimes counterintuitive outcomes that result from complex and unexpected interactions among variables and parameters. For example, in a model of flexible caller/satellite tactics in chorusing frogs (Lucas et al. 1996), the effects of costly singing, predation risk at choruses, variation in female arrival rates, frequency-dependent effects

BOX 18.4

Emerging patterns: why do ARTs differ between major taxa?

When comparing ARTs among major taxa, their prevalence and forms appear to differ substantially. Male ARTs are widespread and variable in **fish**, for example, which may relate to four conditions (Taborsky 2008): (1) The fertilisation mechanism: the vast majority of fish taxa show external fertilisation, which has two important consequences. Firstly, it is difficult for males to monopolise access to partners or fertilisable eggs. Secondly, external fertilisation selects for large numbers of sperm, which is a precondition for male success in sperm competition. External fertilisation also allows for very diverse spawning patterns (e.g., in the water column, on the ground or on/in a substrate), which in turn increases the variability of ARTs. (2) Indeterminate growth: the vast majority of fishes do not stop to grow after maturation, which often causes enormous intrasexual size differences within species (Taborsky 1999). In a sample of eight species of fish with ARTs from which data of male size were available, comprising salmon, sunfish, cichlids, wrasses and blennies, the largest males of a species were on average 18 times heavier than their smallest male conspecifics (Taborsky 1999). In contrast, the intrasexual size dimorphism of animals with determinate growth is much smaller. In 490 passeriform bird species, for example, the largest males were on average only 1.19 times heavier than their smallest male conspecifics (Taborsky 1999). As a consequence, no specialised reproductive parasites are apparently found in passerine birds. (3) Parental roles: paternal investment is particularly widespread in fish (Blumer 1979), which allows male competitors to exploit such investment by the performance of ARTs. In addition, fish show an unprecedented diversity of parental care patterns (Blumer 1982), which relates to a great variability in mating patterns and, consequently ARTs (Taborsky 1994). (4) Variable sex determination: in fishes we find gonochorism, simultaneous and sequential hermaphroditism, and the latter with either males (protandry) or females (protogyny) preceding each other (Shapiro 1987). Gonochorism and sex change may even coexist within species (Robertson et al. 1982). This variability of sex determination and differentiation mechanism might also relate to the evolution of alternative mating tactics in fish, as suggested by the frequent existence of ARTs in simultaneous and sequential hermaphrodites (see Taborsky 2008 for review).

In **insects**, ARTs can be found at all different steps of (male) reproductive behaviour, which include locating a mate, getting access and copulating with her, and showing postcopulatory behaviour serving to raise the fertilisation chances (Brockmann 2008). ARTs are particularly common at the mate searching stage, especially when females mate in diverse locations. In species with maternal care, investing females are often exploited by other females by facultative, intraspecific brood parasitism (Tallamy 2005). The prevalence varies greatly between insect orders, with Hymenoptera and Coleoptera spearheading others, whereas in the also well-studied Hemiptera and

Lepidoptera ARTs are apparently rare. This variation may again relate to parental care, which is more common in the first two orders (Trumbo 1996), providing opportunities for exploitation by male and female parasitism.

In **amphibians**, ARTs are mainly confined to mate acquisition in males (Zamudio and Chan 2008), for example with bourgeois caller and parasitic satellite tactics in frogs and toads. In salamanders, male ARTs involve paedomorphosis (the retention of larval characters in mature adults), female mimicry and sexual interference. Female amphibians hardly show ARTs. In contrast, intraspecific female reproductive parasitism (egg dumping) is widespread in **birds**, where high parental investment makes exploitation worthwhile (Krüger 2008). In male birds, opportunistic simultaneous ARTs are very widespread, with males that invest in resource defence, mate acquisition and parental care also pursuing a parasitic tactic to fertilise neighbouring females (Westneat and Stewart 2003). In **mammals**, harem defence and resource defence polygyny in pinnipeds and ungulates is frequently accompanied by alternative male tactics exploiting the investment of bourgeois males (Wolff 2008). A pattern with territorial bourgeois males and extra-pair fertilisations by satellite, neighbouring or wandering males is also widespread in rodents. In contrast, sexual coercion as an alternative male tactic is most widespread in primates (Smuts and Smuts 1993), where sneak matings by subordinate males with females guarded by dominants also abound (Setchell 2008). Female ARTs are very rare in mammals.

Probably the most obvious general pattern is that ARTs abound where individuals invest heavily in reproduction in a way that can be circumvented and exploited by same-sex competitors. As soon as selection favours investment, there is also potential to select for low-cost tactics to attain the same goal by alternative means (Taborsky 1997, 2001). This reflects disruptive selection on reproductive investment (e.g., Schütz et al. 2010). A second generality may be the important effect of body size variation among same-sex competitors, which may have different causes in the evolutionary ecology of different species, including indeterminate growth, variable growth conditions during ontogeny, and diverging feeding specialisations of juveniles. In species with environmentally determined size variation between competitors, a specialisation should result in bourgeois tactics if large and parasitic tactics if small. This expectation is apparently often met. When comparing gross patterns between taxa the caveat is, however, that our knowledge depends largely on the accessibility of information, conspicuousness of traits, research approach, ideas and hypotheses of researchers, and underlying research traditions. Therefore, the differences we conceive between major taxa must be treated with caution – in the end they might be more apparent than real.

since satellites parasitise the singing behaviour of callers (only callers attract females) and a limited breeding season combined to produce some unexpected results: periods of intense calling followed by periods with no animals present. Such fluctuations in numbers at choruses had been observed but were always assumed to be due to some unknown environmental factors. This model also demonstrated that a variable that had never been measured, female arrival rate, was a crucial parameter in determining the behaviour of the model and the frequency of tactics. Thus, models can identify new important factors; they can evaluate the importance of variables through sensitivity analyses; and they can even suggest new tactics that were not previously suspected.

