20 · Integrating mechanisms and function: prospects for future research

H. JANE BROCKMANN, RUI F. OLIVEIRA, AND MICHAEL TABORSKY

CHAPTER SUMMARY

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

20.1 WHAT IS NEXT IN THE STUDY OF ARTs?

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

20.1.1 Categories of ARTs

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

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

Alternative Reproductive Tactics, ed. Rui F. Oliveira, Michael Taborsky, and H. Jane Brockmann. Published by Cambridge University Press.

ARTs have been categorized in a number of different ways. As discussed in Chapter 1, "tactics" and "strategies" are not easily distinguished and imply a dichotomy between genetic and nongenetic control that is not useful (e.g., nature vs. nurture; see Section 20.3), so we do not support this distinction and refer instead to all cases as tactics. Tactics are governed by evolved decision-making rules, whatever the underlying mechanism. Many authors also distinguish ARTs that are associated with a genetic polymorphism from those that are conditional (i.e., influenced by individual status, condition, age, or environmental conditions). We now know that environmental conditions often affect the expression of genetic polymorphisms (Chapters 10 and 12), that thresholds of genetically based tactic expression may vary even within populations (Chapters 5, 8, and 10), and that genetic differences may affect the expression of condition-dependent tactics (Chapter 5). Therefore, the distinction between genetic polymorphism and conditional tactic does not seem useful. Rather, we consider gene–environment interactions to be of paramount importance in understanding reproductive tactics. Well-adapted animals are expected to switch from one tactic to another so that fitness is maximized, i.e., they should always be making the *best* of their situation. With ARTs individuals allocate resources to either one or the other (mutually exclusive) way of achieving the same functional end (reproductive tactic) using evolved decision-making rules (i.e., the tactics are adaptations). We suggest that ARTs should be categorized in the same way as other alternative allocation phenotypes such as sex allocation (Figure 1.1; Chapter 2) (Henson and Warner 1997, Taborsky 1998, Brockmann 2001) and alternative life histories (West-Eberhard 2003). When this is done, theory developed for other alternative allocation problems (e.g., sex allocation, alternative life histories) can be readily applied to ARTs.

In a remarkable convergence of views, those studying ARTs primarily from an evolutionary perspective (e.g., Taborsky 1998, Brockmann 2001; Chapter 1) and those studying the underlying mechanisms of ARTs (Chapters 6 and 7; Moore *et al.* 1998) have arrived at the same system for classifying ARTs (Figure 1.2). Both approaches view ARTs as either fixed or plastic during the life of an individual and among the plastic tactics, as either irreversible switches that occur at a particular age, condition, or under particular environmental situations, or fully reversible through the adult life of an individual. Fixed ARTs are thought to be due to organizational effects whereas plastic ARTs involve activational processes during the adult life of the individual. In many cases fixed ARTs are known to involve a switch mechanism (Chapters 5, 6, 7, 8, and 10) during the development of the individual (e.g., horned beetles: Chapter 5), so the differences between the two processes may be a matter of developmental timing rather than a fundamental differences in underlying processes. Nonetheless, identifying these patterns has allowed both evolutionary and mechanistic studies to begin to identify the factors controlling the expression and evolution of ARTs.

The ARTs literature has emphasized males but cases of female ARTs are scattered among most taxonomic groups. Female ARTs include brood parasitism (Chapters 8 and 12); tactics to avoid male coercion (Chapters 8 and 18); reproductive dominance and suppression (Chapters 8, 14, and 15); alternative colony-founding tactics (Chapter 8) and cobreeding (Chapter 19); monandry and polyandry (Chapters 12 and 19); differences in fecundity or investment in eggs (Chapters 2 and 12); and consistent differences among females in preferences for males (Chapters 13, 17, and 18). As with males, female ARTs can be expected to evolve under conditions of intense intrasexual or social competition and high reproductive skew. Since females are generally thought to be under less intense sexual selection than males, it is not surprising that female ARTs are less common. Of course, it is also possible that female ARTs, like female sexual behaviors generally, are simply less easily observed than male ARTs. Certainly, condition-dependent and frequency-dependent fitness effects can occur in females so it is important to search for female ARTs more explicitly if we hope to understand the evolution of reproductive behavior.

20.1.2 Crossing fitness curves and beyond: the importance of modeling

ARTs are found across a wide range of taxonomic groups and across different stages of the reproductive process. ARTs occur most often in the context of intrasexual selection when (a) there are reproductive opportunities for those individuals that opt out of costly or high-risk male–male interactions to seek mating opportunities under less competitive circumstances (e.g., fighting vs. dispersing males); or when (b) parasitizing of costly male investment (e.g., bourgeois vs. parasitic males) can result in fitness gains, and (c) patterns arising in response to intersexual selection are much less common but include female choice for direct benefits (e.g., useless nuptial gifts) and mate conflict (e.g., noncourtship and forced copulation). ARTs may also evolve when mating opportunities arise because females are found in different habitats that require different male adaptations. For example, unmated female fig wasps (Chapter 8) can be found both inside and outside the natal fig; males that remain inside must fight for access to females so they develop enlarged heads and mandibles and have reduced wings whereas males that leave the natal fig must fly and they do not have to fight for females so they have normal mandibles and wings. In all cases the model of crossing fitness curves has been used to understand the maintenance of alternative tactics (figures in various chapters). This simplistic model says little more than that individuals switch from one tactic to the other under the conditions that maximize their fitness or that population-wide frequencies of alternative tactics converge on the ESS. Even this simple model, however, is rarely tested experimentally. It should be possible, for example, to change the proportions of the tactics in a population and predict a change in their fitness. It should also be possible to change the pay-offs to the tactics and thereby predict a change in their frequencies. Such experimental approaches are required to determine whether our view of the evolution of ARTs is supported.

Better models are needed for understanding ARTs. Current theory is generally based on fixed rather than dynamic fitness functions. New models need to incorporate differences in individual condition and status and the mechanisms and decision rules by which tactics are switched, as well as frequency and density dependence (and their interactions) (Chapter 4). Such models will require dynamic game modeling as well as measures of physiological condition and the benefits that accrue to alternative tactics. The dynamics of between-sex interactions are as important to understand as the dynamics of within-sex interactions. For this reason both male and female tactics and male–female conflict need to be incorporated into modeling efforts (Chapter 18). Models predict that females should adjust their mating decisions to males of different tactics depending on their condition and the relative fitness gains associated with direct vs. indirect benefits. Multilevel games will be important when female choice affects the pay-offs to males choosing among ARTs and when the frequency of male tactics affects the pay-offs to females in their choice among reproductive tactics. Furthermore, the success of alternative phenotypes often depends on spatial and temporal dynamics. In some well-studied cases (e.g., Chapters 12 and 13), fitness is affected by the number of, distance from, and morph of neighbors, as well as habitat characteristics and seasonal patterns. Recent modeling efforts (Formica *et al.* 2004, Hamilton *et al.* 2006, Koseki and Fleming 2006, Vercken *et al.* 2007) show that the frequency and coexistence of ARTs are shaped by such spatial and temporal dynamics. Modeling of complex systems like ARTs is crucial because it reveals hidden assumptions and often results in counterintuitive predictions.

20.1.3 Equality of fitness?

As Darwin (1871) observed, when two differing male forms are found in the same population at the same time, both must have “certain special, but nearly equal advantages from their differently shaped organs.” This general expectation for equality of fitness and evolutionary stability for alternative phenotypes has been supported in a number of cases where mixed evolutionarily stable states (ESSs) and frequency dependence are involved (e.g., Chapters 9, 10, and 12). However, many studies have demonstrated that alternative phenotypes are maintained in populations without equal fitness. It is generally agreed that the majority of these ARTs are conditional on environmental, social, or individual status (e.g., Chapters 8, 11, 14, and 15). When each individual follows a conditional tactic that maximizes its fitness, equal success among the tactics is unlikely (Chapter 2; Repka and Gross 1995). There are studies, however, in which differences in success between morphs are almost certainly attributable to the fact that it is very difficult to measure the reproductive success of both tactics with equal reliability. In general the sedentary, monopolizing, and higher-variance or bourgeois tactic has been found to have higher fitness than the dispersing, sneaker, lower-variance or parasitic tactic, which is also the tactic whose fitness would be most difficult to measure. In particular, the success of all males must be counted including those that disperse, those that die before reproducing, and those that never inseminate any females (Chapter 9). This almost certainly means that some studies have prematurely claimed unequal fitness between tactics (Shuster and Wade 2003).

Many of the assumptions we have made in the past about costs and benefits of alternative tactics are being challenged. Most studies have assumed that females would not choose to mate with parasitic males if given the option and indeed there is experimental evidence for this in some species (Alonzo and Warner 2000, Gonçalves *et al.* 2005). However, in several recent studies, females have been shown to mate polyandrously both with the faster-growing parasitic males, thereby increasing their indirect benefits, and with parental males, thereby increasing their direct benefits (Chapter 17; Neff 2004). In still other species females apparently mate preferentially with parasitic males to increase genetic benefits but also with aggressive, monopolizer males to reduce the costs of male coercion (Watters 2005). Such female preferences may help to explain the frequency of "cuckoldry" in many ARTs systems and the apparent tolerance that some bourgeois males show toward satellite or parasitic males.

