Effects of parental age and environmental change on offspring sex ratio in a precocial bird

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Summary

1. Variation in offspring sex ratio at the end of parental care may reflect passive sexual differences in offspring survival, or a facultative manipulation by parents to balance trade-offs between sex-specific offspring growth and survival and parental fitness. In contrast, among species with limited size dimorphism, there may be little reason to expect significant sexual differences in offspring survival, and the presence of offspring sex-ratio variation in such species may indicate sex-specific differences in parental investment at some stage. However, sex-ratio variation in monomorphic species with precocial young may be more difficult to explain, since the decreased parental investment, which is largely shared between offspring of either sex, may reduce the opportunity for sex-ratio manipulation.

2. We examined this question by analysing annual variation in fledging sex ratio of an avian herbivore with strong female natal philopatry and precocial young, the lesser snow goose Anser caerulescens caerulescens, using data from a 23-year observational study during a period of marked population growth. Although snow geese show limited sexual size dimorphism, with males being 2–6% larger at all ages post-hatching, growth and survival of snow goose goslings has been shown previously to be extremely sensitive to variation in food supply.

3. The proportion of males at fledging has decreased from ≈51% in the early years, when food at the colony was abundant, to c. 48% in recent years, when food supply has been reduced. Concurrent with this change, the mass and condition of goslings have declined significantly over the years, with males showing a proportionately greater decline than females. Hatching sex-ratio data showed no systematic significant differences overall, and thus the most likely explanation for the change in sex ratio is increased mortality of male goslings between hatching and fledging.

4. The change in fledging sex ratio occurred only among broods from younger adults (age < 5 years). These age-specific differences were evident both among and within individual females. Younger adults may be less able to accommodate long-term changes in foraging conditions successfully, resulting in proportionately greater gosling mortality overall, and increasingly biased mortality of male goslings, which may be more susceptible to food restriction.

5. Despite potential differences in indirect costs of rearing male or female offspring, it is suggested that these results are more consistent with increased mortality of male goslings under increasing food restriction, rather than active parental manipulation.

Key-words: body size, brood rearing, growth rates, philopatry, snow goose, survival.


Introduction

Fisher (1930) showed that lifetime reproductive investment should be equal for the two sexes. However, if costs of rearing offspring are lower for one sex than the other, either in terms of (i) sex-specific differences in the probability of offspring survival and recruitment (Trivers & Willard 1973; Slagsvold, Røkaft & Engen 1986) or (ii) direct fitness costs to parents from producing and rearing an offspring of a given
sex (Clark 1978; Myers 1978), then biasing the offspring sex ratio in favour of the cheaper sex will increase the inclusive fitness of the parent(s).

While a deviation in the secondary sex ratio away from 1:1 may reflect such a facultative adaptation on the part of the parents, this is not necessarily the case. Skewed secondary sex ratios may also result from apparently ‘non-adaptive’ sexual differences in survival (Clutton-Brock 1986). For example, if one sex requires proportionately more food than the other, then when food resources become scarce this sex should experience increased mortality (e.g. Searcy & Yasukawa 1981; Cromilier & Thompson 1981; Weatherhead & Teather 1991).

The contrast between ‘adaptive’ and ‘non-adaptive’ explanations for secondary sex-ratio variation has been studied most intensely in species with (i) sexually size-dimorphic (SSD) young, where differential costs, and survival, of sons and daughters is potentially large (Myers 1978; Richter 1983; Slagsvold et al. 1986; Clutton-Brock 1986; Bednarz & Hayden 1991; Richner 1991; Weatherhead & Teather 1991), and (ii) substantial parental care, where discrimination between male and female offspring may contribute to sexual differences in mortality (McClure 1981; Burley 1986; but see Clutton-Brock 1991). In general, it has proven difficult to resolve unambiguously the competing hypotheses, since both are generally consistent with a bias towards the less expensive sex (Slagsvold 1990; Weatherhead & Teather 1991; Clutton-Brock 1991).

