

Nestling sex ratios in the polygynously breeding Corn Bunting *Miliaria calandra*

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We used a PCR-SSCP assay to sex 288 nestling Corn Buntings *Miliaria calandra* from 113 clutches studied between 1988 and 1990 in the Western Isles, Scotland. In each year the sex ratio was not statistically different from 1:1. Brood sex ratios did not deviate significantly from the binomial distribution when tested by robust randomisation tests. Although the effect was not strong, the proportion of males in broods declined as the breeding season progressed in 1989, although the opposite trend was observed in 1988 and 1990. Overall, we found no effect of year, timing of breeding, levels of polygyny, brood size or female size on brood sex ratios although several terms had significant interactions with year due to the effects of the data collected in 1989. Independently of brood size, the feeding rates of males, females or both combined did not vary in relation to brood sex ratios. However, the proportion of feeds provided by fathers was highest at male-biased broods when brood size was small (1–3 young) but at female-biased broods when brood size was large (4–5 young).

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There are theoretical reasons to expect animals with parental care to manipulate the sex ratios of their offspring in relation to the costs and benefits of rearing sons or daughters (Hamilton 1967); for example, when a parent has above average levels of a critical resource to provide to its offspring, it should invest in the sex which faces greater competition for mates if the added investment increases the reproductive success of those offspring (Trivers and Willard 1973, Charnov 1982, Leimar 1996). Investment may involve allocating the sex to offspring before they are born or hatch, but it could also be the adjustment of resources in relation to the sex of offspring.

In birds, there have been few tests for skewing of sex ratios prior to hatching (Clutton-Brock 1986), mainly because nestlings of most bird species are impossible to sex visually. However, in those species where sexing

nestlings is possible the results suggest that sex ratios in birds could deviate from a random distribution in relation to external influences such as timing of breeding (Howe 1977, Dijkstra et al. 1990, Olsen and Cockburn 1991, Zijlstra et al. 1992, Daan et al. 1996). New molecular techniques now permit screening of the sex of any bird species from hatching onwards (Griffiths and Tiwari 1993, 1995) and recent evidence suggests that offspring sex ratios may vary in response to factors such as parental survival (Svensson and Nilsson 1996), territory quality (Komdeur et al. 1997) and sexually selected traits (Burley 1981, Ellegren et al. 1996).

In this study we present data on offspring sex ratios in a polygynous passerine, the Corn Bunting *Miliaria calandra*. In this species there is a much greater variance in reproductive success among males than females because all females breed whereas some males breed

polygynously (25%) while others are monogamous (50%) or remain unmated during a breeding season (25%) (Hartley et al. 1993, Hartley and Shepherd 1995). Furthermore, although Corn Buntings are not sexually dimorphic in plumage coloration they show relatively extreme sexual size dimorphism for a passerine species, with adult males being approximately 20% heavier than females. The opportunity for selection to influence offspring sex ratios therefore exists because sons are potentially more costly to rear than daughters and there is a large difference in variance in reproductive success between the sexes. The objective of this paper is to test whether brood sex ratios vary in relation to the mating system, timing of breeding, brood size and female body condition.

Methods

Study species and site

Corn Buntings are sexually monochromatic, brown passerine birds in which the males weigh approximately 55 g and females 45 g. Males defend territories in the summer with a relatively simple song and breed with one to three females or remain unmated within a season (Hartley et al. 1993). Females build nests in vegetation on the ground and the males play no role as parents until the young hatch, when they provide an average of up to 22% of the feeds (Hartley and Shepherd 1994a).

Fieldwork was carried out between early May and late August each year from 1988 to 1990 at Balranald (57°37'N, 7°30'W) on the west coast of North Uist, Outer Hebrides, Scotland. The study site was approximately 7 km² and consisted of cultivated land used to grow cereal crops, rough grazing for cattle and uncultivated sand-dunes dominated by hogweed *Heracleum sphondylium* and marram grass *Ammophila arenaria* (Hartley et al. 1995). Most adults in the study population were individually colour-ringed to enable identification in the field (Hartley et al. 1993, Hartley and Shepherd 1994a). Territories were usually checked daily throughout the season to monitor breeding females and nests with chicks were watched for several one-hour periods to assess parental provisioning of nestlings (Hartley and Shepherd 1994a).

