

Sexual size dimorphism and offspring vulnerability in birds

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13.1 Introduction

Evolutionary theories trying to explain the existence and patterns of sexual size dimorphism (SSD) across taxa often focus on selection on body size at the adult stage, mainly driven by sexual selection acting on males or fecundity selection on females. However, the size dimorphism observed in adults can be determined not only by selection during adulthood (Blanckenhorn 2000), but also by selection on growth or size at earlier stages. It is therefore necessary to include ontogeny as an important period for determining final size dimorphism (e.g., Badyaev 2002; see also Chapters 7, 9, 19, and 20 in this volume).

Besides genetic constraints on how to achieve dimorphic growth while conserving the genes for the complete developmental programme in both sexes, physiological constraints during development can also limit final size. In sexually dimorphic species, size-related viability and health costs can become detectable as sex-biased effects. Increased mortality of the larger sex is the most extreme result, but other sub-lethal fitness effects can also be size- and sex-specific. A main focus in this respect is body mass, or size, of offspring, as this is often related to survival or probability of recruitment and regarded as a prime measure of offspring quality (Hochachka and Smith 1991; Potti *et al.* 2002). More recently, aspects of immunocompetence have been investigated as another measure of sex differences in physiological health and quality (Fargallo *et al.* 2002; Tschirren *et al.* 2003; Laaksonen *et al.* 2004; Bize *et al.* 2005; Chin *et al.* 2005; Müller *et al.* 2005a, 2005b). Although

mortality, body mass, and immunocompetence are very diverse aspects of development, sex-biased reductions in offspring quality or survival can all be seen as manifestations of some disadvantage of one sex during the growth period. Collectively, these and any other negative effects on offspring quality and fitness are referred to as offspring vulnerability.

Differential offspring survival in a size-dimorphic species was probably first observed in humans: male fetuses and infants have a higher risk of dying than females (e.g. Süßmilch 1765). Male bias in offspring mortality has also been documented in other mammals (Clutton-Brock *et al.* 1985) and birds (Roskaft and Slagsvold 1985; Teather and Weatherhead 1989; Griffiths 1992; Müller *et al.* 2005a, 2005b). Most of these species have in common that males are the larger sex. To achieve their larger size, males are likely to have higher energy demands during growth, which in turn might make them more vulnerable to a shortage of resources, leading to increased mortality.

Alternative, size-independent explanations have been proposed to explain the observed male-biased offspring vulnerability in many mammals and birds. The one that has received most attention is the male-phenotype hypothesis. Size-independent aspects of physiology, in particular the high levels of testosterone needed for male sexual differentiation, might negatively impact on other aspects of development, such as immunocompetence (Olsen and Kovacs 1996; Fargallo *et al.* 2002). In order to tease apart the importance of male phenotype compared with the size effect on

offspring mortality, it is necessary to include species where females are the larger sex.

In this chapter we will use recent studies of birds to explore patterns of sex-specific offspring vulnerability in relation to SSD in both directions; that is, female-biased as well as male-biased SSD. We will combine results on sex-specific offspring performance, and analyze mortality and plasticity of fledging mass in relation to SSD. If indeed size is the main reason for increased mortality of male offspring, then female offspring of species with female-biased SSD should experience similar disadvantages as males in species with male-biased SSD.

13.2 Measuring sex-biased offspring vulnerability in birds

Studies of sex-specific patterns of growth and mortality in birds have benefited hugely from the development of molecular sexing methods in the mid-1990s (Griffiths 1992; Ellegren 1996; Griffiths *et al.* 1998). Bird nestlings can usually not be sexed visually except in extremely size-dimorphic species, but even then only during the second half of the growth period (Cronmiller and Thompson 1980). A few earlier studies used laparotomy, a surgical incision of the abdomen, to inspect the gonads, but this could only be carried out in older chicks, not in hatchlings (Roskaft and Slagsvold 1985). Reports of sex-specific mortality between hatching and fledging could therefore not be based on individual fates. They were mostly inferred by comparing fledging sex ratios in nests with and without mortality (assuming equal hatching sex ratios in both nest categories), or by comparing fledging sex ratios with a sample of dissected clutches (Howe 1977). As avian hatching sex ratios are frequently skewed in relation to such variables as parental condition or social status, the progressing season or territory quality (e.g. Komdeur *et al.* 1997; Heg *et al.* 2000; Kalmbach *et al.* 2001), comparing hatching and fledging sex ratios between different sub-samples of nests can lead to wrong conclusions about sex-biased mortality.

