

Sexual Competition among Females: What Causes Courtship-role Reversal?

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In most animals, males are the competitive sex whereas females are typically non-competitive and choosy of mates. In a variety of taxa, certain species (or populations within species) show a reversal in these typical courtship roles. Recent research with these organisms supports a central tenet of sexual selection theory: that it is the relative investment of the sexes in offspring that controls the number of males and females available for mating, and thus is the main determinant of the degree of sexual competition in each sex.

For an Indian species of button quail (*Turnix taigoor*) Darwin¹ noted that males brooded eggs and that rivalry between females caused them to be the 'more pugnacious' sex. Such inter-female competition (which led to local natives using the hens rather than 'fighting cocks' in gaming contests¹) is the opposite of the reproductive roles seen in most animals; males are usually non-parental and sexually competitive. The question of what determines which sex takes the more competitive role has continued to interest biologists and prompted Williams² to ask, 'Why are males masculine, females feminine and occasionally vice-versa?' A number of recent studies have examined this question in detailed investigations of role-reversed or 'vice-versa' species.

What is role reversal?

A role reversal involves a change in the behavioural roles; it does not involve a change in sex (sex reversal³). Species in which both courtship and parental roles are reversed (particularly vertebrates; Table 1) have been referred to as showing sex-role reversal (e.g. Ref. 4). A number of species lacking parental care, however, show a reversal only in the courtship roles (several arthropods; Table 1) and it is courtship-role reversal that is the main focus of this review.

Courtship is used here in a broad sense by including not only direct interactions between males and females but also competitive inter-

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actions among members of the same sex for opportunities to mate. Thus, there is a courtship-role reversal when females are sexually competitive, engaging in competitive displays or actual aggression, and males discriminate among females. Females taking the more active or initial role in courtship or 'soliciting' males may also comprise part of the behaviour in courtship-role reversal (Table 1). Courtship reversals can be partial or complete. In complete reversals males show no sexually competitive behaviour.

Although my discussion is primarily concerned with behaviour, the 'typical' and 'reversed' sexual differences observed in various species may include morphological traits. The more sexually competitive sex may exhibit elaborated coloration or other characters that, as Darwin¹ first noted, appear to function either in intrasexual aggression or in attracting mates.

Causes of courtship-role reversal: theory

Parental investment, operational sex ratios and sexual selection

Darwin¹ argued that the direct cause of role reversal is sexual selection for attractive and competition-functioning traits in females, and a relaxation of such selection in males. Selection (natural) is also expected to produce choosiness in males. Despite recent interest in estimating opportunity for sexual selection in nature (using estimates of intrasexual variation in mating success)⁵ (Box 1), there have been no tests of the predicted association between reversed roles and more intense sexual selection on females relative to males. However, an experimental study reporting data on females alone showed a large decrease in the variance in mating frequency of female katydids to be concomitant with a change from complete courtship-role reversal to the more typical courtship roles (Table 1)¹⁰.

Sexual selection on females should increase when there are more sexually receptive females than sexually receptive males, i.e. the operational sex ratio (OSR)¹¹ is

skewed toward a greater number of females. Two factors can theoretically affect the OSR. First is the actual ratio of all adult females and males. Although there is evidence that variation in this ratio can correlate with the degree of mate choice and sexual competition^{12,13}, I am unaware of any studies in nature showing that a skew in the primary adult sex ratio is a cause of courtship-role reversal.

Theory holds that it is the relative investment of the sexes in the production of offspring that exerts the main control on the rates of offspring production by the sexes¹⁴, and thus the OSR, and sexual competition^{6,7}. In most species, parental investment (Box 1) by females is greater than that by males. Due to investment in maternal duties, fewer females than males are available for mating, and thus there is greater sexual selection on males. Courtship-role reversal, therefore, is expected to occur when parental investment by males exceeds that of females, so that there are fewer males than females available for mating.

Although the large gametic investment of females in the production of each zygote predicts a shortage of sexually receptive females in virtually all species¹⁵, male reproductive investment (such as paternal care) can offset and even reverse this initial disparity^{6,7} (see Ref. 14). A relatively greater male parental investment, and the resultant female-biased OSR, lead to greater sexual selection on females. However, the extent of the sexual selection can be influenced by certain ecological factors. For instance, if the environment is structured so that access to receptive males can be easily controlled, sexual selection on females is expected to be high¹¹.

