

# Alternative reproductive strategies and tactics: diversity within sexes

Mart R. Gross

In the minds of many researchers, sexual variation is understood as being the differences exhibited between males and females. However, during the past two decades we have witnessed the discovery of widespread variation among individuals *within* the two sexes<sup>1,2</sup>. Such variation is found in most major taxa and may include significant behavioural, morphological, physiological and life history differences (Table 1). These examples illustrate that, rather than evolution giving rise to a single best male and female phenotype for each species, it has instead resulted in extreme phenotypic diversity. This realization is changing the way biologists view the adaptiveness of organisms.

An important evolutionary force in generating individual variation within a sex is social interaction<sup>3</sup>. Current evolutionary studies are attempting to understand how and why social interactions give rise to often elaborate phenotypic alternatives. Game theory and associated concepts such as the evolutionarily stable strategy (ESS)<sup>4,5</sup> provide a framework for studying alternative phenotypes in terms of their costs and benefits to evolutionary fitness. By contrast, proximate studies are addressing the underlying mechanisms that regulate phenotypic alternatives, such as the roles of genes, hormones and neurons. This article assesses our current understanding of alternative reproductive phenotypes within the sexes, updates our classification and models, and suggests new directions for the future.

## Evolutionary studies

Evolutionary studies are concerned with why and how selection favours alternative phenotypes. In the context of game theory, phenotypic diversity may be categorized as being under the control of three different kinds of strategy: alternative strategies, mixed strategy and conditional strategy (see Box 1).

### Alternative strategies

Alternative strategies are characterized by a genetic polymorphism, with equal fitnesses provided by frequency-dependent selection (see Box 2). How common are alternative strategies in nature? There seem to be only a few candidates, and further tests are needed in each system to demonstrate conclusively the existence of alternative strategies.

One such system is that of a small marine isopod (*Paracerceis sculpta*) that inhabits intertidal sponges. Females are mated by large fighter males, intermediate-sized males that mimic females, or small sneaker males. Shuster and Wade<sup>8</sup>

**Not all members of a sex behave in the same way. Frequency- and status-dependent selection have given rise to many alternative reproductive phenotypes within the sexes. The evolution and proximate control of these alternatives are only beginning to be understood. Although game theory has provided a theoretical framework, the concept of the mixed strategy has not been realized in nature, and alternative strategies are very rare. Recent findings suggest that almost all alternative reproductive phenotypes within the sexes are due to alternative tactics within a conditional strategy, and, as such, while the average fitnesses of the alternative phenotypes are unequal, the strategy is favoured in evolution. Proximate mechanisms that underlie alternative phenotypes may have many similarities with those operating between the sexes.**

---

Mart Gross is at the Dept of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1.

---

conclude that the three phenotypes are due to three alleles at a single autosomal locus, and that the fitnesses of the alternative phenotypes are equal. Unfortunately, measurements of paternity have not yet been obtained for all possible combinations of mate pairings, and the fitness calculations do not incorporate life history differences such as maturation rate or mortality during dispersal – both variables that will affect fitnesses. In addition, the system has not yet been examined for the appropriate frequency-dependent selection.

In the swordtail (*Xiphiphorus nigrensis*), three alleles at a single Y-locus are thought to result in small, intermediate-sized, and large males that respectively sneak, sneak and court, and court, females. Ryan, Pease and Morris<sup>9</sup> calculate both mating success and differential survival due to maturation rate. They conclude that fitnesses are equal, but suggest that the broad confidence limits make

this conclusion questionable. Another concern is that the fitnesses of the intermediate-sized and large males are calculated together, and thus the genotypes and behaviours are not evaluated against each other. The system has not yet been examined for frequency-dependent selection (see also Refs 10 and 11).

A third system is the lek mating system of the ruff (*Philomachus pugnax*)<sup>12</sup>. 'Resident' males are dark in plumage and defend courts on the lek, while 'satellite' males are white in plumage and share courts with the residents. Recently, Lank *et al.*<sup>13</sup> conclude from a breeding study that the alternative males result from two alleles at a single autosomal locus. There are presently no fitness measurements that include both mating success and life history differences, nor are there data to test for frequency-dependent selection.

### Mixed strategy

If frequency-dependent selection can result in equal fitnesses between alternative phenotypes, it is theoretically possible for a mechanism of probabilistic allocation to evolve with individuals each expressing the appropriate mix as alternative tactics (Box 2). However, there is no documented case of such a mixed reproductive strategy within a sex. Such a demonstration would require evidence not only of equal fitnesses and frequency-dependent selection, but a genetic monomorphism among individuals and a purely probabilistic production of the alternative tactics. Earlier suggestions of mixed strategies<sup>4</sup> either have not been supported by recent work or were misclassified.

**Conditional strategy**

The literature contains hundreds of examples of alternative reproductive phenotypes that are most readily interpreted as alternative tactics within a conditional strategy. The key characteristics of a conditional strategy are: (1) the tactics involve a 'choice' or 'decision' by the individual; (2) the decision is made relative to some aspect of the individual's status (see Box 3); (3) individuals are genetically monomorphic for the decision; (4) the average fitnesses of the tactics are not equal, but the fitnesses of the alternatives at the switchpoint are equal; and (5) the chosen tactic results in higher fitness for the individual (Box 3). While no study has yet demonstrated this complete set of characteristics, many systems do demonstrate that individuals are employing tactics according to their status, in a way that would seem to increase their fitness. The fact that tactics in these systems are 'chosen' excludes them from the categories of mixed or alternative strategies (Boxes 1,2).

