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Adaptive sex allocation in birds: the complexities of linking theory and practice

Jan Komdeur[1*] **and Ido Pen**[2†]

[1]*Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*
[2]*Institut des Sciences de l'Evolution, cc065, Université Montpellier 2, Place Eugène Bataillon, 34095 Montpellier, France,*

We review some recent theoretical and empirical developments in the study of sex allocation in birds. The advent of reliable molecular sexing techniques has led to a sharp increase in the number of studies that report biased offspring sex ratios in birds. However, compelling evidence for adaptive sex allocation in birds is still very scant. We argue that there are two reasons for this: (i) standard sex allocation models, very helpful in understanding sex allocation of invertebrates, do not sufficiently take the complexities of bird life histories and physiology into account. Recent theoretical work might bring us a step closer to more realistic models; (ii) experimental field and laboratory studies on sex allocation in birds are scarce. Recent experimental work both in the laboratory and in the field shows that this is a promising approach.

Keywords: sex ratio; parental care; life history; sex determination; sexual selection; fitness

1. INTRODUCTION

Modern empirical sex ratio research began when Hamilton (1967) observed that many insects and mites have highly female-biased sex ratios and that this trait is associated with high levels of brother–sister matings. This could not be explained by the dominant theory at the time, Fisher's (1930) theory of equal allocation to the sexes. Hamilton solved the problem by marrying his theory of kin selection (Hamilton 1964) to sex ratio theory. He showed that the sex with more severe kin competition is less efficient than the opposite sex in exporting parental genes. Hamilton's work greatly boosted further empirical and theoretical research into invertebrate sex ratios. The result is that today we have an excellent understanding of the selective forces that shape sex allocation in invertebrates (review in Godfray & Werren 1996).

Sex allocation in birds, on the other hand, is still far from being well understood (Sheldon 1998; Pen 2000). We review some recent empirical and theoretical developments in the study of sex allocation in birds. Our main objectives are threefold: (i) review the standard sex allocation models focusing on the shortcomings in their application to birds, and discussing recent improvements that may help researchers identify which empirical measurements are important for further progress; (ii) review correlates of sex ratio variation in birds, and determine how well they can be explained by the standard sex allocation models; (iii) review recent experimental approaches to adaptive sex allocation in birds.

2. CLASSIC SEX ALLOCATION THEORY

(a) *Four major ideas*

The classic theory of sex allocation (Charnov 1982) can be regarded as founded on four major ideas. The first and foremost idea was that frequency-dependent selection tends to restore an equal sex ratio. At least in diplo-diploid organisms, the aggregate of all males in the population has a genetic share in the next generation, which is identical to the genetic share of all females. It follows that individuals of the minority sex have a greater per capita share, putting a premium on the production of such individuals. This holds true regardless of which sex is in the minority; hence an equal sex ratio is the unique stable evolutionary outcome. This idea is commonly attributed to Fisher (1930), but its origins can be traced back to Darwin (see Edwards (1998) for a historical account). Nevertheless, Fisher generalized the idea by noting that selection favours equal parental expenditure on the sexes, which implies a sex ratio biased towards the sex that incurs the least amount of expenditure.

The second major idea was that sex-specific kin competition might affect selection on the sex ratio (Hamilton 1967). In general, selection favours a sex ratio biased towards the sex experiencing the least amount of kin competition. For example, this might be the sex with the more even dispersal pattern (Bulmer & Taylor 1980). Conversely, selection may also favour an overproduction of the sex that positively improves conditions for kin (Emlen *et al.* 1986; Lessells & Avery 1987).

The third major idea was that relative fitness costs and benefits of producing sons or daughters may vary according to parental condition, or indeed to any variable, and that selection would favour parents to 'individually optimize' the sex ratio accordingly (Trivers & Willard 1973).

The fourth major idea was that of genetic conflict over the sex ratio (Trivers 1974; Trivers & Hare 1976). For example, according to Fisher's theory, parents favour a

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*Author for correspondence (j.komdeur@biol.rug.nl).
† Present address: Zoological Laboratory, University of Groningen, PO Box 14, 9750AA Haren, The Netherlands (i.r.pen@biol.rug.nl).