The most widely reported measure of nestling mortality is the survival probability from hatching to fledging. Using the difference between hatching

sex ratio and fledging sex ratio as a measure for sex-specific mortality, a relationship between larger size and increased mortality was found across species with different degrees of SSD (Clutton-Brock *et al.* 1985). Sex differences in nestling mortality correlated with adult size dimorphism: the larger the males were in relation to females, the higher their survival disadvantage as nestlings. However, as only one species with female-biased size dimorphism was included in that review (which showed no sex bias in offspring mortality: Eurasian sparrowhawk, *Accipiter nisus*; Newton 1979), the size–mortality relationship therefore was shown only for species with larger males. Additionally, as the study dates before the advent of molecular sexing, its data suffer from the above-described methodological problems of obtaining true hatching and fledging sex ratios within the same nests. We will remedy this problem by employing strict selection criteria for the studies we include in our comparative analysis of nestling mortality (see Section 13.3.1).

Sex-biased mortality represents the extreme case of sex differences in offspring vulnerability. As mentioned above, growth rate and size at fledging are also regarded as a measure of offspring performance. Because of its likely negative impact on future life stages, reduced size at fledging is seen as a manifestation of non-optimal conditions during ontogeny (Hochachka and Smith 1991; Haywood and Perrins 1992; Potti *et al.* 2002). Assuming that under ideal conditions individuals will grow to the maximum possible size (given their species, genes, and sex), the degree of size reduction under suboptimal conditions gives an indication of how much the growing organism was struggling.

Considering that the larger sex is likely to have a higher energy demand during growth than the smaller one, we would predict that during periods of scarce resources the larger sex would be affected disproportionately. To test this prediction, we will compare fledging mass of males and females under varying circumstances (Section 13.3.2). We use mass rather than some structural measure of size, such as wing or tarsus length, for two reasons. Body mass is probably the easiest of those measures to record in the field, and is the one most frequently reported in publications. Second, our

choice of mass reflects the fact that for birds adult SSD is most commonly reported as the dimorphism in mass.

13.3 Comparative analysis of SSD and nestling vulnerability

The modulation of vulnerability differences between the two sexes by environmental conditions is referred to as sex-biased environmental sensitivity. It is generally assumed that poor conditions increase the disadvantage of the weaker sex. In order to investigate environmental sensitivity, comparisons of offspring performance under varying environmental conditions need to be made (Sheldon *et al.* 1998). Most simply, this can be a dichotomy between a "good" and a "poor" environment. Increasingly, these contrasting situations are created by experimental manipulation of the environment during ontogeny. Such experimental approaches include brood size increase and decrease, manipulation of parental condition and workload, provision of supplementary food, or changes of the parasite load (Richner 1992; Sheldon *et al.* 1998; Nager *et al.* 2000; Bize *et al.* 2005; Råberg *et al.* 2005). However, comparisons might also be made

between naturally occurring good and poor conditions, for example between first and last hatchlings in asynchronous broods or between seasons of abundant and low food availability (Wiebe and Bortolotti 1992; Brommer *et al.* 2003; Goymann *et al.* 2005). As restricting data to either experimental or observational studies would greatly reduce the number of available species, we included both types of study in the following comparative analyses.

To correct for the species' phylogenetic relatedness, we employed a comparative approach following the method of phylogenetically independent contrasts (Harvey and Pagel 1991; Garland *et al.* 1992). Contrasts were calculated using the program CAIC (Purvis and Rambaut 1995), and the phylogeny was taken from Sibley and Ahlquist (1990). All statistical results were obtained using this comparative method, and are reported in Table 13.1. However, for illustrative purposes we show species data, including species-level trend lines, in our graphs. These are more accessible because of their biologically interpretable values. Regression lines are only shown for those relationships for which a significant effect was found in the analysis based on phylogenetically independent contrasts.

