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Sex-role reversal in vertebrates: behavioural and endocrinological accounts

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Abstract

Sex-role reversal occurs when females compete more intensely than males for access to mates. In this paper, we survey the occurrence of sex-role reversal in vertebrates: we focus on behavioural aspects of sex-role reversal and we examine possible endocrinological correlates of this phenomenon. The best documented cases among vertebrates of sex-role reversal occur in fish and birds. In nearly all sex-role reversed species or populations, females have higher potential reproductive rates than males. Some species in which females were previously thought to be the predominant competitors for mates (for instance seahorses and a dendrobatid frog), appear not to be sex-role reversed according to recent studies. The endocrinology of sex-role reversal has been studied in only a few species and therefore remains poorly understood. In birds, which probably have been studied the most in this respect, steroid hormones appear to follow the typical ancestral conditions (for instance no reversal of testosterone levels) in sex-role reversed species, whereas prolactin, a principal regulator of the onset and maintenance of incubation, departs from the usual avian pattern in that it is higher in males than in females. The study of sex-role reversed behaviour offers unique opportunities not only to test sexual selection theory, but also to enhance our understanding of the neuroendocrine mechanisms mediating behavioural sex differences. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Since Darwin (1871) proposed the concept of sexual selection to explain the evolution of sex differences, there have been impressive empirical and theoretical advances in this field (Andersson, 1994; Bateman, 1948; Clutton-Brock and Parker, 1992; Emlen and Oring, 1977; Trivers, 1972). Although some degree of competition for mates is common in both sexes of most species, the predominant pattern in animals is that of males competing more intensely for mates than females (Andersson, 1994). In many animals, males also develop secondary sexual characters such as conspicuous colours, exaggerated ornaments, or menacing weapons. In general, female reproductive success is limited by gamete production, whereas

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male success is limited by mate availability (Bateman, 1948). Hence, males are under strong selection to acquire mates. In some animals, nevertheless, females compete more intensely than males for access to mates. Such species are typically described as sex-role reversed (Trivers, 1972; Williams, 1966, 1975) and they provide critical tests of the generality of theories pertaining to the strength of sexual selection (Andersson, 1994; Jones et al., 2000; Okuda, 1999; Vincent et al., 1992). In these species with mainly paternal care, the sex differences in parental roles can apparently override the effects of anisogamy and lead to a reversal of other aspects of sex roles and sexual dimorphism (Andersson, 1994). As we will see later, current parental investment theory asserts that regardless of whether males or females provide parental care, the sex with the higher potential reproductive rate will compete more strongly for mates (Clutton-Brock and Vincent, 1991).

Although studies of reproductive patterns have historically neglected female behaviour and focused instead on the more common phenomenon of male–male competition for access to females or on male secondary sexual characteristics, there has recently been a surge of interest on female sexual behaviour and on female–female competition (Ahnesjö et al., 1993; Berglund et al., 1993; Okuda, 1999; Swenson, 1997; Vincent et al., 1992). Since Darwin (1871) and Williams (1966) drew attention to sex-role reversed behaviour, an increasing number of examples has come to light (Trivers, 1985; Andersson, 1994). Sex-role reversal has now been documented or suggested in insects, fish, amphibians, and birds.

During the last three decades, numerous papers have proposed various determinants of sexual selection. Trivers' concept of parental investment (PI) was a major advance in sexual selection theory that helps to explain sex differences in mating competition and to predict which sex would compete more intensely for mates (Trivers, 1972). The sex that invests less in offspring should compete more for mates because that sex reproduces more often, leading to scarcity of sexually active members of the opposite sex. Trivers' PI theory has subsequently been revised by many researchers who have suggested that it is the operational sex ratio (OSR), rather than the relative PI, that is the causal factor in the evolution of sex roles (see Owens and Thompson, 1994). Emlen and Oring (1977) introduced the concept of the OSR (defined as the ratio of fertilizable females to sexually active males in a population at a given time) as an empirical measure of the sex bias in reproductive animals. Emlen and Oring were the first to suggest that sex roles were determined by the relative abundance of each sex and they argued that the more abundant sex should be the more competitive one. Because PI and OSR can be difficult to measure in nature, the potential reproductive rate (PRR), i.e. the maximum number of independent offspring that each parent can produce per unit of time, has been proposed as an empirical measure for predicting the direction of mating competition (Clutton-Brock and Vincent, 1991). They predicted that the mating competition would be more intense among the sex with higher PRR. Recently, additional theoretical work has suggested that courtship roles are determined by a combination of OSR, PI and the relative time involved in reproductive tasks ('time out') versus the amount of time each sex is available to mate ('time in'; Parker and Simmons, 1996; see also Kvarnemo and Ahnesjö, 1996). Another determinant of mating competition is mate quality: where the PRR is similar in the two sexes, the relative benefits of acquiring qualitatively superior mates, rather than the OSR, may determine the comparative intensity of mating competition in the two sexes (Clutton-Brock and Vincent, 1991; Owens and Thompson, 1994; Petrie, 1983).

