

Review

Adult sex ratios in wild bird populations

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Offspring sex ratios in wild bird populations, and the extent to which they vary from the equality expected by random genotypic sex determination, have received much recent attention. Adult sex ratios (ASRs) in wild birds, on the other hand, remain very poorly described, and many of the questions about them posed by Ernst Mayr in 1939 remain unanswered. This review assesses population-level sex ratio patterns in wild bird populations, with an emphasis on the ASR. A quantitative assessment of over 200 published estimates of ASR, covering species from a wide range of taxa, regions and habitats, supported Mayr's assertion that skewed ASRs are common in wild bird populations. On average, males outnumbered females by around 33%, and 65% of published estimates differed significantly from equality. In contrast, population-level estimates of offspring sex ratio in birds did not generally differ from equality, and mean ASR across a range of wild mammal species was strongly female-skewed. ASR distortion in birds was significantly more severe in populations of globally threatened species than in non-threatened species, a previously undescribed pattern that has profound implications for their monitoring and conservation. Higher female mortality, rather than skewed offspring sex ratio, is the main driver of male-skewed ASRs in birds, and the causes and implications of this are reviewed. While estimates of ASR in wild bird populations may be subject to a number of biases, which are discussed, there is currently no quantitative evidence that an ASR of one male to one female represents the norm in birds. A better understanding and reporting of ASRs in wild bird populations could contribute greatly to our understanding of population processes and could contribute much to theoretical and applied research and conservation.

Keywords: Allee effect, cooperative breeding, demography, heterogamety, operational sex ratio, polygamy

In birds, primary and secondary sex ratios, defined by Mayr (1939) as the ratio of male to female eggs and chicks, respectively, may vary significantly from the 1 : 1 expected if the sex of each individual were determined by random chromosomal (Mendelian) sex determination alone. A huge body of recent research (summarized in Sheldon 1998, Hardy 2002, West *et al.* 2002, Ewen *et al.* 2004) has been directed at describing and explaining variation in offspring sex allocation in plants and animals. The success of sex allocation models in explaining observed patterns has been hailed as one of the great achievements of evolutionary ecology, although its success for birds and mammals appears more modest (Sheldon 1998,

Cockburn *et al.* 2002, Komdeur & Pen 2002, West *et al.* 2002, Ewen *et al.* 2004, Uller 2006). Far less is known about patterns of variation in tertiary sex ratios, or adult sex ratios (ASRs), strictly defined as the sex ratio of breeding adults, but in practice generally measured as the sex ratio of all independent non-juvenile individuals (Mayr 1939). The frequency and causes of ASR variation, the responses of individuals to it and the extent to which the response feeds back into population dynamics are all poorly understood phenomena in populations of humans (Lummaa *et al.* 1998), let alone those of other animals (Le Galliard *et al.* 2005a). The extent to which generally subtle manipulations of offspring sex ratio survive the maelstrom of dispersal, mortality, territory acquisition and eventually mating, and so are detectable in the

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following generation of adults, is practically unknown. This has implications far beyond assessing the success of models developed to explain offspring sex allocation in terms of resultant ASR.

Charles Darwin (1871) was one of the first naturalists to recognize that sex ratios in wild animal populations can be unbalanced. In 1933, Aldo Leopold noted that ASR in wildfowl (Anatidae) were 'seriously deranged' and presciently suggested that the observed excess of males might be associated with population decline or environmental change (Leopold 1933). In 1939, Ernst Mayr published a quantitative overview of ASRs in wild bird populations, asserting that it was a commonly held belief that in many bird populations, males outnumbered females by around 10–20% (Mayr 1939). Mayr concluded that much variation exists in ASR, which can be heavily skewed towards either males or females (though generally towards males), and suggested that sex ratio imbalance might be associated with a number of physiological or behavioural traits. Since Mayr's review, the ASR has been largely neglected, although McIlhenny (1940) and Payevsky (1993) again pointed to evidence of an excess of males across a range of species. A general acceptance of Fisher's (1930) argument for the evolutionary stability of equal investment in the sexes of offspring may have dampened interest in ASRs and led to a general acceptance that they tend to be largely balanced (Breitwisch 1989). Despite this, skewed or variable ASRs remain frequently proposed, though rarely quantified, drivers of a number of behavioural or demographic patterns, such as variation in mating systems, sexual selection, parental care, individual behaviour, migratory strategy or lifetime productivity (Clutton-Brock & Parker 1992, Kvarnemo & Ahnesjö 1996, Le Galliard *et al.* 2005b, Gerber 2006, Kokko *et al.* 2006, Marr *et al.* 2006). While completely new fields of ecological and evolutionary thinking have arisen from studies of the offspring sex ratio, our understanding of the ASR has advanced little since Mayr's review of 1939.

The importance of understanding ASRs

Despite this lack of recent interest, a better understanding of the ASR and its relationship with demography, behaviour and population persistence may contribute a great deal to many areas of research. Behaviours such as polygyny, extra-pair copulation, mate-guarding and co-operative breeding have frequently been linked to skewed ASRs, and indeed may have evolved in response to them (Murray 1991).

Different breeding systems differentially skew the distribution of individual productivity, so the ASR may influence an individual's breeding or social status and lifetime reproductive success (Bertram 1992, Castro *et al.* 2004). The ASR could therefore profoundly influence population dynamics, and requires greater consideration in demographic population models and population viability analyses than has generally been given (Brook *et al.* 2000, Boukal & Berec 2002, Deeming & Wadland 2002, Engen *et al.* 2003, Saether *et al.* 2004, Morales *et al.* 2005, Steifetten & Dale 2006). There is evidence of a general correlation between the ASR and population trend (Nadal *et al.* 1996, Wilkinson *et al.* 2002) or habitat quality (Fretwell & Calver 1970, Butler & Merton 1992, Zanette 2001, Johnson *et al.* 2006), so the ASR might be a useful indicator of a species' population trajectory or conservation status. ASR is already used as an indicator of population status in the management of mammals (McLoughlin *et al.* 2005, Solberg *et al.* 2005), reptiles (Smith & Iverson 2006) and fish (McCleave & Jellyman 2004, Han & Tzeng 2006), but its use in the management of bird populations has yet to be developed. Skewed ASRs might represent an important demographic Allee (small population size) effect in declining or isolated populations (Dale 2001, Engen *et al.* 2003), and understanding their variation and drivers might provide insights for the management of species of high conservation concern or commercial importance (Aldrich 1973, Wildt & Wemmer 1999, Clout *et al.* 2002, Wedekind 2002, Bessa-Gomes *et al.* 2004). The ASR might also explain variation in a number of behavioural or environmental parameters, such as the relative arrival times of male and female long-distance migrants (Kokko *et al.* 2006), territory density (Fretwell & Calver 1970) or range edge effects (Woolfenden *et al.* 2001).

A final reason for desiring a better understanding of ASRs is that it would allow calibration of census and survey data. These are often based on counts of territorial males and so might systematically over- or underestimate the effective population size if the sex ratio is skewed (Newson *et al.* 2005, Amrhein *et al.* 2007). This problem is exacerbated by the fact that unpaired males may be more detectable by human observers, as they often sing more or for longer than paired males, or may defend multiple territories (Donald *et al.* 2003, Amrhein *et al.* 2007). This could theoretically result in a negative relationship between population size estimated by field surveys and true functional population size, clearly a highly undesirable situation.

This review attempts (1) to identify patterns of ASR in wild bird populations and their causes, correlates and variation, (2) to assess the importance to conservation of the observed patterns, (3) to identify problems and biases in estimating ASR and (4) to suggest priority areas for future research. Offspring sex ratios are also briefly reviewed, to illustrate their relevance to understanding ASR, and to compare the magnitude and frequency of their skews to those of adult populations; fuller reviews of offspring sex ratios and their variation have been published elsewhere (Clutton-Brock 1986, Sheldon 1998, Hardy 2002, West *et al.* 2002, Ewen *et al.* 2004). This review focuses on population-level sex ratios, and does not cover the well-documented phenomenon of seasonally or spatially unbalanced sex ratios caused by the non-breeding segregation of males and females into different regions or habitats (e.g. Catry *et al.* 2005, Schwab *et al.* 2005, Fernandez & Lank 2006).