20.1.4 Competition and cooperation in ARTs

Although most male ARTs have been viewed as highly competitive, there is increasing evidence that cooperation can be an adaptive competitive tactic (Taborsky 2001). If females copy the mate choice decisions of other females or if females actively prefer multiple males (for example, to ensure fertilization of all the females' eggs), then a bourgeois male may gain from the presence of satellite males (Chapters 10 and 13). Cooperative behavior offered by reproductive parasites to bourgeois competitors may reduce the costs of competition for both parties, or provide incentives to the bourgeois male to be more tolerant of the parasite's presence. In some species males can increase their success by allowing particular males (e.g. dull yearlings or males of the same morph) to occupy adjacent territories (Chapters 12 and 13) or by forming alliances with other males (Chapters 14, 15, and 19). The pay-offs to competitive interactions are likely to be dynamic and the degree of reproductive skew variable, ranging from competitive to neutral to more beneficial for one party or the other. The spatial and temporal dynamics of reproductive pay-offs will be influenced by individual status, social conditions, and frequency dependence, which means that extensive modeling of these systems will be required.

20.1.5 Evolution of tactic frequencies and the importance of frequency dependence

Models with crossing fitness curves predict the stable frequency of alternative morphs in the population. Considerable theory exists for the evolution of sex ratios (stable frequencies of two sexes in a population: Charnov 1982, Hardy 2002), but there is little information on the population-wide frequency of other alternative phenotypes (Chapter 2). When alternative tactics are frequency dependent then they should evolve like sex ratios. Factors such as the relative costs of producing the two morphs (cost ratios) and the relative reproductive values of the two morphs should affect equilibrium morph ratios as they do sex ratios. To add another level of complexity, combinations of conditional and pure or "mixed strategies" (e.g., gynodioecy) are well-known sex-allocation patterns (Chapter 2) and models suggest that such combinations should also occur in ARTs (Hazel *et al*. 2004, Plaistow *et al*. 2004). Trimorphic ARTs are also frequency dependent, often with rock–paper–scissors intransitivities that result in cyclical patterns of morph frequencies (Sinervo and Calsbeek 2006). However, not all ARTs are frequency dependent; in some cases ARTs evolve in niches in which some fitness can be achieved. In these cases morph ratios should reflect the relative frequencies of the two niches in the environment (Chapter 2).

Both frequency dependence and density dependence can maintain alternative phenotypes in a population. Frequency and density dependence often interact in complex ways (Chapter 19). For example, in the damselfly *Ischnura ramburi*, one female morph mimics males thus avoiding costly matings, but since males learn to recognize male mimics, the system shows negative frequency dependence (the rarer morph is more successful; Chapter 8). However, the mating cost to females (male mimics) is incurred only at high densities, so the intensity of frequency-dependent selection in this system changes with density (Brockmann 2001, Sirot *et al*. 2003). This means that population-level differences in demographic structure (e.g., density and operational sex ratio) can affect the social context for mating and influence the direction of sexual selection at different temporal and spatial scales (Chapter 11).

Although generally regarded as important for the maintenance of ARTs (and for maintaining other polymorphisms), few studies have evaluated frequency dependence experimentally (Conover and van Voorhees 1990, Hori 1993, Basolo 1994, Roff 1996, Giraldeau and Livoreil 1998, Olendorf *et al*. 2006). If frequencies of a morph are manipulated then changes should occur in the reproductive success of the manipulated and alternative morphs and predicted population-wide adjustments in frequencies should follow.

20.1.6 Information is important

Those studying ARTs often stress the importance of knowing the environmental information available to the individual and the value of that information in affecting the expression of alternative tactics. For example, when little information is available about the association between behavior and fitness, then mixed strategies are favored (Brockmann 2001). Environmental predictability is often mentioned as a selective pressure favoring alternative tactics but few studies have examined the ability of individuals to detect and evaluate this variable and to act on the basis of such information. Clearly, the amount and nature of the information available to individuals and the benefits and costs associated with gathering and responding to this information will influence the evolution of ARTs (Leimar *et al*. 2006).

ARTs are also shaped by the communication networks in which they occur. The presence of eavesdroppers such as social competitors and predators will affect the evolution of signals associated with reproductive tactics (Chapter 16). For example, bourgeois males reduce their courtship signaling behavior when the reproductive success of both females and bourgeois males declines with increasing numbers of parasitic males (Alonzo and Warner 1999). Selection will favor females that either thwart or encourage eavesdropping by parasitic males depending on whether females lose or gain fitness from mating with these individuals.

Some ARTs depend on misinformation. For example, male damselflies apparently cannot distinguish male mimics from males (Sherratt 2001) and male peacock blennies cannot distinguish female mimics from females (Gonçalves *et al*. 2005). Such mimicry systems depend on morph-specific costs and benefits as well as on an underlying mechanism for mate recognition. If, for example, mating is costly to females and males learn to recognize females then rare morphs will always have an advantage, a frequency-dependent effect that will maintain variation in female traits (Fincke *et al*. 2005). A quantitative, decision-theory approach (Dall *et al*. 2005) to analyzing the information available to individuals is needed to understand both the evolution of and mechanisms underlying ARTs.

20.1.7 Understanding trade-offs

The evolution of alternative tactics is grounded in the notion of trade-offs: allocating resources in one direction will reduce alternative possibilities. For example, dispersing males reduce the costs of fighting or maintaining territories but they do not attract females, they are exposed to increased levels of sperm competition, and they may have a shorter lifespan. Animals that need wings for flight must expend resources on developing flight muscles, resources that then cannot be used for other activities such as producing eggs. This intuitive concept of trade-offs as direct competition for limited resources among different body functions has been examined in studies of wing-dimorphic crickets. The greater ovarian growth and reduced lipid biosynthesis of the wingless morph relative to the winged morph was found to result from the differential allocation of internal reserves to the two traits (Zera and Harshman 2001). Knowledge of the underlying basis for trade-offs will help evolutionary biologists understand the likely evolutionary trajectory for ARTs and assist physiologists in understanding the developmental expression of ARTs (Emlen 2001, Emlen *et al*. 2005, Simmons and Emlen 2006).

20.1.8 Origin and evolution of ARTs

ARTs are found more commonly in some groups than in others (e.g., Chapters 8 and 11). To some degree this bias results from differences between taxonomic groups in their depth of study, but clearly this is not the only explanation. ARTs occur most commonly in groups with intense sexual selection; where there are large investments by males or females; when males have the ability to monopolize some mating opportunities; and when opportunities exist to partially fertilize clutches of polyandrous females (Chapters 2, 8, and 11). ARTs can magnify intrasexual variance in reproductive success and may lead to more intense sexual selection on some male tactics than on others.

ARTs seem particularly common among fishes (Chapter 10). The factors that may influence the frequent evolution of ARTs in fishes include the presence of indeterminate growth, which results in large size differences among males; external fertilization, which selects for large quantities of sperm and the opportunity for sperm competition; and the frequency of parental care, a high-investment tactic that can be exploited by other males. One tentative conclusion about the phylogeny of male ARTs (as described for three groups of fishes) is that although ARTs arise repeatedly during the course of evolution, they are found only at the tips of branches (Chapter 3). This means that ARTs rarely become permanent features of deeper clades. This is not surprising since the frequency of ARTs is so responsive to environmental and social conditions, which means that one of the morphs can easily go extinct (Chapter 3). However, once ARTs have evolved and there is a developmental uncoupling of dimorphic structures and behavior, then the alternative tactics may evolve at least partially independently (Chapter 5; West-Eberhard 2003).

20.1.9 Integrating mechanisms with evolution

One important remaining challenge for the study of ARTs is to understand how the mechanisms that cause variants to arise are favored by selection. When we say that ARTs have evolved in a lineage, we mean that a developmental process has caused a change in the phenotype of some individuals in that lineage. That process is likely affected by genetic, physiological, and environmental factors. There are two established mechanisms that will produce dimorphism, a threshold mechanism and a change in the scaling of the power relationships among traits (Chapters 5, 6, 9, and 10). When differences in phenotype are due to heritable differences in the underlying mechanism and when these differences result in fitness differences then selection on the mechanisms will occur. When disruptive selection is combined with heritable developmental threshold mechanisms, then genetic correlations between tactics will be minimized by partially uncoupling gene expression of the alternative tactics permitting them to evolve along independent trajectories. This mechanistic model for the evolution of ARTs needs to be verified and many questions remain. What genes are involved in these threshold mechanisms and are there patterns or homologies for the genes affecting ARTs? How does the genetic architecture of ARTs change as tactics evolve and are there common patterns or underlying constraints in this process? Are there constraints on the underlying mechanisms that affect the kinds of options that are available as ARTs or that make some ARTs more common than others (e.g., the frequency of sexual mimicry would suggest that this is the case)? A fully integrative approach is needed to answer these questions, an approach that unites mechanistic studies with evolutionary modeling and empirical tests.