Molecular sexing methods

As part of a study which used DNA fingerprinting to measure reproductive success of individuals (Hartley et al. 1993), we collected blood samples (under Home Office licence) from adults and nestlings. The blood was stored at -70°C in 1 × SSC buffer (Sambrook et al. 1989). DNA was extracted from these samples to sex the individuals using a PCR-single-strand conforma-

tional polymorphism (SSCP) assay (Ellegren et al. 1996). Using Griffiths' primers 2 and 3 (Griffiths and Tiwari 1995) we amplified a highly conserved gene which is found on the avian W-chromosome and another, similar gene found elsewhere in the genome which is inherited autosomally. The two genes of identical size have been shown to differ by several nucleotide positions (R. Griffiths pers. comm.) and so separation of the amplified products was possible using SSCP analysis.

PCR was performed on DNA extracted using techniques described in Kawasaki (1990). Primer 2 was end-labelled with [γ ³³P]-dATP and each reaction contained 3.5 pmol of primer in a volume of 10 μ l. After a hot start, in which DNA was denatured at 94°C for 100 s, each reaction consisted of 40 cycles of 94°C for 15 s, 50°C for 20 s and 72°C for 25 s using a Perkin Elmer Cetus DNA thermal cycler. The amplification products were separated by electrophoresis in a non-denaturing 9% polyacrylamide/10% glycerol gel overnight at 14 W and then visualised by autoradiography. In birds the female is the heterogametic sex and so only females possess the W-chromosome. PCR products from the DNA of females were therefore characterised by a spread of bands representing different single-stranded, heteroduplex or homoduplex variants of the two amplified genes whereas products from male DNA appeared as only two very close bands. A blind run of 37 individuals of known sex revealed that all were correctly sexed using the molecular method and so we can be confident that the technique is robust.

Statistical analysis

Sex ratio is binomially distributed and is therefore best analysed using generalised linear models with binomial errors and logit links (Crawley 1993). The statistical significance of possible explanatory terms is determined by calculating the deviance of the model with and without these terms. The deviance is distributed asymptotically as χ^2 with degrees of freedom equal to the difference in the degrees of freedom between models with and without these terms (Crawley 1993).

To test for departure from the binomial distribution, and hence to determine if there was significant variation in sex ratios between broods, we examined the deviance of the null model. When brood sizes are large, the significance of departure from the binomial distribution can be determined by comparing the null deviance with χ^2 , with the appropriate degrees of freedom (Crawley 1993). When brood sizes are small, however, this method can severely over-estimate the degree of departure from the binomial (Westerdahl et al. 1997, C. M. Lessells pers. comm.) so we examined the robustness of these analyses by performing randomisation tests. These involve comparing the deviance of the null model

with deviances obtained by a series of randomly generated data sets. In practice, we randomised chicks between broods, while maintaining the same distribution of brood sizes and total number of male and female chicks. The deviance associated with this model was recorded and the process repeated 1000 times. The obtained distribution of deviance values then became the null distribution against which our model was compared. To determine the significance level of departure from the binomial distribution, we divided the number of deviance values greater than or equal to our model's null deviance by 1000. Similar methods were used to test the significance levels of the terms in our logistic models.

In all of these analyses the unit of analysis was the brood rather than the chick and sex ratios were weighted by the number of chicks sexed. Departure of population sex ratios from 1:1 was determined by Wilcoxon-signed ranks tests, adjusted for ties. Sex ratios are expressed as the proportion of individuals which were male.