METHODS

Literature searches were undertaken on key words through Web of Science, Google Scholar and SORA (<http://elibrary.unm.edu/sora/index.php>) and by systematically checking through reference lists in each study identified. During this review process, a database was simultaneously compiled of the results of studies containing data on offspring and ASRs in birds. Data on ASR in mammals and other vertebrate groups were collected incidentally, in order to identify similarities or differences that might help explain avian ASRs. For each published estimate of ASR, the database included fields indicating levels of sexual size or plumage dimorphism and fields intended to assess or identify likely bias in (1) methods of ASR estimation and (2) publication bias. For the former, studies were scored on whether or not they identified or tried to correct for potential bias in sex ratio estimation, for example by calibrating different methods, by quantitatively assessing likely sources of bias or by determining the sex of a high proportion of individuals in the study population. The method used to estimate ASR was also recorded, classed into three main types of catching or trapping, direct observation and a small group of less frequently used methods (such as carcass examination). Publication bias was assessed by visual examination of a funnel plot (Palmer 2000) and by comparing estimates of ASR between studies in which estimation of ASR was the primary aim of the work and those in which it was a secondary aim or was collected incidentally.

Because of missing values in many of the fields, and because the aim of the review was to describe patterns, rather than to explain them, univariate analyses were used rather than multivariate models.

The database excluded studies listed by Mayr (1939) or Breitwisch (1989), unless these were picked up independently by the literature searches described, because they were deliberately selected to illustrate male skew in sex ratios. Studies based on recoveries of dead birds, for example through shooting bag records, were also omitted, as an excess of one sex in the sample could indicate either that it was more numerous in the wild, or that it suffered disproportional mortality so that it was less numerous in the remaining wild population. Such data are also severely biased, as hunters preferentially shoot male birds (McIlhenny 1940). This led to the omission of a large amount of hunting data on groups such as ducks, particularly from North America (Bellrose *et al.* 1961), though despite higher hunting pressure, males tend to predominate in wildfowl populations (see below). Studies reporting ASRs based on museum skins were also excluded for sexually dimorphic species, as brighter males might be more vulnerable to collectors (Mayr 1939).

All sex ratios are expressed as the proportion of the population made up by males (Wilson & Hardy 2002). The statistical significance of departure from an expected sex ratio of 0.5 was assessed using Pearson's χ^2 goodness-of-fit statistic, though other methods have been proposed (Wilson & Hardy 2002, Ewen *et al.* 2003). However, the statistical significance of any particular sex ratio skew should be interpreted cautiously. For example, in a remnant population comprising eight males and two females, the sex ratio skew is not statistically significant ($\chi^2 = 3.6$, $P > 0.05$), but is clearly of great biological and conservation significance, perhaps of greater significance than the same sex ratio in a population of 80 males and 20 females, which is highly significantly skewed ($\chi^2 = 36.0$, $P < 0.0001$). For this reason, analyses did not correct for sample size, which anyway was not always given in the original papers. Furthermore, the direction of skew, rather than its magnitude, might carry additional significance; a population of two males and eight females might be easier to save from extinction than a population of eight males and two females (Bessa-Gomes *et al.* 2004, Morales *et al.* 2005), although the overall deviation from 0.5 is the same.

The tertiary sex ratio, as defined by Mayr (1939), relates to the sex ratio of adult birds in the population, though with no definition about what constitutes adulthood. This differs from the more precisely

defined operational sex ratio (OSR), which relates to 'the average ratio of fertilizable females to sexually active males at any given time' (Emlen & Oring 1977). Tertiary and operational sex ratios can clearly differ, in that the former might include non-breeding adults. In monogamous species therefore the OSR is more likely to equate to 0.5 than is the tertiary sex ratio, although the latter is calculated from a larger proportion of the total population. An example of the way the two measures can differ was given by Faaborg *et al.* (1980), whose study of Galapagos Hawks *Buteo galapagoensis* estimated an OSR of 0.7, with high rates of polyandry, though a large non-breeding adult female population meant that the ASR was close to 0.5. Differences between ASR and OSR arise through a range of behaviours that act to reduce the effective population size (Anthony & Blumstein 2000). In extreme cases, ASR and OSR may be skewed in opposite directions, for example in sex-role-reversed species (Emlen & Wrege 2004). In the great majority of cases, published estimates of ASR reflect Mayr's tertiary sex ratio rather than the OSR, so in the few cases where estimates of both were given, the tertiary sex ratio was used.

RESULTS AND REVIEW

Offspring sex ratios

The database contained 140 estimates of offspring sex ratio, from studies of sex ratios in eggs or nestlings of 114 species. Of these, 24 (17%) differed significantly (at $P < 0.05$) from 0.5, 11 skewed towards males and 13 towards females. The distribution of reported offspring sex ratios, which had a median value of 0.5, is shown in Figure 1.

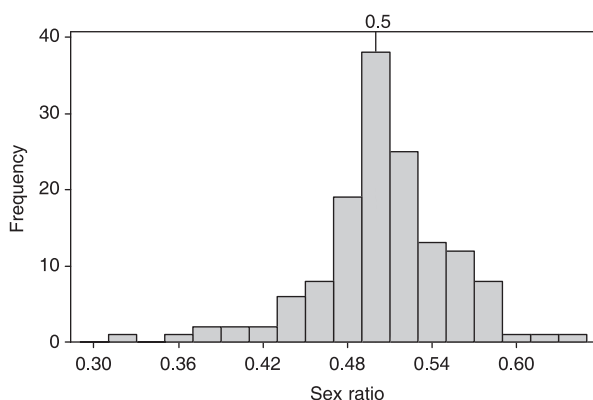


Figure 1. Frequency distribution of 140 published estimates of offspring sex ratio from a wide range of bird species.

Charles Darwin (1871) was one of the first to realize the importance of sex ratios in sexual selection and proposed a model, later elaborated upon by Fisher (1930), to suggest that balanced sex ratios (in mammals and birds at least) are adaptive. Where the cost of production and reproductive value do not differ between male and female offspring, individuals producing an excess of the rarer sex are more likely to pass on their minority sex-producing genes to the next generation, until the other sex becomes the rarer, when individuals producing more of the new minority would gain reproductive advantage. If all parents produce equal numbers of both sexes, an evolutionarily stable strategy results. This model assumes that an individual's tendency to offspring sex allocation is inherited. The problem with this model as evidence for adaptive offspring sex allocation is that its outcome, a sex ratio of 0.5, is indistinguishable from that which would be expected by random Mendelian (meiotic) sex allocation. Studies of the heritability of offspring sex ratio determination in mammals suggest that random allocation may be a better explanation than the Darwin/Fisher adaptive model for the generally balanced offspring sex ratios seen in mammals and birds (Toro *et al.* 2006), though evidence from pre-industrial human societies suggests Fisher's theory may have some explanatory power (Ranta *et al.* 2000). Since the publication of the Darwin/Fisher model, increasingly more complex models of offspring sex ratio, involving sexual selection, parental costs or fitness and gene flow, have been developed (Seeger & Stubblefield 2002). It is unclear which, if any, of these models explain offspring sex allocation in birds better than does simple random meiosis (Cockburn *et al.* 2002, Ewen *et al.* 2004, but see also Cassey *et al.* 2006).

Offspring sex ratios in birds, measured at the level of either the population or the individual, do not normally exhibit the extreme degrees of skew found in apomictic species, or in amphimictic species in which sex allocation is under environmental determination (Cockburn *et al.* 2002). In birds, notable documented exceptions are the Eclectus Parrot *Eclectus roratus* (Heinsohn *et al.* 1997) and the Seychelles Warbler *Acrocephalus sechellensis* (Komdeur 1996), individuals of which consistently produce more of one sex than the other (though the population-level offspring sex ratio in both species is balanced). Doubtless, more examples await discovery. Despite the apparent rarity of extreme offspring sex allocation in birds and mammals, subtle spatial or temporal sex ratio variation, within and between individuals, populations and species, has been reported from a