Table 13.1 Regression results of sex-specific vulnerability against SSD, using phylogenetically independent contrasts. (a) Nestling mortality from hatching to fledging against SSD. The dependent variable was hatching sex ratio, fledging sex ratio, or sex-specific chick mortality (calculated as fledging sex ratio minus hatching sex ratio). (b) Intraspecific fledging mass change under good and poor conditions against SSD. The dependent measure was the mass-change difference (Δfm female– Δfm male; see text), mass-change difference for experimental studies only, male change only, or female change only. SSD is the independent variable in all models. Models are based on phylogenetically independent contrasts. For the analysis presented here we used the molecular phylogeny by Sibley and Ahlquist (1990). The results were qualitatively the same when using a morphological phylogeny. All regressions are forced through the origin. The analyses were run with the program CAIC (Purvis and Rambaut 1995). R^2 is the proportion of variance in the independent variable explained by the predictor variable; r is the Pearson correlation coefficient.

Dependent variable	No. of species	No. of contrasts	R^2	r	P
<i>(a) Nestling mortality</i>					
Hatching sex ratio	45	13	0.02	–0.14	0.622
Fledging sex ratio	45	13	0.09	–0.29	0.303
Sex-specific mortality	45	13	0.29	–0.54	0.047
<i>(b) Fledging mass change</i>					
Female–male difference	21	19	0.32	0.57	0.008
Female–male difference (experimental studies only)	14	13	0.40	0.63	0.015
Male change	21	19	0.25	–0.50	0.025
Female change	21	19	0.00	0.00	0.980

13.3.1 Sex-biased mortality and sex ratios

As highlighted above, for the following sex ratio and mortality analyses, we only used data from studies that report sex ratio at hatching *and* fledging from the same study nests. Sex-ratio data for the cross-species analysis were taken from observational studies or from experimental studies, in cases where the sex ratios between experimental and control treatments did not differ.

Across species, we found a negative correlation between sex-biased mortality and size dimorphism that was consistent for species with male-biased and female-biased SSD (Table 13.1). The larger of the two sexes appears to suffer greater mortality; that is, more females die as nestlings in species with larger females, and more males die in species with larger males. The survival disadvantage increases with increasing size dimorphism. In

other words, the larger sex always suffers higher mortality, indicating that to achieve a larger final body size both males and females pay a survival cost. On the species level, overall nestling mortality seemed slightly male-biased (Figure 13.1). This impression is supported by a negative average mortality value in the comparative analysis, suggesting that offspring survival was negatively affected by male-specific traits other than size.

Neither hatching nor fledging sex ratio showed a correlation with SSD (Table 13.1). At the population level, parents neither overproduced the smaller sex (as predicted by Fisher's (1930b) equal-investment sex-ratio theory) nor the larger sex to compensate for its higher mortality up to fledging. Despite the trend of increased mortality of the larger sex, and the unbiased hatching sex ratios, overall fledging ratios were not significantly biased