**SEX-RATIO VARIATION IN MONOMORPHIC SPECIES WITH PRAECOCIAL YOUNG**

In the absence of large SSD, the growth and survival of male and female offspring should be roughly equal, and the offspring sex ratio should show little or no deviation from 1:1 (e.g. Clutton-Brock, Albon & Guinness 1985). Therefore, a significantly biased sex ratio in such species may be more consistent with a facultative parental manipulation, either at birth (e.g. Patterson & Emien 1980; Weatherhead 1983; Dijkstra, Daan & Baker 1990; Wiebe & Bortolotti 1992), or during the period of parental care following birth (e.g. McClure 1981; Burley 1986; but see Clutton-Brock 1991).

However, several sexually monomorphic species also produce praecocial young. In such species, it would seem unlikely that manipulation of the sex ratio could occur during the period of parental care, since parental care in praecocial species is largely sharable among offspring, regardless of sex (Winkler & Walters 1983).

We examined the pattern of annual variation in the growth and survival of offspring of an avian herbivore with praecocial young, using data from a long-term study of lesser snow geese *Anser caerulescens caerulescens* L. (hereafter snow geese) breeding at La Pérouse Bay (LPB), Manitoba, Canada (58°44’N, 94°28’W). Snow geese exhibit only limited sexual size dimorphism in both growth rates and size at fledging, with males slightly larger (2–6%) at all ages (Cooch, Lank & Cooke 1996). Parental care of goslings following hatching consists primarily of defence against conspecific interference and predation.

There is little reason to expect significant sexual differences in offspring survival during early growth in this species, so any variation in offspring sex ratio may suggest parental manipulation. However, as an adaptation to the short breeding season, goslings of Arctic-breeding geese exhibit extremely rapid growth for a species with praecocial young (Whitehead, Free- land & Tschirner 1990). As a result, growth and survival of geese is highly sensitive to variation in the quality and quantity of food (Cooch et al. 1991a, b; Sedinger & Flint 1991; Larsson & Forslund 1991). Since male goslings are typically larger than female goslings, they may be more sensitive to food restriction than female goslings.

Cooch *et al.* (1996) previously considered this question by examining the effects of seasonal declines in food quality and quantity on growth and survival of goslings at LPB. Among early-hatching goslings (when food is most abundant), females were ≈7–8% lighter than males at fledging, whereas amongst late-hatching goslings this difference declined to ≈5%. Despite these differences in growth, there was no evidence of sexual differences in gosling survival, and no seasonal deviation from a 1:1 fledging sex ratio.

A seasonal decline in food is virtually ubiquitous at Arctic breeding colonies (Cooch *et al.* 1991a; Sedinger & Flint 1991; Larsson & Forslund 1992), and the sexual differences in growth within season may reflect an adaptation to minimize risk of mortality in response to a predictable food restriction (Cooch *et al.* 1996). In contrast, high-intensity grazing and early season grubbing by increasing numbers of geese at LPB has systematically reduced the annual standing crop of food (Williams *et al.* 1993). This long-term decline in food over many years at LPB is less predictable than seasonal changes and as such, goslings may not be able to compensate. The decline over the years in food has led to a long-term decline in both the average gosling size at fledging (Cooch *et al.* 1991b) and first-year survival (Francis *et al.* 1992), with most of this increased mortality occurring during early growth (Francis *et al.* 1992; Williams *et al.* 1993).

In this paper we examine the responses of male and female goslings to the long-term food reduction at LPB. We specifically address the question of whether or not this reduction in food has lead to measurable sexual differences in size at fledging, and changes in fledging sex ratio. We show that growth of male goslings has been significantly more sensitive than that of females to food restriction, similar to the results of our within-season analyses (Cooch *et al.* 1996). In contrast, there has also been a long-term decline in the frequency of male goslings at fledging (Cooke,
Rockwell & Lank 1995). Although apparently consistent with the hypothesis that larger male goslings may be less able to adapt to unpredictable food restrictions, this explanation alone may be insufficient to explain some of the variation in fledging sex ratio over the years.

Methods

Data have been collected annually from LPB from 1969 to the present. General field methods are described in detail in Finney & Cooke (1978), Cooke et al. (1985), and Cooke et al. (1995). Those particular procedures relevant to this study are described briefly here.