number of species (Rosivall *et al.* 2004, Cichon *et al.* 2005). Two mechanisms exist by which sex ratios of chicks leaving the nest can differ from unity: parental manipulation of the primary (egg) sex ratio, which might be controlled by a number of different physiological mechanisms or environmental cues (West *et al.* 2002, Pike & Petrie 2003, Alonso-Alvarez 2006), and differential egg or chick mortality between laying and fledging (Székely *et al.* 2006). Individual offspring sex ratio variation has been related to a large number of factors, including parental body condition, size and age (Yamaguchi *et al.* 2004, Weimerskirch *et al.* 2005, Dowling & Mulder 2006), sexual dimorphism and the relative costs of raising chicks of each sex (Trivers & Willard 1973, Wiebe & Bortolotti 1992), mate attractiveness (Ellegren *et al.* 1996, Griffith *et al.* 2003), clutch size (Dyrce *et al.* 2004), age at first breeding (Daan *et al.* 1996), postnatal dispersal patterns (Gowaty 1993, Julliard 2000), the presence or contribution of nest helpers or brood parasites (Komdeur 1998, Legge *et al.* 2001, Griffin *et al.* 2005, Zanette *et al.* 2005), climate (Weatherhead 2005), habitat fragmentation (Suorsa *et al.* 2003) and the quality and availability of food or nest-sites (Byholm *et al.* 2002, Clout *et al.* 2002, Dubois *et al.* 2006). All these factors are interrelated, and it is not yet clear whether skewed offspring sex ratios are adaptive, or what their proximate or ultimate drivers are (Weatherhead & Teather 1991, Sheldon 1998, Dyrce *et al.* 2004, Ewen *et al.* 2004). Predictors of sex ratio variation appear to differ between species and populations and often appear inconsistent (Hasselquist & Kempenaers 2002, Komdeur & Pen 2002, West *et al.* 2002, Westneat *et al.* 2002, Ewen *et al.* 2004). Even in species with highly skewed individual offspring sex ratios, the population-level offspring sex ratio generally does not differ significantly from 0.5 (Ligon & Ligon 1990, Heinsohn *et al.* 1997, Radford & Blakey 2000, Legge *et al.* 2001, Magrath *et al.* 2002, Paxton *et al.* 2002, Yamaguchi *et al.* 2004, Eraud *et al.* 2006).

Adult sex ratios

Results from analysis of the database

In total, 201 published estimates of ASR were collected from 173 species. Of these, 131 (65%) differed significantly from 0.5, the majority of these (83%) towards males (Table 1). The mean and median ASR were both 0.57 (Fig. 2), and 95% confidence intervals for the mean did not include 0.5. For the subset of estimates for which numbers of males and females were available ($n = 142$), rather than just a ratio,

Table 1. Taxonomic distribution of the 201 estimates of ASR, showing the number of estimates significantly (at $P < 0.05$) skewed towards males or females and the number that did not differ from 0.5. Where multiple estimates of the same species are included in the same ASR category, the number of different species is given in parentheses. A further ten species each had two estimates of ASR falling into different categories. ASR skew was not distributed randomly with respect to taxonomy ($\chi^2 = 57.8$, $df = 32$, $P < 0.005$ for all studies, $\chi^2 = 50.8$, $df = 32$, $P < 0.05$ for individual species), due to the larger than expected number of female-skewed populations in the Apodiformes (see text). Taxonomy follows Sibley and Ahlquist (1990).

Order	Female-skewed	Balanced	Male-skewed
Anseriformes		8	14
Apodiformes	3		1
Bucerotiformes			1
Ciconiiformes	7 (5)	17 (13)	17 (14)
Columbiformes		1	3
Coraciiformes	1	1	1
Cuculiformes			2
Galliformes		1	3 (1)
Gruiformes	3 (1)	4	3
Passeriformes	3	33 (31)	56 (52)
Pelecaniformes			1
Piciformes			1
Procellariiformes		1	1
Psittaciformes		2	5
Sphenisciformes			2
Strigiformes			1
Struthioniformes	2 (1)	2	
Total	19 (14)	70 (64)	112 (105)

logistic regression, with number of males fitted as the numerator and total number of birds as the binomial denominator, estimated an ASR of 0.56 (95% CL: 0.542–0.569). Males appear therefore to outnumber females by around 30–35%.

The ASR in birds, and its absolute deviation from 0.5, differed significantly from the ASR in mammals, which was strongly female-skewed, and from offspring sex ratios in birds, which (as described above) were generally balanced (Fig. 3). The ASR in birds was on average less skewed from 0.5 than the ASR in mammals. There was no significant difference in estimated ASR between di- and monomorphic species with respect to size or plumage, or between migratory and non-migratory species (Mann–Whitney U -tests, $P > 0.05$ in all cases). However, bird species listed by the IUCN as Globally Threatened or Near-threatened showed both a significantly more male-skewed ASR and a greater absolute deviation from 0.5 than non-threatened species (Fig. 4), and there was a tendency for the skew towards males in the ASR to increase with increasing threat status (Fig. 5).

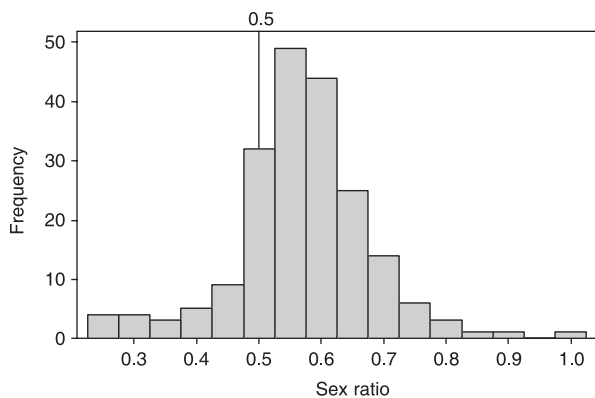


Figure 2. Frequency distribution of 201 published estimates of adult sex ratio from a wide range of bird species.

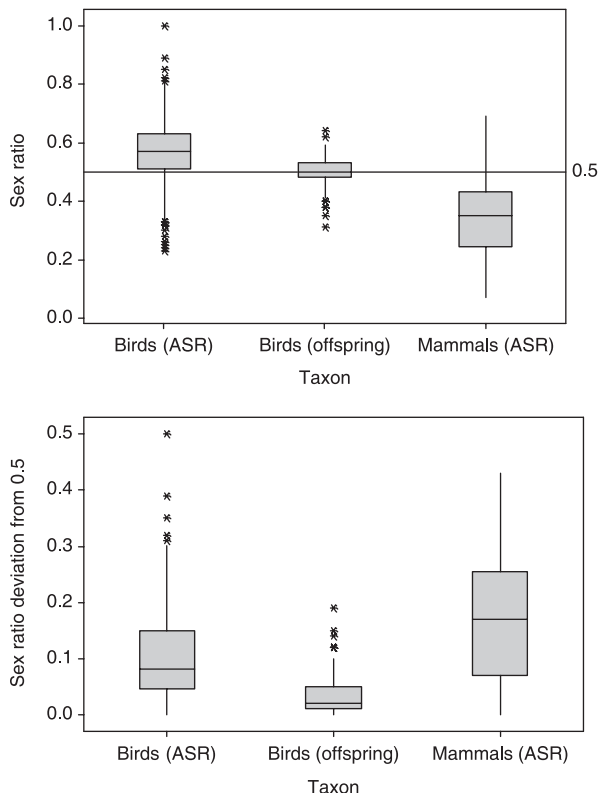


Figure 3. Comparison of sex ratios (upper) and their absolute deviation from 0.5 (lower) in adult birds ($n = 201$), adult mammals ($n = 61$) and bird offspring ($n = 140$). The horizontal line represents the median, the box the interquartile range and the vertical lines span the range of the values lying between the interquartile and 1.5 times the interquartile range. Outliers beyond this are represented by asterisks. The difference was statistically significant across all groups and between each pair of groups in both cases (Kruskal–Wallis tests, $P < 0.0001$).

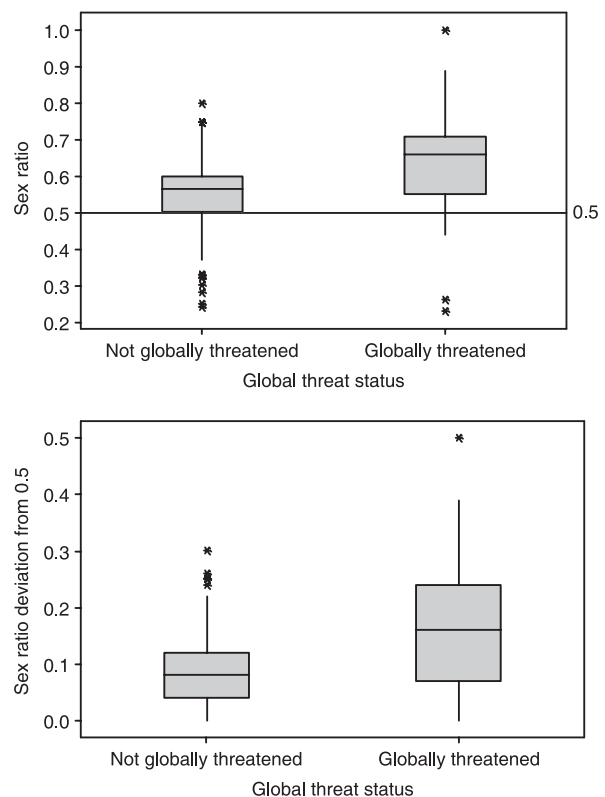


Figure 4. Comparison of ASRs (upper) and their absolute deviation from 0.5 (lower) in species of birds listed by the IUCN as Globally Threatened Species ($n = 37$) and non-threatened species (non-GTS; $n = 164$). The difference was statistically significant in both cases (Mann–Whitney U -tests, $P < 0.001$). The Globally Threatened Species included one extinct form and one species listed as Near-threatened; all others were listed by the IUCN as Vulnerable, Endangered or Critically Endangered. Interpretation of the bars is as in Figure 3.

