

Sexual Dimorphism and Sex Reversal in Birds

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Abstract

The occurrence of plumage dimorphism of birds in Australia, Papua New Guinea, Peninsular Malaysia/Singapore, and Thailand was assessed from published data as being between 32-42 percent. This lies within the range noted in other areas of the world and suggests that tropical areas are not unique in the incidence of dichromatism. Incidents of reverse plumage dimorphism were noted where the male was less conspicuous than the female. Size dimorphism reversal, with the male being the smaller partner, was a feature noted in some birds outside the raptors. A detailed description of sex reversal in a peahen is recorded over a three year period, which resulted in the hen taking on almost indistinguishable male features. These data are supplemented by a review of the bases for sexual dimorphism, particularly plumage features.

Keywords: sexual dimorphism, sex reversal, oestrogen, testosterone levels

Introduction

Dimorphism is high among some bird families, such as in hummingbirds, birds of paradise, pheasants, grouse, manakins and pond ducks (Sibley 1957). Sexual dimorphism in birds is noted particularly in plumage and colouration but can extend to size, structure, and shape. The male is usually larger than the female, but reverse size dimorphism is well known among the raptors, jacanas, buttonquail, and berry pickers (*Melanochoris longicauda* and similar species)---(Swaddle, Karubian et al. 2000; Krüger 2005). Differences in behaviour do not fit well under the heading of sexual dimorphism, but they are frequently considered in an attempt to generate unifying concepts (Campbell and Lack 2013).

Sexual differences noted in plumage, eye, and cere colour are classically observed within the human visual range. When ultraviolet discrimination patterns are involved a majority of apparently monochromatic birds may appear as dichromatic (Eaton 2005). However, the majority of data available involves human visual perceptions. The occurrence of such dichromatism in regions varies with levels ranging from 32 to 39 percent (Wilson and Von Neumann 1972; Bailey 1978)---Europe (32 percent), North America (39 percent), and South America (35 & 39 percent). The concept that birds in the tropics are more susceptible to the development of dichromatism than those at higher latitudes is not supported by careful studies where confounding factors are removed, such as giving proper consideration to phylogenetic relationships and latitudinal range overlap (Bailey 1978; Cardillo 2002). The level of visible sexual dichromatism observed may also differ with geographical regions for the same species (Saino, Romano et al. 2013) and the contrast between male and female is greater at higher latitudes than at lower latitudes. In migratory birds elaborate plumage displays in females is restricted, ostensibly on account of the energy costs and predation risks involved (Bailey 1978; Simpson 2012).

Where dimorphism is under genetic control (ZZ in males and ZW in females), the birds show dimorphism all year long. The removal of testes or ovaries (or adding testosterone or oestrogen) has no effect on the plumage displayed (e.g., sparrow, bowerbirds, birds of paradise). Another possibility is that plumage dimorphism is displayed particularly during the breeding season. In such instances, the default position in both females and males is to develop a showy plumage. However, in females such plumage is not formed on account of the production of oestrogen, making plumage display oestrogen dependent. It is also possible for plumage dimorphism to involve interactions between genetic and hormonal factors in some species (Owens and Short 1995).

In the ruff (*Philomachus pugnans*---a wading bird across northern Eurasia) raising testosterone levels is involved in the development of male breeding plumage. Here the ornamental feathers around the neck (ruff) will develop in response to testosterone injection in females and fail to develop in castrated males (Owens and Short 1995; Lank, Coupe et al. 1999). Testosterone appears also to be involved in the Phalaropes (e.g., Wilson's phalarope---*Phalaropus tricolor*---a wading bird in the Americas), which show reversed sex roles with the females being brightly coloured and the males dull. The skin of female birds is more able to produce an active metabolite from testosterone than the males, hence accounting for the bright plumage developed. The superb blue wren (*Malurus cyaneus*---Australia) may fit into the testosterone-dependent category as well. These males display a dull as well as a bright plumage. Supplementing testosterone levels may induce a moult and lead to the formation of brightly coloured feathers.

Selected weaver and warbler birds, found primarily in North America, respond to rising luteinizing hormone (pituitary origin) levels rather than either oestrogen or androgens (Kimball 2006; Bókony, Garamszegi et al. 2008). These accounts leave us with the obvious conclusion that a great deal is still to be

discovered about factors influencing sexual dimorphism.

