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Short Review

Recent studies of avian sex ratios

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Sex allocation theory, and its success in predicting sex ratios in such taxa as parasitoid wasps, is often cited as one of the crowning achievements of theoretical evolutionary biology. Its success in some vertebrate taxa, particularly birds, has been more modest. I discuss two reasons for this. First, it is difficult to obtain avian sex ratio data before substantial offspring mortality has occurred. Second, the theory and data required to predict sex allocation patterns (let alone sex ratio patterns) in vertebrates are complex and hard to obtain. Recently developed molecular genetic techniques allowing sex identification from DNA samples have largely solved the first problem and there have been several striking empirical demonstrations of sex ratio biases consistent with sex allocation theory in wild bird populations. Solution of the second problem may come with the incorporation of realistic life history data into models and the use of experimental manipulations to reveal the fitness consequences of allocation strategies. Further data concerning sex ratio variation in taxa such as birds, with chromosomal sex determination, are valuable because they allow the investigation of the role of constraint vs. adaptation in evolution.

Keywords: natural selection, sex allocation, sex identification, sex ratio, sexual selection.

Separate sexes are associated with sex-differences in life histories. A consequence of this is that selection acts differently in the two sexes, which can change the relative reproductive value of each sex of offspring. As a result individuals are selected to vary their allocation of resources between the sexes. Major contributions to sex allocation theory were made by Fisher (1930), Hamilton (1967) and Charnov (1982). Three broad classes of process can be expected to influence the optimal sex allocation by parents: differential costs, conditional sex allocation and structured populations (recently reviewed by Hardy, 1997). The success of sex allocation theory in predicting patterns of sex allocation in nature has, in some cases, been extraordinary. Thus, sex allocation theory is able to predict with considerable accuracy the proportion of female eggs that a female parasitoid wasp should lay, dependent on both host size and the number of females that have already laid in a given host (reviewed by Godfray, 1994); the rate of outcrossing of malarial parasites from the sex ratio of gametocytes measured from blood smears of infected hosts (Read *et al.*, 1995); and the timing of sex reversal in marine shrimps on the basis of changes in population structure (Charnov, 1982). It is not surprising that sex allocation theory is often cited in textbooks as one of the most successful areas of theoretical evolutionary biology (e.g. Ridley, 1993).

If one were to restrict an assessment of the predictive success of sex allocation theory to vertebrate taxa with chromosomal sex determination, particularly birds, the verdict would be less favourable. Few studies have been able to make and test quantitative predictions and there is also a paucity of studies showing even minor skews in sex ratio in directions consistent with expectations from theory. Williams (1979) concluded famously, that the best data from birds ‘give no support to any theory of adaptive sex ratio evolution’ and suggested that this reflected a constraint imposed by the Mendelian process of meiosis. Although evidence to support the existence of adaptive sex ratio skews has since been obtained from outcrossed bird and mammal populations, such patterns do not seem to be very common. In this review I describe some recent studies of sex ratio variation in birds, and discuss some ways in which this field may develop. Although this review describes data that are relevant to the theory of sex *allocation*, most of the studies described here have addressed the sex *ratio*. Sex allocation is the quantity on which selection acts, whereas the sex ratio merely describes the relative numbers of sons and daughters; the two need not be equivalent. Unfortunately, the sex ratio is far easier to measure than is sex allocation. For the remainder of this review I assume, as have most studies, that the sex ratio reflects sex allocation. Further, I address only studies relating to adaptive sex allocation at the level of the individual family. Population level patterns of sex allocation are interesting in their own right (Clutton-Brock, 1986), but most recent studies have not been concerned with the population sex ratio, and few have involved samples large enough to detect any but the largest deviations from equality with much power.

I have nothing to say about the genetics of sex ratio variation in birds in this review, other than to repeat the often-noted conclusion (based on selection experiments with poultry) that there is no evidence for any such variation, nor any evidence for the operation of non-Mendelian sex ratio distorters as found more often in invertebrates (Hardy,

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1997). The theories of adaptive sex allocation described below are silent about whether genetic variation for the sex ratio should be present in contemporary populations.