A common conditional reproductive strategy is the use of fighting or sneaking as alternative mating tactics depending on body size. Recent studies have shown that this strategy may be quite sophisticated. For example, in scarab dung beetles of the genus *Onthophagus*, male fighting ability increases with both adult body size and with horn size. Larger larvae develop into the big-horned adults that fight for females, while smaller larvae develop into tiny-horned or hornless males that attempt to sneak matings<sup>15,16</sup>. The distribution of adult horn size and body size in the population is discontinuous, seemingly reflecting different developmental trajectories<sup>17</sup>. The choice of these trajectories can be manipulated by altering larval diet and growth. This suggests that an individual larva uses body size to decide which future tactic – fight or sneak – will maximize its fitness. In the ground-nesting bee *Perdita portalis*, big larvae develop into a fighter phenotype that is flightless, has large mandibles, and that mates within the nest, while smaller larvae metamorphose into a distinctly smaller-headed phenotype with wings, and mate outside the nest<sup>18</sup>. Maternal provisioning has been shown to determine male larval size and thereby the tactic. For both the beetle and bee it is thought that the

**Table 1. Alternative reproductive phenotypes<sup>a,b</sup>**

Species	Alternative phenotypes	Genetic polymorphism	Refs
<i>Caloglyphus berlesei</i> (mite)	Fight/non-fight	N	25,49
<i>Onthophagus</i> sp. (dung beetle)	Fight/sneak	N	15–17
<i>Leistotrophus versicolor</i> (rove beetle)	Dominant/female mimic	N	20
<i>Perdita portalis</i> (bee)	Wingless fighter/winged non-fighter	N	18
<i>Paracerceis sculpta</i> (isopod)	Fight/mimic/sneak	Y	8
<i>Limulus polyphemus</i> (horseshoe crab)	Pair/satellite	N	21
<i>Poecilia reticulata</i> (guppy)	Court/sneak	N	26,27
<i>Xiphiphorus nigrensis</i> (swordtail)	Court/court and sneak/sneak	Y	9–11
<i>Porichthys notatus</i> (midshipman)	Call/sneak	N(?)	33,38,39
<i>Urosaurus ornatus</i> (tree lizard)	Territorial/ranger	Y(?)	31,48
<i>Bucephala islandica</i> (goldeneye duck)	Nest/nest and parasitize	N	22
<i>Philomachus pugnax</i> (ruff)	Territorial/satellite	Y	12,13
<i>Ficedula hypoleuca</i> (pied flycatcher)	Monogamous/polygynous	N	19
Various rodents	Dominant/subordinate	N	36

<sup>a</sup>Examples mentioned in the text are listed. They include most known cases with evidence for genetic polymorphism, but only a small fraction of the known cases without. Many of these papers give additional references.

<sup>b</sup>N, no; Y, yes; ?, unsure.

smaller-male tactic obtains less average fitness than the larger-male tactic. However, this has not yet been well quantified, nor is there any fitness calculation at the switchpoint.

Another common alternative tactic is mimicry of females by males. Young pied-flycatcher (*Ficedula hypoleuca*) males are thought to mimic female plumage to gain access to better

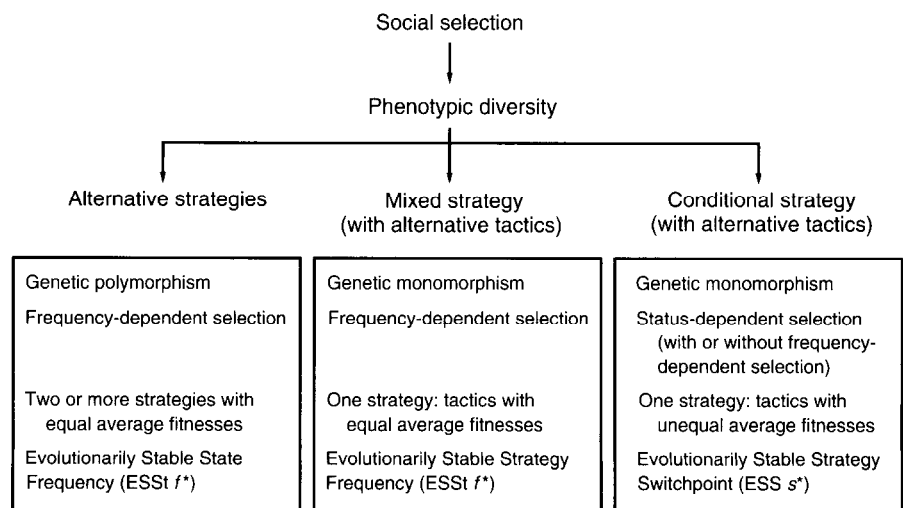
**Box 1. Classifying phenotypic diversity: strategies versus tactics**

While mathematical game theory<sup>6</sup> formally defines two types of strategy – pure and mixed – a review of current biological literature shows that these terms have different meanings for different people. In addition, the literature of biological game theory has added new terms (e.g. conditional strategy<sup>7</sup>) and frequently interchanges the terms strategy and tactic. What follows is an attempt to clarify biological game theory terminology.

**Strategy:** a strategy is a genetically based program (decision rule) that results in the allocation of the somatic and reproductive effort of an organism (such as energy and development) among alternative phenotypes (tactics). An example is the allocation of reproductive effort into fighting versus sneaking. The strategy operates through a mechanism (physiological, neurological or developmental) that detects appropriate cues and puts the strategy's decision rule into effect, such as to fight when larger than *X* and to sneak when smaller (a conditional strategy), or to fight with probability 0.3 and to sneak with probability 0.7 (a mixed strategy).