Secondary sexual characters (combs, wattles, spurs) have been associated usually with testosterone levels, although there are some exceptions such as among the mallards (Keck 1934; Kimball 2006). Where bill pigmentation patterns differ between the sexes, particularly during the breeding season, the feature appears usually to be testosterone dependent. This is observed, for example, in the masked weaver (*Quelea quelea*---Africa) and the paradise whydah (*Vidua paradisaea* or *Steganura paradisaea*---Africa) (Owens and Short 1995). The intensity of the pigmentation shown in the bare integument found between the ocular ring and lores is associated with circulating carotenoid pigments in the plasma. It is suggested that testosterone influences the bioavailability of these pigments in the red-legged partridge, *Alectoris rufa* (European bird, but introduced to various countries) (Blas, Pérez-Rodríguez et al. 2006).

Besides plumage differentiation, there are differences in the occurrence of and/or the form and frequency of singing and aggressive behaviour found between the sexes as a result of elevated levels of testosterone (Adkins-Regan 1999; Ketterson, Nolan Jr et al. 2005).

In rare instances females birds may be transformed so that male plumage and other characteristics develop. This phenomenon is often associated with age, but has been observed in partridge about a year old, which showed a partial male plumage. This state was associated with the presence of a diseased reproductive system. Irrespective of age, interference with ovarian function is correlated with the appearance of masculinized plumage. Multiple causes for such a change are possible (Forbes 1947; Fadly 2008).

Sex-reversal typically is recorded in domesticated, aviary, and zoo birds. In a number of bird genera sex reversal has been observed. This includes domestic fowl (*G. gallus domesticus*), mallard (*Anas boschas*), partridge (*Perdix cinerea*), peahen (*Pavo spp.*), pheasant

(*Phasianus spp.*), pidgeon (*Columba livia*), turkey (*Meleagris sp.*), widgeon (*Anas penelope*), scaup (*Aythya marila*), scoter (*Melanitta nigra*), merganser (*Mergus serrator*), wood grouse (*Tetrao urogallus*), and others (Forbes 1947). In many breeds of birds, removal of the ovary from the female, by surgical means or pathological processes, will lead to the development of some male characteristics, for the rudimentary right gonad begins to differentiate in the absence of oestrogen. This can lead to the secretion of androgens and the development of male characteristics. The extent and permanency of male characteristics will be determined by the degree of reduction in ovary tissues (Domm 1924; Chalmers 1986; Thorne 1997).

In this study, we have estimated the incidence of sexual dimorphism in a number of countries and describe the phenomenon of sex reversal in detail in a blue female peahen with a long history of successful mating and raising young. The female took on male characteristics with aging, which was just one season after her last successful hatching. These data are discussed in relation to other published information.

Study Area and Methods

The incidence of sexual dimorphism was estimated in five countries (Australia, Peninsular Malaysia/Singapore, Papua New Guinea and Thailand by analysing data from published accounts assembled by professional ornithologists (Frith 1977; Coates 1985; Lekagul and Round 1991; Jeyarajasingam and Pearson 2012). Birds showing sexual differentiation in the breeding season or on a continuous basis were assessed as being dimorphic to human vision.

An incidence of sex reversal in peahen is documented. The study area was located at Deuchar, Queensland. Our case report involved a blue female peahen (*Pavo cristatus*) with a long history of successful breeding and with typical plumage. The hen was observed over three years (2007-2010) by the senior author, which was from the time when plumage change

was noted until the death of the bird. The bird had enjoyed a long history of successful breeding, had raised young, and was treated routinely as a female by the resident males.

Results

Findings on the survey of sexual dimorphism in Australian, Papua New Guinean and Southeast Asian birds are presented together with the account of sex reversal in a peahen.

