Parental care and adaptive brood sex ratio manipulation in birds

Dennis Hasselquist[1] and Bart Kempenaers[2*]

[1]*Department of Animal Ecology, Lund University, Ecology Building, 223 62 Lund, Sweden,*
(*dennis.hasselquist@zooekol.lu.se*)
[2]*Reproductive Biology and Behaviour Group, Research Centre for Ornithology of the Max Planck Society, Postfach 1564, D-82305 Starnberg (Seewiesen), Germany*

Under many circumstances, it might be adaptive for parents to bias the investment in offspring in relation to sex. Recently developed molecular techniques that allow sex determination of newly hatched offspring have caused a surge in studies of avian sex allocation. Whether females bias the primary brood sex ratio in relation to factors such as environmental and parental quality is debated. Progress is hampered because the mechanisms for primary sex ratio manipulation are unknown. Moreover, publication bias against non-significant results may distort our view of adaptive sex ratio manipulation. Despite this, there is recent experimental evidence for adaptive brood sex ratio manipulation in birds. Parental care is a particularly likely candidate to affect the brood sex ratio because it can have strong direct effects on the fitness of both parents and their offspring. We investigate and make predictions of factors that can be important for adaptive brood sex ratio manipulation under different patterns of parental care. We encourage correlational studies based on sufficiently large datasets to ensure high statistical power, studies identifying and experimentally altering factors with sex-differential fitness effects that may cause brood sex ratio skew, and studies that experimentally manipulate brood sex ratio and investigate fitness effects.

Keywords: sex ratio; parental care; mating systems; birds; Aves

1. THE STUDY OF SEX ALLOCATION IN BIRDS

The fitness of an individual is determined both by parental genetic effects and by environmental effects during the nestling stage (and later in life). When genetic or environmental factors affect the fitness of sons and daughters differently, then it might be adaptive for the parents to manipulate the sex ratio of their brood in relation to these factors. This hypothesis of adaptive family-level sex ratio adjustment was originally presented by Trivers & Willard (1973) and has subsequently been the focus of much theoretical and empirical research (Charnov 1982; Frank 1990; Gowaty 1991; Hardy 1997; Sheldon 1998). There is now ample support for these theories of sex allocation in haplo-diploid parasitoids (e.g. Godfray 1994).

Our understanding of adaptive sex ratio manipulation in vertebrates, and in birds in particular, is hampered by three problems. First, most of the current sex allocation models fail to take into account the complexities of vertebrate sex determination and life histories (Pen & Weissing 2002a). Second, to test models of sex allocation strategies, detailed knowledge of the fitness functions for parents and offspring of both sexes is required (Leimar 1996; Koenig & Walters 1999; but see Pen & Weissing 2000). For the majority of populations these data are not available and they are not easily obtained (Lessells *et al.* 1996). Sheldon *et al.* (1998) discussed this problem and

suggested experiments to investigate the existence of sex-specific fitness differences in relation to environmental factors. Third, in birds there is as yet no low cost mechanism identified that would allow manipulation of the primary sex ratio (Krackow 1995, 1999), and modelling has suggested that even small costs of sex ratio control may overcome the adaptive value of adjusting the BSR (Pen *et al.* 1999). Adaptive sex ratio manipulation in birds has, therefore, been questioned (Williams 1979; Clutton-Brock 1986; Krackow 1999).

Until recently, another problem was the lack of good data on avian BSRs. Earlier studies relied on sex determination based on external differences (e.g. size or plumage) between the sexes in nestlings, restricting studies to sexually dimorphic species. Moreover, most of these studies measured the secondary BSR, i.e. the sex ratio around the time of fledging (Patterson *et al.* 1980; Burley 1981). This is problematic, because the sex ratio bias at fledging might be adaptive, but it might also be the by-product of differential mortality due to sexual size dimorphism (Cronmiller & Thompson 1981; Blank & Nolan 1983; Angelstam 1984; Clutton-Brock *et al.* 1985; Weatherhead & Teather 1991; Griffiths 1992), different requirements of male and female chicks (Dhondt 1970; Cooch *et al.* 1997), brood reduction (Howe 1976, 1977; Bortolotti 1986) or differential allocation of parental care to chicks of different sexes (Burley 1986; Clotfelter 1996). Thus, a sex ratio bias some weeks after hatching, or at fledging, does not necessarily mean that the primary sex ratio is adaptively biased. The problems of sexing small avian nestlings with any confidence have now been solved, due to

Phil. Trans. R. Soc. Lond. B (2002) **357**, 363–372
DOI 10.1098/rstb.2001.0924

363

the development of simple molecular sex identification techniques (e.g. Griffiths & Tiwari 1993; Griffiths *et al.* 1996; Ellegren & Sheldon 1997; Lessells & Mateman 1996, 1998). Therefore, the data needed to evaluate primary sex ratio manipulation in birds, i.e. sexing newly hatched young from complete egg clutches, can be obtained relatively easily, and recently there has been a rapid increase in the number of studies presenting data on BSR, particularly in passerine birds (Bensch 1999). Hence, data are rapidly becoming available which will make it possible to evaluate the generality of BSR manipulation, as well as which factors might affect BSRs. A problem, in this context, is that negative results, i.e. the lack of biased BSR or that no factor explains the observed BSR pattern, are hard to publish compared with studies finding such relationships. This potential publication bias may result in an exaggeration of the occurrence of adaptive sex ratio manipulation. When many studies are available, statistical techniques can be used to investigate the importance of this potential bias (Palmer 2000). However, such meta-analysis cannot be easily applied to the study of adaptive BSR manipulation for two main reasons. First, as discussed in the previous paragraph, it is difficult to make predictions about the relationship between an investigated factor and BSR. Second, it is unreasonable to assume that there would be a common effect size for all BSR studies. Hence, pooling studies and applying meta-analysis requires caution.

In theory, females (or parents) can manipulate their investment in male and female offspring in a number of ways. First, and most controversially, females could manipulate the primary sex ratio (i.e. bias the sex ratio of the ovulated eggs via a process taking place before or during ovulation). Second, the sex of offspring can be manipulated in relation to the order of laying (where early laid eggs are of one sex and later laid eggs are of the other sex). This primary sex ratio distortion can later be used as a basis for secondary sex ratio manipulation, for example, if chicks from first hatched eggs obtain more parental care. Third, females can exert sex-differential investment in eggs (i.e. sex-differential distribution of maternal effects). Fourth, females/parents can use sex-differential parental investment rules when provisioning chicks ('sex-biased favouritism'; Lessells 2002). With new techniques available to study primary BSR and different maternal effects (e.g. yolk testosterone, Schwabl (1996), Schwabl *et al.* (1997); yolk carotenoids, Blount *et al.* (2000); yolk antibodies, Smith *et al.* (1994)) it is now possible to investigate at which of these levels sex-biased investment occurs.