20.2 WHAT DOES THE STUDY OF ARTs TELL US ABOUT OTHER BIOLOGICAL PROBLEMS?

ARTs provide a valuable tool for understanding biology, from genes through development and physiology to behavior and morphology. The reviews in this book have demonstrated that ARTs are common among organisms and that alternative phenotypic pathways have evolved multiple times (Chapters 3 and 5; Emlen *et al*. 2005). This means that ARTs provide a rich pallet from which to investigate a number of important biological questions. ARTs are also part of a much larger category of alternative allocation phenotypes that covers a wide diversity of animal adaptations (Chapter 2). Just as the study of sex allocation or game theory can improve our understanding of ARTs, the study of ARTs can provide insights into the mechanisms, evolution and maintenance of variation in populations.

20.2.1 The control, origin, and evolution of complex phenotypes (suites of characters)

From a mechanistic perspective, one of the most remarkable (and valuable) features of ARTs is that there is a dissociation between the control and expression of ARTs (Chapter 7, Figure 7.1). Most animals show clear differences in morphology, physiology, and behavior between males and females. But in species with alternative tactics one sex may look and act like the opposite sex. For example in the damselfly *Ischnura ramburi*, females of one morph (andromorphs) are physically and behaviorally similar to males, and they are often treated like males (Chapter 8; Robertson 1985, Sirot *et al*. 2003). In many fish species such as bluegill sunfish and peacock blennies, parasitic males mimic females in appearance and behavior and thereby escape bourgeois male aggression (Chapter 10; Dominey 1980, Gonçalves *et al*. 1996, 2005; see Taborsky 1994 for review). This decoupling of the expression of behavioral and morphological male traits (i.e., secondary sexual characters) from gametogenesis offers unique opportunities to study the proximate mechanisms of reproduction (Moore 1991, Moore *et al*. 1998, Oliveira *et al*. 2005, Oliveira 2006). Causal mechanisms underlying individual variation in reproduction can be studied much better in species with ARTs, since within-sex variation in reproductive traits is not confounded by the effects of gender.

The expression of alternative reproductive tactics is often a function of behavioral plasticity (Gross 1996), which is primarily triggered by structural reorganization (for slow and long-lasting changes) and biochemical switching (involving neuromodulators such as catecholamines, which allows faster and reversible changes: Zupanc and Lamprecht 2000). Both mechanisms usually depend on organizational and activational effects of hormones (Arnold and Breedlove 1985, Moore 1991, Moore *et al*. 1998, Oliveira 2006). In vertebrates sex steroids, glucocorticoids, and neuropeptides are major candidates for the differentiation and maintenance of ARTs (Chapter 7; Brantley *et al*. 1993, Nelson 2005). Because similar regulatory mechanisms are involved in the development and differentiation of sex (Crews 1998, Crews *et al*. 1998, Devlin and Nagahama 2002, Godwin and Crews 2002, Oliveira 2005, Vigers *et al*. 2005), the study of proximate mechanisms underlying ARTs has important general implications. In both cases developmental processes need to be considered to understand how factors taking effect early in ontogeny can shape consistent individual variation within and between sexes (see Crews and Groothuis 2005). Understanding the proximate mechanisms underlying the regulation of ARTs might also help to explain other problems such as alternative life-history patterns (Turner and Grosse 1980, Meyer 1987, Lu and Bernatchez 1999, Jonsson and Jonsson 2001, Kurdziel and Knowles 2002) or the mode of action and importance of threshold mechanisms (Chapter 5; West-Eberhard 1989, Roff 1996, Zera and Denno 1997, Hartfelder and Emlen 2005).

20.2.2 The proximate causes of ARTs and functional genomics

ARTs offer a unique opportunity to study the physiological mechanisms and the genetic architecture underlying the decoupling of traits that are usually present in concordance, since in the parasitic tactic a mosaic of both male and female traits may be present instead of a constellation of gender-specific traits (e.g., species with parasitic males that mimic females in which the maturation of the male gonad is decoupled from the expression of male secondary sex characters and male sexual behavior). Therefore, ARTs provide insight into the proximate mechanisms linking male and female phenotypes under conditions that are not pathological.

Neuroendocrinological studies have shown that different neuropeptides (e.g., GnRH, AVT) and steroids are operating either independently or in concert to coordinate the expression of a suite of characters, characteristic of a given tactic (see Chapters 6 and 7). These studies have also demonstrated that the decoupling of different male traits in parasitic males may be achieved either by differences in hormone levels or by varying the local microenvironments in the different target tissues, due to differential expression of receptors or to differential levels of activity of catabolic enzymes that modulate the availability of the active hormone to specific targets (e.g., 11-β-hydroxilase and 11-β-HSD that metabolize T into KT). These are key steps in the expression of male secondary sex characters, spermatogenesis, and the modulation of the expression of reproductive behavior in male teleosts (Oliveira 2006). For example, in the protogynous wrasse *Halichoeres trimaculatus*, which has ARTs, the relative levels of brain steroid receptors vary between alternative reproductive phenotypes, with levels of androgen receptor transcripts being significantly higher in the brain of terminal-phase males than in initial-phase males, whereas no other significant differences in gene expression were observed either for androgen or for estrogen receptors in the gonads or for estrogen receptors both in the brain and in the gonads (Kim *et al*. 2002). Thus, by varying the expression of androgen receptors in specific tissues (brain vs. gonad), terminal-phase males can both increase their sensitivity to circulating androgen levels in specific targets (the brain), and at the same time decouple the effects of androgens in different target tissues by varying androgen receptor densities, so that unwanted effects of androgens can be avoided. This mechanism hypothetically makes it possible to activate the expression of an androgen-dependent reproductive behavior in bourgeois males without having the associated costs of increasing spermatogenesis or the expression of a sex character, since the androgen action can be independently modulated at each compartment (brain vs. gonad vs. morphological secondary sex character). Studies focusing on target tissues are thus a major avenue for future research in this area.

One emerging approach when studying target tissues has been the use of functional genomics tools that are now becoming more accessible. DNA microarrays allow the monitoring of large sets of genes (thousands) in key tissues (brain, gonads, somatic ornaments), hence making it possible to identify genes and regulatory networks which are consistently up- or downregulated between alternative sex types. Genes that are differentially expressed in alternative morphs are potential candidates to be involved in the expression of the alternative tactics (Hofmann 2003). Since ARTs involve differences in the expression of reproductive behavior between alternative phenotypes, this approach has concentrated on comparing the brain gene expression profiles between morphs. In the Atlantic salmon *Salmo salar*, gene expression profiles were compared between sneaker males and immature juveniles (of the same age) that represent alternative life histories (Aubin-Horth *et al*. 2005). The immature males will later migrate and then return to the breeding grounds where they will reproduce as bourgeois males. Fifteen percent of the genes included in the array (ca. 3000) were expressed differentially between the sneaker and the juvenile immature males (Aubin-Horth *et al*. 2005). In sneaker males most of the upregulated genes are involved in reproduction and related processes (e.g., gonadotrophins, growth hormone, prolactin, and POMC genes) whereas in immature males upregulated genes are associated with somatic growth (e.g., genes involved in transcription regulation and protein synthesis, folding, and maturation). This reflects at the cellular level the classic life-history trade-off between reproduction and growth, illustrated by these two alternative phenotypes. Another set of genes upregulated in sneakers are involved in neural plasticity (e.g., genes coding for synaptic function and for cell-adhesion glycoproteins that have been implicated in memory formation) and in neural signaling (e.g., genes coding for nitric oxide synthesis, a neurotransmitter involved in the regulation of neuropeptide action). This difference has been interpreted as suggesting that the expression of the sneaker tactic is more demanding at the cognitive level (Aubin-Horth *et al.* 2005). Therefore, a functional genomics approach may not only allow the confirmation of expected differences in the profiles of gene expression of specific target tissues between alternative phenotypes, but it may also reveal differences in gene expression between morphs in otherwise unsuspected biological processes (e.g., neural plasticity).

20.2.3 Behavioral syndromes

Ethologists have long realized that there is often consistent behavioral variation between individuals of a species (Bagg 1916, Lorenz 1935, Tinbergen 1951, van Oortmerssen 1971, Huntingford 1976, Benus *et al.* 1987, Clark and Ehlinger 1987, Riechert and Hedrick 1993, Verbeek *et al.* 1994). Interestingly, a broader systematic study of the mechanisms underlying such individual variation has begun only recently, but with all the more vigor (e.g., van Oortmerssen and Bakker 1981, Ehlinger and Wilson 1988, Benus *et al.* 1991, Hessing *et al.* 1994, Dingemanse *et al.* 2002, van Oers *et al.* 2004, 2005, Both *et al.* 2005, Kralj-Fiser *et al.* 2007; reviews in Wilson 1998, Koolhaas *et al.* 1999, Gosling 2001, Sih *et al.* 2004a, b, Groothuis and Carere 2005). The consistent tendency of individuals to behave in a certain way, either in a particular behavioral context (e.g., in resource competition) or across contexts (e.g., in exploration, predator avoidance, and dominance interactions) has been referred to as an animal's coping style, behavioral type, profile, or tendency, or – in analogy to a term used in human psychology – "personality" (Gosling and John 1999, Kolhaas *et al.* 1999, Carere and Eens 2005, Groothuis and Carere 2005). Suites of correlated behaviors have been called behavioral syndromes (Sih 2004a, b), which refers to a property of a population of individuals denoting a correlation between rank-order differences of individuals through time or across situations (Bell 2007).