Whatever the reasons for sex-role reversal (e.g. PRR, OSR, differences in mate quality or parental investment), when it occurs, theory predicts: (1) stronger female than male competition for mates; (2) more critical choice of mate by males; (3) higher variance in female than male mating success; and (4) more pronounced female secondary sex traits and mate-attracting displays (Andersson, 1994; Trivers, 1985).

In this paper, we survey the occurrence of sex-role reversal in vertebrates. We focus on behavioural aspects of sex-role reversal and we examine possible hormonal correlates of this phenomenon.

2. Evidence for sex-role reversal in vertebrates

2.1. Fishes

Although male care of offspring is the dominant parental care pattern in teleost fish, males are also generally the predominant competitors for mates and evidence for sex-role reversal is rare (Vincent, 1992; Vincent et al., 1992). This is probably because the most common forms of paternal care do not usually depress male PRRs below that of females: egg guarding, nest building and fanning do not prevent males from caring simultaneously or in quick succession for several clutches (Clutton-Brock and Vincent, 1991; Vincent, 1992). Nonetheless, some forms of teleost paternal care do not permit the male to care quickly for large number of eggs, and recent theory predicts females to compete more intensely for mates in those species in which females have higher PRRs than males. Such sex-role reversal is most probable in those species in which males bear eggs and/or embryos on their body, and consequently may be severely restricted in the time or space available for brooding eggs, and in species where males provide extraordinarily lengthy care or build specialized nests which limit brood size (Vincent, 1992).

The male pregnancy of pipefishes and seahorses (family Syngnathidae) has often led to the inference that females compete most intensely for access to males, because males limit female reproduction (Trivers, 1972, 1985). However, recent studies have shown that in different species either sex may be the predominant competitor for mates (Vincent et al., 1992). Or, in other words, although males are responsible for extended and specialized brood care in all members of this family, not all syngnathids are sex-role reversed. Vincent et al. (1992) suggested that there is an association between the mating pattern and the sex roles in this family: polygamous species show reversed sex roles whereas monogamous species show conventional sex roles. Given that this relationship between polygamy and sex-role reversal in syngnathid fishes is based on comparisons involving very few species in a family with over 200 species, this suggestion is in need of further evaluation (but see also Masonjones and Lewis, 2000).

A classical example of sex-role reversal is found in pipefishes (Vincent et al., 1992). Two species, *Nerophis ophidion* and *Syngnathus typhle*, have been studied in great detail. In both species, females produce more eggs than the male brood-pouches can accommodate (Berglund and Rosenqvist, 1990; Berglund et al., 1989). This reproductive inequality results in a female-biased OSR, causing the above mentioned sex-role reversal (Clutton-Brock and Parker, 1992). Observational and experimental evidence obtained in these two species is consistent with the predictions of the sexual selection theory. First, females are the predominant competitors for access to mates, and competition is primarily indirect (Berglund, 1991; Rosenqvist, 1990). Second, males are more selective than females in accepting mates (Berglund et al., 1986b; Rosenqvist, 1990). Males benefit directly from being choosy by selecting larger females that provide more and larger eggs (Berglund et al., 1986a,b), which give rise to heavier and higher quality offspring (Ahnesjö, 1992a,b). Third, females of both species appear to be most modified by sexual selection. In *N. ophidion*, sexual dimorphism is most pronounced: females are larger, have a bright blue colouration along their body and develop obvious ventral skin folds (Berglund et al., 1986b). All of these features play a role in mate choice by males (Berglund et al., 1986b). In *S. typhle* females develop a temporary ornament when competing over mates with other females and when performing nuptial dances with males. Berglund et al. (1997) recently showed experimentally that this temporary ornament honestly signals female quality and that ornamentation accurately predicts female mating success.