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sex ratio biased towards the cheaper sex. As a result, in Fisherian equilibrium, the more expensive sex has a higher individual reproductive value, owing to its relative scarcity. An offspring's gene that increases its chances of being in the expensive sex might, therefore, be favoured by selection, even if the gene's action compromises the total number of offspring afforded by the parents.

(b) *Population and individual sex allocation patterns*

A common mistake is to assume that several of the above ideas can be applied at the same time (Frank 1987, 1990). For example, it would be a logical error to use Trivers and Willard's idea to explain the variation in sex allocation between individuals in the population, and to use, at the same time, Fisher's theory to predict the average level of sex allocation in the population. In fact, if the assumptions of Trivers and Willard's hypothesis hold, then sometimes the opposite of what Fisher's theory would predict might apply to the population level. Frank (1995) gives an example of a model in which individual males receive more investment than individual females, but where individual adjustment of the sex ratio, as in Trivers and Wilard, leads to a male-biased sex ratio at the population level, quite the opposite of what Fisher's theory of equal allocation would predict. However, there is currently no theory that can tell us how often the prediction of Fisher's theory is qualitatively incorrect if the assumptions of Trivers and Willard hold. In the same spirit as Frank's model, Pen & Weissing (2000*a*) show that if offspring of one sex become helpers at the nest, and parents adjust the sex ratio to varying benefits of help, then at the population level the sex ratio may be biased towards the non-helping sex.

3. DIFFICULTIES WITH APPLYING CLASSIC SEX ALLOCATION THEORY TO BIRDS

The results of empirical sex ratio studies in birds are often interpreted within the framework of classic sex-allocation theory, even though the life histories of birds clearly violate a number of assumptions of the standard models. We review several of these troubling assumptions and discuss some recent theoretical developments that overcome some of these difficulties. For a fuller discussion of the application of sex ratio theory to birds see Frank (1990) and Pen & Weissing (2002*a*).

(a) *The cost of sex ratio control*

Standard sex-allocation models assume that sex ratio manipulation is without cost to the individual in control (but see Maynard Smith 1980; Eshel & Sansone 1991, 1994). This may be a reasonable assumption for haplodiploid species where females can determine the sex of an offspring by selectively fertilizing eggs with stored sperm. In species with chromosomal sex determination, such as birds, parents may not have a mechanism with which to bias sex ratios at fertilization (Williams 1979; Krackow 1995). If sex ratio manipulation requires selective killing of offspring at some point during development, this is likely to result in a loss of invested resources or time.

Explicitly including the costs of sex ratio control in models typically leads to less biased sex ratios than predicted by the standard models, which is not surprising. However, depending on the relationship between the degree of sex ratio bias and the associated cost, this can either mean that biased sex ratios remain equally frequent but less strongly biased (Leimar 1996) or biased sex ratios become less frequent but equally strongly biased (Pen & Weissing 2002*a*). Moreover, sometimes surprisingly small costs of sex ratio control are sufficient to offset any advantage of manipulating the sex ratio (Pen *et al.* 1999).

(b) *Overlapping generations and reproductive effort*

Standard sex-allocation models assume non-overlapping generations and a fixed amount of resources for reproduction. However, in addition to sex allocation, iteroparous organisms, which include most birds, face a perhaps even more fundamental decision: how much to invest in a particular reproductive episode (Zhang *et al.* 1996). Reproductive effort may be regarded as clutch size multiplied by the average investment per offspring, and sex allocation as the number of sons (daughters) multiplied by the average investment per son (per daughter) divided by reproductive effort. Thus, both reproductive effort and sex allocation may be considered as the outcome of selection on at least four allocation components: the clutch size, the sex ratio, the investment per son, and the investment per daughter. The resulting sex allocation depends strongly on whether or not constraints act on certain allocation components (Pen & Weissing 2000*b*, 2002*b*). For example, in low-fecundity organisms with small clutch sizes, the discrete nature of the clutch size may have a large effect on optimal sex allocation (Williams 1979; Frank 1987).