New techniques for sex identification

Although the adults of many bird species show conspicuous sexual dimorphism in either size or colour, this dimorphism is often reduced or absent among juveniles. For most birds, the proportion of marked juveniles which are recaptured as adults is less than 10 per cent, so that it is usually hopeless to expect sex ratios measured among adults to reveal biases in sex ratio among families. Although some species of birds which exhibit marked sexual size dimorphism (e.g. members of the family Icteridae) can be readily sexed as nestlings on the basis of body size before fledging, these species cannot easily be used to test theories of adaptive sex allocation because sexual size dimorphism is probably correlated with sex differences in mortality (Clutton-Brock *et al.*, 1985). Thus, environmentally caused sex-biased mortality can generate a correlation between environmental quality and sex ratio of the same sign as that expected were parents to adjust sex ratios adaptively. Also, sex cannot be determined for very small nestlings, or nestlings which die before hatching, so that it is difficult to know whether a biased sex ratio reflects biased production or mortality. A reliable means to identify sex at all developmental stages is required in order for sex ratio variation to be described accurately.

Birds, like mammals, have separate sex chromosomes (females ZW, males ZZ), and this makes the isolation of sex-specific genetic markers possible. Although sex-specific genetic markers have occasionally been discovered fortuitously (for example while probing southern blots of genomic DNA with minisatellite sequences), a major step in the development of simple molecular identification techniques was taken with Griffiths & Tiwari's (1993) description of a method, based on randomly primed PCR, for isolating sex-linked markers. Recent developments have involved the characterization of a pair of highly conserved Z and W-linked genes (*CHD1-Z* and *CHD1-W*), for which locus-specific primers are now available, that can determine sex for almost all birds (Griffiths & Tiwari, 1995; Griffiths *et al.*, 1996; Ellegren & Sheldon, 1997). Markers of this type have been used in a growing number of studies of avian sex ratios, often involving retrospective analysis of sex ratio variation in samples originally collected for other purposes (e.g. DNA fingerprinting). A few other recent studies have used a different type of DNA-based sexing technique, flow-cytometry, that detects the difference in nuclear DNA content due to difference in sex chromosomes. The difficulty of determining sex, which handicapped earlier studies of sex allocation, has been effectively removed by the development of these techniques.

Sex allocation theory applied to birds

A comprehensive treatment of sex allocation theory, and its application to birds and mammals is presented by Frank (1990). I mention briefly here two conclusions drawn by Frank, but not always heeded by studies of avian sex allocation. First, if there is selection for biased sex allocation at the family level, then equal allocation at the population level is no longer evolutionarily stable. Second, it is unlikely that studying just the variance in family sex ratios will reveal anything of interest about adaptation.

Some specific characteristics of avian life histories have consequences for predicting sex allocation. For example, the simplest model of sex allocation when fitness varies assumes that the degree of bias in sex allocation is independent of the reproductive value of the clutch (Bull, 1981; Charnov, 1982). If this is the case, the optimum sex ratio is a step function with a threshold at which a switch from production of one sex to the other should occur (Fig. 1). While this assumption may be broadly true for hymenoptera where a female can potentially 'determine' offspring sex by deciding whether to fertilize each egg, it may not be true for birds. If birds are constrained by meiosis to produce an equal sex ratio, sex allocation could only be modified by selectively favouring one sex of offspring over the other, and the sex ratio could only be altered by killing more offspring of one sex. Since such actions would reduce the reproductive value of the clutch, the optimal sex allocation pattern will show a gradual response to variation in the variable with differential effects on fitness. The costs of sex allocation in organisms with chromosomal sex determination (CSD) may therefore be one explanation of why sex ratio biases tend to be weaker than in organisms with more labile sex determination mechanisms. The assumption that CSD is a constraint tends to be made more by default than in response to evidence to this effect. Determining the mechanism(s) by which sex allocation occurs in birds is important because this information suggests how sex allocation theory should be applied.