Sexual dimorphism

In Australian and Malaysian/Singaporean birds reasonably obvious plumage dimorphism was noted in 32 percent of species, in 39 percent of species in Papua New Guinea, and in 42 percent of species in Thailand. In Australia, kingfishers (family Alcedinidae), long-tailed parrots (family Polytelitidae), weavers and allies (family Ploceidae), and wrens (family Maluridae) showed a high proportion of sexually differentiated species compared to other families. In Malaysia and Singapore parrots and allies (family Psittacidae), pigeons (family Columbidae), trogons (family Trogonidae), cuckoo shrikes (family Campephagidae), old world orioles and allies (family Oriolidae), thrushes (family Turdidae), and old world flycatchers (family Muscicapidae) showed the greatest plumage dimorphism. In Papua New Guinea, a high level of differentiation was noted again among the parrots and cuckoo shrikes and their allies, kingfishers (family Alcedinidae), monarch flycatchers (family Monarchidae), whistlers, pitohius and allies (family Pachycephalidae), longbills and berrypickers (family Melanocharctidae), and especially among the bowerbirds (family Ptilonorhynchidae) and birds of paradise (family Paradisaeidae). In Thailand, sexual dichromatism during the breeding season was noted among a large number of shorebirds such as herons (family Ardeidae), plovers (family Charadriidae), sandpipers (family Scolopacidae), gulls and terns (family Laridae). A high degree of continuous differentiation

was noted again among parrots, pigeons, trogons, cuckoo shrikes, thrushes, and old world flycatchers. In addition to these families, ducks (family Anatidae), pheasants (family Phasianidae), woodpeckers (family Picidae), and sunbirds (family Nectariniidae) also showed a high proportion of sexually differentiated species compared to other families.

The male of the species is usually the larger and the more showy sex, but some species displayed a spectacular reverse sexual dichromatism. This is noted in a convincing fashion in the plumage of the eclectus parrot (*Eclectus roratus*---family Psittacidae; found in Australia, Papua New Guinea, Moluccas and selected Pacific islands). The male has a brilliant green plumage whereas the female displays mainly bright red feathers, with purple to blue highlights. In Papua New Guinea the black fantail (*Rhipidura atra*---family Rhipiduridae) and some monarch flycatchers (e.g., *Myiagra alecto*, *M. hebetior*---family Monarchidae) show differentiation in the female to display rich rusty or rufous feathers and other ornaments in contrast to mainly black plumage in the male. The plumage in the red necked phalarope (*Phalaropus lobatus*---family Scolopacidae; found from the arctic to the tropics) is a duller colour in the male than the female.

Reversed size differentiation was noted in some species in the areas surveyed. Here the female was larger than the male. This was noted particularly among the smaller raptors (e.g., *Accipiter nisus*, *Accipiter badius*, *Accipiter virgatus*, *Falco berigora*, *Phalaropus lobatus*), but is found in the barred and red backed buttonquail (*Turnix suscitator*, *T. maculosa* respectively), berry picker (*Melanochoris longicauda* and similar species), and comb crested jacana (*Irediparra gallinacea*).

Sex reversal

The peahen studied began to develop male characteristics at about 23 years of age. The hen showed her first male feather complete with the typical spectacular 'eye' pattern on the tail feathers during the

breeding season (September to January). This unusual development of male characteristics occurred about 12 months after her last successful hatching. As time passed, more male feathers developed and twelve months after the first display of such feathers, she had developed a full set or plume of tail feathers (train). However, these were about half the length of a fully grown male train. Despite this outward appearance of maleness, a white male peacock cohabiting with her for a season treated her as a female preferring to direct his aggression towards other males in adjoining pens.

The peahen continued to display male characteristics (Fig. 1) for a total of three years until she died. As time passed, the train of feathers increased in length until they were about three quarters the length of a typical fully developed male's train (juvenile males take about three years to develop a full train). The transformed peahen did raise the train to create a visual display but not as frequently as a regular male. Peahens have a dull brown crest, as did the peahen which eventually took on male characteristics. In the transformed hen, the crest developed the rich blue colour typical of cocks. She also developed spurs of equivalent length to that of a typical male. Her voice was rather hoarse and not typically male.



Figure 1. Plumage characteristics of the transformed peahen close to the time of death. Background details were eliminated by using Photoshop. Other details were not altered or enhanced.

The most prominent differences shown in the transformed female to a typical cock involved the wing feather patterning and the size of the white feather zone on the face. The brown colouration on the wing feathers was paler than in cocks, making the patterning less prominent. The zone of white feathers on the face was broader, particularly underneath the eye and sweeping towards the ear. To the uninitiated, the bird's visual appearance was almost indistinguishable from that of a typical male. No autopsy was possible on the bird following death. Her genotype was assumed to be ZW on account of her successful breeding until four years before her death and one year before the sex reversal changes began to appear. One of her daughters is now showing sex reversal changes (commenced September 2015) and seven months later has a half developed male display tail.