(c) *Extended biparental care*

Birds usually have extended parental care, often by both parents. Standard sex-allocation models, however, assume uni-parental control and a single short 'burst' of investment. Extended parental care leads to several theoretical and practical difficulties. Theoretically, because little is known about how reproductive costs before egg laying affect sex allocation it is not known whether these costs should be added to the investment in offspring after egg laying, and if so, how they should be divided between sons and daughters. Preliminary analysis (I. Pen and F. J. Weissing, unpublished data) suggests that such pre-laying costs do not affect sex allocation unless they interact non-additively with post-laying costs on parental survival. Practically, extended parental care makes it very hard to estimate relative investment in sons and daughters, especially if differential mortality takes place during the period of parental care.

Because of asymmetries in care, parents need not agree on the optimal sex allocation (Charnov 1982). The outcome of such a conflict strongly depends on which parent controls what aspect of allocation (Pen & Weissing 2002*a*). It is also possible that selection favours each parent to specialize in investing in a particular sex (Lessells 1998).

(d) *Fitness measures*

To test sex-allocation theory in the field it is necessary to have an adequate measure of fitness. The fitness measure of choice is reproductive value (Fisher 1930; Taylor

1990; Pen *et al.* 1999). Reproductive value measures the long-term contribution to the gene pool. In some instances, it is equivalent to a short-term measure of success, such as recruitment. In other instances, such a simple measure does not suffice. For example, Leimar (1996) has shown that even if high-quality males have higher reproductive success than high-quality females, a sufficiently strong correlation between maternal quality and offspring quality may raise the reproductive value of high-quality daughters above that of high-quality males, thus reversing Trivers & Willard's (1973) prediction.

In the context of kin selection, measures of fitness include measures of relatedness between interacting individuals. For example, the inclusive fitness of helpers-at-the-nest depends on their relatedness to their beneficiaries. What is often neglected in studies trying to assess inclusive fitness, is that the indirect benefits of help may be offset later by stronger local competition between previous helpers. Either such long-term effects are included in measurements of reproductive value, or such effects can be controlled for by an appropriate method of measuring relatedness that takes the different spatial scales of helping and local competition into account (Queller 1994).

4. PROXIMATE CAUSES OF BIASED SEX RATIOS IN BIRDS

To test adaptive theories of sex allocation in birds, it is important to know if and how birds might be able to adjust the sex ratio of their offspring. An important first step is to know how early during development biased sex ratios occur. Although the adults of some bird species are sufficiently sexually dimorphic to be able to sex individuals using external characteristics, the adults of many species, and newly hatched young of virtually all species, cannot be sexed in this way. Thus, in early sex ratio studies, where sexing was often done just before fledging, sex specific mortality could usually not be ruled out as a cause of biased sex ratios. With the advent of nearly universal molecular techniques for genetic sexing of birds from the embryonic stage onwards (Quinn *et al.* 1990; Griffiths 1992; Griffiths & Tiwari 1993; Griffiths *et al.* 1992, 1996; Lessells & Mateman 1996, 1998), it is possible to determine the sex ratio before substantial mortality has occurred.

A number of recent studies have demonstrated that some species of birds have biased sex ratios as early as at hatching (e.g. green woodhoopoe (*Phoeniculus purpureus*), Ligon & Ligon (1990); European kestrel (*Falco tinnunculus*), Dijkstra *et al.* (1990); collared flycatcher (*Ficedula albicollis*), Ellegren *et al.* (1996); great tit (*Parus major*), Lessells *et al.* (1996); blue tit (*Parus caeruleus*), Svensson & Nilsson (1996), Sheldon *et al.* (1999); European starling (*Sturnus vulgaris*), Bradbury *et al.* (1997); Seychelles warbler (*Acrocephalus sechellensis*), Komdeur *et al.* (1997); eclected parrot (*Eclectus toratus*); Heinsohn *et al.* (1997); zebra finch (*Taeniopygia guttata*), Clotfelter (1996), Kilner (1998), Bradbury & Blakey (1998); great reed warbler (*Acrocephalus arundinaceus*), Nishiumi (1998); Tengmalm's owl (*Aegolius funereus*), Hörnfeldt *et al.* (2000)). In most of these cases differential mortality between egg laying and hatching can be ruled out. Thus, in these cases, the sex ratio must have been biased inside the mother.