It is important to note that relative parental investment determines the *extent* rather than the *nature* of sexual selection¹⁴. Female-female competition resulting from an excess of sexually receptive females may be expressed in mating strategies of various natures. These include the possibility that not all elements of courtship-role reversal are exhibited, i.e. overt male mate choice may not have evolved because males simply

Table 1. Groups in which courtship-role reversal has been observed

| Taxon | Nature of role reversal | Male-male competition? | Operational sex ratio | What limits female reproduction? |
|--|---|--|--|---|
| Birds | | | | |
| <i>Phalaropus</i> spp. (phalarope) ²⁵ | Fights among females for pre-nesting males | No | Female-biased due to polyandry | Egg incubation exclusively by males |
| <i>Actitis macularia</i> (spotted sandpiper) ²⁶ | Females compete in areas in which males nest; females court males | Some | Female-biased due to polyandry | Egg incubation exclusively by males |
| <i>Gallinula chloropus</i> (moorhen) ¹⁸ | Fights among females for pre-nesting males | Male fights | Male-biased | Phenotype of incubating male |
| Frogs | | | | |
| <i>Dendrobates auratus</i> (poison-arrow frog) ⁴³ | Occasional fights between females; female takes the active role in courtship | Occasional fights | Possibly female-biased | Male tending of eggs |
| Fishes | | | | |
| <i>Nerophis ophidion</i> (pipefish) | Male choice (for larger females) and dominance among females ^{44,45} | No | Female-biased due to brood-size limitation in males ⁴ | Time taken by male to brood eggs on body |
| Crustaceans | | | | |
| <i>Pseudosquilla ciliata</i> (stomatopod) ⁴⁶ | Female initiation of courtship and male choice (for larger females) | Some aggression | | Possibly male-derived nutrients in ejaculate (known as <i>Squilla</i>) ⁴⁷ |
| Insects | | | | |
| <i>Empis borealis</i> (dance fly: Diptera) | Females compete in a lek swarm; males enter the swarm and choose large, young females ^{40,41} | No | Apparently female-biased | Prey item provided by male (females obtain prey only from males) ⁴² |
| <i>Anabrus simplex</i> (Mormon 'cricket': Orthoptera), Zaprochiline katydid (unnamed) (Orthoptera) | In food-limited populations females fight for access to signalling males; male choice (for larger females) ^{10,24,32} | Not in these populations | Female bias caused by food limitation ³³ | Large spermatophore eaten by female, which increases fecundity ^{48,49} |
| Belostomatids (giant water bugs: Heteroptera) | <i>Abedus herberti</i> not completely role-reversed: female initiates mating; male coyness ³⁸ <i>Diplonychus major</i> females fight to lay eggs (in lab) ²⁸ | Male <i>A. herberti</i> display to females ³⁸ | Female-biased but only at certain times of the season in <i>D. major</i> ²⁸ , <i>Belostoma flumineum</i> ²⁹ and <i>A. indentatus</i> ³⁰ | Male's aeration of eggs laid on his wing covers |

mate with winners of competitive bouts.

Courtship-role reversal and male-biased OSRs

Sexual selection theory predicts that a partial courtship-role reversal – the coexistence of male and female choice as well as direct intra-sexual competition by both sexes – can occur if there is a similarity in parental investment by the sexes and thus in the number of receptive males and females present. In theory, however, these behaviours can also be exhibited by both sexes even when the number of receptive females is smaller than the number of available males. If large variation in phenotypic quality exists in both sexes (due to variation either in genetic quality or in the ability to provide direct phenotypic benefits to the opposite sex), females should compete for access to high-quality males and these males are ex-

pected to discriminate in favour of high-quality females^{14,16}. However, not all individuals should exhibit such a role reversal; low-quality males should compete for all females but high-quality females should discriminate against such males¹⁷. Petrie's study of moorhens¹⁸ (Table 1) may be an example of such a scenario. Although there was 'no shortage of available males', female moorhens competed for access to high-quality paternal care from certain males, but males were also noted to compete for females.

Mate choice by males in the absence of a role reversal (i.e. without direct sexual competition among females) is frequently recorded. This is expected when there is variation in female quality and when male mating costs are such that only a small fraction of the available females can be mated by an individual male^{19,20}. Male mating costs may be parental investment, as dis-

cussed above, or mating effort (Box 1) that does not provide direct benefits to the mating female (e.g. certain time costs of mating). Because of the lack of female-female competition, the limitation on male mating frequency does not appear to result in an excess of receptive females. In contrast to male parental investment, such mating effort by males is never expected to result in an excess of sexually receptive females and thus to cause a role reversal in the competitive elements of courtship.