The study of ARTs and behavioral syndromes has much in common. Variation in behavior, regardless of whether it is discontinuous or continuous, is strongly influenced by developmental processes (Caro and Bateson 1986, Meaney 2001, Stamps 2003); it is heritable (Benus *et al.* 1991, Sinervo and Zamudio 2001, Drent *et al.* 2003); it depends on the abiotic, biotic, and social environments (Emlen 1997, Benus and Henkelmann 1998, Groothuis and Carere 2005); and it has profound fitness consequences (Shuster 1989, Ryan *et al.* 1992, Dingemanse and Reale 2005), which affect populations and thereby have important ecological and evolutionary implications (Gross 1991, Bolnick *et al.* 2003, Sih *et al.* 2004a). The most significant difference between alternative allocation phenotypes (AAP) such as ARTs and behavioral syndromes (BS) seems to be the form of the trait distributions. AAP are characterized by discontinuous or bimodal/multimodal phenotype distributions (Chapters 1 and 2), whereas BS usually show a continuous, unimodal distribution (Wilson *et al.* 1994). In both cases, it is of paramount interest to understand the ultimate and proximate mechanisms causing and maintaining behavioral variation within populations.

Students of ARTs can learn from BS research that individual differences in behavior can represent limited plasticity. If behavioral tendencies "carry over" between different contexts due to the make-up of an organism, "optimal" responses to particular problems might not be expected (Sih *et al.* 2004b). Imagine a benefit exists in a population for high aggression levels in competition for food resources. Individuals thereby selected to be very aggressive may not be able to overcome such tendencies in the reproductive context. In other words, they may be predisposed to perform a bourgeois reproductive tactic, even if a parasitic tactic may provide higher rewards. The important message here is that correlations among traits can act as evolutionary constraints (Duckworth 2006). We may not find the expected optimal behavior because correlated responses to selection on nontarget traits can depend on genetic correlations (Lande and Arnold 1983, Roff and Fairbairn 1993). Traits may evolve together as packages. It would be worth studying also in the context of ARTs, which behaviors are correlated across which contexts, how stable these correlations are, and which evolutionary processes and physiological mechanisms might be responsible for the existence of such correlations. This is an addition to the 12 pertinent questions asked in Chapter 1 to aim at a comprehensive understanding of the evolution of ARTs.

In return, research on BS may benefit from the knowledge of principles developed in the long history of AAP studies (Brockmann 2001). The theory developed to explain sex allocation, alternative life histories, and ARTs may yield adequate approaches and methods to resolve questions of the coexistence of alternative coping styles (Chapter 2). Conceptual understanding and empirical results have accumulated in the research of ARTs (Chapter 1) that may significantly further the comprehension of BS, at least by turning the focus towards the most urgent questions. The majority of the 12 questions asked in Chapter 1 are also relevant for the study of BS. For example, it seems presently unclear to what extent behavioral types such as shyness or boldness are flexible (or reversible) over a lifetime (Wilson *et al*. 1993, Coleman and Wilson 1998, Frost *et al*. 2007). Are threshold mechanisms and developmental switches involved in the generation of diverging behavioral profiles (Groothuis and Carere 2005), and if so, to what degree are these switches and threshold mechanisms subject to natural selection (Roff 1998)? The integrative approach to the study of ARTs (Chapters 2, 5, 7, 8, 9, 10, 12, and 15) may be particularly valuable for BS research, because both physiological and evolutionary mechanisms must be considered for a comprehensive understanding of individual variation in behavior (Koolhaas *et al*. 1999, Oliveira *et al*. 2005).

The study of behavioral syndromes still suffers from a lack of quantitative information in most natural systems (Sih *et al*. 2004b). A crucial question in BS research is the nature of phenotype distributions. Is the distribution of shy and bold, proactive and reactive, sedentary and roaming behavioral types indeed continuous and unimodal as is usually assumed or is there sometimes evidence for underlying disruptive selection processes? Surprisingly, this question is hitherto largely neglected in the study of BS (Sih *et al*. 2004a, b, Bell 2007). If disruptive selection is involved, concepts developed in the study of AAP could be applied. If instead BS are characterized by uniform distributions, the persistence of systematic individual differences in behavior despite apparent absence of disruptive selection needs to be explained. What is the importance of density- and frequency-dependent selection under these conditions (Dall *et al*. 2004, Wilson *et al*. 1994)? Why is behavioral plasticity hampered (DeWitt *et al*. 1998, West-Eberhard 2003)? To what extent is state dependence involved in the expression of behavioral phenotypes (Dall *et al*. 2004)? This is where the study of ARTs and BS can effectively complement one another.

20.2.4 The role of ARTs in speciation

Intraspecific alternative adaptations predispose populations to speciation because they represent fitness trade-offs under natural selection (West-Eberhard 2003). When divergence in the form of alternative phenotypes has developed, particular variants may be fixed in certain subpopulations due to assortative mating, environmentally mediated change in expression, or frequency-dependent selection. Examples include (1) socially parasitic inquiline ants that reproduce by laying eggs in the colonies of other ant species; there is evidence that these ants have evolved by sympatric speciation due to parallel size-related alternatives in the two sexes (Buschinger 1986; see Buschinger 1990, Bourke and Franks 1991, West-Eberhard 2003 for review). (2) In pacific sockeye salmon *Oncorhynchus nerka*, some individuals do not migrate to sea but stay in the rivers where they were born to reproduce earlier than the anadromous conspecifics (Thorpe 1989). In the male sex, this usually involves parasitic sneaking behavior. In some populations, the marked size difference between stationary and migratory individuals of both sexes apparently leads to assortative mating by size (Foote 1988, Foote and Larkin 1988), which creates genetic divergence between the anadromous sockeye and nonmigratory kokanee forms (see Foote and Larkin 1988 for references). The ultimate cause for assortative mating in systems with extensive, discontinuous size variation may be the benefit of mating among mates with a similar, precocious life-history type. (3) Lizards have been suggested to nicely demonstrate the importance of secondary sexual signals for the evolution of intrapopulation divergence and sympatric speciation (Lande 1982, West-Eberhard 1983). In lizards with intraspecific and intrasexual color polymorphisms and alternative mating behaviors, frequency-dependent selection in combination with assortative mating between like-types and reduced hybrid fitness may further genetic diversification and speciation (Hochberg *et al*. 2003, Sinervo and Calsbeek 2006). When assortative mating is not linked to resource competition, genetic drift may break the linkage equilibrium between the trait responsible for mate selection and the respective ecological traits (Dieckmann and Doebeli 1999), hence leading to reproductive isolation between ecologically diverging subpopulations. (4) Color polymorphisms and negatively frequency-dependent selection that might be associated also with alternative mating behaviors may cause speciation in the rapidly radiating Lake Victoria cichlids (Seehausen and Schluter 2004). Male–male competition and aggression focused on like-types generates negative assortment of nuptial color patterns among habitats. Whether and to what extent alternative mating behaviors may be involved in this diversification process is yet unclear.

In species with male ARTs, reproductive parasites or "sneakers" may participate in fertilization attempts of other species (Crapon de Caprona 1986, Taborsky 1994, Jansson and Ost 1997, Wirtz 1999) or forcefully copulate with heterospecific females (Seymour 1990, Russell *et al*. 2006). This causes hybridization, a speciation mechanism that is often underrated (Mallet 2007). It may be particularly important in lineages with rapid adaptive radiation such as the cichlids of the Great African Lakes (Salzburger *et al*. 2002, Seehausen 2004). Interspecific fertilization by reproductive parasites is probably a frequent phenomenon because it is inherently "cheap," i.e., reproductive parasites only contribute sperm and do not invest in secondary sexual characters, courtship, nest building, and brood care (Taborsky 1994). This is one likely cause of unidirectional hybridization, which is apparently more frequent than reciprocal hybridization (Wirtz 1999). Phylogenetic analyses of ARTs in fishes suggest that they are distributed near the tips of the phylogenetic trees (Chapter 3), which might indicate a functional link between speciation and the evolution of alternative mating tactics.