Recently, Jones et al. (2000) provided the first empirical test of the sexual selection gradient (also called the Bateman gradient) concept in a sex-role reversed species, namely the pipefish *S. typhle*. In his classic experimental study of sexual selection in *Drosophila*, Bateman (1948) proposed that the strength of sexual selection depends on the relationship between mating success and offspring production. In species with typical sex roles, the Bateman gradient of males is expected to have a steep slope relative to the gradient for females.

Using molecular genetic techniques for assigning parentage, Jones et al. (2000) performed mirror-image experimental tests of the Bateman gradient using the sex-role reversed *S. typhle*. Most importantly, they found that females in this species exhibited a stronger positive association between number of mates and offspring production, thus females clearly having a steeper sexual selection or Bateman gradient. They further showed that, when an excess of males was present in the breeding population, a condition which is known to lessen the strength of sexual selection on females, the Bateman gradients of the sexes did not differ significantly in slope. The relationship between number of mates and fertility thus clearly responded in the predicted fashion to changes in the adult sex ratio. Jones et al.'s findings give empirical support to the idea that the relationship between mating success and number of progeny, as characterized by the Bateman gradient, is a central feature of the genetic mating system affecting the strength and direction of sexual selection.

Although it had been tacitly and explicitly assumed that seahorses were sex-role reversed, more recent studies have shown that they exhibit conventional sex roles: male seahorses compete more intensely than females for access to mates, and only males exhibit uniquely competitive behaviours (Vincent, 1994a; see also Masonjones and Lewis, 2000). On the basis of a laboratory study on the Sri Lankan seahorse *Hippocampus fuscus*, Vincent (1994b) found that the OSR among mated seahorses is unbiased because males and females effectively have equal PRRs. In contrast, the OSR among mate-seeking seahorses is male-biased, because unmated (empty) males can prepare to mate faster and can remain ready to mate for longer than unmated females. In dwarf seahorses *Hippocampus zosterae*, males were found to have higher PRRs and shorter reproductive 'times out' than females (Masonjones and Lewis, 2000). Overall, all the recent studies on seahorses support the original hypothesis of Clutton-Brock and Vincent (1991) that the sex with the higher PRR competes more intensely for mates than does the sex with the lower PRR.

In species with traditional sex roles, a simple prediction originally inspired by Darwin (1871) is

that polygyny results in more intense sexual selection and can lead to the evolution of secondary sexual characters in males (Andersson, 1994). The analogous prediction for sex-role reversed species is that sexual dimorphism and expression of secondary sexual traits in females may be more pronounced in species that are more strongly genetically polyandrous than in species that are less so (Jones and Avise, 1997a). Recently, microsatellite markers have been employed to study the genetic mating system in four species of the Syngnathidae and to address possible relationships between the mating system, sexual selection, and sexual dimorphism in sex-role reversed species (Jones and Avise, 1997a,b; Jones et al., 1998, 1999). The available data on syngnathid genetic mating systems so far are consistent with the hypothesis that the more polyandrous species exhibit greater levels of sexual dimorphism (with females being the sexually selected sex) than those that are less polyandrous (i.e. either monogamous or polygynandrous). *Syngnathus scovelli* is extremely dimorphic and has a primarily polyandrous genetic mating system (Jones and Avise, 1997a), *Hippocampus angustus* appears to be monogamous and is sexually monomorphic (Jones et al., 1998), and both *S. typhle* and *S. floridae* exhibit moderate levels of sexual dimorphism and are genetically polygynandrous (Jones and Avise, 1997b; Jones et al., 1999).