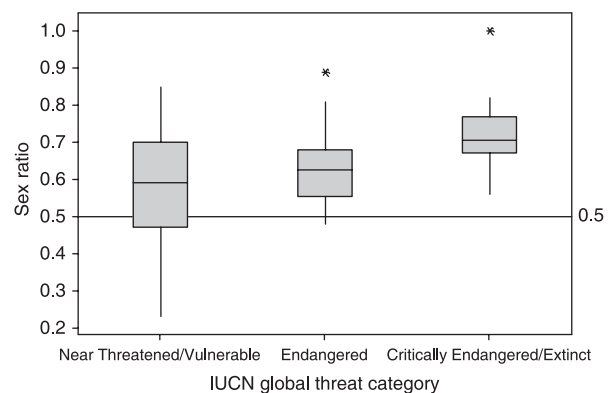


Figure 5. ASRs of birds in different IUCN threat status categories. There was a tendency for ASR skew to increase with increasing threat category (Kruskal–Wallis test, $P < 0.05$). Interpretation of the bars is as in Figure 3.

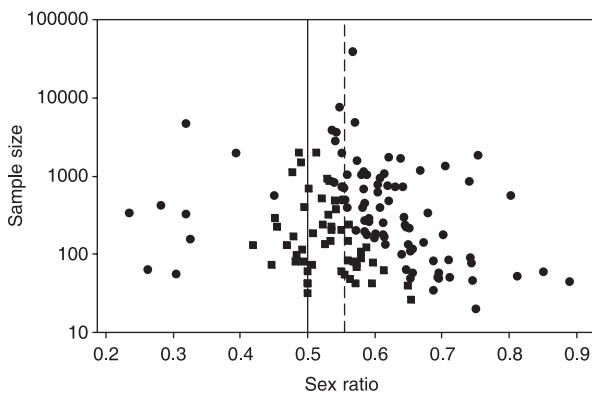


Figure 6. Funnel plot of sample size from which the ASR was estimated against ASR. The dotted line represents the pooled mean ASR. Estimates of ASR that differed significantly from 0.5 are indicated by circles, others by squares.

Neither published estimates of ASR in birds nor their absolute deviation from 0.5 differed significantly between studies in which bias was likely to be low (because a high proportion of the study population was sexed) and studies in which no account was taken of potential bias (Mann–Whitney U -test, $P > 0.05$). Estimates of ASR did not differ systematically with the three main methods (catching or trapping, direct observation or other) used to generate them (Kruskal–Wallis test, $P > 0.05$). There was no significant difference in estimates of ASR or their absolute deviation from 0.5 between studies whose primary interest was ASR and those in which ASR was of secondary or incidental interest (Mann–Whitney U -test, $P > 0.05$), and a funnel plot did not demonstrate extreme asymmetry around the mean (Fig. 6).

Causes and predictors of ASR variation

Given the generally balanced offspring sex ratio, a skewed ASR can only be explained by higher mortality of the rarer sex. Survival rates of female birds appear to be systematically lower than those of males (Searcy & Yasukawa 1981, Promislow *et al.* 1992, Sillett & Holmes 2002, Liker & Székely 2005, Githiru & Lens 2006b), and a number of studies have empirically demonstrated lower survival of the rarer sex, generally the female, as the cause of skew in ASR in birds (Richdale 1957, Shreeve 1980, Burger *et al.* 1995, Blums & Mednis 1996, Gerlach & Le Maitre 2001, Woolfenden *et al.* 2001, Gardner *et al.* 2003, Githiru & Lens 2006b, Székely *et al.* 2006). In a small number of cases, the mechanism of higher female mortality was also identified. For example, female-biased predation of Blackbirds

Turdus merula by Sparrowhawks *Accipiter nisus* was related to significant differences between the sexes in foraging rates and methods, and led to a male-skewed ASR (Post & Götmark 2006). Given the generally balanced offspring sex ratios demonstrated above, this sexual difference in survival rates makes male-skewed ASR inevitable. Skewed ASRs also result from higher mortality of the rarer sex, rather than from skewed sex ratios at birth, in mammals (Owen-Smith 1993, Berger & Gompper 1999, McCullough 1999, Bryja *et al.* 2005, Christe *et al.* 2006) reptiles (Girondot & Pieau 1993, Aresco 2005), fish (Morley *et al.* 2004, Olsen *et al.* 2006) and insects (Stoks 2001).

There are a number of reasons for expecting a sexual difference in avian survival rates. Males and females differ physiologically, ecologically, genetically and behaviourally. In most bird species, females are the more dispersive sex (Greenwood & Harvey 1982, Clarke *et al.* 1997), exposing them to greater risk as they leave the natal area and disperse across unfamiliar territory (Steiffetten & Dale 2006). Moreover, in migratory species, the smaller sex, generally females, tends to migrate further than the larger (Kjellen 1994, Stouffer & Dwyer 2003, Catry *et al.* 2005). During breeding, incubation tends to be undertaken largely or wholly by the female, entailing both increased metabolic demands (Thomson *et al.* 1998) and greater risk of predation. For example, Sargeant *et al.* (1984) demonstrated significantly non-random predation on nesting waterfowl by Red Fox *Vulpes vulpes* in the Dakotas, where the percentage of females among the corpses removed from Fox dens varied between species from 64 to 90%. This high predation of incubating females probably accounts for the significantly male-skewed ASR in North American wildfowl (Bellrose *et al.* 1961, Baldassarre & Bolen 1994). Even cavity-nesting birds, with their generally lower rates of predation, might be prone to high female mortality during incubation, and the proportion of nest predation events that result in the death of the female may be high (Lundberg & Alatalo 1992, O'Donnell 1996). Significant sexual differences in foraging behaviour and distribution, and in energy intake and expenditure, have been recorded in both sexually dimorphic and monomorphic species, leading to higher mortality in one sex (Gonzalez-Solis *et al.* 2000, Lewis *et al.* 2002, Phillips *et al.* 2004, Verhulst *et al.* 2004, Post & Götmark 2006). These may be at least partly driven by competitive exclusion from better habitats of smaller females by dominant males (Benkman 1997,

Marra & Holmes 2001, Pechacek 2006) but could also be adaptive (Morton 1990), allowing males and females to exploit different resources (Hedrick & Temeles 1989, Phillips *et al.* 2004). The mode of brain size evolution has differed between the sexes and many species have sexually size-dimorphic brains (Garamszegi *et al.* 2005). Because brain size is linked to adaptability (Sol *et al.* 2005), intraspecific sexual differences in brain size might lead to intraspecific sexual differences in survival. Relative brain size was found to be a significant predictor of long-term population trends across a range of European farmland species (Shultz *et al.* 2005),

Within birds and mammals, heterogamety is invariable; as far as is known, in all bird species the female is the heterogametic sex, and in all mammals the male. Within other vertebrate groups, however, the heterogametic sex varies within and between orders and families, and may be under environmental as well as genetic control (Kraak & Pen 2002). The unguarded Z chromosome in female birds, or X chromosome in male mammals, and the consequent expression of recessive mutations, might lead to higher mortality of the heterogametic sex (Trivers 1985, Breitwisch 1989, Liker & Székely 2005, Székely *et al.* 2006). In both birds and mammals, adult mortality appears higher in the heterogametic sex (Promislow 1992, Promislow *et al.* 1992, Liker & Székely 2005) and reflects systematic differences in ASR between the two groups (Fig. 3). Parasitic or infectious sex ratio distorters of invertebrate and, more rarely, vertebrate populations (Zakharov & Shaikevich 2001, Arnold *et al.* 2003, Dyson & Hurst 2004, Olsen *et al.* 2006) are undescribed from birds.