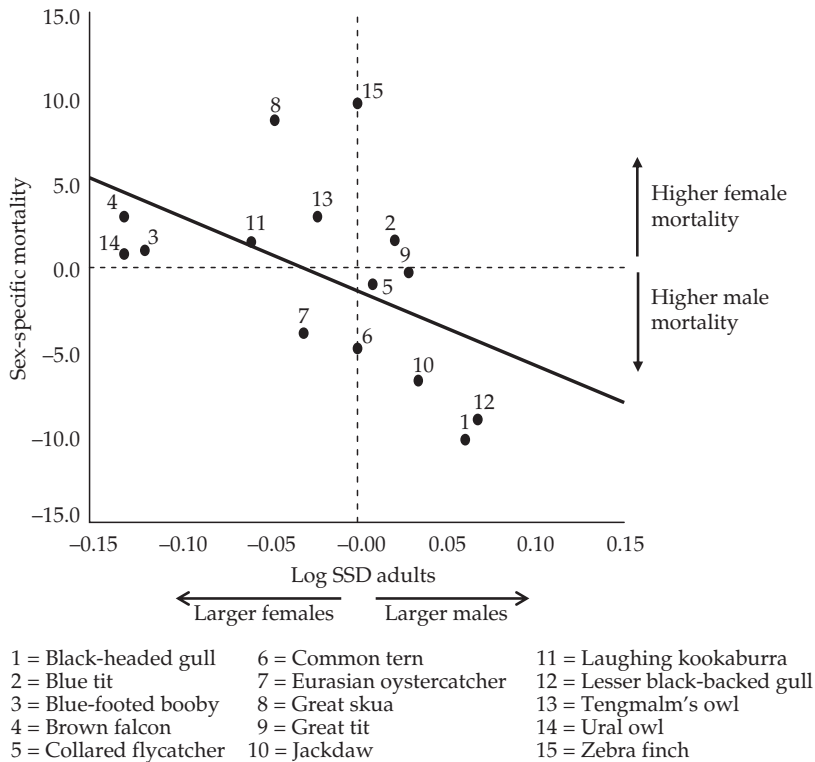


Figure 13.1 Relationship between SSD, calculated as $\log(\text{male adult weight}/\text{female adult weight})$ and sex-specific chick mortality, calculated as fledging sex ratio minus hatching sex ratio. Species references: 1, Müller *et al.* (2005b); 2, Råberg *et al.* (2005); 3, Torres and Drummond (1999); 4, McDonald *et al.* (2005); 5, Sheldon *et al.* (1998); 6, Gonzalez-Solis *et al.* (2005); 7, Heg *et al.* (2000); 8, Kalmbach *et al.* (2005); 9, Oddie (2000); 10, Arnold and Griffiths (2003); 11, Legge *et al.* (2001); 12, Griffiths (1992); 13, Hornfeldt *et al.* (2000); 14, Brommer *et al.* (2003); 15, Bradbury and Blakey (1998).

towards the smaller sex (Table 13.1). This is likely due to the high variation of sex ratios among species and the relatively small number of species we could include based on our methodological criteria.

13.3.2 Fledging mass

In the following cross-species analysis, we used data from studies which reported sex-specific fledging mass under two different conditions that could be classified as either good or poor. In most studies those conditions were created through experimental manipulations, although we also included data from observational studies reporting sex-specific fledging mass (see Table 13.2 for classification of good and poor conditions). For each sex we set the average fledging mass under good conditions as the reference value, and expressed the difference between that and fledging mass under poor conditions as a percentage of the reference mass. We will call this difference Δflm (delta fledging mass). As we are mainly interested in the difference between males and females with respect to their reaction to environmental conditions, we compared Δflm of males and females within each species. We subtracted Δflm of males from Δflm of females to obtain one value per species. When positive, this value indicates that males lose relatively more mass compared to females, whereas when this value is negative males lose relatively less mass. For example, the value of -10.6 for great skua (*Stercorarius skua*) means that males lost 10.6% less of their reference body mass than females during poor rearing conditions (Kalmbach *et al.* 2005).

Across species, and across both directions of size dimorphism, birds of the larger sex suffered a greater mass reduction under poor conditions (Table 13.1; Figure 13.2). For monomorphic species the fledging mass differences are clustered around 0. This suggests that in the absence of size dimorphism neither sex has a consistently higher vulnerability. The overall pattern could indicate that having to grow to a larger size under sub-optimal conditions is similarly difficult for males and females. However, when plotting Δflm for

males and females separately, we see that the pattern is mainly generated by a correlation between male fledging mass reduction and SSD (Figure 13.3). The more male-biased the SSD, the larger the impact of poor rearing conditions on male fledging mass, while female mass differences between good and poor conditions are independent of whether they are the larger or the smaller sex. This pattern remains when non-experimental studies are excluded from the data-set (Table 13.1).

Our results prompt an interesting consideration. The relative demands of having to grow large (for a given species) might not be as high as is generally assumed. Only in conjunction with the rest of the male phenotype does aiming for being large—that is, following a developmental program which leads to large size for a given species—appear to make the growing organism more vulnerable. Testosterone and its allies are much-cited candidates for mediating male vulnerability. Remarkably, in the species with the largest females and highest female mass loss (African black coucal), the breeding system is polyandrous. Although female behavior is ‘masculinized’, daughters’ testosterone levels are lower than those of sons and even lower than those of nestlings of other species (Goymann *et al.* 2005).