Sex-role reversal has been suggested or documented in three other species that bear their young and recently also in one species in which males do not bear eggs or young. In the cardinalfish *Apogon notatus* (Apogonidae), in which males alone mouthbrood the young, the PRR of males is restricted by the lengthy mouthbrooding period and is usually lower than that of females (Kuwamura, 1985). Because females are more active in courtship and attacks against conspecifics (Kuwamura, 1985; Okuda, 1999), this species has often been considered to be sex-role reversed (Swenson, 1997; Vincent, 1992). In a recent study, Okuda (1999) showed however that the OSR is male biased throughout the breeding season, primarily due to a higher mortality in females. In agreement with the sexual selection theory, Okuda found that sexual selection is operating more

strongly on the males (i.e. the sex toward the OSR is biased) and that this fish is not sex-role reversed (despite PRR being higher in females). In a related species *A. doederleini*, several observations suggest that this species might be sex-role reversed: the OSR was female-biased almost throughout the breeding season, and females more frequently moved to search for mates and agonistic encounters occurred more between females (Okuda and Yanagisawa, 1996). In the black-chinned tilapia *Sarotherodon melanotheron*, a paternal mouth brooding cichlid in which the PRR of males is lower than that of females, a clear sex-role reversal has recently been documented. First, females were more aggressive than males both in the presence and absence of potential mates. Second, males appeared to be more choosy for size, preferring large partners over small ones, while females did not discriminate for size (Balshine-Earn and McAndrew, 1995). The most recent reported case of sex-role reversal in fish concerns the tidewater goby *Eucyclogobius neberryi* (Swenson, 1997). In this species in which males do not bear eggs or developing young (but construct a burrow and provide parental care), the intensity of sexual aggression is greater among females than among males. Furthermore, females have a more developed secondary sexual trait (black nuptial coloration) than males. According to Swenson (1997) the sex-role reversed behaviour in this species is unique among fishes because it is the only reported case in teleost males that do not bear eggs or developing young.

We are aware of only one study that has examined the endocrinology of sex-role reversal in fish. Mayer et al. (1993) measured plasma levels of androgens in three species of pipefish to determine whether sex-role reversal and male pregnancy could be correlated with circulating hormone levels. The levels of most measured hormones did not differ consistently between the sexes under the physiological conditions studied. However, in the case of 11-ketotestosterone (the dominant circulating androgen in breeding teleost males), pipefish showed the typical teleost pattern in that levels of this androgen were higher in males than in females, and in that levels were higher in prebreeding than in postbreeding males. Although

Mayer et al. (1993) suggested that the relatively high levels of 17beta-estradiol obtained in breeding males might indicate a partial reversal of the normal teleost steroid pattern between the sexes, this needs to be further verified because their sample size was low and because the single highest 17beta-estradiol level was measured in a female. Overall, however, their data did not suggest that steroid levels in pipefishes were markedly different from the typical teleost pattern. This was certainly the case for testosterone and 11-ketotestosterone, while the data for 17beta-estradiol were somewhat equivocal. To that end, Mayer et al. (1993) suggested that the observed steroid patterns in the pipefishes may be a consequence of male pregnancy rather than of reversed sex roles.

2.2. Amphibians

On the basis of males performing parental care and of more than one female following a single calling male, Trivers (1972, 1985) suggested that sex-role reversal might occur in green dart-poison frogs *Dendrobates auratus*. Wells (1978) subsequently studied this species and he concluded that his observational results were consistent with the hypothesis of sex-role reversal: a small female clutch size and a large time investment by males in parental care may have caused receptive males to become rare compared with receptive females causing female–female competition and female courtship of males. In the most detailed studies so far on this species, it was found however that the intensity and frequency of competition for mates is high in both sexes, and that females are more selective about mating than males, which is contrary to predictions of sex-role reversal (Summers, 1989, 1990). According to Summers, females compete to monopolize the parental care of particular males: females engage in mate guarding to prevent their mates from mating with other females and caring for their offspring.

All *Dendrobates* studied have extended parental care in which one parent carries the tadpoles from an oviposition site in the leaf litter to pools of water. In some species this behaviour is performed by the male, while in others it is performed by the female (Summers, 1992a), making

them extremely interesting for comparative studies. Summers (1992b) compared the results of field investigations of two species of dart-poison frogs, one with male (*D. leucomelas*), the other with female parental care (*D. histrionicus*). The sex-role reversal hypothesis (sensu Trivers, 1972) would predict that male–male aggression should be less common and intense than female–female aggression when males invest more in parental care than females (Summers, 1992a,b). This was clearly not the case when comparing these two species. Observations on aggressive intrasexual interactions in the species with male parental care (*D. leucomelas*) did also not support the sex-role reversal hypothesis: there were more male–male fights than female–female fights. Summers' comparative work also showed that males in species with paternal care were not more selective about mating than males in species with female parental care. In both species, females were more selective than males.