ARTs may result from divergent reproductive niches due to habitat differences or when same-sex competitors show bimodal or multimodal trait distributions caused by natural selection (Chapter 2; Denno 1994, Skúlason and Smith 1995, Pigeon *et al*. 1997, Danforth and Desjardins 1999, Jonsson and Jonsson 2001). Trophic morph divergence, for example, may strongly affect reproductive options and thereby relate to the mating tactics used, such as in Arctic charr (Jonsson and Jonsson 2001, Snorrason and Skúlason 2004). This may drive speciation by disruptive selection under conditions of at least minimum ecological contact between the diverging lines (Smith and Skúlason 1996), whereby reproductive isolation may evolve surprisingly quickly (Hendry *et al*. 2000). When gene flow becomes severely restricted, further morph specialization may ensue, which finally gives rise to new species (Snorrason and Skúlason 2004). This is a promising area for future research into evolutionary mechanisms underlying speciation on the basis of intraspecific morph divergence.

20.3 BROADER IMPLICATIONS OF ARTs

The study of ARTs can contribute much to our understanding of fundamental issues in biology (as discussed above), but it can also contribute to our understanding of applied problems. In this section we address a few of these topics.

20.3.1 ARTs in conservation

Conservation is a growing field of knowledge in which the maintenance of biodiversity is a key goal. In conservation the species is the commonly used unit of biodiversity and intraspecific variations are usually overlooked (but see Bolnick *et al*. 2003). However, intraspecific variation represents an important component of ecologically functional diversity within a species and this translates into adaptive genetic variation of the population and hence its evolutionary potential. This means that polyphenisms including ARTs are a valuable part of biological diversity and should be considered in conservation actions. For example, the occurrence of sneaker males in the peacock blenny *Salaria pavo* is limited to lagoon populations in southern France and in southern Portugal (Ruchon *et al*. 1995, Gonçalves *et al*. 1996). Apparently, the scarcity of nest sites in the near-shore lagoon environments poses a constraint on male reproductive rate in this crevice-nesting species and the operational sex ratios become female biased (J. Saraiva and R.F. Oliveira, unpublished data). This leads to a sex-role reversal in courtship behavior, with females taking the leading role in courtship in the lagoon population (Almada *et al*. 1995). ARTs are also present among males in these populations, with younger and smaller males mimicking female courtship behavior in order to gain access to nests during spawning episodes (Gonçalves *et al*. 1996). Hence, although this species is common in rocky shores in the Mediterranean Sea and in adjacent areas from northern Morocco to the Bay of Biscay (Zander 1986), the lagoon populations deserve a special conservation status for the intraspecific variation they exhibit.

The occurrence of intraspecific diversity should be preserved not only because of their intrinsic interest as unique biological phenomena, but also because such local adaptation adds to the species genetic assets and flexibility and thus can contribute to the evolutionary potential and long-term survival of the species (Buchholz and Clemmons 1997). This is illustrated by our discussion of the potential role of ARTs in speciation. But species with ARTs may also maintain greater intraspecific genetic diversity than populations without such variation. For example, alternative dispersal tactics, which are often associated with ARTs (Chapters 2 and 8), will influence genetic variation and population viability as well as the effectiveness of release programs (Thomas *et al*. 2000). One problem in the conservation of highly sexually selected species, which are some of our most spectacular species, is that genetic diversity and the effective size of the breeding population is constrained by the presence of a few highly preferred males (Parker and Waite 1997). However, when ARTs are present, genetic variance is more likely to be maintained and inbreeding problems reduced.

The presence of ARTs should be considered whenever human intervention is planned. For example, an effort to increase the number of nest sites for rare cavity-nesting birds by placing nest-boxes in the environment at high densities had an unanticipated result, an increase in intraspecific brood parasitism (Eadie *et al*. 1998). This facultative, female reproductive tactic turned out to be density dependent and an increase in nesting sites ended up decreasing population growth. ARTs should also be considered in resource exploitation, since harvesting may lead to the selective removal of one of the reproductive morphs. For example, because bourgeois males are larger than parasitic males, and because harvest activities are usually directed towards the largest individuals in the population, bourgeois males are more likely to be removed. The effects of selective removal of specific morphs on population persistence and genetic diversity are still poorly understood. However, it can be predicted that the removal of larger individuals may influence life-history decisions leading to a reduction in size at sexual maturity and concomitantly to a reduction in female fecundity (assuming size-dependent fecundity) (Vincent and Sadovy 1998). Also, the differential removal of males in a population may lead to sperm limitation and consequently to a reduction in female fecundity with an impact on population persistence (e.g., male biased capture in ungulates: Ginsberg and Milner-Gulland 1994).

Knowledge of ARTs has already influenced management decisions. In the United States, sunfishes (*Lepomis* spp.) are an important resource for sport fishing and some species of sunfish exhibit ARTs consisting of three male types: nest-guarding parental males, female-mimicking satellite males, and sneaker males that dart into the nests of parental males during spawning to release sperm (Gross 1982). The fishery disproportionately removes parental males both because they are larger and because they are site-attached to their nests making them easier to target. As a consequence the unguarded eggs and larvae of captured parental males are cannibalized by other individuals, thus reducing the survival of the young. To control the impact of this selective removal, fisheries management policies were revised and the frequency of alternative males in the population is being controlled (M. Gross, personal communication, in Vincent and Sadovy 1998). Similarly, increased fishing pressure on the large, anadromous, hooknose male salmon may end up increasing the proportion of the less desired, small jacks in the population (Gross 1991b).

20.3.2 ARTs in pest management

The occurrence of alternative reproductive phenotypes can play a key role in the effectiveness of pest management strategies, since variants can be maintained or selectively targeted by specific pest management practices. Red imported fire ants *Solenopsis invicta* introduced into the United States from South America in the 1930s and 1940s rapidly became a pest in southern states because of their negative economic impact. They produce large nest mounds that may damage agricultural equipment or even promote the collapse of road sections by removing the soil under the asphalt; they inflict significant damage to agricultural crops (e.g., soybeans, eggplant, corn, etc.) and livestock; and they have a painful sting that may be dangerous to sensitized people that develop an allergic reaction to their venom. Different pest management methods have been developed to control the populations of the red imported fire ant, including pesticides and biological control agents. Recently a microsporidian pathogen (*Thelohania solenopsae*) with a high prevalence rate that may reduce or even kill colonies has been detected in the US populations of fire ants, thus having a potential role as a biological control agent (Williams *et al*. 2003). Since *T. solenopsae* can be transmitted by the introduction of infected broods into a colony, the degree of inter-colony brood transfer is a key factor for its spread. In fire ants two types of social organization are commonly present: monogyny, in which a single egg-laying queen is present per colony, and polygyny, in which multiple queens are present per colony (Ross and Keller 1995). These two ethotypes also differ in their social behavior: polygyne colonies exchange workers, food, brood and mated females, whereas monogyne colonies are very territorial (Tschinkel 1998). Therefore, the social structure of the colonies is expected to moderate the infection by *T. solenopsae*. As predicted, polygyne colonies have a much higher prevalence of this infection in the field (Oi *et al*. 2004, Fuxa *et al*. 2005) and a longer persistence and faster spread of infections started in the laboratory than monogyne colonies (Oi 2006, Preston *et al*. 2007). Therefore, by affecting the dynamics of the microsporidium infection, the multiple social forms of these fire ant populations play a key role when considering the potential of this pathogen as a biological agent in pest management.

20.3.3 ARTs in medicine

Medical research is mainly focused on explaining how the body systems work and why some people are more vulnerable to a particular disease than others. The proximate mechanisms of disease vulnerability are commonly seen as resulting from evolutionary "defects" and random processes. More recently, the role of evolutionary constraints and host–parasite co-evolution have also been implicated in evolutionary approaches to the study of disease (Nesse and Williams 1998). The study of ARTs provides a different conceptual framework that promotes the view that genetic variants are likely to represent evolved alternative adaptations for different environments instead of the classic view as malfunctioning phenotypes. This ARTs view of adaptive variation is relevant to understanding the evolution of host–parasite interactions, the evolution of and spread of disease organisms, and antibiotic resistance.

20.3.4 ARTs in evolutionary psychology

The study of ARTs may help to explain the evolution of apparently nonadaptive human characters such as homosexuality. Same-sex sexual behavior is present in a large number of species from different vertebrate taxa, and it is commonly associated with ARTs (Bagemihl 1999). In humans sexual orientation shows marked sex differences: male homosexuality presents a somewhat bimodal distribution, whereas female homosexuality displays a more continuous distribution, from strictly heterosexual to strictly homosexual individuals (LeVay 1996). Therefore, the distribution of male homosexuality in humans resembles the discrete distribution of ARTs. However, despite displaying a similar pattern to same-sex sexuality in animals (e.g., female mimicry in males in order to get access to breeding females), human homosexuality does not share the same functional explanation. On the contrary, male homosexual behavior is an evolutionary paradox since it is associated with decreased direct reproduction and other hypotheses, such as kin selection, also fail to account for its maintenance in the population (Bobrow and Bailey 2001). This paradox is further stressed by the prevalence of homosexuality in different cultures and by the fact that at least part of the variation in sexual orientation has a genetic basis (see Bailey *et al*. 2000 and references therein).

Thus, by providing the theoretical basis and the methodologies for the study of discrete, within-sex variation in sexual behavior, the study of ARTs may also contribute to the rigorous study of the complexities of human social behavior.