The colony, presently numbering 15,000-20,000 breeding pairs (Cooke et al. 1995), is on the southern edge of the species' breeding range. Each year, ≈2000 nests were monitored at hatching (modal clutch size at hatch = 4), and each hatching was marked with an individually numbered web-tag. In some years, sex of the goslings at hatch (secondary sex) was also determined (see below). Approximately 5 weeks after hatch, before goslings are fully fledged, the adults moult their primary flight feathers and are temporarily flightless. During this period, ≈1500 families (≈4000–5500 adults and goslings) were rounded up, aged, sexed and ringed. Since 1969, >55,000 goslings have been captured at fledging, sexed and marked with individually numbered tarsal rings. A portion of the goslings caught in these ringing drives have webtags, and thus could be aged precisely (age = days since hatch).

Sampling regions

As the LPB population has increased and food abundance has decreased over time, increasing numbers of family groups have been locally dispersing from the traditional feeding areas during brood rearing. Cooke et al. (1993) demonstrated that goslings from dispersed broods were heavier and had higher survival rates than goslings that remained within LPB itself. In recent years, with progressively deteriorating conditions at LPB, relatively few broods have continued to use the traditional rearing areas. To control for the possible effects of these differences, we generally restricted our analyses to data from the LPB site only. For most of the years of our study (1969–84), this comprised >90% of the broods in the population. The long-term decline in the frequency of male goslings reported by Cooke et al. (1995) involved only goslings reared at LPB. However, in some analyses, we specifically compared sex ratios among brood-rearing sites within a year.

Adult age

Rockwell et al. (1993) showed that several differences in reproductive performance between young and old adults were due to differences in components of brood-rearing success. They suggested that adults of different ages differed in their ability to rear a brood successfully to fledging, and that these differences interacted significantly with long-term changes in food abundance. Thus, we might expect differences in offspring sex ratio as a function of parental age. Precise adult age (years) in this study was determined by the presence of cohort-specific alpha-numeric leg rings. Birds ringed as adults form a sample for which the minimum age is known. Since snow geese do not breed until at least 2 years of age, newly ringed adults are assigned a minimum age of 2 years. We used varying portions of this minimum-aged sample to augment some of our analyses where there were insufficient numbers of known-aged adults. To minimize the possible effects of error in assigning a minimum age estimate, we included such birds only if (i) the estimated age was <4 years, categorized as 'young', or (ii) the estimated age was ≥5 years, categorized as 'old'.

Sex-ratio variation

In all years, overall gosling sex ratio was measured at fledging using data from annual ringing drives. The fledging sex ratio of individual adult females was determined in broods where all goslings in the brood had been web-tagged at hatch.

From 1982 to 1986, the sex of 4524 goslings from 1290 different nests was determined at ringing by cloacal evasion. Only goslings that had emerged completely from the egg were sexed. The sexing of goslings at hatch was not continued in subsequent years, in an attempt to minimize the time spent at each nest during ring-tailing. Only nests for which all goslings in the nest were sexed were used. Although there was a significantly greater probability of misclassifying male goslings at hatch as female than vice versa (Cooch et al. 1996), we found no significant annual variation in this bias. Therefore, we interpret any systematic variation in hatching sex ratio as independent of bias in the misclassification error in assigning sex at hatching. We supplemented this data set by including data from broods where all goslings survived from hatch to fledging (n = 2523 goslings, 729 broods, 1973–89). For such broods, the sex ratio measured at fledging is clearly equivalent to the hatching sex ratio. Such broods may be a biased subset of all broods (i.e. if hatching sex ratio significantly influences the probability that all goslings in a brood will survive to fledging). However, Harmen & Cooke (1983) found no significant deviation in sex ratio from binomial expectations (based on a 1:1 hypothesis) among such broods.

Body size measurements

We compared body size differences between male and female goslings using two different measures of struc-
tural size (culmen and total tarsus length (mm); Dzubin & Cooch 1992) and body mass (g). Within any year, only data from the first capture for each gosling during banding drives were used. Although multivariate measures of structural size (e.g. PC1) are preferred (Rising & Somers 1989; Freeman & Jackson 1990), they are dimensionless variables for which proportional changes (with respect to sex and other variables) are difficult to estimate.

STATISTICAL METHODS

Sex-ratio variation

We used generalized linear models with a logit link function to compare sex ratios among years or groups, and estimate trends in binary sex-ratio data with respect to one or more covariates. Because of the extremely large annual sample sizes, we tested the significance of deviations in the observed sex ratios from a 1:1 expectation using a normal approximation to the binomial distribution (Zar 1984). We used likelihood-ratio tests (LRT) to compare relative fit among nested models.