We must also seek to identify factors that, potentially, can have sex-specific effects on offspring fitness (see also Komdeur & Pen 2002). Such factors include those related to the quality of the parents, the quality of the external and social environment, and to the number and asymmetry among the offspring, and a list of such factors is presented in table 1. The aim of table 1 is to give an overview of factors which, in a broad sense, might reflect or influence parental care, that have been found (or predicted) to show a relationship with biased BSR. It is neither complete (i.e. not all studies are mentioned), nor does it include information on studies showing negative results.

We focus on how parental care might influence BSR manipulation in birds. It is well known that the amount (or quality) of parental care has strong direct effects on offspring fitness and if these effects are sex-biased, we might expect females to adaptively manipulate the BSR. An important assumption is that females are able to estimate the quantity or quality of parental care at the time when offspring sex is determined. The importance of parental care depends on the external environment during chick rearing (e.g. weather, food availability). Some of these environmental factors might be very hard to predict during, or just before, laying when offspring sex is determined. It is also possible that the male's ability to provide parental care reflects his genetic quality, with indirect effects on fitness (through genetically superior offspring). This may influence the optimal BSR if these effects are sex-specific, e.g. if sons of good providers are more attractive because they inherit genes that make them better providers.

The BSR might also influence the pattern of parental care provided by each sex (i.e. sex-biased parental care; Stamps *et al.* (1987); Lessells *et al.* (1998); Radford & Blakey (2000a)). For example, males may prefer to feed male-biased broods (Nishiumi 1998; Westerdahl *et al.* 2000). However, we will not discuss this issue further as sex-biased favouritism in parental care has been discussed in a recent review by Lessells (2002).

2. HOW TO INVESTIGATE ADAPTIVE BSR MANIPULATION IN RELATION TO PARENTAL CARE

When investigating relationships between parental care and BSRs, we suggest the following working schedule. (i) Test whether the population variance in sex ratios among broods differs from expectation under a binomial distribution. Investigate whether distortions from a binomial distribution occur in the primary and/or in the fledgling sex ratio (Burley *et al.* 1989; Weatherhead & Teather 1991; Cooch *et al.* 1997). If the BSRs in the population follow a binomial distribution, it could simply be that no adaptive sex ratio manipulation is occurring. However, it is not possible to exclude the occurrence of BSR manipulations, but that the resulting distribution does not differ from a binomial distribution (for example if early broods are male-biased, mid-season broods have equal BSRs, and late broods are female-biased). If distortions from a binomial distribution are found, then this requires an explanation, even if the factors under scrutiny (e.g. parental care) are not related to the BSR. (ii) Investigate whether and how the relative fitness of producing sons and daughters is affected by environmental conditions and parental care during the nestling phase (Sheldon *et al.* 1998). (iii) Investigate whether the BSR is adjusted according to the identified factors, both in correlative and experimental studies. Currently, only a few studies have investigated whether sex ratio manipulation does lead to increased fitness, even though some studies have presented data suggesting this (Appleby *et al.* 1997; Komdeur 1998). The long-term and inclusive fitness effects of the BSR are still unknown and experimental work in this area is urgently required (see also Komdeur & Pen 2002).

Table 1. Overview of factors that may directly (parental) or indirectly (environmental, social, and offspring) affect parental care and have been shown to relate to biases in avian BSRs.

factors that may affect parental care	references[a]
directly affecting parental care	
A. parental	
parental condition	48
parental age	37, 45
parental breeding experience	45
B. male	
male plumage colour	36, 37
male attractiveness	6, 7, 14
male survival	39
male body size	25
C. female	
female condition	4, 30
female age	3, 37
female breeding experience	18
female size	48
female harem status	31, 32, 35, 46, 47
indirectly affecting parental care	
A. environmental and social	
timing of breeding season	9, 10, 20, 26, 34, 37, 38, 42, 43, 44, 49
stress	28[†], 29
food availability or quality	1, 4, 8, 13, 22, 40, 41, 48
habitat quality	12, 21[†]
territory quality	23, 24
territory availability	23
number of helpers	24, 27
B. offspring	
sex-differential dispersal	15
sexual size dimorphism	2, 13, 20, 31, 32, 33, 35, 46
clutch size	11, 16, 17, 19, 26
hatching asynchrony	5, 26

[a] Key to references. (1) Appleby *et al.* 1997; (2) Bednarz & Hayden 1991; (3) Blank & Nolan 1983; (4) Bradbury & Blakey 1998; (5) Bradbury & Griffiths 1999; (6) Burley 1981; (7) Burley 1986; (8) Burley *et al.* 1989; (9) Daan *et al.* 1996; (10) Dijkstra *et al.* 1990; (11) Dijkstra *et al.* 1998; (12) Dhondt 1970; (13) Dzus *et al.* 1996; (14) Ellegren *et al.* 1996; (15) Fiala 1981; (16) Gowaty 1991; (17) Gowaty 1993; (18) Gowaty & Lennartz 1985; (19) Heinsohn *et al.* 1997; (20) Howe 1977; (21) Julliard 2000[†]; (22) Kilner 1998; (23) Komdeur 1998; (24) Komdeur *et al.* 1997; (25) Kölliker *et al.* 1999; (26) Lessells *et al.* 1996; (27) Ligon & Ligon 1990; (28) McGinley 1984[†]; (29) Myers 1978; (30) Nager *et al.* 1999; (31) Nishiumi 1998; (32) Nishiumi *et al.* 1996; (33) Oddie 2000; (34) Olsen & Cockburn 1991; (35) Patterson *et al.* 1980; (36) Sheldon *et al.* 1997; (37) Sheldon *et al.* 1999; (38) Smallwood & Smallwood 1998; (39) Svensson & Nilsson 1996; (40) Teather 1987; (41) Teather & Weatherhead 1988; (42) Tella *et al.* 1996; (43) Torres & Drummond 1999; (44) Weatherhead 1983; (45) Weimerskirch *et al.* 2000; (46) Westerdahl *et al.* 1997; (47) Westerdahl *et al.* 2000; (48) Wiebe & Bortolotti 1992; (49) Zijlstra *et al.* 1992. (†Theoretical studies.)

