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Anisogamy, chance and the evolution of sex roles

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Recently, several authors have challenged the view that anisogamy, the defining feature of the sexes, is an important determinant of the evolution of sex roles. Sex roles are instead suggested to result from chance, or from non-heritable differences in life histories of females and males. Here, we take issue with these ideas. We note that random processes alone cannot cause consistent differences between the sexes, and that those differences between the sexes in life histories that affect the sex roles are themselves the result of sex-specific selection that can ultimately be traced back to anisogamy. To understand sex roles, one should ask how environmental variation and female–male coevolution cause variation in sex-specific selection in the light of anisogamy.

Sex roles and anisogamy

Since Darwin introduced the basic conceptual framework to understand why the male and female sexes are different [1,2], much research has been devoted to understanding the origin and evolutionary consequences of sexual differences [3–12]. Questions asked include: why are there two sexes, why do the sexes differ in behaviour and morphology, and why is the nature and extent of these differences so variable within and among species?

The sexes are defined by differences in the type of gametes they produce; the female sex produces relatively few, large and usually non-motile gametes (eggs or ovules), whereas the male sex produces many, smaller and often motile gametes (sperm or pollen). Moreover, there is considerable consensus about the probable evolutionary pathways leading to this basic difference [3,13–16]. Definitions of the so-called 'sex roles', however, are more variable. Although males and females typically differ in an array of traits, definitions of sex roles tend to focus on sexual dimorphism in either: (i) the degree of within-sex reproductive competition; (ii) how discriminating individuals are during pair formation; or (iii) the extent to which they exhibit parental care after mating. Sex roles are, however, not restricted to males and females (i.e. species that exhibit life-long sexual dimorphism) but can also relate to the female and male functions of hermaphroditic individuals (see below).

Recently, several authors have questioned whether there are any intrinsic differences between the sexes that shape the extent and nature of diversity in sexual systems and sex roles. In their view, sex roles arise entirely from chance, or from sex differences in environment-driven 'habits of life', such as encounter rates, mortality schedules and re-mating rates [17–22]. The differences in these life-history and mating traits are assumed to be externally imposed, arising from the ecological setting that an individual or species finds itself in, rather than ultimately being a consequence of anisogamy. Were this to be true, sex roles would be variable to the extent that females and males (as defined by anisogamy) would be no more or less likely to have any one sex role. Here, we take issue with this view. We begin by addressing the misconception that random processes can cause consistent differences between the sexes, next we clarify that the idea that sex roles are externally imposed is misinformed, and we end by arguing that sexual selection research has generally embraced, rather than dismissed, the broad variation in sex roles among organisms.

The role of 'chance' for sex differences in the variance in mating success

More than 25 years ago, Sutherland [23] used the term 'chance' when describing a scenario that could generate the higher variance in mating success among males than females first observed by Bateman [24]. A misinterpretation of his work has affected the literature ever since [17–20,22], leading to the erroneous suggestion that sex differences in variance in mating success 'could be due entirely to chance' [20]. These differences cannot arise by chance, and it was not Sutherland's intention to suggest that they could [25]. His original point was that longer re-mating latencies will reduce variance in mating success under random mating (owing to a more even distribution of matings among individuals). If one then assumes longer re-mating latencies in females than males, owing to, for example, maternal care, this will result in higher variance in male than in female mating success [4] under random mating. Thus, it is not 'chance' or stochasticity that produces this difference, but the assumed sex difference in re-mating latency [25]. Similar effects will result from differences in other 'habits of life' between the sexes [17,20], which we discuss next.

Sex roles and the 'habits of life'

A series of simulations has explored the effect of sex differences in life-history and mating traits (referred to

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as 'habits of life'), such as survival rate, mate encounter rate and re-mating latency, on the expression of sex roles [17,18,20] and these simulations have been promoted as providing 'an alternative hypothesis to anisogamy theory' [20]. The simulations treat these sex differences in 'habits of life' as being 'non-heritable and fixed', stemming from external forces [18,19]. Our main issue concerns the fact that these assumed sex differences are themselves the result of sex-specific selection (Box 1).