**Tactic:** a tactic is a phenotype that results from a strategy. An example is to fight for access to a mate, while the alternative tactic may be to sneak. The fight tactic will have associated behavioural, morphological, physiological or life history features that distinguish it from its alternative. The 'decision' about which tactic is expressed is made by the strategy.

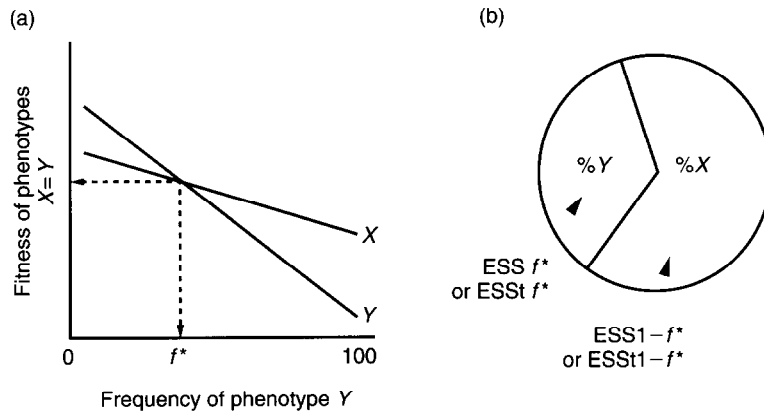
This distinction between strategy and tactic, combined with the mechanisms of frequency- and/or status-dependent selection (Boxes 2 and 3) results in the classification shown in the chart of phenotypic diversity: alternative strategies, mixed strategy and conditional strategy (*f*, frequency; *s*, status).



**Box 2. Frequency-dependent selection**

Frequency-dependent selection arises when the relative fitnesses of alternative phenotypes depend on their frequencies in the population. For instance, a fighter may be more successful than a sneaker when fighters are rare, but less successful when fighters are common.

The essential features of frequency-dependent selection are modelled in (a). When phenotype Y is at low frequency its fitness is greater than phenotype X and consequently it increases in frequency in the population. But when Y is at high frequency its fitness is less than X and consequently it declines in frequency. Where the fitness functions intersect, there is an intermediate frequency  $f^*$  for Y and  $1 - f^*$  for X – at which the average fitnesses of the two phenotypes are equal. Within the population as a whole (b), Y will evolve to give  $f^*$  of the phenotypes and X will evolve to give  $1 - f^*$ . For the model to operate, the fitness functions must intersect and the fitness of at least one phenotype must be negatively frequency-dependent. In this case it is Y.



Game theory allows for two ways in which the alternatives can be biologically organized. One way is as **alternative strategies** with an evolutionarily stable state frequency  $f^*$  (ESS  $f^*$ ). In this way the population is genetically polymorphic with  $f^*$  of individuals carrying allele(s) to express strategy Y, and  $1 - f^*$  of individuals carrying allele(s) to express strategy X. The genetically unique strategies coexist evolutionarily with equal fitnesses due to frequency-dependent selection.

The second way is as alternative tactics within a **mixed strategy**, with an evolutionarily stable strategy frequency  $f^*$  (ESS  $f^*$ ). In this way the population is genetically monomorphic for the strategy and each individual displays a probabilistic mix of the tactics, with Y appearing at frequency  $f^*$  and X at frequency  $1 - f^*$ . The average fitnesses of the alternative tactics are equal due to frequency-dependent selection.

Note that game theory uses this model to make precise predictions about the 'frequencies' and 'fitnesses' of alternatives within a population. The model and its fitness functions do not include the status-dependent selection of Box 3, and make a different set of predictions from Box 3.

territories<sup>19</sup>; mimics do less well than higher-status older males but presumably better than males without territories. There is no calculation of fitnesses at the ontogenetic switchpoint. Male rove beetles (*Leistotrophus versicolor*) also mimic females to reduce their displacement by larger males<sup>20</sup>; however, no data on average fitnesses and switchpoints are yet available.

Many additional variations in the use of alternative tactics have been reported. In the horseshoe crab (*Limulus polyphemus*) it is the older males, typically in relatively poor condition, that adopt the satellite tactic while the younger and stronger males pair with the female. DNA fingerprinting shows that males who adopt the satellite tactic fertilize about 40% of the female's eggs, while those who adopt the pairing tactic fertilize roughly 60% (Ref. 21). By contrast, in the goldeneye duck (*Bucephala islandica*) the oldest females have sufficient condition that they can both maintain their own nests and sneak eggs into the nests of younger females<sup>22</sup>. Similarly, in the fish *Stegastes nigricans*, it is the largest males in a colony that have their own nests and sneak fertilizations in the nests of neighbours<sup>23</sup>. In the blue tit (*Parus caeruleus*), it is the preferred males that can have partners and also sneak extra-pair copulations<sup>24</sup>.

Research in several systems has demonstrated that switchpoints are sensitive to how ecological and demographic events influence tactic fitness functions (see Box 4). Radwan<sup>25</sup> shows in the acarid mite (*Caloglyphus berlesesi*), which has fighter and non-fighter male phenotypes, that density influences the potential success of the alternative

tactics, and that individual choice of tactics is sensitive to density as well as to body size. Eadie and Fryxell<sup>22</sup> show that density influences the potential success from nest parasitism by female goldeneye ducks, and that females adjust their investment into nesting and parasitism in response to density. Godin<sup>26</sup> shows that in the presence of a model predator, the guppy (*Poecilia reticulata*) increases its use of the sneaking tactic and decreases its use of the courting tactic, presumably because the latter makes it more vulnerable to predation (see also Ref. 27). Many other examples of switchpoint adjustment to ecology and demography, including operational sex ratio, exist (e.g. Refs 28–30).