An important factor directly related to parental care is the difference in the costs of producing sons and daughters, which could have different effects on parental fitness. It is therefore important to investigate whether one sex is more costly to produce than the other, for example, because it has a higher metabolic rate (Teather & Weatherhead 1988; Krijgsveld *et al.* 1998), grows faster (Teather 1987) or begs more (Teather 1992). In some species, males are larger than females and this difference may already be visible in the nest (Patterson *et al.* 1980; Weatherhead & Teather 1991; Westerdahl *et al.* 2000), resulting in higher food requirements (Anderson *et al.* 1993; Krijgsveld *et al.* 1998). However, it need not always be true that the cost of producing offspring differs substantially between the larger and the smaller sex. For example, in nestling birds, sex dimorphism in body mass overestimates sex differences in energy requirements (Krijgsveld *et al.* 1998). Conversely, males and females may be similar in size, but one sex may still be more costly to produce. For

example, sons and daughters might differ in competitive ability (aggressiveness) for food delivered by the parents. Under adverse feeding conditions, the more aggressive sex might out-compete the less aggressive sex, leading to higher nestling mortality in the latter (e.g. Oddie 2000). Thus, both the number and the quality of offspring produced need to be considered. We would welcome further experimental tests where food availability and/or parental condition are manipulated (Kilner 1998; Nager *et al.* 1999) and the resulting sex-specific effects on nestling condition were investigated. An even stronger test is to manipulate the BSR and investigate fitness effects for the parents (Komdeur 1998; Lessells *et al.* 1998).

3. BSR MANIPULATION UNDER DIFFERENT PATTERNS OF PARENTAL CARE

We have derived predictions for patterns of BSR manipulation by grouping species based on their predomi-

nant pattern of parental care (table 2). Note that the patterns of parental care are closely connected to social mating systems, and we have used these two factors as a basis for the classification. Table 2 provides a summary of the predictions under different conditions of parental care as discussed.

(a) Uniparental and facultatively biparental care
(i) *Social polygyny*

In socially polygynous species where males do not provide any care at all, i.e. uniparental care systems, the BSR and female investment could be affected by territory, male and female quality. The fact that males breed with multiple females can be used to differentiate between effects of territory and male quality versus female quality. If the former two factors are important, one expects a high repeatability of BSR within males. If female quality is important, the dominance hierarchy within the harem might predict the BSR given that primary females of higher quality can afford to raise more offspring of the costlier sex whereas secondary females of lower quality produce an excess of the less costly sex.

Other socially polygynous species have facultative biparental care. In most cases, males feed almost exclusively at the first nest to hatch in the territory (Alatalo *et al.* 1981; Pinxten & Eens 1990; Yasukawa *et al.* 1990; Webster 1991; Johnson *et al.* 1993; Bensch & Hasselquist 1994; Sejberg *et al.* 2000). Thus, under the latter conditions and assuming that females are aware of their status, one would expect secondary females to produce more chicks of the sex whose fitness is least affected by the reduction in male care. Significant differences in BSRs between females of primary (male-biased BSR) and secondary (female-biased BSR) status have been demonstrated in three species: yellow-headed blackbird *Xanthocephalus xanthocephalus* (Patterson *et al.* 1980), oriental reed warbler *Acrocephalus orientalis* (Nishiumi *et al.* 1996; Nishiumi 1998), and great reed warbler *A. arundinaceus* (Westerdahl *et al.* 1997, 2000). In these species, sons weigh more than daughters and might therefore be more costly to produce. Moreover, in polygynous species, the fledging condition of a male might have a stronger effect on his future reproductive success than the fledging condition of a female. In other species, males use specific feeding rules for how to divide their care over the two (or more) broods. In passerines such as the pied flycatcher *Ficedula hypoleuca* (Lifjeld & Slagsvold 1989), the starling *Sturnus vulgaris* (Smith *et al.* 1994) and the blue tit *Parus caeruleus* (Kempenaers 1995), the amount of paternal care depends on the hatching interval between the clutches of the primary and secondary female. The secondary female obtains progressively less help the later her brood hatches relative to that of the primary female. All other conditions being equal, and assuming that parental care influences the BSR, the difference between the BSR of primary and secondary nests should then increase with the hatching interval. Two factors may confound the relationship between female status and BSR. (i) The quality of the secondary female might also be lower than that of the primary female. This would add to the 'poor environment' in the secondary brood. (ii) Independent of environmental quality, the timing of the breeding season could influence the optimal sex ratio (Daan *et al.* 1996), leading to a similar prediction

that secondary (later breeding) females would produce more daughters (given that sons are more costly to produce and that their fitness is more severely affected by a 'poor environment' late in the season than that of daughters). To test this, the BSR of secondary females could be compared with that of monogamous females breeding at the same time.

(ii) *Social polyandry*

In socially polyandrous species, males usually provide all or most of the care (incubation, feeding), but it is the female that can manipulate the primary BSR. Polyandrous species are interesting, because the same female produces several clutches with different males. This allows investigations of whether the BSR depends on the timing of the season, the individual female and/or on male (parental) quality. Polyandrous shorebirds would be particularly interesting, because variation in clutch size is minimal or absent (usually four eggs). We do not know of any published studies on BSRs in polyandrous species.

(b) Biparental care

Socially monogamous species are generally characterized by biparental care with an equal share of nestling provisioning by males and females. However, several factors have been shown to influence the amount of paternal care a female can expect. Male and female age (or breeding experience), condition and attractiveness could influence the quality of parental care and therefore the BSR (table 1). For example, if a female is paired to a high quality provider, she should produce more sons if this quality is heritable or if sons benefit more from better paternal care.

A male's attractiveness, based on his high quality as a provider, could influence selection on sex ratios in two ways. (i) Via indirect benefits, i.e. good providers produce sexy sons (Weatherhead & Robertson 1979, 1981) or sons that inherit the 'good genes' of the good provider. (ii) Via direct benefits, i.e. attractive males might feed less (Burley 1988), or more (Greig-Smith 1982; Hoi-Leitner *et al.* 1993; Buchanan & Catchpole 2000). If indirect benefits are important, one would intuitively predict that females mated to attractive males should produce more sons. However, Pen & Weissing (2002*b*) formally modelled this using an ESS approach and showed that the outcome depends on the mechanism of sexual selection underlying the evolution of male attractiveness. According to their models, females should produce more sons only under the good genes process of sexual selection, not under the Fisherian runaway process. Some empirical and experimental studies found evidence that females mated to attractive males produce more sons (zebra finch *Poephila guttata*, Burley (1982); collared flycatcher *Ficedula albicollis*, Ellegren *et al.* (1996); blue tit, Svensson & Nilsson (1996), Sheldon *et al.* (1999); great tit *Parus major*, Kölliker *et al.* (1999)). However, we do not know whether attractive males are good providers in any of these cases. Indirect benefits might also be offset against the direct costs of reduced paternal care, and this has been suggested to explain the lack of a relationship between male ornamentation and BSR in the barn swallow *Hirundo rustica* (Saino *et al.* 1999).

Table 2. Predictions of occurrence and expected direction of BSR manipulations under different parental care patterns. The main social mating system under which these care patterns occur is given in parentheses.