13.4 SSD and environmental sensitivity of immunocompetence

The immune system provides a potential link for life-history trade-offs (Sheldon and Verhulst 1996). It is relatively expensive to develop and maintain, but crucial for a successful life. Reduced immune capacity of nestlings is likely to indicate sub-optimal conditions during development when resources have to be invested in other parts of the growing organism. Recently, a few studies investigated sex-linked differences of immunocompetence in varying environmental conditions.

In two of four studies there was no differential decrease in immunocompetence under poor conditions (great tit and alpine swift, adult SSD 1.07 and 1.02, respectively; Oddie 2000; Bize *et al.* 2005). In food-restricted nests of Eurasian kestrels (adult SSD 0.78), the (smaller) males showed a slightly

Table 13.2 Circumstances representing good and poor conditions in the studies which were included in the cross-species analysis of fledging mass. Log SSD is $\log(\text{male adult mass}/\text{female adult mass})$; where available taken from the same study population, otherwise from reference literature. Type of study: obs, observational; exp, experimental.

Species	Log SSD	Type of study	Good/poor environment	Reference
Capercaillie, <i>Tetrao urogallus</i>	0.33	obs	Good against poor growth year due to temperature difference	Lindén (1981)
Helmeted guineafowl, <i>Numida meleagris</i>	-0.02	exp	Summer against winter rearing conditions	Baeza <i>et al.</i> (2001)
Lesser snow goose, <i>Anser caerulescens caerulescens</i>	0.06	obs	Seasonal environmental decline; earliest against penultimate category	Cooch <i>et al.</i> (1996)
African black coucal, <i>Centropus grillii</i>	-0.23	obs	Hatching order; "middle" against "late" chicks; earliest chicks were older at fledging	Goyman <i>et al.</i> (2005)
Alpine swift, <i>Apus melba</i>	0.01	exp	De-parasitized against parasitized broods	Bize <i>et al.</i> (2005)
Ural owl, <i>Strix uralensis</i>	-0.13	obs	Good and poor food years (vole cycles)	Brommer <i>et al.</i> (2003)
Great skua, <i>Stercorarius skua</i>	-0.05	exp	Control eggs against small replacement eggs	Kalmbach <i>et al.</i> (2005)
Lesser black-backed gull, <i>Larus fuscus</i>	0.06	exp	Control against poorer condition parents	Nager <i>et al.</i> (2000)
Black-headed gull, <i>Larus ridibundus</i>	0.06	exp	First against last hatched chick in all female and all male broods	Müller <i>et al.</i> (2005b)
Common tern, <i>Sterna hirundo</i>	0	obs	First against third hatched chicks	Becker & Wink (2003)
Eurasian kestrel, <i>Falco tinnunculus</i>	-0.07	exp	(a) Unisex broods in poor food years; (b) control against enlarged brood	(a) Laaksonen <i>et al.</i> (2004); (b) Dijkstra <i>et al.</i> (1990)
American kestrel, <i>Falco sparverius</i>	-0.06	obs	Good against poor food years	Wiebe & Bortolotti (1992)
Blue-footed booby, <i>Sula nebouxii</i>	-0.12	exp	Feather-clipping of mothers; chicks of control against chicks of clipped mothers	Velando (2002)
Carrion crow, <i>Corvus corone</i>	0.05	exp	Food-supplemented against un-supplemented nests in a food-limited population	Richner (1992)
Collared flycatcher, <i>Ficedula albicollis</i>	0.01	exp	Reduced against enlarged broods	Sheldon <i>et al.</i> (1998)
Great tit, <i>Parus major</i>	0.03	exp	Experimental nests of "large" and "small" nestlings; "large" against "small" nestlings	Oddie (2000)
Blue tit, <i>Parus caeruleus</i>	0.02	exp	Reduced against enlarged broods	Råberg <i>et al.</i> (2005)
Zebra finch, <i>Taeniopygia guttata</i>	0	exp	Abundant against restricted food	Kilner (1998)
Red-winged blackbird, <i>Agelaius phoeniceus</i>	0.21	exp	Control against enlarged broods	Cronmiller and Thompson (1980)
Boat-tailed grackle, <i>Quiscalus major</i>	0.29	obs	First against third hatched chicks	Bancroft (1984)
Great-tailed grackle, <i>Quiscalus mexicanus</i>	0.28	exp	Experimentally synchronized last hatchlings; having female nest mate against having male nest mate	Teather and Weatherhead (1989)

stronger decrease of cell-mediated immunity (CMI) than the (larger) females compared with control nests (Fargallo *et al.* 2002). CMI of male nestlings (larger sex) in large broods of European

starlings (adult SSD 1.05) also decreased more strongly than CMI of female nestlings compared to values in smaller broods (Chin *et al.* 2005). So far these studies have reported either no sex bias or a