There are therefore many possible explanations for sex-biased survival in birds. Trivers (1972) suggested that the apparently high incidence of male-skewed ASRs in birds resulted from higher female reproductive effort, leading to lower survival, an assertion supported by Bennett and Owens (2002). However, Breitwisch (1989) suggested that higher female mortality in populations of birds with skewed ASR actually occurs before first breeding and during the non-breeding season, and is not related directly to reproductive input. Liker and Székely (2005) again challenged the assumption that lower female survival was the result of greater parental investment by females, given that variation in female care appeared unrelated to sexual differences in mortality. However, the appearance of a skewed ASR might be an inevitable step in the evolution from promiscuity with no parental care, the situation found in most

reptiles, to the social monogamy with parental care that typifies avian mating systems (Burley & Johnson 2002).

A number of studies have demonstrated trends in ASR across age cohorts, providing longitudinal evidence of increasingly skewed ASR with age. For example, Williams (1957) demonstrated a progressive change in California Quail *Callipepla californica* sex ratios from 0.28 in 6–9-week-old chicks, to 0.54 in 14–17-week-old birds, to 0.64 in adults. Similarly, Coulson (1960) found a shift in the sex ratio in juvenile Starlings *Sturnus vulgaris* from 0.46 immediately after the end of parental care to 0.63 during the first year. In a detailed long-term study of Yellow-eyed Penguins *Megadyptes antipodes*, Richdale (1957) noted that as cohorts grew older, so the lower annual survival of females caused the ASR to become increasingly skewed towards males (Fig. 7). A similar pattern has been demonstrated in another long-lived bird, the Wandering Albatross *Diomedea exulans*, in which ASRs in all but the oldest cohorts were balanced (Weimerskirch *et al.* 2005). Age at first breeding has been shown by a range of studies to be significantly earlier in females than in males, possibly a response to male-skewed ASR and perhaps further increasing female mortality (Olsson & van der Jeugd 2002).

While natural mortality in birds appears generally to be higher in females, human-induced mortality might be higher for males. Where this happens, for example through trophy hunting of male Great

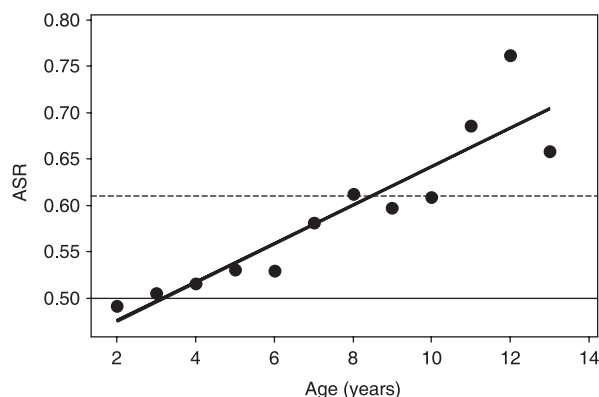


Figure 7. Adult sex ratio (ASR) variation across different age cohorts in a population of Yellow-eyed Penguins *Megadyptes antipodes*, drawn from data in Richdale (1957). The highest age class (13) includes a small number of individuals older than this. The ASR of the whole population was 0.61 (dotted line), significantly skewed from a balanced sex ratio (solid line). The significant positive correlation results from higher female mortality, possibly due to predation of incubating females by introduced mammals.

Bustards *Otis tarda* (Alonso *et al.* 2005), or higher accidental fisheries by-catch of male albatrosses (Awkerman *et al.* 2006), the ASR can become strongly female-skewed. Selective hunting of male Willow Ptarmigan *Lagopus lagopus* in winter balanced higher natural mortality of females during the breeding season, leading to a balanced ASR overall (Hannon *et al.* 2003). This pattern of persecution-induced ASR is more frequently encountered in mammals (Berger & Gompper 1999, Forsyth 1999, Solberg *et al.* 2005), and ASRs reach extremes (sometimes lower than 0.05) in species in which males have commercial value, such as elephants (Vidya *et al.* 2003). However, higher male mortality is also common in mammals that are not hunted (Promislow 1992).

Another mechanism proposed to explain generally male-skewed ASR in birds, particularly in isolated populations, is greater female postnatal dispersal (Dale 2001, Steifetten & Dale 2006), although this could also act through raising female mortality. There is good evidence for a general pattern of female-biased dispersal in birds, measured both as the proportion of individuals that move from the natal area and as the average distance moved (Greenwood & Harvey 1982, Gowaty 1993, Clarke *et al.* 1997, Dale 2001, Steifetten & Dale 2006). However, higher female natal dispersal might also lead to a female-skewed ASR in newly established or rapidly expanding populations, as has been demonstrated for gulls *Larus* in North America (Fry *et al.* 1987). Even in groups in which males are the more dispersive sex, such as the Anatidae (Gowaty 1993), male-skewed ASR can still predominate (Bellrose *et al.* 1961).

There might also be phylogenetic patterns in ASR. Male-skewed ASR might be common, for example, in honeyeaters (Meliphagidae) (Mayr 1939, McFarland & Ford 1987, Clarke *et al.* 2002) and wildfowl (Baldassarre & Bolen 1994; Table 1). In contrast, ASRs in gulls and terns (Laridae) appear to be regularly female-skewed (Conover & Hunt 1984, Fry *et al.* 1987, Nisbet & Spendelov 1999). In the 201 estimates of ASR collected for this review, ASR was not distributed randomly across orders (Table 1), the significant interaction resulting from the higher than expected number of female-skewed populations in the Apodiformes (within which all four species for which ASR estimates were available were hummingbirds, Trochilidae). When this small number of estimates from this order was removed, there was no association between ASR and order.

Another predictor of ASR appears to be the arrival time of long-distance migrants, in which protandry

(earlier male arrival) is a common phenomenon (Rubolini *et al.* 2004, Kokko *et al.* 2006). Recent models, backed by field observations, suggest that protandry is likely to be associated with, and may be the result of, male-skewed sex ratios, and that protogyny, the rarely observed earlier arrival of females, is only likely to occur when the sex ratio is balanced or female-dominated (Kokko *et al.* 2006, Amrhein *et al.* 2007). Annual variation in the time of male settlement might be related to variation in ASR (Neergaard & Arvidson 1995). However, protandry is also associated with levels of extra-pair paternity (Coppack *et al.* 2006) and sexual plumage dimorphism (Rubolini *et al.* 2004), both of which might also be related to the ASR.

Studies of temporal or spatial variation in ASR within species are rare. There is evidence that in some species at least, even skewed ASRs might exhibit stability. Examination of subfossil cave remains of the critically endangered Kakapo *Strigops habroptilus* suggested that the extremely male-skewed ASR evident in today's remnant population was also evident in populations pre-dating the arrival of people in New Zealand (Trewick 1997). In invertebrates, extremely skewed ASRs may persist over hundreds of generations (Dyson & Hurst 2004, Perotti *et al.* 2004).

Spatial variation in ASR has been documented in the Brown-headed Cowbird *Molothrus ater*, from balanced in eastern USA to heavily male-skewed (0.66) in western USA, possibly because of declining quality in wintering conditions (Woolfenden *et al.* 2001). ASR in the Dickcissel *Spiza americana* became increasingly male-skewed away from the centre of its range, where it was balanced, and also varied between habitats (Fretwell & Calver 1970). Temporal changes in ASRs have been recorded in declining populations of Capercaillie *Tetrao urogallus* (Helle *et al.* 1999, Wilkinson *et al.* 2002). In an analysis of museum skins of a number of sexually monomorphic North American gulls *Larus*, Conover and Hunt (1984) documented a significant change in the ASR from 0.52 before 1940 to 0.45 after 1950. These authors dismissed previous claims that this was due to feminization of male embryos by DDT poisoning and instead hypothesized that it was due to reduced male survival, although the reasons for this were not identified.

Female-skewed ASRs, the most common pattern in mammals, appear rare in birds, and were recorded in just 19 (9.5%) studies of 14 species. Within this small sample there was consistency within species;

all three estimates of ASR in Great Bustard were significantly female-biased (possibly because of trophy hunting of males), as were both estimates of ASR for Ostrich *Struthio camelus* and Wilson's Phalarope *Phalaropus tricolor* and two of four estimates for Capercaillie. All these species have unusual mating systems, with lekking in two species and high male parental care in the other two. Female-skewed ASRs were also significantly over-represented in the hummingbirds (Table 1), another group that often exhibits lekking or harem behaviour. It may be therefore that species that exhibit breeding behaviours that resemble those more commonly found in mammals might also exhibit ASRs more similar to those recorded in mammals (Fig. 1). However, significant female skew was also recorded in the ASR of a number of species that exhibit the socially monogamous mating systems and high female parental care more typical of birds.

