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\(^1,2\). 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 boat 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\(^3\). 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)\(^4,5\) 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 (Para cerceis sculp ta) that inhabits intertidal sponges. Females are mated by large fighter males, intermediate-sized males that mimic females, or small sneaker males. Shuster and Wade\(^6\) 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 (Xiphophorus 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\(^7\) 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)\(^12\). ‘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.\(^13\) 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\(^8\) 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 decreases with both adult body size and 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. The distribution of adult horn size and body size in the population is discontinuous, seemingly reflecting different developmental trajectories. 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. 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 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 nymphy of females by males. Young pied-flycatchers (*Ficedula hypoleuca*) males are thought to mimic female plumage to gain access to better

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**Table 1. Alternative reproductive phenotypes**

<table>
<thead>
<tr>
<th>Species</th>
<th>Alternative phenotypes</th>
<th>Genetic polymorphism</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caloglyphus berlesei</td>
<td>Fight/non-fight</td>
<td>N</td>
<td>25,49</td>
</tr>
<tr>
<td>(mite)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Onthophagus sp.</td>
<td>Fight/sneak</td>
<td>N</td>
<td>15–17</td>
</tr>
<tr>
<td>(dung beetle)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leptochirus versicolor</td>
<td>Dominant/female mimic</td>
<td>N</td>
<td>20</td>
</tr>
<tr>
<td>(rove beetle)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perdita portalis</td>
<td>Wingless fighter/</td>
<td>N</td>
<td>18</td>
</tr>
<tr>
<td>(bee)</td>
<td>winged non-fighter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paracoccid sculptra</td>
<td>Fight/mimic/sneak</td>
<td>Y</td>
<td>8</td>
</tr>
<tr>
<td>(isopod)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Limulus polyphemus</td>
<td>Pair/satellite</td>
<td>N</td>
<td>21</td>
</tr>
<tr>
<td>(horsehoe crab)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porcella reticinata</td>
<td>Court/sneak</td>
<td>N</td>
<td>26,27</td>
</tr>
<tr>
<td>(guppy)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xiphophorus nigrensis</td>
<td>Court/court and sneak/sneak</td>
<td>Y</td>
<td>9–11</td>
</tr>
<tr>
<td>(swordtail)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porichthys notatus</td>
<td>Call/sneak</td>
<td>N(?)</td>
<td>33,38,39</td>
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<tr>
<td>(midshipman)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ursus arctos maritimus</td>
<td>Territorial/ranger</td>
<td>Y(?)</td>
<td>31,48</td>
</tr>
<tr>
<td>(tree lizard)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bucculohela labiata</td>
<td>Nocturnal and parasitic</td>
<td>N</td>
<td>22</td>
</tr>
<tr>
<td>(goldeneye duck)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philomachus pugnatus</td>
<td>Territorial/satellite</td>
<td>Y</td>
<td>12,13</td>
</tr>
<tr>
<td>(ella)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ficedula hypoleuca</td>
<td>Monogamous/polygamous</td>
<td>N</td>
<td>19</td>
</tr>
<tr>
<td>(pied flycatcher)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Various rodents</td>
<td>Dominant/subordinate</td>
<td>N</td>
<td>36</td>
</tr>
</tbody>
</table>

*Species 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.*

*N, no; T, yes; ?, unsure.*

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

While traditional game theory 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) 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 male, while the alternative tactic may be to sneak. The fight tactic will have associated behavioural, morphological, physiological, and/or colouration 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 sneakier 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, $Y$ 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 $Y$.

![Diagram of frequency-dependent selection](image)

Gomo 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 $f^*$ (ESSI $f^*$). 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 $f^*$ (ESST $f^*$). 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.

tactics, and that individual choice of tactics is sensitive to density as well as to body size. Eade and Fryxell show that density influences the potential success from nest parasitism by female goldeneye ducks, and that females adjust their investment into nestling and parasitism in response to density. Godin 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 switch-point adjustment to ecology and demography, including operational sex ratio, exist (e.g. Refs 28-30).

Proximate studies

Moore 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 developmentally 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. This demonstrates that a simple proximate mechanism, such as hormone level early in life, can organize the development of a complex suite of functional 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, 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. It is also interesting to note that exposure to hormones leading to sibmates while in the womb, or to hormones within an egg, can generate marked differences in later adult reproductive behaviour.

Finally, researchers are beginning to examine neurobiological differences in the organization of the brain of territories; 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 beetle Leiotorphus vernicolor also mimic females to reduce their displacement by larger males; 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. Similarly, in the fish Stogastus nigricans, it is the largest males in a colony that have their own nests and sneak fertilizations in the nests of neighbours. In the blue tit Parus caeruleus, it is the preferred males that can have partners and sneak extra-pair copulations. Research in several systems has demonstrated that switchpoints are sensitive to how ecological and demographic events influence tactic fitness functions (see Box 4). Radwan shows in the acarid mite Caloglyphus beriolelt, which has fighter and non-fighter male phenotypes, that density influences the potential success of the alternative
alternative sexual phenotypes. Studies by Bass and colleagues 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 focused on attention 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 evokes 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. In Box 4, for example, as the switchpoint moves from $s^*$ to $s^*$ 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. 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

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**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. Individuals 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 fitness depend on the status of the individuals expressing the phenotype. Where the fitness functions intersect, the phenotype showing highest fitness in $X$ and $Y$ will be adopted by individuals of status less 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 $s^*$).

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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 selection41.

- 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 selection41. Future researchers should consider the possibility of sneak having higher average fitness. For example, the conditional strategy of male coho salmon (Oncorhyncus 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 fight42. The sneak life history tactic is chosen by faster-growing juveniles43, 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 biologists44. 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 sexes45. 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 sexes33,34. 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 adults32, 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).

![Diagram](image-url)

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**X** (or ESS f**Y**) of the Y phenotype, from f**X** to f**X**. In status-dependent selection (b), ecological factors are now rendering phenotype Y relative to X, and the ESS switchpoint f**X** moves to a lower status, from s**X** to s**X**. 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 trio to hold a territory. Thus, f**X** 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 selectional 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 systems45, and the value of pairing with specific males50, 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 plants51.

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 polymorphisms52.

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References


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The evolution of human sexuality
Randy Thornhill and Steve W. Gangestad

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, new research reveals that the sexual selection that designed human secondary sexual traits was functional rather than strictly fisherian.

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short-term, sexual relations (e.g. one-night stands) 18.

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 15. 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 23.

Fantasies function to motivate individuals to achieve social goals that typically promoted the reproductive success of human ancestors 5. 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 20.

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 5. 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