Results

We determined the sexes of 288 young from 113 clutches. Chicks were generally sexed when 6–7 days old, before which time approximately 25% of eggs had either failed to hatch (14%) or had hatched but the chick had died (11%). This mortality limited the proportion of chicks in each brood that could be sexed successfully (median proportion of each brood sexed = 0.75, range = 0.2–1.0). We compared the sex ratios of broods in which there was no mortality with those in which one or more embryos had died prior to hatching. The mean sex ratio of intact clutches was 0.520 ($n = 43$), while for partial clutches it was 0.488 ($n = 28$) (Mann Whitney U test, $z = 0.304$, $P = 0.760$). Furthermore, the sex ratio of broods in which no mortality occurred between hatching and fledging (mean = 0.510, $n = 29$) was not significantly different from that of broods in which some hatchling mortality had occurred (mean = 0.496, $n = 47$) (Mann Whitney U test, $z = 0.178$, $P = 0.858$). For broods where clutch size was known, the proportion of eggs which were sexed was not correlated with the brood sex ratio ($r_s = 0.16$, $n =$

71, N.S.) which suggests that any potential sex-biased mortality was unrelated to clutch size.

Considering the study overall, and each year in isolation, the population sex ratio was male-biased, but not significantly so (Table 1). To determine if there was significant variation in the proportion of males between broods, the deviance in the null model was compared with the χ^2 distribution (see Methods). Using this method, there appears to be significant departure from the binomial distribution (all years; $P < 0.001$, 1988; $P = 0.029$, 1989; $P = 0.009$, 1990; $P = 0.065$: Table 1). However, using the more robust randomisation tests described in the Methods section, the distribution of sex ratios was not significantly different from the binomial, either overall or in any individual year, although 1989 comes close to significance (Table 1). This result undermines any claims for a systematic departure from a binomial distribution of brood sex ratios, although it does not exclude the possibility.

To determine which factors might influence brood sex ratio, we performed a series of logistic regressions in which the dependent variable was sex ratio and a series of independent terms were tested for inclusion in the models individually, as main effects (Table 2a). These analyses suggested that none of the factors examined were significantly associated with variation in brood sex ratio although some terms were significant in interaction with year (Table 2b). These included the date that the first egg of the clutch was laid, harem size (i.e. whether the focal male bred with more than one female in that year) and female body mass. Further analyses suggested that these significant interaction terms were primarily a consequence of trends arising in just one year of the study; 1989. We therefore repeated the above analysis for 1988 and 1990 combined (Table 2c) and 1989 (Table 2d), for those variables for which there was a significant year interaction. For 1988/90, there was no significant interaction between years and only the date of laying the first egg was significantly associated with sex ratio (a marginally significant increase in sex ratio with laying date). This relationship was not statistically significant for 1988 or 1990 alone. In 1989, only laying date showed a significant association with brood sex ratio but the trend was in the opposite direction to that found for 1988/90; the predicted sex ratio declined through the season (Table 2d). While this

Table 1. Yearly variation in Corn Bunting sex ratio (proportion of males) and its standard error. Null deviance and degrees of freedom refer to those associated with the logistic model. * Deviation from the binomial distribution determined by randomisation procedures (see main text). ** Deviation from 50:50 sex ratio determined by Wilcoxon signed ranks tests, corrected for ties.

Year	Sex ratio	SE	Null deviance	Null d.f.	P (deviation from binomial)*	P (deviation from 50:50 sex ratio)**
1988–1990	0.525	0.032	164.08	113	0.131	0.123
1988	0.541	0.046	77.81	57	0.355	0.095
1989	0.505	0.072	44.43	26	0.051	0.316
1990	0.513	0.057	41.28	30	0.283	0.375

Table 2. Correlates of Corn Bunting sex ratios (proportion of males). (a) significance levels for terms in logistic model as main effects; (b) significance levels of terms in interaction with year (a factor with 3 levels, 1988–1990); (c) significance levels of terms in logistic model that includes data only for the years 1988 and 1990; (d) significance levels for terms in logistic model for 1989 only. Significant relationships ($P < 0.05$) marked with an asterisk.