One further factor with potential influence on sex allocation strategies concerns the extent to which parents are able to estimate the value of any variable with sex-specific effects on offspring fitness at the time when offspring sex is deter-

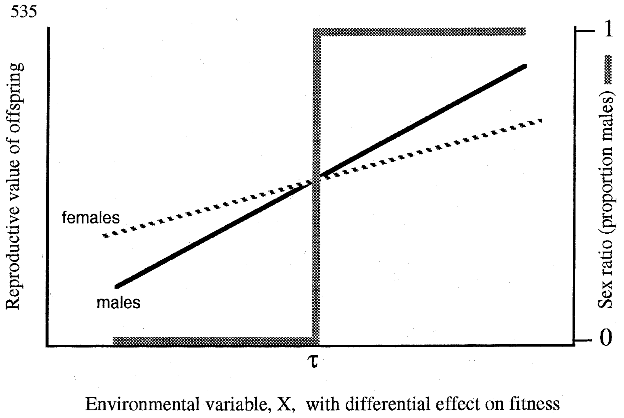

Fig. 1 A simple model for biased sex allocation (after Bull, 1981; Charnov, 1982). In this case the ESS sex ratio is for only females to be produced for any values of $X < \tau$ and only males to be produced for any values of $X > \tau$, where τ is the threshold value of X at which the reproductive value of sons and daughters is equal.

mined. In the simplest 'parasitoid' case, the size of a host, and hence the relative effect of host size on fecundity of sons and daughters, may be quite accurately estimated by an ovipositing female. In contrast, if a female bird is trying to produce the optimum sex ratio in response to food availability several weeks or months in the future, or in response to the additive genetic component of a mate's sexual ornament, the likelihood of estimating these parameters correctly will probably be much lower. The increased likelihood of error in estimating fitness-related variables will have the effect of selecting for bet-hedging (Gillespie, 1977) in sex allocation strategies: fewer extreme family sex ratios would then be expected (Charnov, 1982).

Realistic models of sex allocation strategies in vertebrates can be constructed, despite the difficulties outlined above (Leimar, 1996). They require quite detailed knowledge of fitness functions for both parents and offspring of both sexes. Such data are available for some exceptionally well studied vertebrate populations. An alternative means of generating them is to combine experimental manipulations with measurements of sex-specific responses (e.g. Lessells *et al.*, 1996; Sheldon *et al.*, 1998).

Recent empirical studies

Although Burley (1981) showed that captive zebra finch *Taeniopygia guttata* sex ratios were modified in response to both male and female attractiveness determined by different coloured plastic rings, it seems that her work was not very widely accepted. Perhaps the combination of sex ratio skews in response to both male and female attractiveness, with the fact that the response was to an artificial ornament, was too much to accept given scepticism about the existence of adaptive biases in sex ratios at that time. There were few studies of sex ratio variation in birds which supported adaptive sex allocation until Dijkstra *et al.* (1990) showed that the brood sex ratios of European kestrels *Falco tinnunculus* varied systematically with hatching date. Kestrel sex ratio variation was apparently adaptive, since the reproductive value of male and female nestlings was differentially affected by hatching date. These early studies have been backed up by further reports of skews in family sex ratios that are also consistent with adaptive sex allocation (although adaptiveness has only been assessed in rather general terms). These studies are united by their reliance on the core theory that differences in reproductive value of the sexes cause selection for variable sex allocation. An exhaustive listing is beyond the scope of this review, so here I describe briefly a few representative studies, which should serve as an indication of the richness of patterns of avian sex ratio variation.

(i) Sex ratio variation in relation to the external environment

It is easy to see how the basic model applies if the sexes of offspring differ in body size and there is variation in food availability in the environment. Many species of birds face predictable environmental variation in food availability as food supply usually declines over the course of the breeding season. This results in a corresponding change in the relative reproductive value of the two sexes. Intuitively, the reproductive value of the larger sex is expected to decline more steeply as food becomes scarcer.