Since females are the heterogametic (ZW) sex in birds, this implies that either during meiosis the Z or the W chromosome has a larger chance of ending up in the egg, or that before laying sex-specific egg mortality occurs. It has been argued (Emlen 1997) that sex-specific resorption of eggs might be a potential mechanism of maternal sex ratio control. This would be a costly mechanism because it takes time to replace a resorbed egg with a new one. This might cause a later laying date, which in itself can compromise offspring survival (Klomp 1970), and it might cause more pronounced hatching asynchrony, which may also compromise offspring survival. To prevent laying gaps, it might pay to adjust the sex ratio of the first-laid egg only. Emlen (1997) argued that this could explain why the strongest sex ratio biases have been observed in a species (the Seychelles warbler, Komdeur *et al.* (1997)) laying single-egg clutches. However, in the meantime, biased sex ratios have also been observed in eggs other than the first-laid, without laying gaps (Seychelles warbler: Komdeur *et al.* 2002). In other species with multi-egg clutches laid without laying gaps, non-random sex allocation in laying sequence has also been observed (e.g. snow geese (*Chen caerulescens*), Ankney (1982); ring-billed gulls (*Larus delawarensis*), Ryder (1983); European kestrel, Dijkstra *et al.* (1990); zebra finch but with contrasting results, Clotfelter (1996) (males in earlier laid eggs) and Kilner (1998) (females in earlier laid eggs)).

It has been argued that maternal hormones might influence the sex ratio in birds (Krackow 1995). Recently, Williams (1999) observed biased sex ratios at fledging in zebra finches after injection of 17β oestradiol. However, it appears that the effect of this hormone is wholly through sex-specific mortality after hatching (N. Von Engelhart, personal communication).

Obviously biased sex ratios at hatching do not preclude sex-specific mortality after hatching. In order to detect sex-specific mortality, it is necessary to measure the sex ratios of the same broods on at least two consecutive occasions. In several species sex ratio shifts after hatching have been observed (e.g. great-tailed grackle (*Quiscalus mexicanus*), Teather (1987); lesser black-backed gull (*Larus fuscus*), Griffiths (1992); marsh harrier (*Circus aeroginosus*), Dijkstra *et al.* (1998), C. Dijkstra, unpublished data).

5. CORRELATES OF SEX RATIO VARIATION IN BIRDS

Reviews from the 1980s were unanimous in that they found significant sex ratio variation in birds to be very rare, of very minor magnitude and of little or no adaptive significance (Charnov 1982; Clutton-Brock 1986; Bull & Charnov 1988). Since then, the number of sex ratio studies in birds has increased sharply. There are now many more studies that report significant sex ratio variation, some of which support an adaptive explanation. However, truly convincing evidence for adaptive biased sex ratios remains extremely scarce. We review several recent correlational studies, classified according to the most common types of factors that were found to correlate with sex ratios in birds. In § 6 we focus on experimental studies.

(a) *External environment*

Several studies have reported a seasonal variation in offspring sex ratios. The first to report this was Howe (1977), who showed that in great-tailed grackles the sex ratio becomes more female-biased later in the season. This was attributed to increasing differential mortality biased towards males (the larger sex) due to decreasing food availability (Teather 1987; Teather & Weatherhead 1988). Among raptors, seasonal sex ratio trends seem to be common. Interestingly, despite the similar ecology and comparable sexual size dimorphism, the direction of sex ratio trends differs between species. Among small falcons (European kestrel, Dijkstra *et al.* (1990), Korpimäki *et al.* (2000); lesser kestrel (*Falco naumanni*), Tella *et al.* (1996); American kestrel (*Falco sparverius*), Smallwood & Smallwood (1998)), the proportion of sons declines during the season, whereas in larger species (peregrine falcon (*Falco peregrinus*), Olsen & Cockburn (1991); marsh harrier, Zijlstra *et al.* (1992); sparrowhawk (*Accipiter nisus*) and goshawk (*Accipiter gentilis*), Daan *et al.* (1996)) the proportion of daughters decreases with time. Another study on sparrowhawks (Newton & Rothery 2000) and a study on Montagu's harriers (*Circus pigargus*, Leroux & Bretagnolle (1996)) failed to find seasonal sex ratio trends. Only in the European kestrel and American kestrel is there evidence that suggests the sex ratio trend might be adaptive: in those kestrels the probability to start breeding as a yearling decreases with birth date for males, while it does not depend on birth date for females. However, caution is required in interpreting these research findings; another study on the American kestrel found no relationship between laying date and the proportion of sons produced (Wiebe & Bortolotti 1992). Pen *et al.* (1999) developed evolutionary models that showed this argument may explain the sex ratio trend in the European kestrel, provided costs of sex ratio control are very small. Their models also predicted that seasonal trends should be less steep at higher latitudes, a prediction that was supported by the studies on American kestrels (Smallwood & Smallwood 1998). In the great tit the hatching sex ratio became more male-biased later in the season, but the functional significance of the sex ratio variation is unknown (Lessells *et al.* 1996), and the sex ratio trend was not observed in other years (C. M. Lessells, unpublished data). This inconsistency of seasonal sex ratio variation has also been observed in other tit species (B. C. Sheldon, personal communication).