Recently, Pröhl and Hödl (1999) analyzed the direction of mating competition for the first time in terms of PRR and OSR in a dendrobatic frog. They recorded that PRRs of males of the strawberry dart-poison frog *Dendrobates pumilio* are much higher than those of females, rendering females the limiting sex in the mating process. As the adult sex ratio did not seem to deviate from unity, the unequal PRR of the sexes generated a male-biased OSR, the main determinant of mating competition. Pröhl and Hödl concluded that the discrepancy in PRRs between the sexes due to differences in parental investment and the prolonged breeding season are sufficient to explain the observed mating pattern (i.e. selective females, high variance in male mating success, and the considerable opportunity for sexual selection).

In conlusion, the available evidence in dendrobatic frogs with male parental care seems to indicate that they are not sex-role reversed (contra Trivers, 1972). Given that PRRs have been determined in few dendrobatic frogs and that they show great variation in mating patterns ranging from species with exclusively male or female parental care, through biparental care to temporal pair bonding (Pröhl and Hödl, 1999), they are ideal subjects for further research into the relationships between PRRs, mating systems and differences in sexual selection between the sexes.

Females have also been observed to compete aggressively in midwife toads *Alytes* (Family Discoglossidae) in which only males provide parental care carrying fertilized eggs entwined around the hind limbs. In *Alytes obstetricans* observed in laboratory conditions, males did not exhibit direct aggressive interactions with one another for access to mates. Females, however, engaged in intense competitive behaviour including frequent physical displacement of the amplectant male by an unpaired female (Verrell and Brown, 1993). In another species of this genus, the facultatively sex-role reversed Majorcan midwife toad *Alytes muletensis*, increased ambient temperature has been shown to affect the sexual difference in PRR by increasing the reproductive rates of males: as temperature changes, the sexual difference in PRR, and consequently OSR and levels of sexual selection, change in the course of the breeding season (Bush 1993 cited in Kvarnemo and Ahnesjö, 1996).

2.3. Birds

2.3.1. Behavioural evidence

In the vast majority of avian species, females incubate alone or males and females share incubation duties approximately equally, and males compete for mates more intensely than do females. In a small proportion of avian species, males provide most or all parental care and a reversal of the usual sex-role pattern occurs: females show higher levels of intrasexual aggressiveness and they are larger and more brightly coloured than males (Oring, 1982, 1986). Sex-role reversal is found in jacanas (Jacanidae), plovers (Charadriidae), sandpipers (Scolopacidae), coucals (Centropodidae) and buttonquail (Turnicidae) (Andersson, 1994; Ligon, 1999).

The spotted sandpiper *Actitis macularia* is probably the most thoroughly studied bird species with sex-role reversal. In the population studied by Oring and co-workers (Oring, 1986; Oring and Lank, 1986; Oring et al., 1991a,b), males perform most of the incubation and care for the young. Females can lay up to five clutches in succession

for different males, whereas males never raise more than one clutch per season. Because most males incubate or care for broods, there is usually a strongly female-biased OSR. Detailed observations in the spotted sandpiper clearly corroborate predictions from sexual selection theory: females, which are the sex with the highest PRR, show a suite of behavioural adaptations that augment mating success in a competitive environment.

Contrary to the usual pattern among birds, female spotted sandpipers which are larger than males, are the first to arrive on the breeding grounds and they compete for multi-purpose territories to which they attempt to attract multiple mates. Older females succeed in attracting a greater number of males. Fights among females are often severe: 10% of the breeding females have visible injuries, some being crippled for life (Andersson, 1994; Maxson and Oring, 1980). Spotted sandpipers also differ from most other birds in showing female-biased philopatry, which may have to do with advantages of site familiarity for the sex that defends territories (Oring and Lank, 1982). The number of offspring produced by a female spotted sandpiper appears to increase markedly with her number of mates. Although one would expect the variance in female mating success to exceed that of males in polyandrous species, male spotted sandpipers had a higher coefficient of variation in reproductive success than females. This was because males were relatively more likely than females to produce no young.