Relative investment as a cause of courtship-role reversal: empirical studies

Complete or partial reversals in the typical courtship roles have been reported in birds (about 30 species), frogs, fishes, crustaceans and insects and, as predicted, are almost invariably associated with paternal investment (Fig. 1 and Table 1). Such investment comes in

Box 1. Sexual selection, male investment and courtship-role reversal

Sexual selection is the differential reproduction of individuals due to competition for mates. Various statistical measures of variation in mating frequency are used to estimate opportunity for sexual selection⁶.

Parental investment represents investment in offspring at the cost of investing in other offspring⁶. Courtship-role reversal occurs when male investment in 'goods and services' to females or offspring greatly reduces the number of males available for mating. Such male investment was originally referred to as parental investment⁶ and I continue with the usage in this article. However, there is some argument as to whether the *evolved function*⁷ of prezygotic investments by males (such as courtship feeding) is parental investment, i.e. investment in the male's own offspring⁶. The alternative is that feeding the female evolved as mate-benefiting 'mating effort'⁸, i.e. it functions to obtain copulations or fertilizations of ova. The key point for the present review is that, no matter what the selective history (function), if the male investment influences offspring number or survivorship (even if this is achieved through the increased survival of the mother) it can potentially cause courtship-role reversal.

two forms (Fig. 1): (1) parental care, in vertebrates and giant water bugs; and (2) in several invertebrates, male 'courtship feeding' (see Box 1) in which nutrients provided to the female during mating are eaten (e.g. dance flies), or absorbed from the ejaculate (e.g. certain stomatopod crustaceans).

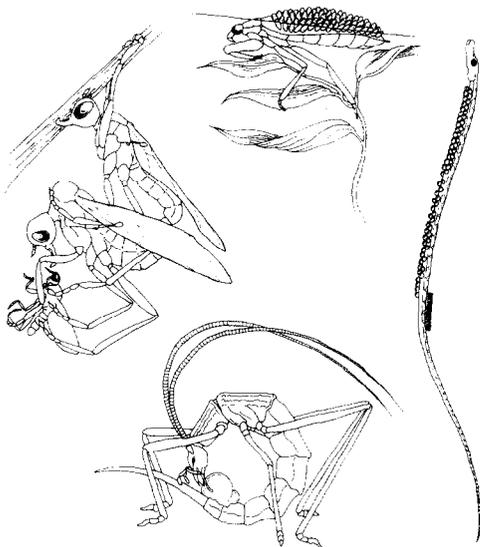


Fig. 1. The form of male investment in four species that show courtship-role reversal. Clockwise from top: male water bug, *Abedus herberti*, brooding (aerating) eggs at the water surface (by R.L. Smith, with permission); male pipefish, *Nerophis ophidion*, brooding eggs (from I. Ahnesjö, artwork by A. Robertson, with permission); female katydid (an undescribed zaprochiline species) eating the large spermatophore; and a copulating pair of dance flies, *Empis borealis*, showing the female about to feed on the courtship gift of prey held by the male's hind legs. The last two figures are original drawings by Heather Proctor from photographs (the *Empis* is from Fig. 1 of Ref. 42).

Sexual selection theory⁶ makes the precise prediction that such reversals should occur when parental investment by the male exceeds that by the female. Initially it may seem that a cross-species confirmation of this prediction would be a comparative association of courtship-role reversal with exclusive male parental care. Such a high degree of paternal care, however, may not necessarily select for such altered roles: for example, 61% of teleost fish families with parental care show exclusive male care²¹ and yet courtship-role reversal has been observed in very few of these (Table 1). Such data suggest that only certain types of exclusive male parental care are of a sufficiently high cost to exceed female parental investment; it is the cost of parental investment (Box 1) rather than its benefit to offspring that is thought to control sexual differences⁶.

In order to associate such costs with behavioural differences, a quantification of parental expenditure by the sexes is required. However, such an endeavour is nearly impossible due to problems both in equating currencies of investment components – such as energy, risks taken and 'value' of care (which is higher if brooding space is more limited) – to determine costs in terms of future offspring²², and in summing all of these components for each sex. Indeed, efforts to estimate relative investment and relate this to sexual differences have failed to find the predicted association^{4,23,24}. One way of estimating whether male investment is relatively greater than that of the female is to determine whether paternal contributions change the OSR by decreasing the average number of male mating opportunities to below those of the female, thus limiting the reproduction of females.