**Proximate studies**

Moore<sup>31</sup> has recently developed a theoretical perspective for the hormonal control of alternative phenotypes within a sex. He proposes two categories of alternative phenotype: developmentally fixed alternatives and developmentally plastic alternatives, each with different hormonal influences. In devel-

opmentally fixed alternatives the steroid hormones play an organizational role during the pre-adult stage and there are no hormonal differences among sexually mature adults. In developmentally plastic alternatives, the steroid hormones play an activational role when tactic switching is occurring among adults, and thus hormonal differences are present.

In an experiment using the developmentally fixed phenotypes of the tree lizard *Urosaurus ornatus*, where two male colour morphs are associated with differences in territorial behaviour, castration on the day of hatching results in all males becoming one phenotype at adulthood, while addition of testosterone at hatching turns almost all males into the alternative phenotype at adulthood<sup>32</sup>. This demonstrates that a simple proximate mechanism, such as hormone level early in life, can organize the development of a complex suite of behavioural and morphological traits associated with an alternative male reproductive phenotype later in life.

Although the hormonal regulation of developmentally plastic alternatives has not been equally examined, and some question remains about the hypothesis<sup>33</sup>, the present findings provide a striking parallel to the physiological and developmental control mechanisms that are believed to turn many organisms into males or females<sup>34,35</sup>. It is also interesting to note that exposure to hormones leaking from sibmates while in the womb<sup>36</sup>, or to hormones within an egg<sup>37</sup>, can generate marked differences in later adult reproductive behaviour.

Finally, researchers are beginning to examine neurobiological differences in the organization of the brain of

alternative sexual phenotypes. Studies by Bass and colleagues<sup>38,39</sup> have revealed marked differences in neurobiological and other traits of parental and sneaker males in the plainfin midshipman fish (*Porichthys notatus*).

**Conclusions**

Three major conclusions can be drawn about alternative reproductive strategies and tactics within sexes:

(1) While biological game theory is an important theoretical tool for studying the evolution of alternative reproductive phenotypes, its importance can be further enhanced by clarifying the terminology (e.g. Box 1). Early applications<sup>4</sup> focused attention on frequency-dependent selection and equality of average fitnesses. This suggested the evolution of the mixed strategy with probabilistic tactic expression within individuals, or alternative strategies with genetic polymorphism among individuals. Recent empirical research does not, however, support the existence of the mixed strategy, and alternative strategies are rare.

(2) New theory and recent empirical research suggest that the conditional strategy, in which individuals choose among alternative tactics, is the most common form of phenotypic diversity within the sexes. By using some clue about their status relative to a switchpoint (itself a response to tactic fitness functions), individuals are able to choose the tactic that provides them with the highest fitness. This ability to choose evolves even though the average fitnesses of the alternative tactics are not equal in the population. The evolution of the switchpoint, and the appropriate allocation of alternative tactics for fitness maximization, is not yet well tested. However, the models in Boxes 3 and 4 provide a powerful framework for studying the conditional strategy.

(3) Theoretical frameworks suggest that proximate mechanisms similar to those that determine and develop the differences between the sexes may also function in the determination and development of phenotypic diversity within the sexes. Evidence suggests that alternative tactics may be regulated by relatively minor hormone differences. Therefore, proximate mechanisms, once thought to be severely limiting to phenotypic diversity, may be minor constraints to alternative tactic evolution.

**Future directions**

- A complete theoretical framework for the evolution

of alternative tactics has yet to be developed. In particular, there is a need for new theoretical modelling to combine frequency- and status-dependent selection and solve for their joint equilibrium<sup>40,41</sup>. In Box 4, for example, as the switchpoint moves from  $s_1^*$  to  $s_2^*$  in (b), the relative frequency of phenotype X to phenotype Y also increases, so frequency-dependent selection in (a) may resist the move. When the fitnesses of alternative tactics are functions of both tactic frequency and the status of the individual, then the switchpoint that evolves must balance between these two often opposing selection pressures.

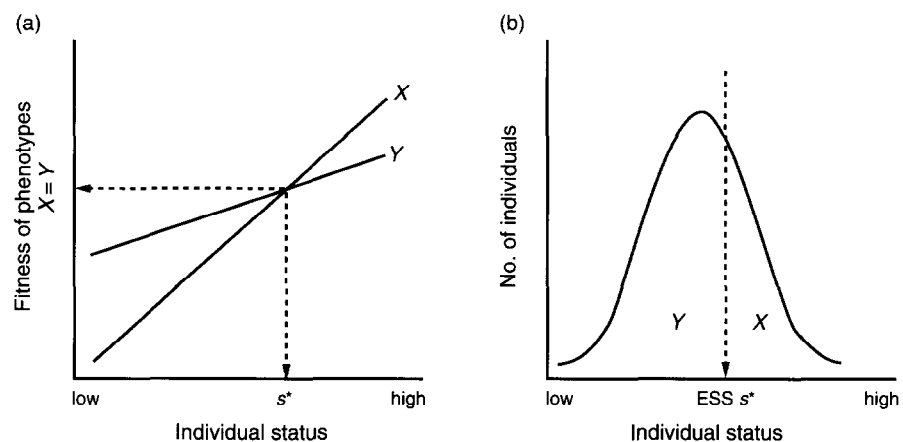
- Additional empirical studies of frequency- and status-dependent selection are needed. At present, only two studies of frequency-dependent selection have been conducted in the field<sup>22,42</sup>. Isopods, poeciliid fish and ruffs may be particularly rewarding to study because of their potential to exhibit alternative strategies. It would be valuable to demonstrate negative frequency-dependent selection for these systems as any calculation of equal fitnesses without such a mechanism will be questionable. If alternative strategies are suspected, it may also be useful to demonstrate that

**Box 3. Status-dependent selection**

I suggest here a model of status-dependent selection for alternative reproductive tactics within a sex. Status-dependent selection arises when the fitnesses of alternative phenotypes, relative to each other, depend on the competitive ability or 'state' of individuals in the population. Individual state always differs because of environmental influences (e.g. disease, trauma, energy), genetic variance (e.g. recombination, mutation) and stage of development (e.g. ontogeny, age). When through social interactions these differences in state also determine the fitnesses that can be obtained from a phenotype, then the individuals differ in their **status**.