---

uni- or facultative biparental care (social polygyny)

(A) facultative biparental care
  males primarily help with feeding in the 1st nest to hatch on his territory
  1. male chicks larger and more costly to raise
    prediction: (i) primary females produce male-biased or no skew in BSR (depending on how costly sons are to produce and how much they benefit by higher parental investment relative to daughters)
    (ii) secondary (non-primary) females produce more daughters
  2. no sex differences in size and costs of raising chicks
    prediction: no primary BSR skew. Secondary females lay smaller clutches. Sex-differential chick mortality may still occur resulting in biased fledging sex ratios

(B) uniparental care
  no (or very limited) parental care provided by the male
  1. differences in territory (nest) quality
    prediction: all females in a harem produce more sons when breeding in high quality territories
  2. difference in female quality (dominance, condition)
    prediction: high quality (dominant) females produce more sons
  3. difference in male quality
    (i) male quality heritable to sons
    prediction: male-biased BSR
    (ii) male quality heritable to all offspring independent of sex
    prediction: no BSR skew
    (iii) male quality not heritable
    prediction: no BSR skew

---

biparental care (social monogamy)

(A) males differ in their ability to provide parental care
  1. females mated to a high quality provider of parental care
    (a) male parental care quality inherited by sons
    prediction: (i) similar survival of sons and daughters: male-biased BSR
    (ii) sons have lower survival than daughters: no BSR bias
    (b) male parental care quality not heritable
    prediction: (i) same fitness value of sons and daughters: no BSR bias
    (ii) sons have higher fitness value than daughters: male-biased BSR
  2. females mated to low quality provider of parental care
    (a) male parental care quality inherited by sons
    prediction: female-biased BSR
    (b) male parental care quality not heritable
    prediction: (i) same cost to produce sons and daughters: no BSR bias
    (ii) sons more costly to produce: female-biased BSR

(B) species with large size-dimorphism (e.g. raptors). sibling competition intense. Nestlings of large sex out-compete small sex for parental care
    prediction: (i) a consistently small-sex biased primary sex ratio to compensate for their higher nestling mortality
    (ii) a bias in favour of nestlings of the large sex during favourable conditions, e.g. high parental and/or territory quality (Olsen & Cockburn 1991)
    (iii) broods with all chicks of same sex (Newton 1986; Olsen & Cockburn 1991; Heinsohn et al. 1997)
    (iv) chicks of the smaller sex hatch first in broods with asynchronous hatching

---

(Continued)

Table 2. (*Continued*)

multi-individual care systems (helper systems)

only one sex stays and helps
   1. dense populations—territories limited
     (a) groups with no/few helpers

prediction:	BSR skew in favour of the helping sex because helpers substantially increase reproductive success (LRE; Emlen *et al.* 1986)

     (b) groups with (several) helpers already present

prediction:	(i) cost of dispersal lower than of staying BSR skew in favour of the dispersing sex because too many helpers decrease reproductive success (LRC; Clark 1978)
prediction:	(ii) Cost of dispersal higher than of staying BSR skew in favour of the staying sex because production of the dispersing sex would yield even lower reproductive success

   2. sparse populations—territories available

prediction:	BSR skew in favour of the dispersing sex because taking up a new territory is more rewarding than to stay and help (Pen & Weissing 2000)

(c) *Multi-individual care systems*

In cooperative breeders with helpers, chicks of one sex are often more likely to stay and help with parental care, whereas offspring from the other sex are more likely to disperse (Emlen 1997). Thus, the value of sons and daughters depends on the costs/benefits of obtaining another helper, which might be related to the quality of the territory (Komdeur *et al.* 1997). Females are expected to produce more of the helping sex if they benefit from the extra parental care, the so-called LRE hypothesis (Gowaty & Lennartz 1985; Emlen *et al.* 1986; Lessells & Avery 1987). The LRC hypothesis, on the other hand, predicts that when local resources are scarce (e.g. in a low quality territory), or when the number of helpers is already high enough to result in competition, females should produce more of the dispersing sex; when resources are abundant or there are no/few helpers, females should produce more of the helping sex (Clark 1978; Clutton-Brock & Iason 1986; Emlen 1997). In the Seychelles warbler *Acrocephalus seychellensis*, both the LRE and the LRC model have been supported (Komdeur *et al.* 1997; Komdeur 1998), and the LRE hypothesis also seems plausible in some other species of birds with helper systems (Gowaty & Lennartz 1985; Ligon & Ligon 1990; however, see Koenig & Walters (1999)). In general, we expect both the LRE and the LRC hypothesis to be working at the same time in most bird species with helper systems, because different groups are exposed differently to factors such as local competition and number of helpers already present in the group.

(d) *Paternity and parental care*

Theoretical models predict (at least under certain circumstances) and some empirical studies have shown, that paternal care is influenced by the real or perceived share of paternity a male achieves in the nest (see review by Sheldon 2002). Females might anticipate the reduction in paternal care and adjust the BSR accordingly. For example, if the genetic contribution from the extra-pair male is independent of offspring sex and sons suffer more from reduced care, one would predict that females engaging in EPFs produce more daughters. Moreover, if cuck-

olded males are less attractive, a female bias among the nestlings sired by the pair male is also predicted if sons sired by less attractive males have a lower fitness value.

If females seek EPF from attractive males to gain indirect benefits through their sons' higher attractiveness or quality, extra-pair young should be male-biased and females might provide more care for these broods (or specifically to the extra-pair sons). In a study of blue tits, extra-pair young were more likely to be males and they survived better as nestlings than nest mates sired by the pair male (Kempenaers *et al.* 1997). In other studies of passerines, however, there was no tendency for a male bias among extra-pair young (Westneat *et al.* 1995; Sheldon & Ellegren 1996; Westerdahl *et al.* 1997; Saino *et al.* 1999).

4. CASES WHERE EVIDENCE FOR ADAPTIVE SEX RATIO MANIPULATION IS LACKING

Many studies failed to find BSR manipulation despite adequate sample sizes (Newton & Marquiss 1979; Blums & Mednis 1996; Koenig & Dickinson 1996; Pagliani *et al.* 1999). Several studies show that effects may be present in some years, but not in others (Lessells *et al.* 1996; Radford & Blakey 2000b; see also review by Bensch (1999)). How can we explain these results? First, females might be unable to adjust their BSR even if it were to be adaptive. Given that the possible mechanisms for BSR manipulation in birds are likely to be costly, Krackow (1999) suggested that adaptive BSR manipulations should only evolve under circumstances where the benefits of such manipulations would be high. If so, this suggests that pathways with a direct effect on fitness, that is environmental factors and parental care, should be more likely to lead to the evolution of BSR manipulation than indirect pathways through the transmission of beneficial genes to offspring (see Kirkpatrick & Ryan 1990; Kirkpatrick & Barton 1997). In accordance with this, in great reed warblers, male help with nestling feeding was related to BSR skew whereas male attractiveness characteristics were not (Westerdahl *et al.* 1997, 2000). Similarly, in blue tits, female age and nest box area had stronger effects on BSR skew than male ultraviolet (UV) coloration (Sheldon *et*

al. 1999). Second, different factors might cause opposite selective pressures on the optimal BSR (e.g. attractive males providing less care, see Saino *et al.* (1999)). Third, environmental factors during chick rearing that are unpredictable during the determination of offspring sex (e.g. weather) might have such strong effects that females do better by not manipulating the BSR.