ASRs, offspring sex ratios and avian mating systems

In the studies of offspring sex ratio collected in the database, only 16% demonstrated a sex ratio signifi-

cantly differing from equality, compared with the 65% reported in adult populations, and absolute departures from a sex ratio of 0.5 were significantly greater in ASRs than in offspring sex ratios (Fig. 3). Some studies published estimates of offspring sex ratio and ASR for the same study populations (Table 2). These show that offspring sex ratios may be positively related, negatively related or unrelated to ASRs, but that the most frequently recorded pattern was, as predicted, a balanced offspring sex ratio and a male-skewed ASR. Estimates of offspring and ASRs from different populations of the same species support this; for example, offspring sex ratios in wildfowl (Anatidae) in North America are generally balanced (Blums & Mednis 1996), whereas ASRs are generally male-skewed (Baldassarre & Bolen 1994). Even within closely related species, the offspring and ASRs can be positively or negatively related. Three co-operatively breeding Australian miner *Manorina* species make an interesting comparison; in all three species, the ASR was significantly male-skewed, whereas the offspring sex ratio was variously male-skewed, female-skewed or balanced (Table 2). How ASR influences offspring

Table 2. Relationship between adult sex ratio (ASR) and offspring sex ratio from studies in which both were measured in the same population. Data from Diamond (1973), Reyer (1980), Shreeve (1980), Curry and Grant (1989), Ligon and Ligon (1990), Major (1992), Russell and Rowley (1993), Lindsey *et al.* (1995), Arnold *et al.* (2001), Ewen *et al.* (2001), Fancy *et al.* (2001), Clarke *et al.* (2002), McIntosh *et al.* (2003), Doutrelant *et al.* (2004), Legge *et al.* (2004), Sandercock *et al.* (2005) and Weimerskirch *et al.* (2005).

	ASR		
	Male-skewed	Balanced	Female-skewed
Offspring sex ratio			
Male-skewed	Bell Miner <i>Manorina melanophrys</i> 'Ôma'o <i>Myadestes obscurus</i>	Wandering Albatross <i>Diomedea exulans</i>	
Balanced	Palila <i>Loxioides bailleui</i> White-fronted Chat <i>Epthianura albifrons</i> Eclectus Parrot <i>Eclectus roratus</i> Grey-crowned Rosy Finch <i>Leucosticte tephrocotis</i> Kentish Plover <i>Charadrius alexandrinus</i> Little Grassbird <i>Megalurus gramineus</i> Noisy Miner <i>Manorina melanocephala</i> Pied Kingfisher <i>Ceryle rudis</i>	Galapagos Mockingbird <i>Nesomimus parvulus</i> Splendid Fairy-wren <i>Malurus splendens</i> Sociable Weaver <i>Philetairus socius</i>	Green Woodhoopoe <i>Phoeniculus purpureus</i>
Female-skewed	Black-eared Miner <i>Manorina melanotis</i> Magnificent Frigatebird <i>Fregata magnificens</i>		

sex ratio is unclear, though studies of the Great Reed Warbler *Acrocephalus arundinaceus* suggest that females do not vary their offspring sex ratio in relation to local ASR (Bensch *et al.* 1999).

Breitwisch (1989) suggested that there has been a general supposition that unbalanced ASRs are the result, rather than the cause, of different mating systems. However, there is evidence that mating systems may be flexible, and dictated by the ASR, and that mating system is a major determinant of the effective population size in populations with skewed sex ratios (Nomura 2002). For example, a detailed 11-year ringing study of Galapagos Mockingbird *Nisomimus parvulus* demonstrated considerable annual variation in the ASR (Curry & Grant 1989). In this highly variable environment, the ASR ranged from 0.39 to 0.64, and mating systems varied accordingly. In years where the ASR skew towards males was high, a higher proportion of males became nest helpers. In years where the ASR was skewed towards females, all females were able to breed as the shortage of males was compensated for by polygyny. Similarly, Song Sparrows *Melospiza melodia* were monogamous in years when there was an excess of males but tended towards polygyny when the ASR approached or fell below 0.5 (Smith *et al.* 1982). A number of other species demonstrate flexible mating systems that respond causally to ASR, including Spotted Sandpiper *Actitis macularia* (Oring *et al.* 1983), Kaka *Nestor meridionalis* (Greene & Fraser 1998), Lesser Spotted Woodpecker *Picoides minor* (Wiktander *et al.* 2000, Rossmanith *et al.* 2006), Blue Tit *Cyanistes caeruleus* (Kempnaers 1994), Louisiana Waterthrush *Seiurus motacilla* (Mulvihill *et al.* 2002) and Bicknell's Thrush *Catharus bicknelli* (Goetz *et al.* 2003). Extrinsic factors, such as an enforced period of monogamy or synchronous nesting, might preclude polygyny even where the skew in the ASR lowers the polygyny threshold (Tershy & Croll 2000). Where variation in ASR does not influence the incidence of polygyny or polyandry, it may significantly affect parental investment patterns (Burley & Calkins 1999), increase mate-guarding behaviour by males (Major 1992) and result in a population of non-breeding male 'floaters' (Githiru *et al.* 2006). Flexibility in mating systems might buffer populations from the increased extinction risk associated with skewed ASR (Rossmanith *et al.* 2006), and much of the variation in mating systems observed in birds might be a simple response to variation in the ASR caused by other factors. The ASR, or more specifically the OSR, might provide a useful empirical estimate of the intensity of sexual

selection (Emlen & Oring 1977, Kvarnemo & Ahnesjö 1996, Wiegmann & Nguyen 2006) or the relative annual reproductive success of males and females (Murray 1991, Clutton-Brock & Parker 1992, Castro *et al.* 2004, Gerber 2006).

Care needs to be taken when ascribing a particular form of breeding behaviour to ASR, as mating system might be independent. For example, Ridpath (1972) noted a high incidence of mate sharing in a male-skewed population of Tasmanian Native-hen *Gallinula mortierii* and assumed a causal link, but Goldizen *et al.* (2002) described the same behaviour in populations of the same species in which there was no skew in the ASR. Polyandry and polygyny can both occur in populations with balanced ASRs (Valle 1995).

The majority of bird species are socially monogamous (Cockburn 2006). A male-skewed ASR might promote monogamy and male-male competition, as a single female would be of great value to a male in a system where females are in short supply (Ligon 1999). In kiwi *Apteryx* spp., the normal pattern of high mate fidelity appears to break down when the ASR becomes female-skewed, leading to a reduction in territoriality and high rates of mate switching (Taborsky & Taborsky 1999). Skewed ASRs have also been implicated in high rates of divorce in other species (Choudhury 1995), and might also lead to higher rates of hybridization (Whittam 1998) and to abnormal behaviour, such as the formation of same-sex 'pairs' (Conover & Hunt 1984). It might also drive evolutionary processes; in a study of Great Frigatebirds *Fregata minor*, a species unusual in that the males are highly ornamented but also share in all aspects of parental care, Dearborn *et al.* (2001) documented only a single extra-pair fertilization. The authors suggested that a heavily male-skewed ASR might create sufficient variance between males in mating success to drive the evolution of male sexual ornaments.

A male-skewed ASR has also been suggested as a necessary condition for co-operative breeding, which occurs in between 3 and 9% of bird species (Bennett & Owens 2002, Cockburn 2006). In the Eclectus Parrot, a scarcity of females and a scarcity of tree nesting holes may enforce co-operative breeding in males (Heinsohn & Legge 2003). If ASR is important in driving co-operative breeding, the proportion of nest helpers in a population should vary with ASR (Brown 1987). However, a study of the Splendid Fairy Wren *Malurus splendens* showed that there was no correlation between the ASR and the proportion

of groups with nest helpers (Rowley & Russell 1990). In the 15 studies of co-operative breeders included in the review, nine had a male-skewed ASR, five a balanced ASR and one a female-skewed ASR, a distribution not greatly different from that found across all species.