In recent years, it has become increasingly clear that sexual competition does not always come to an end at mating (Andersson and Iwasa, 1996). It can continue in several forms, two important of which are infanticide and sperm competition. Infanticide refers to the killing of conspecific young (or destroying eggs). In species with 'traditional' sex roles, infanticide often occurs in polygynous mating systems where males compete for breeding opportunities with females. According to the hypothesis of sexually selected infanticide, the benefit gained from killing conspecific young (or destroying eggs) is increased access to reproductive partners that would otherwise be unavailable (Hrdy, 1979). This hypothesis would clearly gain additional support if in species in which sex roles are reversed, females would commit infanticide to maximize their reproductive success. Observations in two species of sex-role reversed, polyandrous jacanas, *Jacana spinosa* and *J. jacana*, in which females may kill dependent young in order to obtain males to mate with, are consistent with the above-mentioned hypothesis (Emlen et al., 1989; Stephens, 1982).

Recently there has been great interest in the frequency of extra-pair fertilizations in sex-role reversed, polyandrous bird species in which males perform most or all of the parental care. Theoretical models for the evolution of male uniparental care suggest that the parental male's confidence of paternity must be very high (Whittingham et al., 1992). Nevertheless, sperm competition is likely to be intense in polyandrous bird species in which a single female mates and provides clutches for multiple males. Males receive three possible risks to their paternity (see Emlen et al., 1998): (1) fertilizations by males outside the pair or female's group; (2) fertilizations by males previously mated to the female; (3) fertilizations by other males simultaneously paired to the same female (in case of simultaneously polyandrous species). Males in sex-role reversed species appear to have evolved several behaviours to reduce the risk of extra-pair paternity. These include the avoidance of pairing with females that have already been paired with a male earlier in the season, mate guarding, strategic timing of copulations, and possibly also clutch desertion when the risk of being cuckolded is high (Dale et al., 1999; Owens et al., 1995; Whitfield, 1990). In the bronze-winged jacana *Metopidius indicus*, a simultaneously polyandrous sex-role reversed bird in which the ratio of PRRs is skewed to females by about 4:1 (Butchart, 2000) and in which sperm competition is likely to be intense, males in polyandrous harems compete for sexual access to the female by giving a call, termed the 'yell', to attract her (Butchart et al., 1999). Males yelled at higher rates in larger harems, and when the female was further from the yeller or on a co-mate's territory. Males that yelled at the highest rate within polyandrous harems received the most copulations.

In agreement with theory, the reported values of the frequency of extra-pair fertilizations in five sex-role reversed species are considerably lower than those reported for the majority of socially monogamous species studied so far: they range from 0% in the Wilson's phalarope *Phalaropus wilsonia* (Delehanty et al., 1998) to 8.6% in the spotted sandpiper (Oring et al., 1992). Four out of five studied species are sequentially polyandrous sex-role reversed. Available evidence seems to suggest here that the major source of extra-pair fertilizations is sperm stored from previous mates. In the simultaneously polyandrous wattled jacana *Jacana jacana*, however, few if any fertilizations resulted from sperm stored from a previous mating. Here the risk of cuckoldry was strongly associated with the presence of available co-mates: it was 0% in monandrous pairings, rose to 41% of broods (17% of chicks) in polyandrous associations where an additional male was present, and increased to 74% of broods (29% of chicks) where the female was observed to copulate with multiple males (Emlen et al., 1998).