A number of studies of species in which there is sex-role reversal have provided evidence of an association between such limitation and a reversal in the courtship roles. For example, the rate at which male red-necked phalaropes²⁵ and spotted sandpipers²⁶ can incubate eggs is less than the rate at which females produce them. This appears to cause certain females to be excluded from reproduction. Male pipefishes and giant water bugs

(Fig. 1) brood eggs on specialized areas of the body (Table 1). For both taxa, data suggest that the restricted space available for male parental investment can limit female reproduction: in two pipefish species, males are capable of brooding only about half the number of eggs that females can produce during one male 'pregnancy'²⁷; in three species of giant water bugs it was found that male dorsal area can limit female reproduction, but only at certain times of the season^{28–30}.

In katydids, which show paternal investment in the form of spermatophore feeding (Table 1, Fig. 1), courtship-role reversal also appears to be a result of the investment limiting female reproduction. Three species have been observed to show role reversal in nature, but only in certain populations^{10,24,31,32}. Altered roles appear to occur in food-stressed populations in which the number of males able to produce spermatophores is lower than the number of sexually active females. An experimental decrease in food availability produces such a female-biased OSR by decreasing the number of males able to supply spermatophores and increasing the mating (spermatophore-acquiring) frequency of hungry females³³.

For katydids, the fact that courtship roles are environmentally determined³¹ allowed a direct test of the hypothesis that it is an increase in relative male parental investment that causes reversed roles^{6,7}. As relative availability of sexually signalling males (those able to produce spermatophores) decreases in food-depleted habitats, the value of the male offering (male parental investment) increases^{14,31}. To put it another way, when food availability decreases, the percentage of material of male origin in individual eggs probably increases. The hypothesis was supported in a study of an Australian zaprochiline katydid in which a late-season loss of role reversal was correlated with the flowering of a plant with abundant pollen food³². Field experiments with role-reversed populations confirmed that it was additional pollen that increased the number of sexually receptive males, decreased the opportunity for sexual selection on females and caused a change to the more typical courtship roles¹⁰.

Parental investment and courtship roles: can causes and consequences be distinguished?

Sexual selection theory^{6,7} is clear in its claim that relative parental investment patterns control differential sexual selection and thus the different mating strategies of males and females. The experiment with katydids¹⁰ supports this claim; in ecological time, variations in relative parental investment determine variation in courtship roles. The reverse argument, however, has also been presented; a decrease in effort used to compete sexually or to attract multiple mates results in increased male parental investment³⁴⁻³⁶. This argument is usually concerned with factors that select for the origin of male parental investment. Suggested causes of savings in mating effort are: (1) a scarcity of females, (2) the fact that males of low 'genetic quality' might enhance reproductive success by increasing investment in offspring³⁵, and (3) a decrease in the potential for polygyny¹¹ in the environment that selects for males who sequester individual females rather than opting for 'scramble' type competition for mates³⁶.

Future research directions

Considering the current interest in patterns of sexual selection in animals (and plants)³⁷, there has been relatively little empirical testing of factors hypothesized to control sexual selection and, thus, the courtship roles. In the first place, the link between the latter two factors is virtually untested: is the opportunity for sexual selection on females greater than that on males in species (populations) showing courtship-role reversal? And what about controlling factors? A quantitative cross-species test of the association between parental investment patterns and courtship roles has yet to be done. Because exact measures of relative investment are difficult, studies of paternally investing species should provide data on the numbers of males and females available for mating, so that the predicted association between this variable and courtship roles can eventually be examined in a comparison of taxa.

Additional tests of factors controlling sexual selection will be those

that further relate intraspecific variation in the courtship roles to patterns of parental investment and operational sex ratios. Research with giant water bugs has revealed seasonal variation in the availability of male brooding space²⁸⁻³⁰; but it is not clear to what extent the courtship roles are reversed in these insects³⁸ (Table 1). The obvious prediction is that altered roles will occur when male dorsal space is limiting.

In certain insects, courtship roles may vary over quite brief time periods. Male dance flies (Empididae) provide prey items to females at mating (Fig. 1). Although in most species females mate after visiting swarms of males³⁹, Svensson *et al.*⁴⁰⁻⁴² have reported observations of a courtship-reversed species in which prey-bearing males enter all-female 'lekking' swarms and choose mates (Table 1). The intriguing possibility that courtship roles may reverse over periods as short as several hours comes from observations of *Rhamphomyia longicauda* by Downes (pers. commun.), which indicate that swarms of apparently competing individuals change from all male to all female. The causes of such rapid mating-system shifts are well worth future study.

Acknowledgements

Thanks to Gunilla Rosenqvist and Andy Snedden for useful comments on the manuscript, to Heather Proctor for her excellent artwork, to Bob Smith and Annika Robertson for permission to reproduce artwork, and to Antony Downes, John Reynolds and especially Bill Brown and Tim Clutton-Brock for discussion.

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