20.3.5 ARTs in education and the public understanding of science

Finally, we would like to finish the last chapter of this book by drawing attention to the fact that ARTs are an excellent topic for popular science films and books since they provide strong narratives that may increase the impact of science communication (Dingwall and Aldridge 2006). In this respect it is worth mentioning that one of the first scientific studies of ARTs was published by Desmond Morris (Morris 1952), one of the most active popular-science writers today. Moreover, since the boom in popular-science publishing during the 1990s, ARTs are being portrayed in many wildlife films and documentaries and featured in popular books (e.g., Judson 2002, Crump 2005). These popular accounts of ARTs communicate to the public both fascinating biology and important biological concepts, such as the role of evolution in maintaining variation in populations.

We hope that in the near future ARTs can be further used in conveying to the general public one of the basic advances in biology in the last few decades that two levels of explanation are needed for the full understanding of any biological trait: (1) an evolutionary explanation regarding its function; and (2) a proximate explanation for how it works. These two levels should not be taught separately since they complement one another; the teaching of this emerging corollary of modern biology to the general public will be a challenge that represents "integration" at still a higher level.

References

Almada, V. C., Gonçalves, E. J., Oliveira, R. F., and Santos, A. J. 1995. Courting females: ecological constraints affect sex roles in a natural population of the blenniid fish *Salaria pavo*. *Animal Behaviour* **49**, 1125–1127.

Alonzo, S. H. and Warner, R. R. 1999. A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success. *Behavioral Ecology* **10**, 105–111.

Alonzo, S. H. and Warner, R. R. 2000. Dynamic games and field experiments examining intra-and intersexual conflict: explaining counterintuitive mating behavior in a Mediterranean wrasse, *Symphodus ocellatus*. *Behavioral Ecology* **11**, 56–70.

Arnold, A. B. and Breedlove, S. M. 1985. Organizational and activational effects of sex steroids on brain and behavior: a reanalysis. *Hormones and Behavior* **19**, 469–498.

Aubin-Horth, N., Landry, C., Letcher, B., and Hofmann, H. 2005. Alternative life histories shape brain gene expression profiles in males of the same population. *Proceedings of the Royal Society of London B* **272**, 1655–1662.

Bagemihl, B. 1999. *Biological Exuberance: Animal Homosexuality and Natural Diversity*. New York: St. Martin's Press.

Bagg, H. J. 1916. Individual differences and family resemblances in animal behavior. *American Naturalist* **50**, 222–236.

Bailey, J. M., Dunne, M. P., and Martin, N. G. 2000. Genetic and environmental influences on sexual orientation and its correlates in an Australian twin sample. *Journal of Personality and Social Psychology* **78**, 524–536.

Basolo, A. L. 1994. The dynamics fisherian sex-ratio evolution: theoretical and experimental investigations. *American Naturalist* **144**, 473–490.

Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B-Biological Sciences* **274**, 755–761.

Benus, R. F. and Henkelmann, C. 1998. Litter composition influences the development of aggression and behavioural strategy in male *Mus domesticus*. *Behaviour* **135**, 1229–1249.

Benus, R. F., Koolhaas, J. M., and van Oortmerssen, G. A. 1987. Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour* **100**, 105–122.

Benus, R. F., Bohus, B., Koolhaas, J. M., and van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia* **47**, 1008–1019.

Bobrow, D. and Bailey, J. M. 2001. Is male homosexuality maintained via kin selection? *Evolution and Human Behavior* **22**, 361–368.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., *et al.* 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1–28.

Both, C., Dingemanse, N. J., Drent, P. J., and Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology* **74**, 667–674.

Bourke, A. F. G. and Franks, N. R. 1991. Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biological Journal of the Linnean Society* **43**, 157–178.

Brantley, R. K., Wingfield, J. C., and Bass, A. H. 1993. Sex steroid levels in *Porichthys notatus*, a fish with alternative reproductive tactics, and a review of the hormonal bases for male dimorphism among teleost fishes. *Hormones and Behavior* **27**, 332–347.

Brockmann, H. J. 2001. The evolution of alternative strategies and tactics. *Advances in the Study of Behavior* **30**, 1–51

Buchholz, R. and Clemmons, J. 1997. Behavioral variation: a valuable but neglected biodiversity. In J. Clemmons and R. Buchholz (eds.) *Behavioral Approaches to Conservation in the Wild*, pp. 181–211. Cambridge, UK: Cambridge University Press.

Buschinger, A. 1986. Evolution of social parasitism in ants. *Trends in Ecology and Evolution* **1**, 155–160.

Buschinger, A. 1990. Sympatric speciation and radiative evolution of socially parasitic ants: heretic hypotheses and their factual background. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **28**, 241–260.

Carere, C. and Eens, M. 2005. Unravelling animal personalities: how and why individuals consistently differ. *Behaviour* **142**, 1149–1157.

Caro, T. M. and Bateson, P. 1986. Organization and ontogeny of alternative tactics. *Animal Behaviour* **34**, 1483–1499.

Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton, NJ: Princeton University Press.

Clark, A. B. & Ehlinger, T. J. 1987. Pattern and adaptation in individual behavioral differences. In: *Perspectives in Ethology, Vol. 7* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 1–47. New York, Plenum.

Coleman, K. and Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour* **56**, 927–936.

Conover, D. and van Voorhees, D. 1990. Evolution of a balanced sex ratio by frequency dependent selection in a fish. *Science* **250**, 1556–1558.

Crapon de Caprona, M. D. 1986. Are preferences and tolerances in cichlid mate choice important for speciation? *Journal of Fish Biology* **29**, 151–158.

Crews, D. 1998. On the organization of individual differences in sexual behavior. *American Zoologist* **38**, 118–132.

Crews, D. and Groothuis, T. 2005. Tinbergen's fourth question, ontogeny: sexual and individual differentiation. *Animal Biology* **55**, 343–370.

Crews, D., Sakata, J., and Rhen, T. 1998. Developmental effects on intersexual and intrasexual variation in growth and reproduction in a lizard with temperature-dependent sex determination. *Journal of Comparative Physiology C* **119**, 229–241.

Crump, M. 2005. *Headless Males Make Great Lovers*. Chicago, IL: University of Chicago Press.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* **7**, 734–739.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., and Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* **20**, 187–193.

Danforth, B. N. and Desjardins, C. A. 1999. Male dimorphism in *Perdita portalis* (Hymenoptera, Andrenidae) has arisen from preexisting allometric patterns. *Insectes Sociaux* **46**, 18–28.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Denno, R. F. 1994. The evolution of dispersal polymorphism in insects: the influence of habitats, host plants and mates. *Researches on Population Ecology* **36**, 127–135.

Devlin, R. H. and Nagahama, Y. 2002. Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. *Aquaculture* **208**, 191–364.

DeWitt, T. J., Sih, A., and Wilson, D. S. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13**, 77–81.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature* **400**, 354–357.

Dingemanse, N. J. and Reale, D. 2005. Natural selection and animal personality. *Behaviour* **142**, 1159–1184.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., and van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* **64**, 929–938.

Dingwall, R. and Aldridge, M. 2006. Television wildlife programming as a source of popular scientific information: a case study of evolution. *Public Understanding of Science* **15**, 131–152.

Dominey, W. J. 1980. Female mimicry in male bluegill sunfish: a genetic polymorphism? *Nature* **284**, 546–548.

Drent, P. J., van Oers, K., and van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London B* **270**, 45–51.

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology* **17**, 1011–1019.

Eadie, J., Sherman, P., and Semel, B. 1998. Conspecific brood parasitism, population dynamics, and the conservation of cavity-nesting birds. In T. Caro (ed.) *Behavioral Ecology and Conservation Biology*, pp. 306–340. Oxford, UK: Oxford University Press.

Eberhard, W. G. and Gutiérrez, E. E. 1991. Male dimorphisms in beetles and earwigs and the question of developmental constraints. *Evolution* **45**, 18–28.

Ehlinger, T. J. and Wilson, D. S. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences of the United States of America* **85**, 1878–1882.

Emlen, D. J. 1996. Artificial selection on horn length–body size allometry in the horned beetle *Onthophagus acuminatus*. *Evolution* **50**, 1219–1230.

Emlen, D. J. 1997. Diet alters male horn allometry in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society of London B* **264**, 567–574.

Emlen, D. J. 2001. Costs and the diversification of exaggerated animal structures. *Science* **291**, 1534–1536.

Emlen, D. J., Marangelo, J., Ball, B., and Cunningham, C. W. 2005. Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution* **59**, 1060–1084.

Fincke, O. M., Jodicke, R., Paulson, D. R., and Schultz, T. D. 2005. The evolution and frequency of female color morphs in Holarctic Odonata: why are male-like females typically the minority? *International Journal of Odontology* **8**, 183–212.

Foote, C. J. 1988. Male mate choice dependent on male size in salmon. *Behaviour* **106**, 63–80.

Foote, C. J. and Larkin, P. A. 1988. The role of male choice in the assortative mating of anadromous and non-anadromous sockeye salmon (*Oncorhynchus nerka*). *Behaviour* **106**, 43–62.