Even some of the best-studied ART systems at the empirical level have never been modelled and our understanding of the factors that shape their evolution has not been tested. We do not know, for example, whether the effects of frequency and density-dependence are sufficient to maintain alternative tactics at observed frequencies in most systems or even what factors might be creating frequency-dependent effects (e.g. female choice traits, interactions among males, heterozygote advantage). To create a model of an ART system, the factors affecting fitness must be hypothesised, formalised and their functional relationships with other variables specified. Even simple models would take us a long way toward incrementing our understanding of ARTs.

In addition, few alternative phenotype systems have been critically tested at the empirical level. Experimental testing requires manipulating the frequencies of tactics to see whether fitness changes in the predicted directions (Bleay et al. 2007). Alternatively, increasing or decreasing the fitness of one of the tactics should show whether the frequencies of tactics change in the predicted directions or whether selection differentials are affected correspondingly (Lande and Arnold 1983). While such experiments are not easy to carry out, they will reveal whether our picture of the evolution and maintenance of alternative tactics is realistic.

ARTs, along with other sorts of alternative tactics, provide one important source of variation upon which evolution acts (West-Eberhard 2003). A well studied discontinuous distribution of reproductive traits is male and female function. Animals may either pursue a fixed tactic by adopting one of the two sexes for a lifetime (gonochorism); develop both sexual functions simultaneously and use them interchangeably depending on circumstances (simultaneous hermaphroditism); or switch from one sexual function to the other either once or repeatedly (sequential hermaphroditism with fixed or reversible sequence) depending on age or condition (Anthes this volume). Hence the same scheme that we used to classify ARTs also applies to sex allocation (Fig. 18.1). There is a large literature on sex allocation (Charnov 1982), both at the ultimate and proximate levels, and incorporating this aspect of ARTs here was beyond the scope of this chapter. However, it is important to consider that the mechanisms underlying systematic variation in reproductive tactics between sexes and within a sex are similar (Brockmann 2001).

Studies of populations with different frequencies of alternative phenotypes can provide insight into the factors that influence phenotypic evolution (Bailey et al. 2008, Pizzo et al. 2008). Alternative phenotypes also provide a unique opportunity to study the underlying genetic architecture of adaptations. For example, the parasitic tactic is often a mosaic of both male and female phenotypes (e.g. sexual mimicry), which evolves through the decoupling of traits that usually occur together (Brockmann et al. 2008). ARTs allow an opportunity to study the nature of correlated traits and the mechanisms by which they may be decoupled (Gonçalves et al. 2008). Further, genes that are differently expressed in alternative phenotypes make it possible to identify the genes and regulatory mechanisms that are consistently up- or down-regulated between alternative phenotypes (Aubin-Horth et al. 2005b, Toth et al. 2007, Gonçalves et al. 2008, Renn et al. 2008, St-Cyr and Aubin-Horth 2009). The study of alternative phenotypes provides a special opportunity for studying the evolution of the mechanisms that underlie adaptation.

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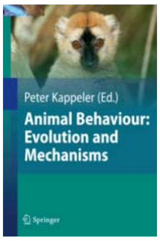

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The study of animal behaviour is one of the fastest growing sub-disciplines in biology. The resulting diversity of conceptual approaches and methodological innovations makes it increasingly difficult for professionals and students to keep abreast of important new developments. This edited volume provides up-to-date reviews that facilitate orientation in key areas of animal behaviour, including communication, cognition, conflict, cooperation, sexual selection and behavioural variation. The contributions address evolutionary and proximate aspects of behaviour and also cover both invertebrates and vertebrates. Important concepts are dealt with in separate glossaries and key examples highlighted in separate text boxes. Richly illustrated with colour figures, this volume offers a well structured overview of all the main developments in current animal behaviour research. It is ideal for teaching upper-level courses, where it will be essential reading for advanced students familiar with basic concepts and ideas.

Content Level » Upper undergraduate

Keywords » Animal Behaviour - Applied Ecology - Behaviour - Behavioural Ecology - Behavioural Variation - Cognition - Communication - Conflict - Cooperation - Ethology - Evolution - Invertrebrates - Sexual Selection - Vertebrates

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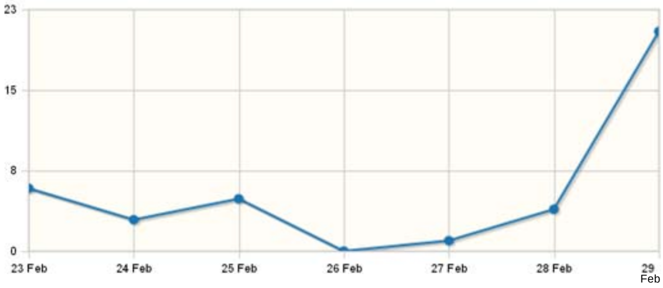

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