Tawny owls (*Strix aluco*) apparently adjust the primary sex ratio within broods to vole densities on breeding territories (Appleby *et al.* 1997). The higher the vole densities on breeding territories, the more the primary sex ratios become biased toward females (the larger sex). This seems to be adaptive, because the breeding success of females was positively related to the densities of voles on their natal territory when the females were reared, while male breeding success was not affected by the vole density they had experienced as a nestling. This may be responsible for giving these chicks their initial competitive advantage over food allocation by their parents.

(b) *Paternal quality*

If male attractiveness (e.g. expressed as large sexual ornaments or large song repertoire) is related to male reproductive success, and if these traits are inherited by the sons, then sons of attractive males might be of higher reproductive value than the daughters of such males. The reverse would be true for offspring of less attractive males. It has been argued that it would therefore be adaptive to modify sex ratios in response to male attractiveness. However, as shown by game-theoretical and population genetic models, whether this argument actually works may depend on the mechanism of sexual selection (Pen & Weissing 2000*c*). For example, a male trait that has evolved via Fisher's runaway process does not give a net fitness benefit to males because in equilibrium the mating benefits conferred by higher attractiveness are exactly counterbalanced by lower survival.

Several studies have investigated whether there is a relationship between male traits and the sex ratio of their offspring. Positive evidence has been obtained from three studies. In the collared flycatcher, brood and recruit sex ratios were male-biased when the male rearing the brood had a large forehead patch (Ellegren *et al.* 1996), which is a heritable secondary sexual character implicated in female choice (Sheldon *et al.* 1997). Female blue tits produce more sons if they mate with a male having good survival prospects (Svensson & Nilsson 1996). In the great tit, male foraging potential and fertilization success depend on male body size and plumage traits. (Kolliker *et al.* 1999). The proportion of male eggs and male recruits increased significantly with male body size.

Five other studies found no relationship between male characters and the sex ratio. In the great reed warbler, where song repertoire size is related to male survival and implicated in female choice, no correlation was found between song repertoire size and offspring sex ratio (Westerdahl *et al.* 1997). In the barn swallow (*Hirundo rustica*), females do not adjust sex ratio in relation to their partner's tail length (Saino *et al.* 1999), a cue which is implicated in female choice (Møller 1995) and which appears to be 'honestly signalling' viability (Møller 1994). In the collared flycatcher (Sheldon *et al.* 1997), the great reed warbler (Westerdahl *et al.* 1997), and the red-winged blackbird (*Agelaius phoeniceus*, Westneat *et al.* (1995)) attractive males father more extra-pair young in the nest of less attractive males. However, there is no evidence that the sex of these extra-pair offspring is male-biased (Sheldon & Ellegren 1996; Westerdahl *et al.* 1997; Westneat *et al.* 1995, respectively).

(c) *Social environment*

In cooperatively breeding species, where helping tendencies of offspring are sex-specific, selection is expected to favour biased sex ratios (see § 5b). A study of red-cockaded woodpeckers (*Picoides borealis*; Gowaty & Lennertz (1985)) found population sex ratios biased towards the helping sex. However, a much larger study on the same species (Walters 1990) found no effect on the population sex ratio. In the Seychelles warbler, helping (mainly by daughters) is frequent. Having 'helpers' around is costly for parents inhabiting poor territories, because helpers deplete insect prey, but is beneficial to parents (higher reproductive success) inhabiting rich territories (Komdeur 1994). Breeding pairs produced 77% sons when breeding on poor territories and 13% sons when breeding on rich territories (Komdeur *et al.* 1997).