In birds, the sex of offspring often correlates with laying order (Howe 1976; Ankney 1982; Ryder 1983; Weatherhead 1985; Bortolotti 1986; Edmunds & Ankney 1987; Dijkstra *et al.* 1990; Olsen & Cockburn 1991; Bednarz & Hayden 1991; Clotfelter 1996; Dzus *et al.* 1996; Leroux & Bretagnolle 1996; Heinsohn *et al.* 1997; Kilner 1998; Albrecht 2000; Velando *et al.* 2000). This may be a side effect of other (e.g. hormonal) factors that are altered during the laying sequence. However, it may also be a mechanism for adaptive BSR manipulation (Krackow 1999). In birds with clutches larger than a single egg, the last eggs in the clutch often do worse when compared to the first eggs (e.g. fledgling mass is often inversely related to hatching order), particularly in situations where parental food provisioning is a limiting factor. Under such circumstances, females might be expected to produce males first, if fledging mass influences fitness of sons more than that of daughters. A recent study on house wrens (*Troglodytes aedon*) indeed showed that last-hatched offspring (most probably hatched from last-laid eggs) were more likely to be females and were fledging in poorer condition relative to their siblings (Albrecht 2000). This suggests adaptive BSR manipulation to produce last-hatched chicks of the smaller, cheaper sex. Alternatively, one could argue that the last-hatched offspring should be of the more competitive sex, because they might still be able to compete for food even with larger siblings of the less competitive sex in the nest (Bednarz & Hayden 1991; Dzus *et al.* 1996; Oddie 2000; see also table 2). However, to convincingly show that biased BSRs in relation to laying sequence are adaptive, nestling translocation experiments need to be performed. For example, one could create broods with a size hierarchy among the nestlings, so that the larger ones are males and the smaller ones females, and vice versa.

5. CONCLUSIONS AND FINAL REMARKS

From being a topic frustrating researchers due to notorious problems with collecting reliable data, the recent developments in molecular techniques, which allow fast and easy sex determination of most or all bird species, now open up a fruitful and exciting research area. The number of studies on avian BSRs has increased dramatically over recent years and many factors have been reported to correlate with skews in BSRs (table 1). Nevertheless, there are a number of published studies that find no bias in BSR, and due to the problem of publication bias against non-significant results there are undoubtedly other such studies that remain unpublished. To get a better understanding of the general patterns and occurrence of BSR manipulation in birds, we encourage researchers to investigate BSR on large datasets. This is important because it increases the probability of detecting relatively small effects because the statistical power will be high enough to warrant publication of studies that find no evidence for BSR manipulation.

Despite problems with identifying mechanisms and finding consistent patterns of BSR manipulation in birds, some recent studies have presented convincing experimental evidence that it occurs. In these studies, manipulation of factors previously found to correlate with BSR skew have resulted in the predicted effect (e.g. female condition in gulls, Nager *et al.* (1999); male quality (crest feather colour) in the blue tit, Sheldon *et al.* (1999)). Another problematic issue has been the lack of consistency in relationships between a given factor and BSR skew between species (Bensch 1999; Krackow 1999). Cases where the same factors have been found to have similar effects on the BSR in different species are therefore very important. One such example is the consistent findings of BSR skew in relation to female harem status in socially polygynous birds (Patterson *et al.* 1980; Nishiumi *et al.* 1996; Nishiumi 1998; Westerdahl *et al.* 2000).

Three major challenges will determine the future of this field. First, we need to understand the mechanism by which females can manipulate BSR. Second, we need a better understanding of when BSR manipulation should be expected (theory), and when it occurs (data). Third, there is a need for long-term studies of fitness effects of BSR manipulation. We hope that this review will encourage researchers to conduct and publish studies based on large datasets, even when no skew in BSRs is found. This is essential to evaluate how common adaptive BSR manipulation is in birds and which factors underlie such manipulations.

REFERENCES

Alatalo, R. V., Carlson, A., Lundberg, A. & Ulfstrand, S. 1981 The conflict between male polygamy and female monogamy: the case of the pied flycatcher *Ficedula hypoleuca*. *Am. Nat.* **117**, 738–753.

Albrecht, D. J. 2000 Sex ratio manipulation within broods of house wrens, *Troglodytes aedon. Anim. Behav.* **59**, 1227–1234.

Anderson, D. J., Reeve, J., Martinez Gomez, J. E., Waethers, W. W., Hutson, S., Cunningham, H. V. & Bird, D. M. 1993 Sexual size dimorphism and food requirements of nestling birds. *Can. J. Zool.* **71**, 2541–2545.

Angelstam, P. 1984 Sexual and seasonal differences in mortality of black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scand.* **15**, 123–134.

Ankney, C. D. 1982 Sex ratio varies with egg sequence in lesser snow geese. *Auk* **99**, 662–666.

Appleby, B. M., Petty, S. J., Blakey, J. K., Rainey, P. & MacDonald, D. W. 1997 Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? *Proc. R. Soc. Lond.* B **264**, 1111–1116. (DOI 10.1098/rspb.1997.0153.)

Bednarz, J. C. & Hayden, T. J. 1991 Skewed brood sex ratio and sex-biased hatching sequence in Harris's hawks. *Am. Nat.* **137**, 116–132.

Bensch, S. 1999 Sex allocation in relation to parental quality. In *Proc. 22 Int. Ornithol. Congr. Durban* (ed. N. J. Adams & R. H. Slotow), pp. 451–466. Johannesburg: BirdLife South Africa.

Bensch, S. & Hasselquist, D. 1994 Higher rate of nest loss among primary than secondary females: infanticide in the great reed warbler? *Behav. Ecol. Sociobiol.* **35**, 309–317.

Blank, J. L. & Nolan, V. 1983 Offspring sex ratio in red-winged blackbirds is dependent on maternal age. *Proc. Natl Acad. Sci. USA* **80**, 6141–6145.

Blount, J. D., Houston, D. C. & Møller, A. P. 2000 Why egg yolk is yellow. *Trends Ecol. Evol.* **15**, 47–49.

Blums, P. & Mednis, A. 1996 Secondary sex ratio in Anatidae. *Auk* **113**, 505–511.

Bortolotti, G. R. 1986 Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* **127**, 495–507.

Bradbury, R. B. & Blakey, J. K. 1998 Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. *Proc. R. Soc. Lond.* B **265**, 895–899. (DOI 10.1098/rspb.199 8.0375.)