Consider, for example, the well-established observation that the re-mating latency in the fruit fly *Drosophila melanogaster* is longer in females than in males [26,27]. This difference is no doubt in part the result of sex-specific selection in females, for example, because they require more time to regain energy before they can benefit from re-mating. However, the difference in re-mating latency in this species also has another important component; sex-specific selection has favored males that reduce the risk of sperm competition by inducing a long re-mating latency in their mates through the transfer of seminal fluid substances [27,28], as recognized also by [18]. Experimental prevention of the transfer of some of these substances leads to much shorter re-mating latencies in females [29,30], clearly demonstrating that females are physiologically capable of re-mating earlier. Thus, the difference between the sexes in re-mating latency is not an arbitrary result of the external environment, but probably an evolutionary consequence of sex-specific selection in both sexes and coevolution between sex-specific adaptations in both sexes [31–34]. Similar scenarios apply to other sex differences in life-history and mating traits, such as longer time to maturity in male *Drosophila* species with longer sperm [35], or higher female mortality rates in female *D. melanogaster* exposed to seminal fluid [36], to name but a few.

The conclusion that 'sex differences in typical reproductive decisions may have more to do with what Darwin called habits of life, rather than to [anisogamy]' [20] is thus misleading. The basic problem with these simulations is that they disregard the fact that any difference between the sexes, such as, for example, in re-mating latency, must to some extent be the result of sex-specific selection (Box 1) and at their root these differences must thus arise from anisogamy, the defining feature that distinguishes the sexes.

In essence, these simulations simply convert the general question about sex differences into a model assumption.

Box 1. An outline of the evolution of sex roles

Simulations have shown that if sexual dimorphism in a life-history and mating trait is assumed and is not allowed to evolve (i.e. considered a 'fixed sex difference'), then sex roles will diverge [17,18,20]. This has been taken to suggest that 'sex differences in typical reproductive decisions may have more to do with what Darwin called habits of life rather than to [anisogamy]' [20] (Figure Ia). This inference [21] is, however, misleading because the sexual dimorphisms in life-history and mating traits are themselves the result of sex-specific selection, owing ultimately to the sex differences that are inherent to anisogamy [7,44] (Figure Ib).

Specifically, the fact that there are two distinct paths to successful reproduction in every sexual lineage (associated with producing either many small or few large gametes) inevitably means that selection will act somewhat differently to maximize success along these paths. This sex-specific selection will create differences between the sexes in life-history and mating traits that underlie the sex roles and, thus, sex-specific selection can ultimately only be understood in light of anisogamy. In fact, the only general alternative to sex-specific selection as a cause of sexual dimorphisms would seem to be genetic drift affecting genes with sex-limited expression, which cannot account for the non-random distribution of sexual dimorphism seen across taxa [7,8].