Explanatory term	(a) main effect				(b) year-interaction			(c) 1988/90				(d) 1989			
	n	df	χ^2	P	df	χ^2	P	n	df	χ^2	P	n	df	χ^2	P
Year	113	2	0.5508	0.4579											
Date first egg laid	113	1	0.8122	0.3675	2	7.8618	0.0196*	87	1	3.8927	0.0485*	26	1	4.2954	0.0382*
Nest status (monog/polyg)	112	1	0.1258	0.7227	2	5.2958	0.0708								
Harem size (1 or >1)	112	1	0.0639	0.8003	2	9.1076	0.0105*	86	1	0.6251	0.4291	26	1	3.4888	0.0617
Brood size at fledging	108	1	0.0008	0.9781	2	0.0296	0.9852								
Brood size at hatching	77	1	0.3621	0.5473	2	2.2839	0.3192								
Clutch size	71	1	0.0897	0.7645	2	2.4251	0.2975								
Female tarsus length	56	1	2.2634	0.1325	2	2.8924	0.2355								
Female body mass	42	1	0.1263	0.7223	2	6.0035	0.0497*	28	1	0.6576	0.4174	14	1	3.7189	0.0537
Female condition (mass/tarsus ²)	42	1	2.1036	0.1469	2	1.4854	0.4758								

relationship was only marginally significant, it was robust as determined by a randomisation test. In 1989, there was a non-significant trend towards a relationship between harem size and brood sex ratio, with harems of more than one being slightly male biased. There was also a non-significant trend for a relationship between female body mass and brood sex ratio in the 1989 data, with heavier females tending to have male biased broods.

One possibility that could account for the between-year effects is different levels of nestling mortality between years but this was unlikely to be the case in this analysis as there was no significant difference between years for either the proportion of eggs which hatched in a clutch or the proportion of hatchlings which fledged (One-way ANOVA with arcsine transformed proportions; hatching success: $F_{2,68} = 0.80$, $P = 0.46$; fledging success: $F_{2,72} = 0.12$, $P = 0.88$). With a larger sample of nests, and data from four years, a separate analysis found a significant year effect on hatching success but not on fledging success (Hartley and Shepherd 1994b). It is, therefore, unlikely that post-hatching mortality was the cause of between year variation in brood sex ratio, but we cannot exclude the possibility of differential hatching success of male and female embryos.

To determine whether males or females adjusted their provisioning rates in relation to brood sex ratio, we performed linear regressions between the absolute number of feeds given to a brood of 8–12 day old chicks and the sex ratio of the brood. This was repeated for males and females separately, as well as for both sexes combined (Table 3). The total number of feeds and the number of feeds by females showed no relationship with brood sex ratio, but males showed a trend for a higher provisioning rate to female-biased broods ($P < 0.08$). Although provisioning rates may also be correlated with brood size (Hartley and Shepherd 1994a), when it was entered into the model it did not alter the conclusions of the analysis (Table 3). The greatest shift

in behaviour was in terms of the relative provisioning rates of the two sexes. This was determined by performing logistic regressions in which sex ratio and brood size were explanatory variables and the response variable was the proportion of feeds provided by the male, weighted by the total number of feeds to the brood. These analyses indicate that males provided a greater proportion of the feeds to chicks when the brood was large and biased towards females. The analysis also indicated a significant interaction between brood size and sex ratio. Closer analysis of these data suggests that when brood sizes were small (1–3 chicks) males invested more in male-biased broods (Fig. 1a), whereas when they were large (4–5 chicks) they invested more in female-biased broods (Fig. 1b).

To determine whether there was a sex bias in chick survival from early or late nests, we looked at the effect of nesting date on the recruitment of offspring into the breeding population the following year by comparing the start date of clutches from which male or female recruits were produced. If males benefitted more than females from an early start in life we might expect male recruits to have fledged from relatively early nests compared to females. Data were sparse (22 males and 20 females) but we found no evidence to suggest that male recruits came from earlier or later nests than female recruits (dates between years were standardised around a common mean to allow for between year variation in mean nesting dates: Unpaired t-test; $t_{40} = 0.47$, $P = 0.6$).