Appleby *et al.* (1997) showed that the primary sex ratio within broods of tawny owls *Strix aluco* was related to vole densities (which show large-scale temporal and spatial variation) on breeding territories: females (the larger sex) were overproduced on territories with high vole densities. They were also able to show that the reproductive success of female owls was positively related to the density of voles on the territory of their parents when the females were reared, while male reproductive success was unaffected by vole density they had experienced as a nestling, thus supporting the contention that the sex ratio variation was adaptive. Daan *et al.* (1996) examined the relationship between timing of breeding and the sex ratio close to fledging produced by five species of diurnal raptors. In three of the species (goshawk *Accipiter gentilis*, sparrowhawk *A. nisus* and marsh harrier *Circus aeruginosus*) the sex ratio was increasingly male-biased the later the clutch was laid, whereas in two species of falcons (European kestrel and lesser kestrel *Falco naumanni*) sex ratios became increasingly female-biased as laying date increased. They argued that the different patterns resulted from differing life-histories followed by the two groups of species. Males of the two falcon species regularly breed in their first year, and empirical data for one species show that a male's probability of doing so decreases the later it is born, while this probability is independent of birth date for females. In the three larger species, females are more likely to breed in their first year than are males. Computer simulations using data from the one species with good estimates of the relevant parameters predicted a seasonal pattern of sex ratio decline close to that observed in nature, supporting the authors' suggestion that the patterns were likely to represent adaptive sex allocation.

(ii) Sex ratio variation in relation to the social environment

In a small proportion of bird species young from previous breeding attempts may remain on their natal territories and assist their parents in rearing future siblings. This, coupled with a sex-bias in dispersal (females are usually the dispersive sex), and hence a sex-bias in helping behaviour, changes the relative reproductive value of male and female offspring to parents. In effect, because one sex remains and helps with rearing their siblings, they 'repay' part of the cost of the parental care that they received (Emlen *et al.*, 1986). In general, this hypothesis suggests that populations of co-operative breeders should overproduce the helping sex, and there is some evidence for biases of this kind (e.g. Gowaty & Lennartz, 1985). However, biases in sex allocation could be much more subtle than this: each breeding pair may have different optima depending upon whether they already have some helping offspring (the effect of helpers on fitness is likely to be a function with diminishing returns; helpers may even have a net cost if they use scarce resources on a territory), and the ability of their territory to support extra adults.

Komdeur *et al.* (1997) have demonstrated remarkably strong among-family biases in the nestling sex ratio of the Seychelles warbler *Acrocephalus sechellensis* along these lines. When the habitat is saturated with breeding pairs, helping (usually by daughters) is frequent because offspring have few opportunities to disperse. Daughters which help are costly to parents inhabiting poor territories, probably because they deplete insect prey. Komdeur *et al.* (1997) found that breeding pairs produced only 13 per cent sons when breeding on high quality territories, but 77 per cent sons while breeding on a low quality territory: hence the direction of sex ratio biasing was as expected. Experimental manipulations which caused pairs to change territory quality resulted in corresponding changes in sex ratio. The sex ratios were obtained from DNA samples taken from small nestlings, and it could be shown that the sex ratio biases must have been present at oviposition. There are, as yet, no other studies of related phenomena, and Komdeur *et al.*'s study is also exceptional because of the relatively extreme nature of the sex ratio biases observed.

(iii) Sex ratio variation in relation to parental quality

Trivers & Willard (1973) pointed out that the environment that parents provide for their offspring can affect their reproductive value differentially, and thus cause selection for variable sex allocation. Although this suggestion has been applied most often to the idea that mothers may transmit something of their physical condition to offspring during parental care, it can apply to any quality which parents transmit to offspring. For example, if male reproductive success is related to the size of a secondary sexual character, then it is likely that the sons of males with large sexual ornaments will be of higher reproductive value than the daughters of such males. The reverse applies for the offspring of males with small sexual ornaments.