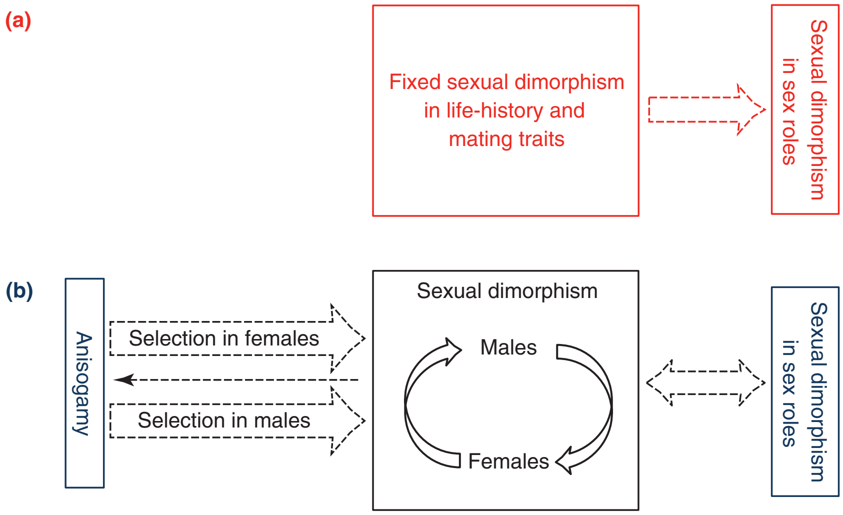

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Figure I. Ways to think about the evolution of sex roles. **(a)** The studies we criticize suggest that sex-role differences (e.g. in mate choice, parental care and mating competition) result from sexual dimorphism in life-history and mating traits (e.g. re-mating latency, survival rate, mate encounter rate and variance in fitness). The latter are considered non-heritable and externally imposed. **(b)** We argue that it is sex-specific selection, ultimately arising from anisogamy, which drives the evolution sexual dimorphism in any trait. Sex-specific selection can result either from differences in male and female life histories or from male–female coevolution. Moreover, sex roles can feed back and affect the evolution of sexual dimorphism and, ultimately, anisogamy. This represents a more dynamic and, we think, more realistic view of sex role evolution (see also [45]).

For example, the simulations assume sex differences in one or several variables (e.g. x_1, x_2 and x_3), which in turn affect the sex-specific optima in another focal variable (x_4). The variables x_1, x_2 and x_3 are referred to as 'habits of life', whereas x_4 is referred to as the 'sex role' (here representing indiscriminate or choosy behaviour). In fact, these are all evolved sex differences, which arguably jointly comprise the sex roles, and the sex specificity of these variables results from sex-specific selection (Box 1). The sex differences in behaviour that are the output of the simulation result directly from the assumption of sex differences in x_1, x_2 and x_3. Indeed, 'the [simulation] predicts that if [the parameters] are the same for all tested individuals, males and females will show no significant differences in their accept/reject behavior' [20]. These simulations therefore illustrate that a single key assumption about a difference between the sexes can cascade into a set of new sex differences, which can be seen as comprising the more or less distinct sex roles. In keeping with classic theory in this field, we suggest that this single key difference is anisogamy: because of anisogamy, selection will simply never be precisely 'the same' for males and females (Box 1).

Variability in sex roles

It has also been suggested that sex roles, and even sex, should be viewed as continuous, environmentally determined traits, and that current research focuses too little on within-species variation in sex roles [20–22]. Yet, with regards to gamete size, males and females form two distinct phenotypic classes in species with separate sexes, or two distinct sexual functions in hermaphrodites (Box 2). It is this difference in gamete size that ultimately causes the sex specificity of selection on male and female traits and phenotypes (Boxes 1 and 2). Instead of relegating anisogamy to a bit part, we believe that it must be the starting point when striving to unravel how sex-specific selection has then acted to generate the tremendous diversity and degree of sexual differences observed today. Furthermore, we suggest that ignoring the fact that male and female gametes are distinctly different will hinder efforts to improve understanding of how sex-specific selection has generated the variance in sex roles that is seen both within and between species.

Although it is no doubt true that stereotypic views of the sexes can affect directions of study in the evolution of sex roles [37], we stress that significant elements of research in this domain over the past several decades have embraced variation at all levels. Acknowledging the fundamental role of anisogamy does not lead inexorably to a deterministic and stereotypic view of sex roles. Indeed, it is the observed diversity of sexual differences that has constituted the very fuel of this research. Variation in male, female and mutual mate choice, sex allocation, parental investment and mating systems has been the main focus of empirical research in this area for many decades. This is true both with respect to within-species variation, where experiments are used to generate variation and identify proximal causation, and with respect to comparative studies, where variation among populations or species is capitalized upon in an effort to improve understanding of the evolution of sex roles. Furthermore, classical theory in this field is less stereotypic than is commonly thought and instead embraces much of this variation. For example, shortly after Trivers developed his theory relating parental investment to sexual selection [4], Parker presented the first theoretical frameworks for both evolutionary conflicts between females and males [5] and for the evolution of mutual mate choice [38]. Similarly, sex allocation theory embraced variation early on [6,39] and has successfully predicted much of the variation seen in sex allocation both within and among species.