In (a), the phenotypes X and Y have status-dependent fitness functions: their fitnesses depend on the status of the individuals expressing the phenotype. Where the fitness functions intersect, the phenotype showing highest fitness changes with status. As a result, individuals of high status obtain greater fitness through phenotype X than through phenotype Y, while individuals of low status obtain greater fitness through phenotype Y than through phenotype X.

There is an intermediate status,  $s^*$ , at which the fitnesses of the two phenotypes are equal. Within the population (b), X will be adopted by individuals of status greater than  $s^*$ , and Y will be adopted by individuals of status less than  $s^*$ . Therefore,  $s^*$  is the switchpoint between phenotypes. Note that the average fitnesses of the alternative phenotypes will be unequal in the population [this can be seen in (b) by summing up the fitnesses for Y and X individuals, and dividing by their number]. Instead, the fitnesses of the alternative tactics are equal at the switchpoint. This is the evolutionarily stable strategy switchpoint  $s^*$  (ESS  $s^*$ ).



This model provides a theoretical framework for a game theoretic **conditional strategy**, a strategy that allows an individual to incorporate information about its ability to obtain fitness through alternative phenotypes and express the phenotype that maximizes its fitness. The conditional strategy dictates the location of the switchpoint, and thus the appropriate tactics. Since the expression of a tactic is not determined by alternative alleles, but by a single conditional strategy, the population is genetically monomorphic.

Parker<sup>5</sup> provided an important theoretical foundation by recognizing the equality of fitnesses at the switchpoint in a conditional strategy. My model differs from so-called condition-dependent models<sup>14</sup> that map investment to a continuously distributed phenotype (e.g. amount of display colour) because my fitness functions map discontinuous or discrete alternatives. Finally, to clarify the difference between status and condition or state, consider two groups of the same organism. In group 1, individual A is 10 cm in size and sneaks, while individual B is 15 cm and fights. In group 2, individual C is 5 cm and sneaks, while individual D is 10 cm and fights. Individuals A and D have the same condition or state (10 cm) yet they express different tactics. This is because they have different status in their group. Status is a useful term for understanding the selection modelled here.

individuals at the pre-differentiation stage do not respond to reasonable manipulations of status. In systems tested for a conditional strategy, it would be useful to identify the existence of a switchpoint, and then to use the switchpoint to predict the tactics employed when status is manipulated and fitness functions are held constant, or when individual status is held constant and the fitness functions are manipulated (see Box 4). Although equal fitnesses are hard to demonstrate, one would ideally test the equality of fitnesses between tactics at the switchpoint. The test of the switchpoint may need to consider the joint interaction of frequency- and status-dependent selection<sup>41</sup>.

- For many years, individuals that sneak received labels like 'making the best of a bad job' because it was assumed that they have lower average fitness than individuals that fight. The other possibility was that they had equal fitness through frequency-dependent selection<sup>4</sup>. Future researchers should consider the possibility of sneakers having *higher* average fitness. For example, the conditional strategy of male coho salmon (*Oncorhynchus kisutch*) has two tactics: to mature precociously as a 'jack' and sneak on the spawning grounds, or to mature when older as a 'hooknose' and fight<sup>43</sup>. The

sneaker life history tactic is chosen by faster-growing juveniles<sup>44</sup>, which are therefore likely to be the highest-status individuals in the population. The choice of sneaking by high-status individuals makes sense only if that life history provides greater average fitness (see Box 3). This suggests that the jack life history has higher average fitness than the hooknose life history. The theory of status-dependent selection and the conditional strategy (Box 3) therefore provides future researchers with a new interpretation for the evolution of alternative life histories in salmon.

- Phenotypic plasticity and reaction norms have captured the interest of many developmental and evolutionary biologists<sup>45</sup>. Much of their research is presently oriented toward understanding responses to heterogeneity in the environment rather than responses to social interactions. However, the concepts in adaptive phenotypic plasticity should in fact be similar to many of those being developed by researchers studying thresholds and switchpoints in alternative reproductive tactics. Research that combines the knowledge and theories of both groups could lead to new insights.

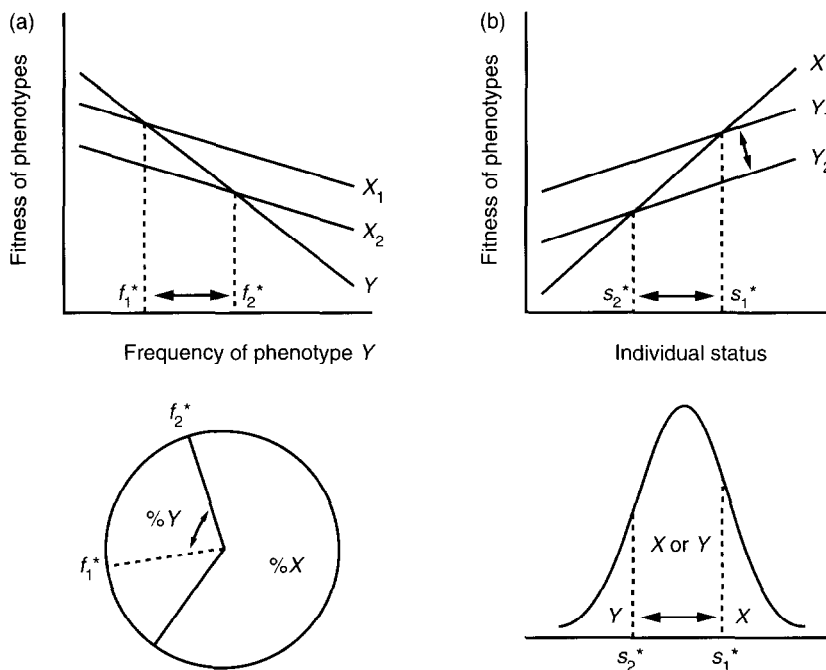
- A large body of physiological and developmental information has been accumulated by researchers studying the