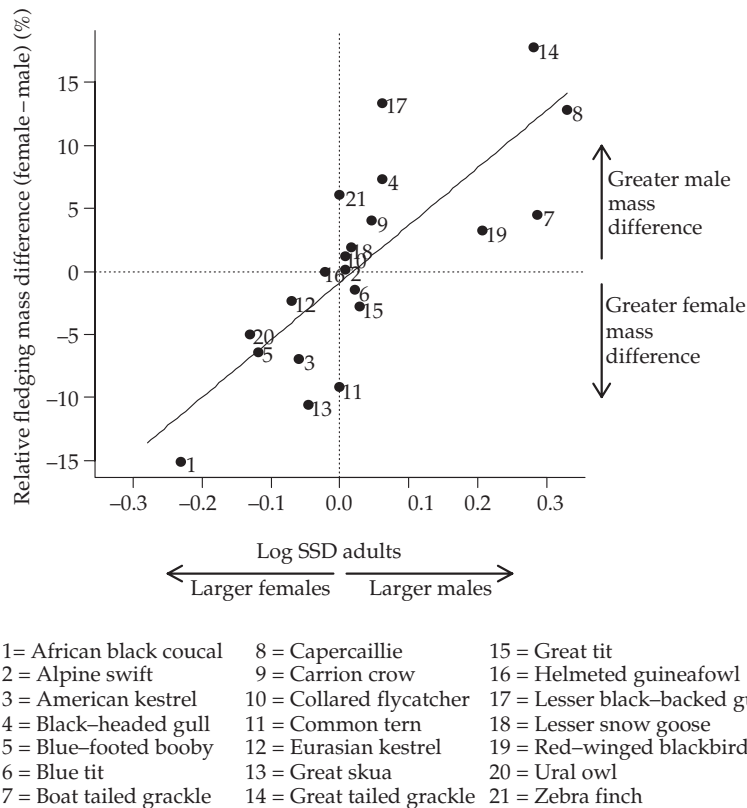


Figure 13.2 Relative change of fledging mass between good conditions and poor conditions against SSD, calculated as $\log(\text{male adult weight}/\text{female adult weight})$. Each species value is calculated as female difference ($\Delta f/m$ of females) minus male difference ($\Delta f/m$ of males). Negative values indicate that males lost relatively less mass than females; that females are more vulnerable. Positive values indicate that males lost relatively more mass than females; that males are more vulnerable. The relationship between sex-specific change of fledging mass and SSD is significant using phylogenetic contrasts ($P=0.008$; see Table 13.1). See Table 13.2 for references.

male bias, but no study has yet found decreased CMI for female nestlings. A second study of Eurasian kestrels, which investigated haematocrit as a measure of physiological condition, found a lower value for (larger) females under increased competition (Laaksonen *et al.* 2004).

The small number of studies and remaining controversy over the interpretation of CMI tests as well as hematocrit values make it clear that at this point no generalization about SSD and immunocompetence of fledglings can be made.

13.5 Intra-brood competition and size-related vulnerability

The dichotomy of good and poor conditions for reasons of comparison is of course a simplification

of the much more complex, naturally occurring situation. In reality, rearing conditions vary across a multitude of gradually changing and interacting factors, not just in two extremes (although the latter happens, to some extent, in experimental studies). So far we have assumed physiological disadvantages of large size, which could be regarded as intrinsic vulnerability of the larger sex. However, nestlings interact with each other and size is often implicated in the outcome of intra-brood competition. Following the terminology of intrinsic vulnerability, we will call growth and viability disadvantages that result from social interactions extrinsic vulnerability.