Bradbury, R. B. & Griffiths, R. 1999 Sex-biased nestling mortality is influenced by hatching asynchrony in the lesser black-backed gull *Larus fuscus*. *J. Avian Biol.* **30**, 316–322.

Buchanan, K. L. & Catchpole, C. V. 2000 Song as an indicator of male parental effort in the sedge warbler. *Proc. R. Soc. Lond.* B **267**, 321–326. (DOI 10.1098/rspb.2000.1003.)

Burley, N. 1981 Sex ratio manipulation and selection for attractiveness. *Science* **211**, 721–722.

Burley, N. 1982 Facultative sex-ratio manipulation. *Am. Nat.* **115**, 223–246.

Burley, N. 1986 Sex ratio manipulation in color-banded population of zebra finches. *Evolution* **40**, 1191–1206.

Burley, N. 1988 The differential-allocation hypothesis: an experimental test. *Am. Nat.* **132**, 611–628.

Burley, N., Zann, R. A., Tidemann, S. C. & Male, E. B. 1989 Sex-ratios of zebra finches. *Emu* **89**, 83–92.

Charnov, E. L. 1982 *The theory of sex allocation*. Princeton University Press.

Clark, A. B. 1978 Sex ratio and local resource competition in a prosomian primate. *Science* **201**, 163–165.

Clotfelter, E. D. 1996 Mechanisms of facultative sex-ratio variation in zebra finches (*Taeniopygia guttata*). *Auk* **113**, 441–449.

Clutton-Brock, T. H. 1986 Sex ratio variation in birds. *Ibis* **128**, 317–329.

Clutton-Brock, T. H. & Iason, G. R. 1986 Sex ratio variation in mammals. *Q. Rev. Biol.* **61**, 339–374.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1985 Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**, 131–133.

Cooch, E., Lank, D., Robertson, R. & Cooke, F. 1997 Effects of parental age and environmental change on offspring sex ratio in a precocial bird. *J. Anim. Ecol.* **66**, 189–202.

Cronmiller, J. R. & Thompson, C. F. 1981 Sex ratio adjustments in malnourished red winged blackbirds. *Auk* **97**, 559–565.

Daan, S., Dijkstra, C. & Weissing, F. J. 1996 An evolutionary explanation for seasonal trends in avian sex ratios. *Behav. Ecol.* **7**, 426–430.

Dhondt, A. A. 1970 The sex ratio of nestling great tits. *Bird Study* **17**, 282–286.

Dijkstra, C., Daan, S. & Buker, J. B. 1990 Adaptive seasonal variation in the sex ratio of kestrel broods. *Funct. Ecol.* **4**, 143–147.

Dijkstra, C., Daan, S. & Pen, I. 1998 Fledging sex ratios in relation to brood size in size-dimorphic altricial birds. *Behav. Ecol.* **9**, 287–296.

Dzus, E. H., Bortolotti, G. R. & Gerrard, J. M. 1996 Does sex-biased hatching order in bald eagles vary with food resources? *Ecoscience* **3**, 252–258.

Edmunds, S. R. & Ankney, C. D. 1987 Sex ratios of hatching mourning doves. *Can. J. Zool.* **65**, 871–874.

Ellegren, H. & Sheldon, B. C. 1997 New tools for sex identification and the study of sex allocation in birds. *Trends Ecol. Evol.* **12**, 255–259.

Ellegren, H., Gustafsson, L. & Sheldon, B. C. 1996 Sex allocation in response to paternal attractiveness in a wild bird population. *Proc. Natl Acad. Sci. USA* **93**, 11 723–11 728.

Emlen, S. T. 1997 When mothers prefer daughters over sons. *Trends Ecol. Evol.* **12**, 291–292.

Emlen, S. T., Emlen, J. M. & Levin, S. A. 1986 Sex-ratio selection in species with helpers-at-the-nest. *Am. Nat.* **127**, 1–8.

Fiala, K. L. 1981 Sex ratio constancy in the red-winged blackbird. *Evolution* **35**, 898–910.

Frank, S. A. 1990 Sex allocation theory for birds and mammals. *A. Rev. Ecol. Syst.* **21**, 13–55.

Godfray, H. C. J. 1994 *Parasitoids: behavioural and evolutionary ecology*. Princeton University Press.

Gowaty, P. A. 1991 Facultative manipulation of sex ratios in birds. Rare or rarely observed? *Curr. Ornithol.* **8**, 141–171.

Gowaty, P. A. 1993 Differential dispersal, local resource competition, and sex ratio variation in birds. *Am. Nat.* **141**, 263–280.

Gowaty, P. A. & Lennartz, M. R. 1985 Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. *Am. Nat.* **126**, 347–353.

Greig-Smith, P. W. 1982 Seasonal patterns of song production by male stonechats *Saxicola torquata*. *Ornis Scand.* **13**, 225–231.

Griffiths, R. 1992 Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. *Ibis* **134**, 237–244.

Griffiths, R. & Tiwari, B. 1993 The isolation of molecular genetic markers for the identification of sex. *Proc. Natl Acad. Sci. USA* **90**, 8324–8326.

Griffiths, R., Daan, S. & Dijkstra, C. 1996 Sex identification in birds using two CHD genes. *Proc. R. Soc. Lond.* B **263**, 1251–1256.

Hardy, I. C. W. 1997 Possible factors influencing vertebrate sex ratios: an introductory review. *Appl. Anim. Behav. Sci.* **51**, 217–241.

Heinsohn, R., Legge, S. & Barry, S. 1997 Extreme bias in sex allocation in *Eclectus* parrots. *Proc. R. Soc. Lond.* B **264**, 1325–1329. (DOI 10.1098/rspb.1997.0183.)

Hoi-Leitner, M., Nechtelberger, H. & Dittami, J. 1993 The relationship between individual differences in male song frequency and parental care in blackcaps. *Behaviour* **126**, 1–12.

Howe, H. F. 1976 Egg size, hatching asynchrony, sex, and brood reduction in common grackle. *Ecology* **57**, 1195–1207.

Howe, H. F. 1977 Sex ratio adjustment in the common grackle. *Science* **198**, 744–747.

Johnson, L. S., Kermott, L. H. & Lein, M. R. 1993 The cost of polygyny in the house wren *Troglodytes aedon*. *J. Anim. Ecol.* **62**, 669–682.

Julliard, R. 2000 Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionary stable offspring sex ratios. *Behav. Ecol.* **11**, 421–428.

Kempenaers, B. 1995 Polygyny in the blue tit: intra- and intersexual conflicts. *Anim. Behav.* **49**, 1047–1064.

Kempenaers, B., Verheyen, G. R. & Dhondt, A. A. 1997 Extra-pair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**, 481–492.

Kilner, R. 1998 Primary and secondary sex ratio manipulation by zebra finches. *Anim. Behav.* **56**, 155–164.

Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preference. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286.

Kirkpatrick, M. & Ryan, M. J. 1990 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Koenig, W. D. & Dickinson, J. L. 1996 Nestling sex-ratio variation in western bluebirds. *Auk* **113**, 902–910.

Koenig, W. D. & Walters, J. R. 1999 Sex-ratio selection in species with helpers at the nest: the repayment model revisited. *Am. Nat.* **153**, 124–130.

Kölliker, M., Heeb, P., Werner, I., Mateman, A. C., Lessells, C. M. & Richner, H. 1999 Offspring sex ratio is related to male body size in the great tit (*Parus major*). *Behav. Ecol.* **10**, 68–72.

Komdeur, J. 1998 Long-term fitness benefits of egg sex modification by the Seychelles warbler. *Ecol. Lett.* **1**, 56–62.

Komdeur, J. & Pen, I. 2002 Adaptive sex allocation in birds: the complexities of linking theory and practice. *Phil. Trans. R. Soc. Lond.* B **357**, 373–380. (DOI 10.1098/rstb.2001.0927.)

Komdeur, J., Daan, S., Tinbergen, J. & Mateman, A. C. 1997 Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* **385**, 522–525.

Krackow, S. 1995 Potential mechanisms for sex ratio adjustment in mammals and birds. *Biol. Rev. Camb.* **72**, 225–241.

Krackow, S. 1999 Avian sex ratio distortions: the myth of maternal control. In *Proc. 22 Int. Ornithol. Congr. Durban* (ed. N. J. Adams & R. H. Slotow), pp. 425–433. Johannesburg: BirdLife South Africa.

Krijgsveld, K. L., Dijkstra, C., Visser, G. H. & Daan, S. 1998 Energy requirements for growth in relation to sexual size dimorphism in marsh harrier *Circus aeruginosus* nestlings. *Physiol. Zool.* **71**, 693–702.

Leimar, O. 1996 Life-history analysis of the Trivers and Willard sex-ratio problem. *Behav. Ecol.* **7**, 316–325.

Leroux, A. & Bretagnolle, V. 1996 Sex ratio variations in broods of Montagu's harriers *Circus pygargus*. *J. Avian Biol.* **27**, 63–69.

Lessells, C. M. 2002 Parentally biased favouritism: why should parents specialize in caring for different offspring? *Phil. Trans. R. Soc. Lond.* B **357**, 381–403. (DOI 10.1098/rstb.2001.0928)

Lessells, C. M. & Avery, M. I. 1987 Sex-ratio selection with helpers at the nest: some extensions of the repayment model. *Am. Nat.* **129**, 610–620.

Lessells, C. M. & Mateman, A. C. 1996 Molecular sexing of birds. *Nature* **383**, 761–762.

Lessells, C. M. & Mateman, A. C. 1998 Sexing birds using random amplified polymorphic DNA (RAPD) markers. *Mol. Ecol.* **7**, 187–195.

Lessells, C. M., Mateman, A. C. & Visser, J. 1996 Great tit hatchling sex ratios. *J. Avian Biol.* **27**, 135–142.

Lessells, C. M., Oddie, K. R. & Mateman, A. C. 1998 Parental behaviour is unrelated to experimentally manipulated great tit brood sex ratio. *Anim. Behav.* **56**, 385–393.

Lifjeld, J. T. & Slagsvold, T. 1989 Allocation of parental investment by polygynous pied flycatcher males. *Ornis Fenn.* **66**, 3–14.

Ligon, J. D. & Ligon, S. H. 1990 Female-biased sex ratio at hatching in the green wood hoopoe. *Auk* **107**, 765–771.

McGinley, M. A. 1984 The adaptive value of male-biased sex ratios among stressed animals. *Am. Nat.* **124**, 597–599.

Myers, J. H. 1978 Sex ratio adjustment under food stress: maximization of quality or number of offspring. *Am. Nat.* **112**, 381–388.

Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson, R. 1999 Experimental demonstration that offspring sex ratio varies with maternal condition. *Proc. Natl Acad. Sci. USA* **96**, 570–573.

Newton, I. 1986 *The sparrowhawk.* Calton: Poyser.

Newton, I. & Marquiss, M. 1979 Sex ratio among nestlings of the European sparrowhawk. *Am. Nat.* **113**, 309–315.

Nishiumi, I. 1998 Brood sex ratio is dependent on female mating status in polygynous great reed warblers. *Behav. Ecol. Sociobiol.* **44**, 9–14.

Nishiumi, I., Yamagishi, S., Maekawa, H. & Shimoda, C. 1996

Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. *Behav. Ecol. Sociobiol.* **39**, 211–217.

Oddie, K. 2000 Size matters: competition between male and female great tit offspring. *J. Anim. Ecol.* **69**, 903–912.

Olsen, P. D. & Cockburn, A. 1991 Female-biased sex allocation in peregrine falcons and other raptors. *Behav. Ecol. Sociobiol.* **28**, 417–424.

Pagliani, A. C., Lee, P. L. M. & Bradbury, R. B. 1999 Molecular determination of sex ratio in yellowhammer *Emberiza citrinella* offspring. *J. Avian Biol.* **30**, 239–244.

Palmer, A. R. 2000 Quasireplication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *A. Rev. Ecol. Syst.* **31**, 441–480.

Patterson, C. B., Erckman, W. J. & Orians, G. H. 1980 An experimental study of parental investment and polygyny in male blackbirds. *Am. Nat.* **116**, 757–769.

Pen, I. & Weissing, F. J. 2000 Sex ratio optimization with helpers at the nest. *Proc. R. Soc. Lond.* B **267**, 539–544. (DOI 10.1098/rspb.2000.1034.)

Pen, I. & Weissing, F. J. 2002*a* Optimal sex allocation: steps towards a mechanistic theory. In *The sex ratio handbook* (ed. I. Hardy). Cambridge University Press (In the press.)

Pen, I. & Weissing, F. J. 2002*b* Sex allocation and sexual selection. *Selection* (In the press.).

Pen, I., Weissing, F. J. & Daan, S. 1999 Seasonal sex ratio trend in the European kestrel: an evolutionary stable strategy analysis. *Am. Nat.* **153**, 384–397.

Pinxten, R. & Eens, M. 1990 Polygyny in European starling: effect on female reproductive success. *Anim. Behav.* **40**, 1035–1047.

Radford, A. N. & Blakey, J. K. 2000*a* Intensity of nest defence is related to offspring sex ratio in the great tit *Parus major*. *Proc. R. Soc. Lond.* B **267**, 535–538. (DOI 10.1098/rspb.2000.1033.)

Radford, A. N. & Blakey, J. K. 2000*b* Is variation in brood sex ratio adaptive in the great tit (*Parus major*)? *Behav. Ecol.* **11**, 294–298.