differentiation of individuals into the two sexes<sup>35</sup>. This information may prove valuable for gaining insight into the proximate control of alternative phenotypes within a sex; conversely, alternative phenotypes within a sex may be an important means for better understanding the differentiation between sexes<sup>31,34</sup>. It will be interesting to see whether the machinery for diversity within sexes may, in some cases, have been coopted from that between sexes, and vice versa. The future will hopefully see close collaboration between physiologists studying within-sex and between-sex diversity.

- Some past interpretations of heritability have proved to be fallacious. One such fallacy is to equate heritability of alternative tactics with the genetic polymorphism of alternative strategies. For example, final body size in larval dung beetles, a cue for development into horned or horn-less adults<sup>15</sup>, probably has underlying additive genetic variance. This pooling of genetic variance into horned and horn-less adults as a consequence of the decision mechanism will result in a statistically demonstrable parent-offspring regression (with large sample sizes). However, unless the pooling evolves into discrete alternative genetic mechanisms (a

**Box 4. Ecology and demography**

Social interactions generate the frequency- and status-dependent selection that are the driving forces in the evolution of alternative reproductive strategies and tactics. But ecology and demography are also important through their influence on the pay-offs, or fitnesses, of the frequency- and status-dependent fitness functions (Boxes 2 and 3).



This influence is in two ways. First, ecology and demography influence whether the fitness functions from alternative phenotypes intersect, a necessary condition for the evolutionary origin of the alternatives. Second, ecology and demography influence where the intersection takes place, and thus the ESS distribution of alternatives in the population.

The fitness function for a phenotype will vary with ecological circumstances that determine its functionality, such as suitability to a habitat or need for food resources, and also its costs, such as predators and parasites. In frequency dependent selection (a), the fitness of phenotype X changes relative to phenotype Y with the introduction of a predator that prefers X over Y. This has the effect of increasing the ESS frequency  $f^*$  (or ESS  $f^*$ ) of the Y phenotype, from  $f_1^*$  to  $f_2^*$ . In status-dependent selection (b), ecological factors are now hindering phenotype Y relative to X, and the ESS switchpoint  $s^*$  moves to a lower status, from  $s_1^*$  to  $s_2^*$ . The Y phenotype will therefore be restricted to yet lower status individuals in the population, and also to fewer individuals.

Now hold ecology constant and consider demography, for example density. In (a), the fitness of phenotype X changes relative to phenotype Y because an increase in population size and thus density causes greater interference to X than Y, perhaps because X tries to hold a territory. Thus,  $f^*$  increases and more individuals will become phenotype Y. In (b), demography has a greater influence on Y than X, and the switchpoint moves down and favours an increase in phenotype X. Ecology and demography can also work in concert.

genetic polymorphism), the recombination and fluctuating selection pressures will maintain the genetic variance only as a contributing factor and not as a regulator of the alternative phenotypes. Claims of genetic polymorphism should be supported by evidence of mendelian segregation of alternative alleles that dictate the phenotype into which the individuals develop. Several potential candidates for genetic polymorphisms exist, but the segregation of alleles has not yet been shown (e.g. Refs 46–49).

- Current theories and classifications of mating patterns between the sexes do not incorporate alternative reproductive phenotypes. Future syntheses would probably benefit from incorporating the fact that many members of a sex are following alternative patterns of mating.

- Studies of male animals provide most of the examples of alternative reproductive phenotypes. This may not be surprising since many of these phenotypes are an outcome of sexual selection for access to members of the opposite sex. However, increasing awareness of female control of mating systems<sup>14</sup>, and the value of pairing with specific males<sup>50</sup>, suggests that competition and therefore alternative tactics could be more common in females than we presently recognize. There is also a shortage of comparable studies in plants<sup>51</sup>.

In summary, the study and models of alternative reproductive phenotypes within a sex are proving to be an exciting and productive area of research that has much to tell us about the genetics, development, physiology, morphology, behaviour, ecology and evolution of the phenotype. In addition, the models discussed here may prove useful in understanding diversity between the sexes, and the evolution of ecological polymorphisms<sup>52</sup>.

### Acknowledgements

I appreciate helpful comments from Andrew Bass, Mark Forbes, Nancy Gerrish, Diana Hews, Dov Lank, Carin Magnhagen, Michael Moore and the members of my laboratory and especially Joe Repka. Luca Cargnelli produced the figures.