In contrast to intrinsic disadvantages, larger individuals generally have a competitive advantage at the behavioral, extrinsic level (Anderson

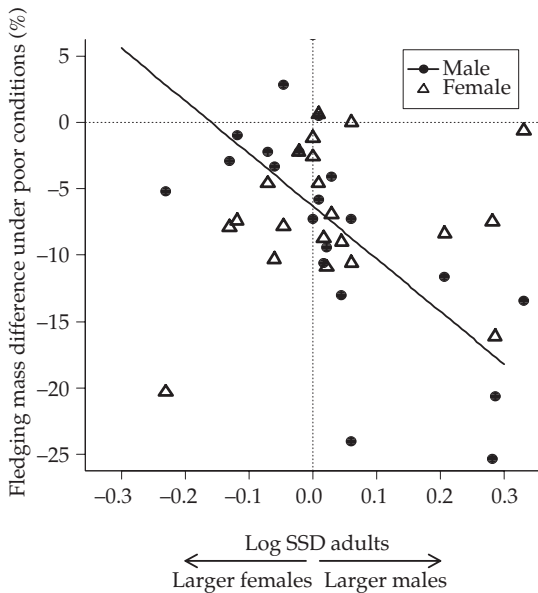


Figure 13.3 Relative difference of fledging mass between good and poor conditions against SSD, calculated as $\log(\text{male adult weight}/\text{female adult weight})$ for male and female nestlings separately. The regression, based on phylogenetic contrasts, is significant for male nestlings, but not for female nestlings ($P=0.025$ for males and $P=0.978$ for females; see Table 13.1).

et al. 1993). Oddie (2000) showed experimentally that increased mortality of the smaller female great tit nestlings was mainly due to their competitive disadvantage. Similarly, Råberg *et al.* (2005) found that female blue tit nestlings (again the smaller sex) suffered more (reduced fledging size). They suggested that brood size, as an indication of the strength of intra-brood competition, could explain part of the variation around the overall pattern. Besides brood size, sex composition, and size and age differences among nest mates determine within-brood dynamics and add another layer of complexity. Depending on the social circumstances, for example in large broods, the competitive disadvantage of the smaller sex can outweigh its physiological advantages.

13.6 Sex-biased vulnerability and the evolution of SSD

Our cross-species comparison highlights two aspects of size-related offspring vulnerability

that affect the extent of SSD exhibited in adult birds. First, across species there is a pattern that the larger sex has a viability disadvantage during ontogeny. This will cause a certain amount of viability selection during ontogeny against growing large. How strong this selection is will depend on many other aspects of each species' particular life history. For example it will be modulated by the ability of parents to adaptively skew primary sex ratios in response to environmental conditions, by the strength of sibling competition, by the type of breeding system and reproductive skew between the sexes, or by differential food allocation to offspring (Anderson *et al.* 1993; McDonald *et al.* 2005; Råberg *et al.* 2005).

Second, we found that across species the larger sex shows a stronger modulation of its relative fledging mass according to environmental circumstances. This can lead to a smaller degree of size dimorphism than would be predicted as optimal for adults. In the short term, sex-biased size reduction during ontogeny will create shifting patterns of SSD between cohorts or even within a season, tracking changes in environmental conditions (Cooch *et al.* 1996). If environmental degradation is a continuing process, size dimorphism in a population could decrease over time even though fecundity and sexual selection favor an increase.

Our results show a size-dependent modulation of male fledging mass in response to environmental conditions, but a size-independent mass reduction in female nestlings. This pattern suggests greater plasticity of male growth. On average, quantitative genetic studies indicate a slightly higher heritability of size in female birds (e.g. Jensen *et al.* 2003), which could reflect greater size plasticity in male fledglings. It remains a challenge to uncover the mechanisms permitting sex-biased evolution of growth patterns despite the shared gene pool between the sexes (Merilä *et al.* 1998; see also Chapters 16, 17, and 19).