To determine any benefits to sons and daughters of being raised in differently sized broods we compared the weights and tarsi lengths of nestlings in large versus small broods. Brood size was the number of chicks alive in the nest on day 6 or 7 when the measurements were made. As each chick is not an independent data point, we averaged the measurements of sons and daughters separately within each brood before carrying out the analysis. We found no differences in weight or tarsus length for either sons or daughters in large versus

small broods (t-tests; daughters' tarsus lengths $t_{22} = 1.34$; daughters' weights $t_{22} = 0.02$; sons' tarsus lengths $t_{24} = 1.45$; sons' weights $t_{24} = 0.81$; all N.S.).

Discussion

Overall sex ratio

Sex ratio skews within avian broods could be caused by either a bias in the sex allocation to the eggs or differential mortality at any stage after laying (Landauer and Landauer 1931). This study was not able to distinguish between these two causes of brood sex ratio skew because sexing was carried out at the nestling stage. Although there were no significant differences in the sex ratios of broods in which no mortality occurred prior to sexing compared to broods in which at least one hatchling died, we cannot be certain that no sex-biased mortality occurred. As Fiala (1980) points out, it is not safe to assume that sex ratios measured at different ages are directly comparable unless the relative survival of male and female embryos is known. In other words, unless one already knows the primary sex ratio, it is not possible to derive it. However, sex biased mortality can produce similar patterns to adaptive sex ratio skews (Clutton-Brock et al. 1985).

There is growing evidence to suggest that adaptive sex ratio skews can occur in birds through non-random sex allocation rather than differential mortality (Daan et al. 1996, Ellegren et al. 1996, Lessells et al. 1996, Svensson and Nilsson 1996, Komdeur et al. 1997). The mechanism for controlling sex allocation in birds is unknown but suggestions include differential survival or growth of male and female follicles in the ovary or female controlled chromosomal segregation (Godfray and Harvey 1986, Hardy 1997). In birds, females are the heterogametic sex so some form of chromosomal sex control mechanism is possible.

Our robust analysis using randomisation tests showed that there was no evidence for a non-binomial distribution of brood sex ratios in our study population, nor was there any evidence for a significant deviation from a 1:1 population sex ratio in any year. Only

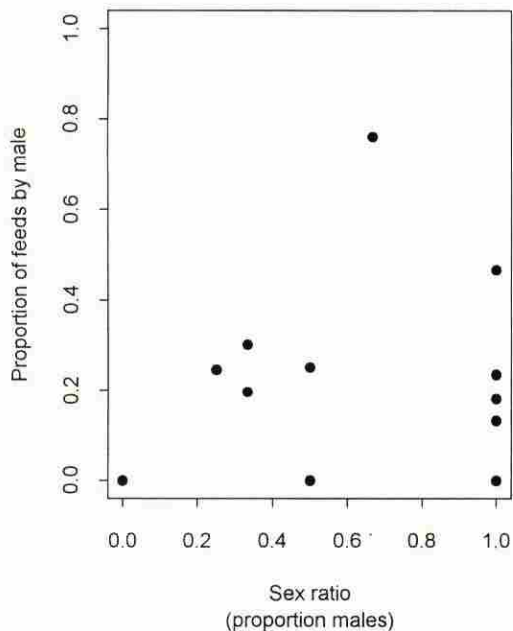
in 1989 was there any hint that sex ratios of nestlings might deviate significantly from binomial but the results were only bordering on significant and with several related statistical tests the probability of making a false rejection of a null hypothesis is increased.