### References

- Field, J. (1992) **Intraspecific parasitism as an alternative reproductive tactic in nest-building wasps and bees**, *Biol. Rev.* 67, 79–126
- Taborsky, M. (1994) **Sneakers, satellites, and helpers: parasitic and cooperative behaviour in fish reproduction**, *Adv. Stud. Behav.* 23, 1–100
- West-Eberhard, M.J. (1991) **Sexual selection and social behavior**, in *Man and Beast Revisited* (Robinson, M.H. and Tiger, L., ed.), pp. 159–172, Smithsonian Institution Press
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press
- Parker, G.A. (1984) **Evolutionary stable strategies**, in *Behavioural Ecology: An Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 30–61, Sinauer
- van Damme, E. (1991) *Stability and Perfection of Nash Equilibria*, Springer-Verlag
- Dawkins, R. (1980) **Good strategy or evolutionarily stable strategy?** in *Sociobiology: Beyond Nature/Nurture* (Barlow, G.W. and Silverberg, J., eds), pp. 331–367, Westview Press
- Shuster, S.M. and Wade, M.J. (1991) **Equal mating success among male reproductive strategies in a marine isopod**, *Nature* 350, 608–610
- 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**, *Am. Nat.* 139, 21–31
- Erbelding-Denk, C. et al. (1994) **Male polymorphism in *Lima perugiae* (Pisces: poeciliidae)**, *Behav. Genet.* 24, 95–101
- Zimmerer, E.J. and Kallman, K.D. (1989) **Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis***, *Evolution* 43, 1298–1307
- van Rhijn, J.G. (1991) *The Ruff*, Poyser
- Lank, D.B. et al. (1995) **Genetic polymorphism for alternative mating behaviour in lekking male ruff, *Philomachus pugnax***, *Nature* 378, 59–62
- Andersson, M. (1994) *Sexual Selection*, Princeton University Press
- Emlen, D.J. (1994) **Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae)**, *Proc. R. Soc. London Ser. B* 256, 131–136
- Cooke, D.F. (1990) **Differences in courtship, mating and post-copulatory behaviour between male morphs of the dung beetle *Onthophagus binodis* Thunberg (Coleoptera: Scarabaeidae)**, *Anim. Behav.* 40, 428–436
- Eberhard, W.G. and Gutierrez, E.E. (1991) **Male dimorphisms in beetles and earwigs and the question of developmental constraints**, *Evolution* 45, 18–28
- Danforth, B.N. (1991) **The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae)**, *Behav. Ecol. Sociobiol.* 29, 235–247
- Slagsvold, T. and Saetre, G. (1991) **Evolution of plumage color in male pied flycatchers (*Ficedula hypoleuca*): evidence for male mimicry**, *Evolution* 45, 910–917
- Forsyth, A. and Alcock, J. (1990) **Female mimicry and resource defense polygyny by males of a tropical rove beetle, *Leistotrophus versicolor* (Coleoptera: Staphylinidae)**, *Behav. Ecol. Sociobiol.* 26, 325–330
- Brockman, H.J., Colson, T. and Potts, W. (1994) **Sperm competition in horseshoe crabs (*Limulus polyphemus*)**, *Behav. Ecol. Sociobiol.* 35, 153–160
- Eadie, J.M. and Fryxell, J.M. (1992) **Density dependence, frequency dependence, and alternative nesting strategies in goldeneyes**, *Am. Nat.* 140, 621–641
- Karino, K. (1993) **Reproductive behaviour of the territorial herbivore *Stegastes nigricans* in relation to colony formation**, *J. Ethol.* 2, 99–110
- Kempenaers, B. et al. (1992) **Extra-pair paternity results from female preference for high-quality males in the blue tit**, *Nature* 357, 494–496
- Radwan, J. (1993) **The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlessei***, *Behav. Ecol. Sociobiol.* 33, 201–208
- Godin, J.-G.J. (1995) **Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*)**, *Oecologia* 103, 224–229
- Reynolds, J.D., Gross, M.R. and Coombs, M.J. (1993) **Environmental conditions and male morphology determine alternative mating behaviours in Trinidadian guppies**, *Anim. Behav.* 45, 145–152
- Carroll, S.P. and Corneli, P.S. (1995) **Divergence in male mating tactics between two populations of the soapberry bug: II. Genetic change and the evolution of a plastic reaction norm in a variable social environment**, *Behav. Ecol.* 6, 46–56
- Crespi, B.J. (1988) **Alternative male mating tactics in a thrips: effects of sex ratio variation and body size**, *Am. Midl. Nat.* 119, 83–92
- Lucas, J. and Howard, R.D. (1995) **On alternative reproductive tactics in anurans: dynamic games with density and frequency-dependence**, *Am. Nat.* 146, 365–397
- Moore, M.C. (1991) **Application of organization-activation theory to alternative male reproductive strategies: a review**, *Horm. Behav.* 25, 154–179
- Hews, D.K., Knapp, R. and Moore, M.C. (1994) **Early exposure to androgens affects adult expression of alternative male types in tree lizards**, *Horm. Behav.* 28, 96–115
- 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**, *Horm. Behav.* 27, 332–347
- Crews, D. (1994) **Animal sexuality**, *Sci. Am.* 270, 108–114
- Marx, J. (1995) **Tracing how the sexes develop**, *Science* 269, 1822–1824
- Clark, M.M. and Galef, B.G., Jr (1995) **Prenatal influences on reproductive life history strategies**, *Trends Ecol. Evol.* 10, 151–153
- Schwabl, H. (1993) **Yolk is a source of maternal testosterone for developing birds**, *Proc. Natl Acad. Sci. USA* 90, 11446–11450
- Bass, A. (1992) **Dimorphic male brains and alternative reproductive tactics in a vocalizing fish**, *Trends Neurosci.* 15, 139–145
- Brantley, R.K. and Bass, A.H. (1994) **Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae)**, *Ethology* 96, 213–232