13.7 Future studies

An important aspect of sex-specific environmental sensitivity is the timing of the occurrence of poor conditions relative to critical stages of offspring

development. When cell numbers of specific organs are limited during a small time window of development, metabolism and growth during all subsequent stages can be affected. Such a mechanism is thought to be involved in increased health risks of persons who showed poor growth during gestation (Bateson *et al.* 2004). It is likely that the metabolic machinery to build differently sized individuals of the same species differs from early development onwards. Sex differences in energy allocation to specific organs might already cause higher vulnerability of the eventually larger sex before size dimorphism and differential energy requirements become apparent (Kalmbach *et al.* 2005). Similarly, poor conditions during a developmental phase when the sexes are still equal in size can cause sex- or size-specific effects later (Gorman and Nager 2003). Physiological studies are required to determine sex differences in physiology and energy allocation at very early stages. To tease apart intrinsic and extrinsic size-related vulnerability, growth experiments with hand rearing, having chicks raised as singletons by parents (Kalmbach *et al.* 2005), or creating same-sex and same-size broods (Oddie 2000; Müller *et al.* 2005b), will be useful.

The measures we used for the present analysis are rather broad, including the necessary dichotomous classification into good and poor conditions for the analysis of fledging mass. This was mainly determined by the availability of comparable variables for a larger number of species. Although mortality is no doubt an aspect of fitness, and fledging mass also appears to be fitness-related (Haywood and Perrins 1992; Potti *et al.* 2002), other aspects of an organism's state might be crucial for its subsequent performance. Studies of immunocompetence address this issue.

The between-sex effect of expected size (predicted by the average size of males and females of the species) on mortality and fledging mass indicates that size-related viability selection also occurs within each sex. To address this, it would be necessary to have prior individual-level knowledge of expected size, beyond the classification by sex, and to investigate how individuals of different predicted sizes of a given sex react to varying conditions. This approach was taken by

Weatherhead and Dufour (2005), who analysed 30 years' of data for red-winged blackbirds. They found no survival differences between (predicted) large and (predicted) small males. As a predictor of size they used the mid-parent value, but the chicks were reared by their natural parents. A phenotypic correlation between large size and good parental abilities might thus mask size-related offspring vulnerability. The sizes of parents are themselves modulated by plasticity and are not a direct measure of genetic size. Using multi-generation animal models of wild populations or captive selection lines could reduce this problem (e.g. Kruuk *et al.* 2001; Teuschl *et al.* 2007).

13.8 Summary

We found cross-species correlations between sex-biased vulnerability (mortality and reduced fledging mass under poor conditions) and the extent of SSD in both directions (males or females larger). This indicates that being programmed to grow large carries viability costs. However, our comparison between fledging mass reached in good and poor environments suggests that having to grow large is mainly disadvantageous when coupled with the male phenotype. Female fledging mass differences between good and poor conditions were independent of SSD. On a behavioral level, larger size generally influences competitive ability positively. Despite physiological disadvantages of the larger sex, in unmanipulated broods the smaller sex might *de facto* be more vulnerable; that is, exhibit higher mortality or stunted growth (Anderson *et al.* 1993; Oddie 2000; Råberg *et al.* 2005).

Differences in environmental sensitivity between the two sexes during ontogeny, in the form of either increased mortality or reduced size, may select against dimorphism during development, affecting existing patterns of SSD in a given species. As such, environmental conditions are likely to play a major role in modulating SSD within or between generations. Given that there is a correlation of vulnerability with size predicted by sex, a similar size-related vulnerability would be expected within sexes. However, to determine the predicted size of an individual is much more difficult. We suggest that more experimental

studies should be carried out with the aim of distinguishing between the physiological basis for vulnerability of being large and behavioral factors that can counteract such disadvantages.

13.9 Suggested readings

- Kalmbach, E., Furness, R.W., and Griffiths, R. (2005) Sex-biased environmental sensitivity: natural and experimental evidence from a bird species with larger females. *Behavioral Ecology* **16**, 442–449.
- Le Galliard, J.F., Ferriere, R., and Clobert, J. (2005) Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* **111**, 368–376.
- Råberg, L., Stjernman, M., and Nillsson, J.-Å. (2005) Sex and environmental sensitivity in blue tit nestlings. *Oecologia* **145**, 496–503.
- Sheldon, B.C., Merilä, J., Lindgren, G., and Ellergren, H. (1998) Gender and environmental sensitivity in nestling collared flycatchers. *Ecology* **79**, 1939–1948.