2.3.2. Endocrinological aspects of sex-role reversal

The endocrinology of sex-role reversal has been studied in detail in three bird species. As mentioned earlier, in most avian species, males are socially dominant and females share equally, or perform most, parental care. In these typical species, testosterone (T) levels of males exceed those of females, whereas prolactin levels during incubation are higher in females (Oring and Fivizzani, 1991). Although early work reported that elevated androgen levels were responsible for the sex-role reversed behaviour (Höhn and Cheng, 1967), more recent studies failed to confirm that females of sex-role reversed species have unusually high levels of T. In all three sex-role reversed species that have been studied in detail (spotted sandpiper, Wilson's and red-necked phalarope), T levels of males greatly exceeded those of females before incubation and males exhibited seasonal T profiles characteristic of monogamous passerine birds (Fivizzani and Oring, 1986; Fivizzani et al., 1986; Gratto-Trevor et al., 1990; Oring et al., 1988; Oring and Fivizzani, 1991; Rissman and Wingfield, 1984). High levels of intrasexual competition for mates among females appear not to be based upon a total reversal of the normal male/female levels of androgens. Although T levels in females do not rival those of males, relative changes in T between unpaired and paired females indicate that this hormone may play a role in mate acquisition and territoriality in sex-role reversed females: for instance, female spotted sandpipers sampled after pairing exhibited a 7-fold increase in T suggesting that the availability of receptive males has a positive impact on T levels of females (Fivizzani and Oring, 1986). In a recent study on sex-role reversed moorhens *Gallinula chloropus*, Eens and co-workers. (Eens et al., 1998, 2000, unpublished data) suggested that the aggressive behaviour of females is very likely related to their elevated T levels. In this species, females are more aggressive in winter flocks where mate choice is taking place and they are also more active than males in courtship (Petrie, 1983). They found that, in the period when most aggressive interactions occur, females have similar T levels as males. Furthermore, they observed that the heaviest females, which tend to win most of the competitive interactions (Petrie, 1983), had higher T levels than lighter females. Although the moorhen is probably the first sex-role reversed species in which both sexes have similar T levels, in general it appears that major changes occurring in the reproductive behaviour in sex-role reversed species do not appear to be accompanied by a radical reorganization of endocrine secretions (Ball, 1991). The lack of reversal of T, as well as other sex steroids, perhaps stems from the fact that these steroids have primary reproductive functions in development and maturation of germ cells and reproductive tracts (Oring and Fivizzani, 1991). The physiological basis for female aggression in sex-role reversed bird species is still largely unknown. It may be expressed independent of hormonal variation, or there may be non-gonadal endocrine influences. Alternatively, female aggressiveness may be due to enhanced neural sensitivity to normal female levels of gonadal steroids. This enhanced sensitivity could result from increased density of steroid receptors in neural cells, or by neural differences established during a critical pe-

riod of embryonic development (Oring and Fivizzani, 1991).

Whereas steroid hormones appear to follow the typical ancestral conditions in sex-role reversed species, levels of the hormone prolactin, a principal regulator of the onset and maintenance of incubation, are consistently lower in prelaying and laying females of both spotted sandpipers and Wilson's phalaropes than in males at the same stage of the nesting cycle (Oring et al., 1986, 1988). Prolactin thus clearly departs from the usual avian pattern in that it is higher in males than in females (Fivizzani et al., 1986; Ligon, 1999). Bunting et al. (1998) recently examined the distribution of prolactine binding sites in the brain of the sex-role reversed Wilson's phalarope and explored the question of whether binding of prolactine to receptors in specific regions of the central nervous system varies with sex or, in the case of males, with parental state. Overall, no striking quantitative or qualitative sex differences were apparent in the pattern of prolactine binding activity in the brain, despite the strong sexual dimorphism in parental duties in this sex-role reversed species. Nevertheless, a trend toward enhanced prolactine binding activity in the preoptic area and in the lateral septum was observed in males during incubation, a physiological state that is characterized by elevated plasma prolactine levels and an associated decrease in prolactine binding in most other brain regions. Based on work in other avian species, Bunting et al. (1998) predicted that an increase in prolactine sensitivity at these sites could facilitate the parental responsiveness and the gonadal suppression that accompanies this reproductive state.

Ligon (1997, 1999) recently suggested that in sex-role reversed coucals, males possess a unique gonadal condition that may proximately promote 'feminization' via a reduction by one-half of the primary source of T. A morphological trait possibly related to sex-role reversal in this group is asymmetry in size and development of the testes. In at least some species, the left testis is atrophied, rudimentary, or even absent. Ligon (1997) speculated that the loss of one functional testis has the effect of reducing the level of circulating

T relative to hormones important in nest building, incubation, etc. Thus, the absence of a functional testis may be causally related to the evolved sex-role reversal in coucals. Unfortunately, hormone levels have not been measured in any coucal species in order to be able to confirm this suggestion.