Sex ratios and conservation

The general relationship between global conservation threat status and level of skew in ASRs appears not to have been described previously. The heavily skewed ASRs in populations of Globally Threatened Species suggests that their extinction risk could be higher, and their reproductive population sizes lower, than currently estimated. Theoretical models incorporating Allee effects predict that in monogamous mating systems the extinction probability of small populations is likely to be lowest when the sex ratio is balanced, and in polygynous systems extinction risk is lowest when the ASR is female-skewed (Bessa-Gomes *et al.* 2004). Extinction risk is not distributed symmetrically either side of an ASR of 0.5, and in both breeding systems is predicted to increase more rapidly with increasingly male-skewed ASR than with female-skewed ASR. Such patterns have been demonstrated in population viability analyses; estimates of population persistence of Little Bustard *Tetrax tetrax* populations in Spain were more sensitive to shortages of females than to shortages of males (Morales *et al.* 2005). The same authors predicted that population viability would start to decline when the ASR rose above 0.55, whereas even at sex ratios of 0.1, population survival probability remained over 90%. Studies of mammals also suggest that significant additional mortality of males through trophy hunting is sustainable (Langvatn & Loison 1999). Heavily skewed ASRs also appear to be common in the populations of threatened and declining species in non-avian taxa (Frankham & Wilcken 2006). For example, a sex ratio of 0.63 in an isolated Tuatara *Sphenodon guntheri* population is seen as a major threat, particularly as global warming is likely to skew the sex ratio further, as sex determination in reptiles is temperature-dependent (Nelson *et al.* 2002). Similarly, there is a heavily skewed ASR (0.69, a male skew unusual in mammals) in the small remaining population of the Northern Hairy-nosed Wombat *Lasiornhinus krefftii* (Banks *et al.* 2003) and in small, isolated populations of otherwise common rock-wallabies *Petrogale* spp. (Eldridge *et al.* 1999). Population collapse of a Yellow Perch *Perca flavescens* population in Lake Michigan was accompanied by

an ASR of 0.99 (Marsden & Robillard 2004). There is even evidence in the fossil record of a correlation between extinction risk and ASR (Berger *et al.* 2001).

Heavily skewed ASRs might pose further threats to small populations. A skewed ASR might explain higher levels of sexual selection in threatened than in non-threatened bird species (Morrow & Pitcher 2003), with potentially harmful consequences. The best documented example of this effect comes from a study of Common Lizards *Lacerta vivipara* (Le Galliard *et al.* 2005a), which found that a male-skewed ASR led not to the expected increase in productivity of females able to choose the best mates, but to increased female mortality and reduced fecundity through aggressive competition by males. This amplified the male skew in the ASR, leading to rapid population collapse. The authors concluded that this potential Allee effect might operate when breeding carries substantial costs for the female and when the ASR is skewed towards males, conditions that appear to be met by a high proportion of threatened bird species. Several examples of this effect have been noted in wild bird populations. Aggressive nest intrusions by unpaired males, resulting in egg loss or infanticide, have been noted in male-skewed populations of the Humboldt Penguin *Spheniscus humboldti* (Taylor *et al.* 2001) and the Nazca Booby *Sula granti* (Anderson *et al.* 2004). Similar adverse consequences of exaggerated sexual selection resulting from heavily skewed ASRs have also been documented in threatened mammals (Hiruki *et al.* 1993, Gilmartin & Eberhardt 1995), amphibians (Byrne & Roberts 1999) and fish (Magurran & Seghers 1994), and in invertebrates in which the ASR is skewed by parasitic infection (Charlat *et al.* 2007). At the opposite extreme, it is possible that an excess of males is required to stimulate pair formation or breeding through group courtship (Aldrich 1973).

At present, it is not clear why threatened populations should exhibit such highly skewed ASRs, but there are at least five, non-independent, possibilities: (1) Heavily skewed ASRs in threatened populations may represent one end of a general correlation between population trend or density and sex ratio, the mechanism of which is unknown (though it might be related to any of the following possibilities). Such a relationship has been documented in at least one globally threatened bird, the Seychelles Magpie Robin *Copsychus sechellarum* (Gerlach & Le Maitre 2001), and similar patterns have been noted in other species of birds (Oring *et al.* 1983, Fry *et al.* 1987, Nadal *et al.* 1996, Helle *et al.* 1999, Wilkinson *et al.*

2002), mammals (Fortier *et al.* 2000, Solberg *et al.* 2005) and reptiles (Hailey & Willemsen 2000, Smith & Iverson 2006). However, this relationship is complicated by the increased stochastic variation in ASR estimates as populations decline.

(2) ASR skew in small populations might represent an effect of inbreeding, leading to the spread of deleterious alleles. Where such alleles reside on the sex chromosomes, it could be that their lethal effects have a greater impact on the heterogametic females and contribute to their generally higher mortality (Breitwisch 1989, Lee *et al.* 2002, Liker & Székely 2005), and its effect might be greater in small populations through inbreeding. However, distortions in the ASR are not a consistent signal of inbreeding depression (Marr *et al.* 2006) and inbreeding has been predicted to reduce the numbers of the homogametic sex (Frankham & Wilcken 2006), the opposite of the direction observed. In other taxa, a heavily skewed ASR has been shown to entail rapid loss of genetic diversity (Briton *et al.* 1994, Eldridge *et al.* 1999) and may exacerbate, or result from, inbreeding depression and asymmetric gene flow, contributing to the likelihood of extinction (Mills & Smouse 1994, Eldridge *et al.* 1999, Telschow *et al.* 2006). Where this further increases skew in the ASR, rapid population collapse might occur.

(3) It is possible that threatened populations have become so because they face a shortage of resources. If this is the case, then it might be that the generally larger males outcompete females for scarce resources (Marra 2000, Pechacek 2006, Donald *et al.* 2007), possibly reducing their survival (Benkman 1997, Marra & Holmes 2001). Similarly, increasing intra-sexual competition for resources in a recovering population of Tuatara might explain the greater degree of long-term loss of body condition in females and the heavily male-skewed ASR (Hoare *et al.* 2006).

(4) Many globally threatened species are confined to small and isolated populations, in which male-skewed ASR is a common phenomenon (Dale 2001). Higher female dispersal, a common pattern among birds (see above), might bring about male-skewed ASRs through the dispersal of females into an unsuitable and largely unoccupied habitat matrix (Steifetten & Dale 2006). Furthermore, the immigration of females from other areas is likely to be limited in isolated populations.

(5) A high proportion of threatened bird species owe their poor conservation status to the effects of introduced predators, which may reduce populations of naïve native birds in non-random ways, with greater predation of incubating females. The predation

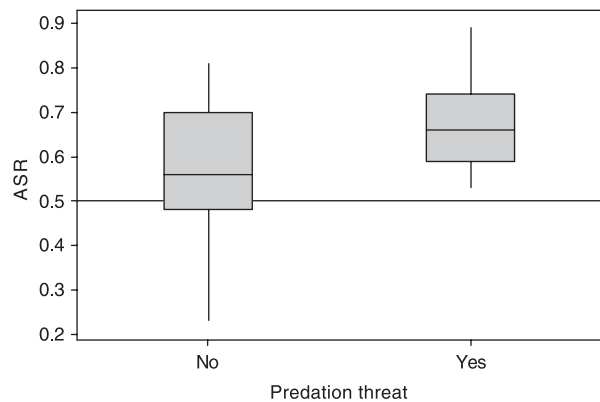


Figure 8. ASR of Globally Threatened Species for which introduced predators are listed as a major threat and of Globally Threatened Species for which they are not. Threats were taken from www.birdlife.org/datazone/species/index.html. The difference was statistically significant (Mann–Whitney *U*-test, $P < 0.05$). Interpretation of the bars is as in Figure 3.

hypothesis has some support from published studies, threatened species for which introduced predators are listed by the IUCN as a severe threat having significantly more skewed ASRs on average than other threatened species (Fig. 8). Mainland populations of New Zealand's endangered Kaka, exposed to a variety of introduced predators, have a strongly male-skewed ASR of 0.74, and occasionally up to 0.88, whereas populations of the same species on predator-free islands have a balanced ASR (Greene & Fraser 1998). The arrival of rats *Rattus* on Big South Cape Island, New Zealand, in 1964 led to rapid skew in the ASR of the last remaining native population of the South Island Saddleback *Philesturnus carunculatus carunculatus*, which slipped from 0.66 to 0.8 in a single year (Merton 2004). In contrast, populations of the same subspecies established on rat-free islands had a balanced ASR (D. Merton pers. comm.). Male skew in the ASR of the endangered Kokako *Callaeas cinerea* changed from 0.9 in 1989 before predator control to 0.6 in 1996 after predator control, with a consequent increase in productivity (Greene & Fraser 1998). Similar returns to more balanced ASRs following predator removal were documented for the Mohua *Mohoua ochrocephala* (Dilks 1999), the North Island Robin *Petroica australis longipes* (Powlesland *et al.* 1999) and the Kakapo (Merton 1999). Predation of incubating females by introduced predators has been suggested as the most likely cause of male-skewed ASR in other threatened species (Lindsey *et al.* 1995, O'Donnell 1996) and in non-threatened species (Nadal *et al.* 1996).