In another polygynously breeding passerine, the Great Reed Warbler *Acrocephalus arundinaceus*, Nishimi et al. (1996) report no skews in overall brood sex ratio in their Japanese population although they did not test for deviation from a binomial distribution. In a Swedish population of the same species, Westerdahl et al. (1997) found that the overall brood sex ratio did not differ from unity but that the variation in brood sex ratios was significantly larger than that expected from a binomial distribution. We might have expected that the costs of rearing larger sons, and/or differential mating success among males in polygyny, might have led to broods with skewed sex ratios in Corn Buntings, as found in the Swedish Great Reed Warblers. It is unclear why Corn Buntings do not skew brood sex ratios; it is either not possible for them or ecological factors which influence sex ratios in other species do not apply to Corn Buntings. In a congener of the Great Reed Warbler, the Seychelles Warbler *A. sechellensis*, experiments have shown that extreme natal sex ratio skews are not only possible, but can be adapted by individuals to maximise fitness under different ecological conditions (Komdeur et al. 1997). In this species, sex ratio skews are related to the need for helpers at the nest on high quality territories and the cost of helpers as competitors for food on low quality territories. The factors which result in sex ratio skews are still not known. As birds can be quite flexible for many life-history traits, such as clutch size (Lessells 1991) or mating system variables (Davies 1991, Davies and Hartley 1996), we probably should expect to find more primary sex ratio skews in other species when the pay-offs for skewing are high. Having established that primary sex ratios can be adaptively skewed within broods, an experimental approach will be needed to test the effects of life history strategies or ecological factors on the extent of those skews. It is also important to obtain more data on the real costs of raising sons versus daughters.

Table 3. Relationships between brood size, sex ratio and chick feeding rates in Corn Buntings. Test statistics and significance levels for (a) sex ratio effects, (b) brood size effects and (c) the interaction between brood size and sex ratio. F ratios are indicated for linear regressions (male feeds, female feeds and total feeds) and Chi-square values for logistic regressions (proportion of feeds by male). Significant relationships ($P < 0.05$) marked with an asterisk.

Explanatory term	(a) Sex ratio				(b) Brood size			(c) Interaction		
	n	df	F/ χ^2	P	df	F/ χ^2	P	df	F/ χ^2	P
Male feeds	33	1	3.355	0.0757	1	3.197	0.0833	1	2.491	0.1251
Female feeds	33	1	0.864	0.3592	1	0.428	0.5177	1	0.079	0.7806
Total feeds	33	1	2.782	0.1045	1	2.096	0.1574	1	0.389	0.5375
Proportion of feeds by male	36	1	6.235	0.0125*	1	7.459	0.0063*	1	6.934	0.0085*

(a) Small broods (≤ 3 chicks)



(b) Large broods (> 3 chicks)

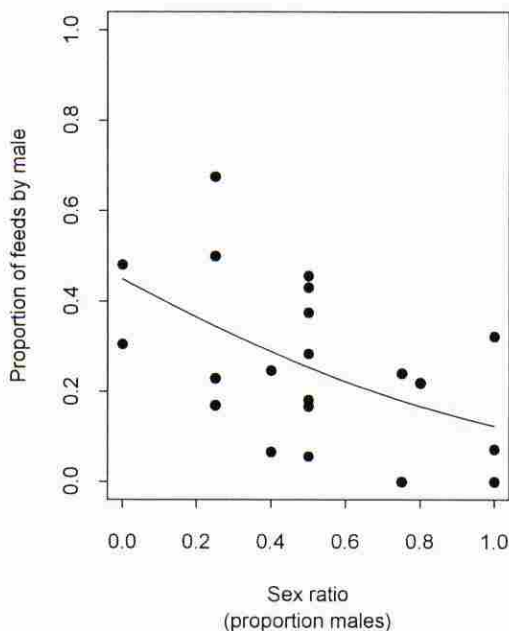


Fig. 1. Scattergrams showing the relationship between brood sex ratio (proportion of sons) and the proportion of feeds provided to the nestlings by the male for (a) small broods (1–3 chicks) and (b) large broods (4–5 chicks). See Table 3 for statistical details.

Timing of breeding and brood sex ratios

Nestling sex ratios did not differ from a binomial distribution overall and brood sex ratios were unrelated to levels of polygyny, brood size or female biometrics. The analysis, however, was complicated by the fact that several terms had significant interactions with year, largely due to the effects from the data collected in 1989 when nestling sex ratios tended to be more male biased earlier in the breeding season and more female biased later. This was in direct contrast to years 1988 and 1990, when broods tended to be female biased early in the season and male biased later. The reasons for this difference are unclear although 1989 had a relatively cold spring and nests were started an average of 8 days later than in other years (Hartley and Shepherd 1994b). One possibility could be that the different weather conditions resulted in differential mortality of male and female chicks but this is unlikely as nestling mortality did not differ between years in this study or in an analysis of a larger sample of nests from the same population (Hartley and Shepherd 1994b).