2.4. Mammals

Although in 25% of mammalian species females are larger than males and although females can be very aggressive in a variety of social situations, males are generally more aggressive than females (Monaghan and Glickman, 1992; Nelson, 1995). To the best of our knowledge, no clear case of sex-role reversal has been documented in mammals. Although spotted hyenas *Crocuta crocuta* present a unique syndrome of reversal in anatomical and behavioural distinction between the sexes (with females exhibiting remarkably masculinized external genitalia and being larger, more aggressive, and behaviourally dominant over males), females do not appear to compete for mates in this species (Frank, 1986, 1996, 1997; Drea et al., 1999).

3. Discussion

In this paper, we surveyed the occurrence of sex-role reversal in vertebrates, focusing in particular on behavioural aspects of sex-role reversal and on endocrinological correlates of this phenomenon. We did not pay attention to the reasons for sex-role reversal in the animals mentioned which are still obscure and debated (Andersson, 1994).

As mentioned earlier, the OSR is central in predicting the intensity of mating competition and which sex is competing for which (Kvarnemo and Ahnesjö, 1996). The initial role of parental investment in predicting sexual selection has recently been complemented by the use of sexual differences in PRRs. The concept of PRR has proven to be an extremely useful concept in determining courtship roles. In their review, Kvarnemo and Ahnesjö (1996) pointed out

that "thanks to recent theoretical and empirical advances, particularly by exploring the concept of OSR, sexual selection studies are becoming more fine-tuned and dynamic". Although typical sex roles can be attributed to most species, there are now several examples of species showing predominant male competition for mates in some populations but reversed sex roles (i.e. females being predominant competitors for mates) in others, or even switching of sex roles within a population over time (Kvarnemo and Ahnesjö, 1996). For instance, in the blennid fish *Salaria pavo*, in which males provide parental care in nests, males court females in most populations. However, the reverse is true in a population with a severe shortage of nest sites, where the OSR is biased towards females because all females are producing eggs but only a small proportion of the males acquire nests (Almada et al., 1995). Thus, sex-role reversal does not need to be a characteristic of a species. Species or populations may switch between exhibiting reversed sex roles and conventional sex roles if fluctuating ecological or physical factors affect PRRs of the two sexes differently, thus shifting OSR biases in space and time (Vincent et al., 1992).

Since the PRR has been advocated as a general measure for predicting the direction of mating competition (Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992), empirical measures of PRR have been very useful. In nearly all vertebrate species where sex-role reversal has been documented, females have higher PRRs than males. Furthermore, in several species which previously were thought to be sex-role reversed but do not appear to be so (such as seahorses and dendrobatic frogs), PRRs of females are lower than those of males. Vincent (1992) proposed that the assessment of PRRs in male and female teleost fishes (and probably in other vertebrate taxa as well) might reveal more examples of sex-role reversal and could contribute to the development of hitherto largely unformulated generalizations about sex differences. Masonjones and Lewis (2000) recently also suggested that fish provide a good model system to evaluate the value of estimates of PRR in predicting courtship roles, because they display

male care of offspring, estimates of parental investment are difficult and males are the predominant competitors for mates. Recent work suggests that apart from relative reproductive rates, sperm competition and quality variation among mates affect the strength of sexual selection (Simmons, 1995; Andersson and Iwasa, 1996).

After having successfully characterized the Bateman gradient in a sex-role reversed pipefish, Jones et al. (2000) suggested that the Bateman gradient surpasses some other important conceptualizations of the measurement of sexual selection in that it can be relatively easily quantified using molecular markers. They propose that future work should concentrate on a broad comparative analysis of Bateman gradients among populations and species. Jones et al. (2000) conclude that "among other factors, parental investment, the OSR and PRRs are certainly important to the process of sexual selection, but perhaps they should be seen as affecting sexual selection through their impact on the realized relationship between mating success and fertility, Bateman's true cause of sexual selection".

Although few studies have looked at hormonal correlates of sex-role reversed behaviour, a picture emerging at present is that reversal of sex roles is not often accompanied by a (dramatic) endocrinological reversal. Further work is however needed in this area. The study of sex-role reversed behaviour offers unique opportunities not only to test sexual selection theory, but also to enhance our understanding of the neuroendocrine mechanisms mediating behavioural sex differences.

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