The transformations observed were the first cases noted in over 40 years of experience by the senior author with breeding and keeping peafowl.

Discussion

The occurrence of visible dichromatism in the tropical regions surveyed was 32-42 percent; the level recorded was no doubt influenced by the discriminating parameters chosen by the observers. Comparative studies in other areas were in the range 32 to 39 percent (Wilson and Von Neumann 1972; Bailey 1978). The idea that birds in the tropics are more susceptible to the development of dichromatism was not supported by our data, in agreement with the observations of others (Bailey 1978; Cardillo 2002).

Colour differentiation classically is thought to give males a competitive advantage, which is an explanation that appears to account for the marked differentiation noted in birds at higher latitudes. The drabness displayed by females generally is considered to function to protect birds during nesting (Simpson 2012). However, this is not a consistent finding, for phenotypic traits are not consistently related to sexually dimorphic traits

(Huang and Rabosky 2015). An added difficulty is that what the birds perceive differs from that observed by humans. This means that explanations regarding the ecological significance of colour differentiation will continue to be expanded.

Phenotypic sex in vertebrates is influenced by both genes and the environment. In birds the sex determination is based on a ZZ/ZW system. In genetic males (ZZ), two testes develop, whereas in genetic females (ZW) the left gonad develops into an ovary whereas the right gonad remains in a rudimentary state (Thorne 1997).

Sex reversal is related to the health and effectiveness of the left gonad. In fact, even at four days development of the left ovary is favoured in chicks destined to be hens. The right gonad does not develop and is reduced to a vestige, which remains attached to the cloaca. In the rooster, both gonads develop (Frankenhuis and Kappert 1980). If the left ovary is destroyed either surgically, through disease, or is reduced due to senile processes this can lead to the growth of the right gonad into a testis or ovo-testis. Usually the growth of the ova-testis tissues does not permit spermatogenesis, but there is one recorded case of such an event. In this instance, an adult hen that had laid eggs was subsequently able to fertilize eggs (Chalmers 1986; Fadly 2008). When resort to experimental transplantation is attempted, then spermatogenesis might be anticipated. For example, when the right gonad of the domestic fowl (*G. gallus*) was introduced into a capon (castrated male), the animal developed sperm and these, when harvested directly from the gland and used to inseminate normal hens, led to fertilization and the development of normal pullets and cockerels (Frankenhuis and Kappert 1980). The implantation of embryonic testes into incubating eggs similarly led to change of female chick embryos into males with all the characteristic features except feather colour (Rashedi, Maraud et al. 1983). Such sex reversals remain permanent (van Krey 2003).

Transformation of females into birds with male characteristics in nature is often associated with age, as observed in our peahens. Irrespective of age, interference with ovarian function is correlated with the appearance of masculinized plumage. Multiple causes for such a change are possible (Forbes 1947; Fadly 2008). However, at the fundamental level, it is the cessation of oestrogen production and the expression of underlying biochemical phenomena determined by the genotype that accounts for the plumage displayed (Owens and Short 1995).

Conclusions

The sexual dichromatism noted in Thai birds corresponded with general expectations from reports made elsewhere in the tropics. There were differences among the countries surveyed in the families showing the highest proportion of dichromatic members. Not surprisingly, Thailand showed greater similarities to trends among the avifauna in Malaysia/Singapore than in Papua New Guinea and Australia. Plumage dimorphism was commonly observed among the families Campephagidae, Columbidae, Muscicapidae, Trogonidae, and Turdidae in the former territories. Papua New Guinea showed spectacular dichromatism among bowerbirds (family Ptilonorhynchidae) and birds of paradise (family Paradisaeidae). Reversed size and plumage dimorphism was noted among a small proportion of birds in all territories surveyed; no surprise elements occurred. Explanation for plumage differentiation among species acknowledged the role of oestrogen, testosterone, and luteinizing hormone. This information was used to explain sex reversal noted in peahens. Much exploratory work remains to be completed in understanding dichromatism and its significance in the natural world.

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