The ASR is a potentially useful demographic in guiding conservation efforts. As well as improving estimates of effective population size, viability and possibly trend, the ASR might provide a useful metric of habitat suitability. Intensive studies of the threatened Chatham Island Black Robin *Petroica traversi* (Butler & Merton 1992) suggested that rapid habitat degradation led to increased exposure of nests to predators and competitors, resulting in higher female mortality and a male-skewed ASR. In good quality habitats, male and female survival was more similar and the ASR balanced. Similarly, Sun *et al.* (2003) considered that an ASR of 0.68 in Chinese Grouse *Bonasa sewerzowi* was the result of habitat degradation caused by fragmentation, and forest fragmentation was also implicated in changes in ASRs in Capercaillie populations in Finland (Helle *et al.* 1999). Fragmentation has been shown to influence ASR in other bird species (Zanette 2001), mammals (Estrada *et al.* 2002, Banks *et al.* 2005) and amphibia (Prohl 2002). However, Sodhi (2002) found that sex ratios did not differ between forest fragments and continuous forests, and Githiru and Lens (2006a) could find no effect of fragment size on ASR.

The ASR might also be a useful metric in guiding reintroduction programmes. Attempts to translocate the threatened Ōma'o *Myadestes obscurus* ran into problems when the donor population was found to have a strongly male-skewed ASR (Fancy *et al.* 2001), and skewed ASRs might arise rapidly in translocated populations (Mumme & Below 1999). Population viability analysis, incorporating ASR, of a small and isolated population of the Red-cockaded Woodpecker *Picoides borealis* suggested that the population stood the best chance of long-term survival if the number of females introduced each year was higher than the number of males (Haig *et al.* 1993). Reintroduction projects that aim to release females to balance skewed ASRs in wild populations may need first to establish why the ASR is skewed, otherwise the released females might not live long enough to fulfil the purposes of their reintroduction. In heavily managed populations it might be possible to correct male-skewed ASRs by manipulating offspring sex ratios (Wildt & Wemmer 1999, Clout *et al.* 2002, Pike & Petrie 2003), the short-term risks of increased inbreeding being outweighed by the long-term benefits of increased population growth (Wedekind 2002). The further implications of offspring sex allocation for conservation are discussed elsewhere (Ewen *et al.* 2001, Clout *et al.* 2002, Sutherland 2002, Wedekind 2002, Linklater 2003, Robertson *et al.* 2006).

The ASR is clearly an important and largely overlooked parameter in the conservation and monitoring of threatened populations. The possibility exists that populations with a highly skewed ASR might become functionally extinct, with the death of the last female, many years before the death of the last male brings about total extinction. In the case of the Dusky Seaside Sparrow *Ammodramus maritimus nigrescens* in Florida, the last six known individuals were all males. The last female was seen in 1975, and the last male died in captivity in 1987; the deaths of last known representatives of each sex were therefore separated by 12 potential generations. A number of potential generations also separated the deaths of the last female and male South Island Saddlebacks on Big South Cape Island in New Zealand, though fortunately translocation of birds to rat-free islands saved the form from extinction (Bell & Merton 2002). Of the last 12 known Heath Hens *Tympanuchus cupido cupido*, only two were females, and the last few individuals seen before its extinction in 1932 were all males. The last 25 Kakapo located on mainland New Zealand in the 1960s and 1970s were all males (Merton 1999). In sexually monomorphic species, the disappearance of females may be difficult to discern, as in the absence of females, males may form same-sex 'pairs', and even build nests; such behaviour was recorded from relict Kokako populations in New Zealand in which females had been totally extirpated by introduced predators (I. Flux pers. comm.). The management of critically endangered populations, and analyses of their viability, should routinely include assessment of a species' ASR (Lens *et al.* 1998, Ewen *et al.* 2001, Donald *et al.* 2005, McCartney *et al.* 2006).

Problems and bias in sex ratio estimation

It is perhaps easy to understand why the majority of published studies on avian sex ratios confine themselves to offspring sex ratios. Not only is this an interesting area of research in the field of evolutionary ecology, it is a relatively easily measured demographic. Estimates are generally unbiased, as they represent the complete clutches or broods, and chemical analysis of genetic material (which can be collected non-invasively; Handel *et al.* 2006) means that individuals can be sexed without error (Griffiths *et al.* 1996). Variation in offspring sex ratios can be discretely related to biometric measurements or other qualities of their parents, their parents' behaviour or the local environment, and revisiting nests allows estimation

of differential chick growth and mortality rates. Chicks in the nest are easily colour-ringed for future measurement and monitoring. In contrast, ASRs are difficult to estimate in an unbiased way. As noted above, the two sexes of any particular species differ in a large number of ways in their behaviour and ecology, making it difficult to sample individuals in an unbiased way. This bias has been demonstrated empirically (Domenech & Senar 1998, Vanderkist *et al.* 1999).

Even where estimates of ASR can be collected in an unbiased way, for example by sexing every individual in the study population, explaining their variation is extremely difficult. ASR may vary seasonally, spatially or between age groups, and may require specific definitions about what constitutes an adult. Studies of long-lived birds have demonstrated varying ASR across age cohorts (Fig. 7). Unless demographic processes can be quantified at every stage, it is impossible to relate observed variation in ASR to factors such as mortality or emigration.

It is likely that the relative lack of interest in ASR results at least partly from the difficulty of obtaining unbiased estimates of it and that the development of a simple and robust method of estimating it in the field will stimulate an increase in research into ASR variation. Less biased methods of assessing ASR might include genetic analyses of non-invasively collected samples such as faecal droppings (Banks *et al.* 2003, Dallas *et al.* 2003, Eggert *et al.* 2003, Vidya *et al.* 2003) or shed feathers (Rudnick *et al.* 2005), removal experiments (Marra & Holmes 1997, Marra 2000) or molecular sexing of prey remains or carcasses (Dallas *et al.* 2003, Nebel *et al.* 2004). Furthermore, if skews in ASR result solely from differential mortality between the sexes, estimates of the difference between male and female survival might explain most of the variation in ASR.

Whether the general pattern of male skew in ASR results entirely from bias in estimation cannot be determined, though there are a number of reasons for assuming it is not. ASR estimated from studies in which potential bias was not considered did not differ from those estimated from populations in which most or all individuals were sexed, and which were therefore likely to be unbiased. Furthermore, if estimates of ASR in wild populations are biased, it is unclear why such a bias should operate in opposite directions in birds and mammals. Balanced offspring sex ratios, estimated without bias, and equally unbiased estimates of higher female mortality, make the overall pattern of male-skewed ASR in birds inevitable.

Estimates of sex ratio appear to be particularly prone to publication bias, compounded by a general lack of true replication (Palmer 2000), with non-significant departures from the 'expected' ratio of 0.5 less likely to be submitted or accepted for publication than those demonstrating significant deviations. Publication bias can be subtle; it is interesting to note that the majority of published studies of offspring sex ratio showed no significant departure from overall equality, suggesting that a general acceptance of adaptive sex allocation theory means that a lack of deviation from the expected binomial distribution is seen as a publishable finding. The extent to which publication bias is responsible for the general apparent male-skew in avian ASR is difficult to assess, though if sex ratios were distributed around a mean of 0.5, there appears to be no reason why publication bias should favour male-skewed ASRs over female-skewed ASRs. Furthermore, among the sample of published estimates identified in this review, ASR from studies that were not primarily about sex ratios did not differ from those from studies in which sex ratio was the main focus. A funnel plot (Fig. 6) suggested that estimates given in this review were not simply the result of publication bias.

CONCLUSIONS

This review supports previous assertions that skewed ASRs are common in wild bird populations, and are probably the result of differential mortality between the sexes rather than skewed offspring sex ratios. Skews in ASR have implications for ecology, monitoring and conservation. An important finding was that Globally Threatened Species tend to have particularly skewed ASRs, with a number of implications for their conservation. The review also highlights the paucity of our knowledge of ASR and its variation. In addition to needing more descriptive information on the frequency of sex ratio skew, a number of key questions arise from this review:

- (1) To what extent does offspring sex ratio manipulation influence the ASR, and vice versa?
- (2) Can ASR variation be explained entirely by sexual differences in adult mortality?
- (3) To what extent are behaviours such as polygyny and nest-helping the result of skewed sex ratios, and to what extent the cause?
- (4) To what extent is ASR phylogenetically determined?
- (5) How stable are ASRs in space and time?
- (6) How strong is the relationship between ASR and population trajectory and what are its drivers?

(7) Why are skewed ASRs so prevalent in populations of threatened species, and how can knowledge of skewed ASR help conserve them?

(8) How can ASR and its variation be estimated in an unbiased way?

It is hoped that this review will reawaken interest in the ASR and its practical applications, and that it will encourage researchers to attempt to answer some of these questions.

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