(d) *Sexual size dimorphism*

Sex ratios have frequently been studied in sexually size-dimorphic species, because size differences between sons and daughters are likely to reflect sex-specific costs to the parents (Stamps 1990; Anderson *et al.* 1993; Krijgsveld *et al.* 1998). A comparative analysis of all published studies shows that sex ratios at fledging at the population level are on average biased towards the smaller sex (Pen 2000), contrary to previous analyses based on a smaller number of species (Clutton-Brock 1986). Only one recent study has found a biased sex ratio at hatching in a strongly size-dimorphic species (blue-footed booby (*Sula nebouxii*), Torres & Drummond (1999)). Thus, it appears that differential mortality biased towards the larger sex is a general phenomenon (see also Dijkstra *et al.* 1998). Since mortality of the larger sex reduces the cost differential between the sexes, the adaptive value of sex ratios biased towards the smaller sex may be much smaller than suggested by size differences and differences in food intake alone.

6. EXPERIMENTAL APPROACHES TO ADAPTIVE SEX ALLOCATION

Even though many studies have found sex ratio variation to correlate with certain variables, the number of studies producing no correlations may be extensive due to a publication bias towards positive results (Bensch 1998; Palmer 2000). In order to demonstrate causal relationships between sex ratio variation and properties of organisms or their environment it is necessary to carry out experimental manipulations, a common practice in the study of other life history traits (Lessells 1991). Such experiments are also necessary to demonstrate trade-offs between alternative sex allocation 'decisions' and to study their fitness consequences. Such experiments have only recently begun in the study of sex allocation in birds, proof that this field is still far from maturation.

Currently, there have only been seven experimental studies that have manipulated an aspect of birds or their environment: habitat quality (Komdeur *et al.* 1997; Hörnfeldt *et al.* 2000), maternal condition (Bradbury & Blakey 1998; Kilner 1998; Nager *et al.* 1999), and paternal attractiveness (Burley 1981, 1986; Sheldon *et al.* 1999). There is only one study which has manipulated broad sex ratios (BSRs) in order to study the effects on fitness components (Lessells *et al.* 1998), and one study in which the accrued fitness benefits of sex ratio adjustment were calculated (Komdeur *et al.* 2002). We will briefly discuss these studies.

(a) *Manipulations of cues for sex ratio adjustment*

The Seychelles warbler experimental manipulations, which caused pairs to change territory quality, resulted in corresponding changes in egg sex ratios (Komdeur *et al.* 1997). The reproductive success of female zebra finches reared when food is scarce is more adversely affected than that of males (De Kogel 1997). Female zebra finches in good condition significantly adjusted their offspring sex ratio, but the direction of sex ratio differs between studies. Females with experimentally restricted food intake gained a lower body condition and subsequently produced significantly more male-biased sex ratios than when experiencing high food availability (Kilner 1998). Conversely, females on high-quality diets gained a lower body condition (because they did not lay down fat reserves), and produced significantly more female-biased sex ratios than females on low-quality diets (Bradbury & Blakey 1998). In the sexually dimorphic lesser black-headed gull (males larger) the survival to fledgling of male, but not female, young was substantially reduced if they came from less well-provisioned eggs (Bolton *et al.* 1992). As a female's condition, and thereby her capacity to produce high-quality eggs declined, she progressively skewed the sex ratio of her eggs toward females; the sex with the higher survival prospects. If maternal conditon was enhanced through supplementary feeding, the quality of eggs improved (Bolton *et al.* 1992), there was a corresponding decline in the survival of male offspring and the sex ratio bias toward females was removed (Nager *et al.* 1999). Blue tits are sexually dichromatic in ultraviolet/blue spectral purity (chroma) of the crown patch (Hunt *et al.* 1998). The crown of the male, which is displayed in courtship, plays an important role in mate selection (Hunt *et al.* 1998). Ultraviolet reflectance of the crown predicted male survival to the following breeding season, suggesting a viable indicator of male quality (Sheldon *et al.* 1999). The hatching sex ratio produced by the females was positively correlated with the ultraviolet plumage ornamentation of their mates. Masking male ultraviolet reflectance reversed a positive correlation to a negative one. Whether this can be interpreted as a causal effect of male ultraviolet ornamentation on offspring sex ratio (Sheldon *et al.* 1999) is unclear. In the zebra finch male, beak colour is a sexually selected trait (Price & Burley 1994) and is related to paternal investment (Burley 1986, 1988). Females paired to brighter bill 'attractive' males produced a higher proportion of sons among their offspring (Burley 1981). However, another study failed to show a relationship between male beak coloration and sex ratios produced in the breeding pairs (Bradbury & Blakey 1998). In addition, band colours have a well-known effect on female mating preferences (Burley *et al.* 1982). If the external appearance of males was experimentally altered to manipulate the male's attractiveness, females paired to red-banded 'attractive' males produced a higher proportion of sons among their offspring than females paired to green-banded 'unattractive' males (Burley 1986). A recent study, which attempted to replicate Burley's experiment failed to find a consistent effect of band colour on offspring sex ratios (C. Dijkstra, personal communication). However, none of these studies has yet determined the fitness consequences of different sex allocation decisions: (i) it is currently unknown whether males inherit the attractiveness from their fathers, and (ii) the fitness of offspring has not been monitored.