Although evolved sex differences ultimately rest on anisogamy, it is important to note that we do not expect variation in sex roles among species to map exactly to variation in the relative size of male and female gametes. This is in part because the degree and direction of sex-specific selection depends on: (i) the environmental context, which in turn is variable in time and space, and (ii) the contingencies of female–male coevolution, and (iii) because sex-specific selection has occurred over a very long time in every sexual lineage (i.e. ever since its ancestor evolved anisogamy), allowing evolution to explore a great expanse of the potential trait space. Despite these diversifying processes, we note that there are clear non-random patterns in the distribution of sex roles and sexual dimorphism throughout the animal kingdom [7,8]. For example, a recent study has suggested that, although there is ample variation, even between closely related species, females across a broad range of species on average tend to invest

Box 2. Sex roles in hermaphrodites

Anisogamy, and the resulting sex-specific selection, does not only lead to distinct sex roles and sex differences in life-history and mating traits in species with separate sexes, but also in organisms where each individual exhibits both the male and female sex, either sequentially or simultaneously.

In sequential hermaphrodites, individuals start life as one sex and then change sex once they reach a certain size, age, or competitive rank in a social group [6,46,47]. Here, each individual has the potential to function as both sexes at different stages of its life, and the two stages are often very distinct, be it in terms of morphology, coloration, mating behaviour, physiology, territoriality and/or life-history traits [46,48–50]. This shows that the type of gamete produced at each life stage cascades, through sex-specific selection, into major differences in traits, resulting in clear differences in sex roles exhibited over the lifetime of an individual.

In simultaneous hermaphrodites, the two sex functions, although generally present throughout the lifetime of an individual, are also associated with sex-specific traits. These include male-interest adaptations to manipulate the sperm storage patterns in the recipient [51,52] and female-interest adaptations to control the fate of incoming ejaculates [51,53,54], which are clearly the result of sex-specific selection. In addition, although hermaphroditic individuals are not expected to exhibit clear-cut sexual dimorphisms consistently, in many species, individuals share a preference for performing a specific sex role in a mating interaction [55], as exemplified by conditional egg-trading behaviour [56,57], rejection of mates that do not donate sperm [58], or unilateral sperm donation in species with hypodermic insemination [59,60]. Moreover, the extent to which individuals emphasize their male and female sides is often highly variable, and can depend on the sex allocation [61], which in turn depends on individual size [62], and the nutritional and social environment [6,63].

Thus, hermaphrodites illustrate that distinct sex roles are associated with different types of gamete, even in situations where individuals do not necessarily differ in their life-history or mating traits.

over 1000× more resources in the production of eggs than males do in the production of sperm [40]. Similarly, sex-role reversal has arisen in a range of animal taxa [8,41], but it is generally the exception and does not occur in half of the species (as might be expected if anisogamy was unimportant). A similar point can be made about males being the ornamented sex more often than females [2,8,42]. Finally, whereas males and females differ in size in most taxa, there are clear clade-specific differences in the direction of these differences [8,43], again demonstrating that sex-specific selection is prevalent.

Concluding remarks

Sex roles can neither be caused by 'chance' alone, nor be externally imposed by 'habits of life'. Because of anisogamy, there are two distinct paths to successful reproduction in every sexual lineage (associated with producing either many small or few large gametes) and selection will act somewhat differently to maximize success along each path. It is this sex specificity of selection, coupled with historical contingency, that has led to the diversity of differences between the sexes in sex roles that are seen in nature. Research efforts should therefore be concentrated on elucidating how variation in the environment and female–male coevolution have shaped sex-specific selection to create sex role variation, given that anisogamy is the root cause of sex-specific selection and, therefore, the sex roles.

Acknowledgments

We thank J. Abbott, I. Ahnesjö, A. Berglund, P. Innocenti, M. Jennions, D. McLennan, S. Ramm, D. Vizoso, and M. Wyman for comments and discussion, and the Swiss National Science Foundation, the Swedish Research Council, the European Research Council, the Natural Sciences and Engineering Research Council, and the Canada Research Chairs program for financial support.

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