Formica, V. A., Gonser, R. A., Ramsay, S., and Tuttle, E. M. 2004. Spatial dynamics of alternative reproductive strategies: the role of neighbors. *Ecology* **85**, 1125–1136.

Frost, A. J., Winrow-Giffen, A., Ashley, P. J., and Sneddon, L. U. 2007. Plasticity in animal personality traits: does prior experience alter the degree of boldness? *Proceedings of the Royal Society of London B* **274**, 333–339.

Fuxa, J. R., Milks, M. L., Sokolova, Y. Y., and Richter, A. R. 2005. Interaction of an entomopathogen with an insect social form: an epizootic of *Thelohania solenopsae* (Microsporidia) in a population of the red imported fire ant, *Solenopsis invicta*. *Journal of Invertebrate Pathology* **88**, 79–82.

Garant, D., Fontaine, P.-M., Good, S. P., Dodson, J. J., and Bernatchez, L. 2002. Influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). *Evolutionary Ecology Research* **4**, 537–549.

Ginsberg, J. R. and Milner-Gulland, E. J. 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology* **8**, 157–166.

Giraldeau, L.-A. and Livoreil, B. 1998. Game theory and social foraging. In L. Dugatkin and H. K. Reeve (eds.) *Game Theory and Animal Behavior*, pp. 16–37. Oxford, UK: Oxford University Press.

Godwin, J. and Crews, D. 2002. Hormones, brain and behavior in reptiles. In D. W. Pfaff, A. P. Arnold, A. M. Etgen, S. E. Farbach, and R. T. Rubin (eds.) *Hormones, Brain and Behavior*, vol. 2, pp. 649–798. New York: Academic Press.

Gonçalves, D., Matos, M., Fagundes, T., and Oliveira, R. F. 2005. Bourgeois males of the peacock blenny, *Salaria pavo*, discriminate females from female-mimicking males? *Ethology* **111**, 559–572.

Gonçalves, E. J., Almada, V. C., Oliveira, R. F., and Santos, A. J. 1996. Female mimicry as a mating tactic in males of the blenniid fish *Salaria pavo*. *Journal of the Marine Biological Association of the United Kingdom* **76**, 529–538.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin* **127**, 45–86.

Gosling, S. D. and John, O. P. 1999. Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science* **8**, 69–75.

Groothuis, T. G. G. and Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews* **29**, 137–150.

Gross, M. R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie* **60**, 1–26.

Gross, M. R. 1991a. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions of the Royal Society of London B* **332**, 59–66.

Gross, M. R. 1991b. Salmon breeding behavior and life history evolution in changing environments. *Ecology* **72**, 1180–1186.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution* **11**, 92–98.

Hamilton, I. M., Haesler, M. P., and Taborsky, M. 2006. Predators, reproductive parasites, and the persistence of poor males on leks. *Behavioral Ecology* **17**, 97–107.

Hardy, I. C. W. (ed.) 2002. *Sex Ratios: Concepts and Research Methods*. Cambridge, UK: Cambridge University Press.

Hartfelder, K. and Emlen, D. J. 2005. Endocrine control of insect polyphenism. In L. I. Gilbert, K. Iatrou, and S. S. Gill (eds.) *Comprehensive Molecular Insect Science*, vol. 3, *Endocrinology*, pp. 651–703. Boston, MA: Elsevier.

Hazel, W., Smock, R., and Lively, C. M. 2004. The ecological genetics of conditional strategies. *American Naturalist* **163**, 888–900.

Hendry, A. P., Wenburg, J. K., Bentzen, P., Volk, E. C., and Quinn, T. P. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* **290**, 516–518.

Henson, S. A. and Warner, R. R. 1997. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annual Review of Ecology and Systematics* **28**, 571–592.

Hessing, M. J. C., Hagelso, A. M., Schouten, W. G. P., Wiepkema, P. R., and van Beek, J. A. M. 1994. Individual behavioral and physiological strategies in pigs. *Physiology and Behavior* **55**, 39–46.

Hochberg, M. E., Sinervo, B., and Brown, S. P. 2003. Socially mediated speciation. *Evolution* **57**, 154–158.

Hofmann, H. A. 2003. Functional genomics of neural and behavioral plasticity. *Journal of Neurobiology* **54**, 272–282.

Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**, 216–219.

Huntingford, F. A. 1976. Relationship between anti-predator behaviour and aggression among conspecifics in threespined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour* **24**, 245–260.

Jansson, H. and Ost, T. 1997. Hybridization between Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in a restored section of the River Dalalven, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2033–2039.

Jonsson, B. and Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. *Journal of Fish Biology* **58**, 605–638.

Judson, O. 2002. *Dr. Tatiana's Sex Advice to All Creation*. New York: Henry Holt.

Kim, S. J., Ogasawara, K., Park, J. G., Takemura, A., and Nakamura, M. 2002. Sequence and expression of androgen receptor and estrogen receptor gene in the sex types of protogynous wrasse, *Heliochoeres trimaculatus. General and Comparative Endocrinology* **127**, 165–173.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., *et al.* 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews* **23**, 925–935.

Koseki, Y. and Fleming, I. A. 2006. Spatio-temporal dynamics of alternative male phenotypes in coho salmon populations in response to ocean environment. *Journal of Animal Ecology* **75**, 445–455.

Kotiaho, J. S. and Tomkins, J. L. 2001. The discrimination of alternative male morphologies. *Behavioral Ecology* **12**, 553–557.

Kralj-Fiser, S., Scheiber, I. B. R., Blejec, A., Moestl, E., and Kotrschal, K. 2007. Individualities in a flock of free-roaming greylag geese: behavioral and physiological consistency over time and across situations. *Hormones and Behavior* **51**, 239–248.

Kurdziel, J. P. and Knowles, L. L. 2002. The mechanisms of morph determination in the amphipod *Jassa*: implications for the evolution of alternative male phenotypes. *Proceedings of the Royal Society of London B* **269**, 1749–1754.

Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* **36**, 213–223.

Lande, R. and Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226.

Leimar, O., Hammerstein, P., and Van Dooren, J. M. 2006. A new perspective on developmental plasticity and the principles of adaptive morph determination. *American Naturalist* **167**, 367–376.

LeVay, S. 1996. *Queer Science: The Use and Abuse of Research into Homosexuality*. Cambridge, MA: MIT Press.

Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie* **83**, 137–215; 289–413.

Lu, G. Q. and Bernatchez, L. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution* **53**, 1491–1505.

Mallet, J. 2007. Hybrid speciation. *Nature* **446**, 279–283.

Meaney, M. J. 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience* **24**, 1161–1192.

Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* **41**, 1357–1369.

Moore, M. C. 1991. Application of organization–activation theory to alternative male reproductive strategies: a review. *Hormones and Behavior* **25**, 154–179.

Moore, M. C., Hews, D. K., and Knapp, R. 1998. Hormonal control and evolution of alternative male phenotypes: generalizations of models for sexual differentiation. *American Zoologist* **38**, 133–151.

Morris, D. 1952. Homosexuality in the ten-spined stickleback (*Pygosteus pungitus* L.). *Behaviour* **4**, 233–261.

Neff, B. D. 2004. Increased performance of offspring sired by parasitic males in bluegill sunfish. *Behavioral Ecology* **15**, 327–331.

Nelson, R. J. 2005. *An Introduction to Behavioral Endocrinology*, 3rd edn. Sunderland, MA: Sinauer Associates.

Nesse, R. M. and Williams, G. C. 1998. Evolution and the origins of disease. *Scientific American* **279**, 86–93.

Oi, D. H. 2006. Effect of mono- and polygyne social forms on transmission and spread of a microsporidium in fire ant populations. *Journal of Invertebrate Pathology* **92**, 146–151.

Oi, D. H., Valles, S. M., and Pereira, R. M. 2004. Prevalence of *Thelohania solenopsae* (Microsporidae: Thelohaniidae) infection in monogyne and polygyne red imported fire ants (Hymenoptera: Formicidae). *Environmental Entomology* **33**, 340–345.

Olendorf, R., Rodd, F. H., Punzalan, D., *et al.* 2006. Frequency-dependent survival in natural guppy populations. *Nature* **441**, 633–636.

Oliveira, R. F. 2006. Neuroendocrine mechanisms of alternative reproductive tactics in fish. In K. A. Sloman, R. W. Wilson, and S. Balshine (eds.) *Fish Physiology*, vol. 24, *Behavior and Physiology of Fish*, pp. 297–357. New York: Elsevier.

Oliveira, R. F., Ros, A. F. H., and Gonçalves, D. M. 2005. Intra-sexual variation in male reproduction in teleost fish: a comparative approach. *Hormones and Behavior* **48**, 430–439.

Parker, P. G. and Waite, T. 1997. Mating systems, effective population size, and conservation of natural populations. In J. Clemmons and R. Buchholz (eds.) *Behavioral Approaches to Conservation in the Wild*, pp. 243–261. Cambridge, UK: Cambridge University Press.