Ryder, J. P. 1983 Sex ratio and egg sequence in ring-billed gulls. *Auk* **100**, 726–728.

Saino, N., Ellegren, H. & Møller, A. P. 1999 No evidence for adjustment of sex allocation in relation to paternal ornamentation and paternity in barn swallows. *Mol. Ecol.* **8**, 399–406.

Schwabl, H. 1996 Maternal testosterone in the avian egg enhances postnatal growth. *Comp. Biochem. Physiol.* A **114**, 271–276.

Schwabl, H., Mock, D. W. & Gieg, J. A. 1997 A hormonal mechanism for parental favouritism. *Nature* **386**, 231.

Sejberg, D., Bensch, S. & Hasselquist, D. 2000 Nestling provisioning in polygynous great reed warblers: do males bring larger prey to compensate for fewer nest visits? *Behav. Ecol. Sociobiol.* **47**, 213–219.

Sheldon, B. C. 1998 Recent studies of avian sex ratios. *Heredity* **80**, 397–402.

Sheldon, B. C. 2002 Relating paternity to paternal care. *Phil. Trans. R. Soc. Lond.* B **357**, 341–350. (DOI 10.1098/rstb.2001.0931.)

Sheldon, B. C. & Ellegren, H. 1996 Offspring sex and paternity in the collared flycatcher. *Proc. R. Soc. Lond.* B **263**, 1017–1021.

Sheldon, B. C., Merilä, J., Qvarnström, L., Gustafsson, L. & Ellegren, H. 1997 Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond.* B **264**, 297–302. (DOI 10.1098/rspb.1997.0042.)

Sheldon, B. C., Merilä, J., Lindgren, G. & Ellegren, H. 1998 Gender and environmental sensitivity in nestling collared flycatchers. *Ecology* **79**, 1939–1948.

Sheldon, B. C., Andersson, S., Griffith, S. C., Örnborg, J. &

Sendecka, J. 1999 Ultraviolet colour variation influences blue tit sex ratios. *Nature* **402**, 874–877.

Smallwood, P. D. & Smallwood, J. A. 1998 Seasonal shifts in sex ratios of fledgling American kestrels (*Falco sparverius paulus*): the early bird hypothesis. *Evol. Ecol.* **12**, 839–853.

Smith, H. G., Ottosson, U. & Sandell, M. 1994 Intrasexual competition among polygynously mated female starlings (*Sturnus vulgaris*). *Behav. Ecol.* **5**, 57–63.

Smith, N. C., Wallach, M., Miller, C. M. D., Morgenstern, R., Braun, R. & Eckert, J. 1994 Maternal transmission of immunity to *Eimeria maxima*: enzyme-linked immunosorbent assay analysis of protective antibodies induced by infection. *Infect. Immun.* **62**, 1348–1357.

Stamps, J. A., Clark, A., Kus, B. & Arrowood, P. 1987 The effect of parent and offspring gender on food allocation in budgerigars. *Behaviour* **101**, 177–199.

Svensson, E. & Nilsson, J. Å. 1996 Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond.* B **263**, 357–361.

Teather, K. L. 1987 Intersexual differences in food consumption by hand reared great-tailed grackles (*Quiscalus mexicanus*) nestlings. *Auk* **104**, 635–639.

Teather, K. L. 1992 An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behav. Ecol. Sociobiol.* **31**, 81–87.

Teather, K. L. & Weatherhead, P. J. 1988 Sex-specific energy requirements of great-tailed grackle (*Quiscalus mexicanus*) nestlings. *J. Anim. Ecol.* **57**, 659–668.

Tella, J. L., Donazar, J. A., Negro, J. J. & Hiraldo, F. 1996 Seasonal and interannual variations in the sex-ratio of lesser kestrels *Falco naumanni* broods. *Ibis* **138**, 342–345.

Torres, R. & Drummond, H. 1999 Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* **118**, 16–22.

Trivers, R. L. & Willard, D. E. 1973 Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–92.

Velando, A., Graves, J. & Freire, J. 2000 Sex-specific growth in the European shag *Stictocarbo aristotelis,* a sexually dimorphic seabird. *Ardea* **88**, 127–136.

Weatherhead, P. J. 1983 Secondary sex ratio adjustment in red-winged blackbirds (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.* **12**, 57–61.

Weatherhead, P. J. 1985 Sex ratios of red-winged blackbirds *Agelaius phoeniceus* by egg size and laying date. *Auk* **102**, 298–304.

Weatherhead, P. J. & Robertson, R. J. 1979 Offspring quality and the polygyny threshold: 'the sexy son hypothesis'. *Am. Nat.* **113**, 201–208.

Weatherhead, P. J. & Robertson, R. J. 1981 In defence of the 'sexy son' hypothesis. *Am. Nat.* **117**, 349–356.

Weatherhead, P. J. & Teather, K. L. 1991 Are skewed fledgling sex ratios in sexually dimorphic birds adaptive? *Am. Nat.* **138**, 1159–1172.

Webster, M. S. 1991 Male parental care and polygyny in birds. *Am. Nat.* **137**, 274–280.

Weimerskirch, H., Barbraud, C. & Lys, P. 2000 Sex differences in parental investment and chick growth in wandering albatrosses: fitness consequences. *Ecology* **81**, 309–318.

Westerdahl, H., Bensch, S., Hansson, B., Hasselquist, D. & von Schantz, T. 1997 Sex ratio variation among broods of great reed warblers *Acrocephalus arundinaceus*. *Mol. Ecol.* **6**, 543–548.

Westerdahl, H., Bensch, S., Hansson, B., Hasselquist, D. & von Schantz, T. 2000 Brood sex ratios, female harem status and resources for nestling provisioning in the great reed warbler *Acrocephalus arundinaceus*. *Behav. Ecol. Sociobiol.* **47**, 312–318.

Westneat, D. F., Clark, A. B. & Rambo, K. C. 1995 Within-brood patterns of paternity and paternal behavior in red-winged blackbirds. *Behav. Ecol. Sociobiol.* **37**, 349–356.

Wiebe, K. L. & Bortolotti, G. R. 1992 Facultative sex ratio manipulation in American kestrels. *Behav. Ecol. Sociobiol.* **30**, 379–386.

Williams, G. C. 1979 The question of adaptive sex ratio in outcrossed vertebrates. *Proc. R. Soc. Lond.* B **205**, 567–580.

Yasukawa, K., McClure, J. L., Boley, R. A. & Zanocco, J. 1990 Provisioning of nestlings by male and female red-winged blackbirds, *Agelaius phoeniceus*. *Anim. Behav.* **40**, 153–166.

Zijlstra, M., Daan, S. & Bruinenberg-Rinsma, J. 1992 Seasonal variation in the sex ratio of marsh harrier *Circus aeruginosus* broods. *Funct. Ecol.* **6**, 553–559.