(b) *Inclusive fitness benefits of sex ratio adjustment*

The great tit experimental manipulations of BSRs (either all male, all female or approximately half male) within days of hatching, did not provide any evidence for an effect of BSR on any aspect of parental behaviour (Lessells *et al.* 1998). Currently, only one study has tested for optimal sex allocation experimentally and adequately (Komdeur *et al.* 2002). It has been demonstrated that female Seychelles warblers increase their short-term fitness by adaptively modifying the sex of their single-egg clutch according to environmental and social circumstances (Komdeur *et al.* 1997). Against this background, an experiment was undertaken in 1994–1996 by selecting breeding pairs on low- and high-quality territories that were feeding a nestling of the adaptive sex. Through swaps of nestlings immediately after hatching, some breeding pairs were forced to raise a stepson and some to raise a stepdaughter, and subsequently the inclusive fitness accrued to foster breeding pairs to raise the less adaptive sex and the adaptive sex was calculated. Inclusive fitness was calculated as the sum of fitness obtained through breeding offspring (grandchildren) and the fitness obtained through helping offspring (in the form of extra offspring produced by the breeding pair through help). In the experiment the step-offspring were regarded as offspring produced by the female of the breeding pair, because under natural circumstances when breeding in pairs, the pair female was always the mother of the offspring, none of the offspring being produced by extra-group females (Richardson *et al.* 2000). Given that almost the entire adult population and all the young were blood sampled from 1994 until the present time, and that the entire population is confined to one small island, the total number of yearlings produced over a step-offspring's entire lifetime was precisely determined through microsatellite DNA fingerprinting (Komdeur *et al.* 2002). On low-quality territories females raising stepsons gained significantly higher inclusive fitness benefits than by raising step-daughters, and vice versa on high-quality territories with females raising stepdaughters (Komdeur *et al.* 2002). Given that females control the egg's sex and the high rates of extra-pair paternity (41.4%, $n = 87$ offspring; Richardson *et al.* (2000)), there may be conflict over egg sex modification between breeding males and females. There is good experimental evidence that the inclusive fitness consequences of sex allocation in the Seychelles warbler are adaptive for the breeding female, but are currently unknown for the breeding male. One should keep in mind that estimates of inclusive fitness should include the reproductive success of all sons and all daughters produced over the breeding female's and male's lifetime.

7. CONCLUDING REMARKS

The advent of molecular sexing techniques has meant that the study of sex allocation in birds is enjoying a welcome renaissance. However, both theory and fieldwork still have a lot of maturation ahead of them. Just as insects have inspired much of classic sex-allocation theory, the complications arising from bird life-histories and physiology are inspiring further theoretical developments. Fieldwork must now graduate from a correlational approach to an experimental approach, the first results of which are promising.

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