Evidence that offspring sex ratios may be adjusted in response to characteristics of their father has been obtained from two studies of passerine birds. Ellegren *et al.* (1996) investigated sex ratio variation in relation to the size of the white forehead patch of male collared flycatchers *Ficedula albicollis*. This trait is known to be heritable and under directional selection due to female preference (Sheldon *et al.*, 1997). As expected, brood sex ratios were male-biased when the male rearing the brood had a large forehead patch. Brood sex ratio was also, as expected, related to prior experimental manipulations of male reproductive effort (which affect forehead patch size of males). No such relationship was observed for females (Ellegren *et al.*, 1996). Other work on this species has shown that male flycatchers with large forehead patches tend to father extra-pair young in the nests of males with smaller forehead patches (Sheldon *et al.*, 1997). As a consequence, it would presumably be adaptive for females to skew the sex ratio of extra-pair offspring in favour of males, since they inherit genes for large forehead patches. Sheldon & Ellegren (1996) found no evidence for such a tendency; nor did Westerdahl *et al.* (1997) in a study of great reed warblers *Acrocephalus arundinaceus*, or Westneat *et al.* (1995) in a study of red-winged blackbirds *Agelaius phoeniceus*. This may reflect an absence of female ability to control the sex ratio of extra-pair offspring (Sheldon & Ellegren, 1996). Although Svensson & Nilsson (1996) also report a correlation between male quality and offspring sex ratio, not all recent studies have found such a relationship. Westerdahl *et al.* (1997) found no correlation between song repertoire size and sex ratio in a large population of great reed warblers, although it seems reasonable to have expected such a correlation.

Mechanisms for adjusting sex allocation

Apart from being interesting in its own right, the range of mechanisms by which sex allocation can be varied in birds has implications for which parts of sex allocation theory should be applied. Very little is known about which of several potential mechanisms to adjust sex ratios actually operate in birds (Krackow, 1995), but there are potentially many mechanisms due to the prolonged parental care found in birds.

The use of molecular sexing techniques to sex offspring even before hatching (e.g. Lessells *et al.*, 1996) has meant that several studies have been able to determine the primary sex ratio with enough accuracy to rule out selective mortality as a cause of biased sex ratios (Lessells *et al.*, 1996; Appleby *et al.*, 1997; Komdeur *et al.*, 1997). Hence, the sex ratio biases demonstrated in these studies must have been present at oviposition. Some authors have therefore suggested that female birds may, by an unknown mechanism, be able to control segregation of the sex chromosomes during meiosis (Dijkstra *et al.*, 1990; Ellegren *et al.*, 1996; Lessells *et al.*, 1996).

However, Emlen (1997) has pointed out that a sex ratio bias at oviposition might also arise from selective resorption, or dump-laying, of ova of the 'wrong' sex. Because the sex of an egg is not determined until the final meiotic division, which occurs only hours before ovulation, this would result in delays in breeding or gaps in laying sequences; the occurrence of such gaps does not suggest they result from sex ratio skewing. Another possibility suggested by Emlen (1997), is waiting until an egg of the 'right' sex is ovulated before beginning the clutch, but then relying on the 'meiotic luck-of-the-draw'. This is appealing because it provides an explanation for the extreme patterns of sex ratio bias observed by Komdeur *et al.* (1997): the warblers in this study have a median clutch size of just one egg. If this is the main mechanism by which sex ratios are adjusted in birds, then across species there should be a negative relationship between clutch size and degree of sex ratio skew: those species that lay large clutches will have very little scope for adjusting the sex ratio of their offspring. In fact, quite strong skews in sex ratio have been observed in two species of tit with mean clutch size as large as 8.4 and 11.0 eggs (Lessells *et al.*, 1996; Svensson & Nilsson, 1996, respectively).

There are three recent studies which suggest that the sex ratio is not always subject to a Mendelian lottery. Heinsohn *et al.* (1997) presented data concerning the sex ratio in successive broods of a small number of captive breeding female *Eclectus* parrots. Although the 'population' sex ratio did not differ from equality, females tended to produce very long runs of nestlings of the same sex (up to 20 same-sexed offspring in succession). In addition, in broods where both nestlings survived (clutch size is almost invariably two), there were many fewer mixed-sex broods than expected. Heinsohn *et al.* were able to show that a large part of the bias must have been present at oviposition. There is no evidence that the patterns observed reflect adaptive biases in sex allocation, nor is it easy to imagine why such biases should be so extreme, but the data do suggest that the female parrots have a remarkable degree of control over the sex ratio of their offspring.