- 40 Parker, G.A. (1984) **The producer/scrounger model and its relevance to sexuality**, in *Producers and Scroungers: Strategies of Exploitation and Parasitism* (Barnard, C.J., ed.), pp. 127–153, Croom Helm
- 41 Repka, J. and Gross, M.R. (1995) **The evolutionarily stable strategy under individual condition and tactic frequency**, *J. Theor. Biol.* 176, 27–31
- 42 Gross, M.R. (1991) **Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish**, *Philos. Trans. R. Soc. London Ser. B* 332, 59–66
- 43 Gross, M.R. (1985) **Disruptive selection for alternative life histories in salmon**, *Nature* 313, 47–48
- 44 Gross, M.R. (1991) **Salmon breeding behavior and life history evolution in changing environments**, *Ecology* 72, 1180–1186
- 45 Via, S. et al. (1995) **Adaptive phenotypic plasticity: consensus and controversy**, *Trends Ecol. Evol.* 10, 212–217
- 46 Clark, D.L. and Uetz, G.W. (1992) **Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour**, *Anim. Behav.* 43, 247–254
- 47 Skúlason, S. et al. (1993) **Genetically based differences in foraging behaviour among sympatric morphs of Arctic charr (Pisces: Salmonidae)**, *Anim. Behav.* 45, 1179–1192
- 48 Thompson, C.W., Moore, I.T. and Moore, M.C. (1993) **Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative reproductive strategies**, *Behav. Ecol. Sociobiol.* 33, 137–146
- 49 Radwan, J. (1995) **Male morph determination in two species of acarid mites**, *Heredity* 74, 669–673
- 50 Reynolds, J.D. and Gross, M.R. (1992) **Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata***, *Proc. R. Soc. London Ser. B* 250, 57–62
- 51 Barrett, S.C.H. and Harder, L.D. (1995) **Ecology and evolution of plant mating**, *Trends Ecol. Evol.* 11, 73–79
- 52 Skúlason, S. and Smith, T.B. (1995) **Resource polymorphism in vertebrates**, *Trends Ecol. Evol.* 10, 366–370

# The evolution of human sexuality

Randy Thornhill and Steve W. Gangestad

**T**he evolution of human sexuality is receiving considerable attention from biologists, psychologists and anthropologists. Pioneers in the 1970s and 1980s demonstrated the scientific promise of applying modern darwinism, with its emphasis on genic and individual selection and adaptation, to a wide range of human activities<sup>1–4</sup>, including human sexuality<sup>5</sup>. The current inspiration and motivation to study human sexuality stems from these earlier successes, and to a significant extent from the recent focus on human psychological adaptations, which has generated the discipline of darwinian or evolutionary psychology (EP)<sup>6</sup> (Box 1).

Evolutionary psychology emphasizes that universal mental adaptations will sometimes be sex-

specific in design because males and females, consistently throughout human evolutionary history, faced sex-specific adaptive problems in the domain of sexual matters<sup>5,12,13</sup>. A vast body of empirical evidence, based on studies of heterosexuals' interests, behavior and motivations, now demonstrates that men's and women's sexual psyches show the sex-specific design<sup>5,13–15</sup> predicted by sexual selection and related theory<sup>16</sup>. Men are more eager and indiscriminate than women in mating decisions. Women value resources and status of potential mates more, and physical attractiveness and youth of a potential mate less, than men do. A potential mate's personality is generally more important to women than to men, particularly in traits associated with male willingness to invest<sup>17</sup>. Men, as predicted, become discriminating of mates when they will invest. For example, for long-term romantic relationships, both men and women value highly and equally intelligence of a mate, but women's standard for intelligence is significantly higher than men's in

**The study of human sexuality from the darwinian perspective is in an explosive phase. Recent research is diverse; for instance, the dynamics of heterosexual relationships, the role of honest advertisement in attractiveness, the role of fluctuating asymmetry in sexual competition, and sexual conflict over fertilization, seen in sperm competition adaptations of men and possible cryptic sire-choice adaptation of women. Also, recent research reveals that the sexual selection that designed human secondary sexual traits was functional rather than strictly fisherian.**

---

Randy Thornhill is at the Dept of Biology and Steve W. Gangestad is at the Dept of Psychology, University of New Mexico, Albuquerque, NM 87131-1091, USA.

---

short-term, sexual relations (e.g. one-night stands)<sup>18</sup>.

Although the sexes predictably use some similar mate attraction tactics, certain tactics that heterosexual men and women use to spark sexually dimorphic mate preference priorities differ<sup>19</sup>. For example, men display resources, status and athleticism more than women do. Women display attractiveness and sexual restraint more than men do. These sex differences in mate attraction tactics are reflected also in tactics of (1) mate retention behaviors, (2) derogation of sexual competitors, and (3) deceptions used in sexual competition<sup>13</sup>.

Fantasies function to motivate individuals to achieve social goals that typically promoted the reproductive success of human ancestors<sup>5</sup>.

They reveal our evolved preferences more clearly than actual behavior does, because behavior is necessarily constrained by many real-life exigencies. Thus, each sex's distinct sexual nature pertaining to mating decisions is acutely revealed by studies of sex differences in sexual fantasies. Men's fantasies have more explicit sexual content, partner variety and sexual content alone, whereas women's fantasies have more implicit sexual content, non-sexual content, affection, commitment, tenderness and emotionality<sup>20</sup>.

Homosexuality has received considerable attention because such sexual behavior is not constrained by the opposite sex, and therefore provides a good test-case for differences in sexual psyches<sup>5</sup>. Homosexual and heterosexual men have the same motivation for non-committal sex and high partner number, but homosexual men score higher in the number of actual brief sexual liaisons and partners in a lifetime. Homosexual and heterosexual women, however, score the same (and much lower than men) in