Pigeon, D., Chouinard, A., and Bernatchez, L. 1997. Multiple modes of speciation involved in the parallel evolution of sympatric morphotypes of lake whitefish (*Coregonus clupeaformis*, Salmonidae). *Evolution* **51**, 196–205.

Plaistow, S., Johnstone, R. A., Colegrave, N., and Spencer, M. 2004. Evolution of alternative mating tactics: conditional versus mixed strategies. *Behavioral Ecology* **15**, 534–542.

Preston, C. A., Fritz, G. N., and Vander Meer, R. K. 2007. Prevalence of *Thelohania solenopsae* infected *Solenopsis invicta* newly mated queens within areas of differing social form distributions. *Journal of Invertebrate Pathology* **94**, 119–124.

Repka, J. and Gross, M. R. 1995. The evolutionarily stable strategy under individual condition and tactic frequency. *Journal of Theoretical Biology* **176**, 27–31.

Riechert, S. E. and Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioral traits in the spider *Agelenopsis aperta* (Aranae, Agelenidae). *Animal Behaviour* **46**, 669–675.

Robertson, H. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Animal Behaviour* **33**, 805–809.

Roff, D. A. 1994. Evidence that the magnitude of the trade-off in a dichotomous trait is frequency dependent. *Evolution* **48**, 1650–1656.

Roff, D. A. 1996. The evolution of threshold traits in animals. *Quarterly Review of Biology* **71**, 3–35.

Roff, D. A. 1998. The maintenance of phenotypic and genetic variation in threshold traits by frequency-dependent selection. *Journal of Evolutionary Biology* **11**, 513–529.

Roff, D. A. and Fairbairn, D. J. 1993. The evolution of alternate morphologies: fitness and wing morphology in male sand crickets. *Evolution* **47**, 1572–1584.

Ross, K. G. and Keller, L. 1995. Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annual Review of Ecology and Systematics* **26**, 631–656.

Rowland, J. M. and Qualls, C. R. 2005. Likelihood models for discriminating alternative phenotypes in morphologically dimorphic species. *Evolutionary Ecology Research* **7**, 421–434.

Rowland, J. M., Qualls, C. R., and Beaudoin-Ollivier, L. 2005. Discrimination of alternative male phenotypes in *Scapanes australis* (Boisduval) (Coleoptera: Scarabaeidae: Dynastinae). *Australian Journal of Entomology* **44**, 22–28.

Ruchon, F., Laugier, T., and Quignard, J. P. 1995. Alternative male reproductive strategies in the peacock blenny. *Journal of Fish Biology* **47**, 826–840.

Russell, S. T., Ramnarine, I. W., Mahabir, R., and Magurran, A. E. 2006. Genetic detection of sperm from forced copulations between sympatric populations of *Poecilia reticulata* and *Poecilia picta*. *Biological Journal of the Linnean Society* **88**, 397–402.

Ryan, M. J., Pease, C. M., and Morris, M. R. 1992. A genetic polymorphism in the swordtail, *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. *American Naturalist* **139**, 21–31.

Salzburger, W., Baric, S., and Sturmbauer, C. 2002. Speciation via introgressive hybridization in East African cichlids? *Molecular Ecology* **11**, 619–625.

Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* **19**, 198–207.

Seehausen, O. and Schluter, D. 2004. Male–male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society of London B* **271**, 1345–1353.

Seymour, N. R. 1990. Forced copulation in sympatric American black ducks and mallards in Nova Scotia. *Canadian Journal of Zoology/Revue Canadienne de Zoologie* **68**, 1691–1696.

Shuster, S. M. 1989. Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among a-, B-, and g-males. *Evolution* **43**, 1683–1698.

Shuster, S. M. and Wade, M. J. 2003. *Mating Systems and Strategies*. Princeton, NJ: Princeton University Press.

Sih, A., Bell, A., and Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* **19**, 372–378.

Sih, A., Bell, A. M., Johnson, J. C., and Ziemba, R. E. 2004b. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* **79**, 241–277.

Simmons, L. W. and Emlen, D. J. 2006. Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 16346–16351.

Sinervo, B. and Calsbeek, R. 2006. The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. *Annual Review of Ecology Evolution and Systematics* **37**, 581–610.

Sinervo, B. and Zamudio, K. 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. *Journal of Heredity* **92**, 198–205.

Sirot, L. K., Brockmann, H. J., Marinis, C., and Muschett, G. 2003. Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Animal Behaviour* **66**, 763–775.

Skúlason, S. and Smith, T. B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology and Evolution* **10**, 366–370.

Smith, T. B. and Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fish, amphibians and birds. *Annual Review of Ecology and Systematics* **27**, 111–134.

Snorrason, S. S. and Skúlason, S. 2004. Adaptive speciation in northern freshwaterfishes: patterns and processes. In U. Dieckmann, H. Metz, M. Doebeli, and D. Tautz (eds.) *Adaptive Speciation*, pp. 210–228. Cambridge, UK: Cambridge University Press.

Stamps, J. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. *Animal Behaviour* **66**, 1–13.

Taborsky, M. 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior* **23**, 1–100.

Taborsky, M. 1998. Sperm competition in fish: "bourgeois" males and parasitic spawning. *Trends in Ecology and Evolution* **13**, 222–227.

Taborsky, M. 2001. The evolution of parasitic and cooperative reproductive behaviors in fishes. *Journal of Heredity* **92**, 100–110.

Thomas, C. D., Bagguette, M., and Lewis, O. T. 2000. *Butterfly movement and conservation in patchy landscapes*. In L. M. Gosling and W. J. Sutherland (eds.) *Behaviour and Conservation*, pp. 85–104. Cambridge, UK: Cambridge University Press.

Thorpe, J. E. 1989. Developmental variation in salmonid populations. *Journal of Fish Biology* **35** (Suppl. A), 295–303.

Tinbergen, N. 1951. *The Study of Instinct*. Oxford, UK: Clarendon Press.

Tomkins, J. L., Kotiaho, J. S., and LeBas, N. R. 2005. Matters of scale: positive allometry and the evolution of male dimorphisms. *American Naturalist* **165**, 389–402

Tschinkel, W. R. 1998. The reproductive biology of fire ant societies. *BioScience* **48**, 593–605.

Turner, B. J. and Grosse, D. J. 1980. Trophic differentiation in *Ilyodon*, a genus of stream-dwelling goodeid fishes: speciation versus ecological polymorphism. *Evolution* **34**, 259–270.

van Oers, K., Drent, P. J., de Goede, P., and van Noordwijk, A. J. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London B* **271**, 65–73.

van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B., and Drent, P. J. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour* **142**, 1185–1206.

van Oortmerssen, G. A. 1971. Biological significance, genetics and evolutionary origin of variability in behaviour within and between inbred strains of mice (*Mus musculus*): behaviour genetic study. *Behaviour* **38**, 1–92.

van Oortmerssen, G. A. and Bakker, T. C. M. 1981. Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behavior Genetics* **11**, 115–126.

Verbeek, M. E. M., Drent, P. J. and Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* **48**, 1113–1121.

Vercken, E., Massot, M., Sinervo, B. and Clobert, J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* **20**, 221–232.

Vigers, R. S., Silversides, D. W., and Tremblay, J. J. 2005. New insights into the regulation of mammalian sex determination and male sex differentiation. *Vitamins and Hormones: Advances in Research and Applications* **70**, 387–413.

Vincent, A. and Sadovy, Y. 1998. Reproductive ecology in the conservation and management of fishes. In T. Caro (ed.) *Behavioral Ecology and Conservation Biology*, pp. 209–245. Oxford, UK: Oxford University Press.

Watters, J. V. 2005. Can the alternative male tactics "fighter" and "sneaker" be considered "coercer" and "cooperator" in coho salmon? *Animal Behaviour* **70**, 1055–1062

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**, 155–183.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics* **20**, 249–278.

West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford, UK: Oxford University Press.

Williams, D. F., Oi, D. H., Porter, S. D., Pereira, R. M., and Briano, J. A. 2003. Biological control of imported fire ants (Hymenoptera: Formicidae). *American Entomologist* **49**, 150–163.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B* **353**, 199–205.

Wilson, D. S., Coleman, K., Clark, A. B., and Biederman, L. 1993. Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology* **107**, 250–260.

Wilson, D. S., Clark, A. B., Coleman, K., and Dearstine, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution* **9**, 442–446.

Wirtz, P. 1999. Mother species–father species: unidirectional hybridization in animals with female choice. *Animal Behaviour* **58**, 1–12.

Zander, C. D. 1986. Blenniidae. In P. J. P. Whitehead, M. L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese (eds.) *Fishes of the North-Eastern Atlantic and the Mediterranean*, vol. 3, pp. 1096–1112. Paris: UNESCO.

Zera, A. J. and Denno, R. F. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Entomology* **42**, 207–230.

Zera, A. J. and Harshman, L. G. 2001. The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics* **32**, 95–126.

Zupanc, G. K. H. and Lamprecht, J. 2000. Towards a cellular understanding of motivation: structural reorganization and biochemical switching as key mechanisms of behavioral plasticity. *Ethology* **106**, 467–477.