Seasonal effects on brood sex ratios in birds have mostly been reported in birds of prey, where the direction of the skew appears to be related to the relative benefits of breeding at an early age (Daan et al. 1996). We should, therefore, expect that variation in sex ratios within seasons should be related to the relative benefits to each sex of getting an early start in reproductive life.

In Corn Buntings, we found no evidence to suggest that there were sex differences in the probability of recruitment into the following year's breeding population for chicks hatched early or late in the season, although more data are needed.

Effects of brood sex ratios on provisioning of nestlings

Male Corn Buntings contributed very little to provisioning of nestlings prior to day four after hatching and thereafter provided an average of only 22% of feeds (Hartley and Shepherd 1994a). This analysis shows that the numbers of feeds provided by males and females, and the total of parental feeds combined, was unrelated to brood sex ratios. The proportion of feeds provided by the male, however, varied significantly with brood sex ratio (Table 3). We found that males invest relatively more in son-biased broods than daughter-biased broods when there are fewer than four nestlings but more in daughter-biased broods when the brood size is four or greater. This would make sense if sons and daughters were of different reproductive values in small and large broods. The large sexual size dimorphism in Corn Buntings suggests that being a large male has advantages in intrasexual competition and we know from our previous work that only males defending territories will be able to mate (Hartley et al. 1993). In

small broods, sons may suffer less sibling competition and develop faster, or further, than sons in large broods. We found no evidence to support this, however, as neither sons nor daughters were larger or heavier in small compared to large broods.

Following the trends of other polygynously breeding passerines we might have expected male, but not female, biases in provisioning to nestlings in relation to brood sex ratios. There are few studies of birds that have demonstrated biased parental investment in relation to offspring sex independently of brood size. In the polygynously breeding Red-winged Blackbird *Agelaius phoeniceus*, males fed son-biased broods at higher rates than daughter-biased broods independently of brood size (Searcy and Yasukawa 1995). In Great Reed Warblers, the frequency of provisioning of nestlings by males, but not females, increased with the proportion of sons in the brood rather than brood size (Nishiumi et al. 1996). It would be especially useful to have more studies which look at relative investment in sons and daughters and the relative benefits to offspring of differential parental investment. There is currently little evidence from bird studies to suggest that sons and daughters benefit differently from increased parental care. We also know very little about how sexual discrimination might be implemented by parents when provisioning their brood.

It has been suggested that parental care biased towards offspring of one sex should be most commonly found in those species where parents can provide enough food for all offspring to survive (Nishiumi et al. 1996). We might extend this idea to individuals within a species and suggest that when parents are not working at their full rate, either because food is plentiful or because one sex is taking most of the parental care burden, then there is the opportunity to allocate extra resources if the investment is worthwhile. In polygynous bird species this would usually mean that females are working to capacity while males have the option of increasing their provisioning rate if the brood either demands more feeds or is worth the investment of extra resources. The evidence from Corn Buntings would seem to support this hypothesis because the males, but not the females, show variation in provisioning rate with respect to brood sex ratio. Male Corn Buntings tend to provide much less parental care than females and, within the range of variation, provisioning behaviour of males did not influence fledging success, whereas females which delivered more large food loads fledged the most young (Hartley and Shepherd 1994a). It would seem, therefore, that male Corn Buntings are in a position to increase their parental care in accordance with the Nishiumi et al. (1996) hypothesis but further work on parental discrimination is clearly needed. It is important to distinguish between parental discrimination between young within a nest and differences in feeding rates due to other, correlated factors.

For example, if a female in good condition is likely to have more sons than daughters, males might provide more food to her young as a result of her quality rather than the sex of the nestlings.

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