Anderson *et al.* (1997) reported data on the relationship between egg size, sex and subsequent growth in broods of American kestrels *Falco sparverius*, a species with quite marked sexual size dimorphism (females 17 per cent larger than males). They suggest that females attempt to reduce the disadvantage of smaller sons in sibling competition by increasing the size of male eggs relative to female eggs. Consistent with this, they showed that males hatched from larger eggs than did females and that egg size affected growth and dominance throughout the nestling period. As in other birds, eggs are ovulated and fertilized sequentially, and yolk size determined before fertilization, while the albumen (= white) and shell are deposited round the egg as it passes down the oviduct. The short time involved in determination of egg size suggests either a surprising degree of linkage between a female's ability to determine the sex of an egg and her ability to control the size of that egg, or that females are able to influence the sex of the egg in order for it to match its size.

Finally, Kilner (1998) has shown that there are clear associations between ovulation order and sex ratio of zebra finch eggs and that the primary sex ratio can be modified by experimentally varying food availability. These data again suggest control of meiosis. Elucidating whether female birds really can influence the outcome of meiosis in developing ova is something which will probably require the development of a good laboratory model, with strong sex ratio skews. Kilner's (1998) work suggests that zebra finches might provide such a model.

Extensive parental care, often by both parents, characterizes birds, and increases the scope for biased sex allocation without changing the sex ratio. Such effects have not been studied much, although there are demonstrations that both sexes of parents feed the larger sex more frequently in sexually size-dimorphic species such as Icterids (e.g. Westneat *et al.*, 1995), and Nishiumi *et al.* (1996) found that male great reed warblers fed male-biased broods at a higher rate. An important step in studies of this kind is Lessells *et al.*'s (1996) demonstration that it is possible to perform experimental manipulations of brood sex ratios within days of hatching. Lessells *et al.* studied the effects of brood sex ratios on parental behaviour of great tits by creating experimental broods that were either all male, all female or approximately half male. Their experiments did not provide any evidence for an effect of brood sex ratio on any aspect of parental behaviour. Nevertheless experimental manipulations of this kind are very important because they open the possibility of investigating the influence of sex ratio on parent and offspring fitness free of the influence of other variables which might be confounded with sex ratio (for example breeding date in the case of great tits; Lessells *et al.*, 1996). They also offer the chance to measure the relative costs of rearing differently sexed offspring, something which had not previously been amenable to measurement. Sex-biases in parental behaviour are unsurprising in sexually size dimorphic species; perhaps more surprisingly they can also be evolutionarily stable in other systems (C.M. Lessells, personal communication), in which case the question of under what conditions offspring should signal their sex to their parents, and what form these signals should take arises. This question forms part of the larger question of which conditions favour the signalling of individual identity (e.g. Johnstone, 1997).

Concluding remarks

Although there are now a number of studies showing that birds adjust sex ratios in apparently adaptive directions, as the application of molecular sexing techniques has grown there are also studies, based upon respectable sample sizes, where no adaptive skews in sex ratios can be detected even in circumstances where it seems reasonable to expect them (e.g. Westerdahl *et al.*, 1997; Simon Griffith, pers. comm.). How common such patterns are will only become apparent as more empirical studies are performed, and it will be necessary to demonstrate selection for biased sex allocation before concluding that there is an absence of adaptation. Equally, more studies that claim evidence for adaptive biases need to support that claim with evidence of selection for bias, and there is a pressing need for more experimental studies. Because there are, in principle, many ways in which allocation can be adjusted, further studies of avian sex ratios have the potential to reveal the way in which mechanisms set limits for the extent of bias in allocation, potentially in a broader context than just avian sex ratios. For example, the difference between the weak biases in sex ratios typical for studies of birds and mammals and the strong biases found in some invertebrates is striking, and explanations of this based on constraints of sex determination seem appealing. Nevertheless, the possibility that the difference reflects adaptation to the degree to which individuals making allocation decisions have information about the environment that their offspring will inhabit should be investigated. Because of the wealth of natural history information available about birds, they are very suited to provide a test of these ideas. If carried out, such a study might prove to be an instructive investigation of the role of adaptation and constraint in shaping variation in nature.

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