The large number of missing values in most of our longitudinal samples (i.e. years in which the sex ratio of an individual female was unknown), and the asymmetrical structure of the data matrix (not all birds observed for the first time in the same year), forced us to use an ad hoc method for analysis of sex-ratio variation within individual adult females. For each individual, we calculated the difference between the first and last recorded sex ratio, and regressed this difference on the number of years between the observations. This technique is robust under the assumption that within-individual changes in sex ratio with year are linear and monotonic (i.e. that the actual year of observation does not influence the magnitude of the difference).

Body size variation

We followed approaches described in detail in Cooch et al. (1996). Briefly, we used annual differences in the magnitude of sexual size dimorphism for goslings of a given age to test for differential sensitivity to variation in growth conditions. We controlled for differences in gosling age (days since hatch) by analysing residuals of regressions of body size (body mass, culmen and tarsus length) on age. Since growth rate is linear over the range of ages encountered during annual ringing drives (Cooch et al. 1991a), differences in these adjusted values reflect differences in actual growth rates. Thus, differences in ‘growth rates’ or ‘body size’ are functionally equivalent in our study. All analyses of body mass, culmen and tarsus length refer to these adjusted values. Year was included as a linear covariate. We included brood size measured at hatching as a classification variable in our starting models for analysis of variation on body size. Brood size at hatch was used instead of final brood size (measured at ringing), since the greatest influence of brood size on growth and survival probably occurs within the first 10 days following hatching (Williams et al. 1993). To avoid biasing the results of our analyses towards larger broods, we used average male and female sizes within each brood. In cases where both male and female goslings in a brood survived to fledging, we randomly selected one or the other sex to control for possible non-independence within broods. Since the results of any single analysis are dependent upon the particular random sample of goslings, we repeated each analysis 25 times, each time using a new randomly selected data set, and report the significance of the mean test statistics.

Results

OVERALL VARIATION IN GOSLING SEX RATIO

Gosling sex ratio varied annually among > 51 000 goslings sampled at fledging ($\chi^2_{2} = 41.90, P < 0.01$), with a highly significant linear decrease in the proportion of male goslings at fledging over time ($\chi^2 = 12.63, P < 0.001$; Fig. 1). The fledging sex ratio differed significantly from 1:1 in only six of 23 years. In the early years of our study (1969–79), when food at LPIB was abundant, the fledging sex ratio was significantly biased towards males (12 908 males, 12 541 females; $Z = 3.22, P < 0.01$). In contrast, in recent years, when food supply at the colony had declined precipitously, there was a significant bias towards females (1981–92: 10 673 males, 11 028 females; $Z = 3.42, P < 0.005$). The fit of the regression model to the data did not differ significantly from the fit of the factorial model ($\chi^2_{2} = 29.3, P < 0.108$), indicating that a significant proportion of the overall variation in fledging sex ratio is due to the long-term decline. Since the regression model was the most parsimonious (i.e. fewest parameters), we used it as the starting model for further analyses over the years.

Attempts to explain residual variation in sex ratio in terms of other covariates (hatch date, average gosling age at ringing, measures of average fledging mass and above-ground biomass; $P > 0.5$ for all variables) were not successful. This is perhaps not surprising given that the predicted values from the linear-decline model were within 95% sampling error in 21/23 years (Fig. 1).

Young (precise age = 2–4 years; $n = 892$) and old (precise age = 5+ years; $n = 1106$) females differed significantly in the pattern of variation in fledging sex ratio across years (1973–88; $\chi^2_{9} = 9,87, P < 0.002$). The proportion of male goslings in broods of younger adults declined significantly over time, from 58% to 39% (−1.2%/year; $\chi^2_{1} = 7.77, P = 0.005$), while the sex ratio of broods from older birds did not show a systematic change ($\chi^2 = 2.54, P = 0.110$; Fig. 2).
Fig. 1. Long-term variation in sex ratio of goslings captured at fledging at LPB, 1969–91. Sex ratio is expressed as the proportion of male goslings in the overall sample. Sample sizes represent the total number of male and female goslings in an annual sample. Error bars indicate 95% confidence limits for the sample. Open symbols indicate years in which the sex ratio deviated significantly (α = 0.05) from 1:1 (significance estimated using the normal approximation of the binomial distribution). The regression line is drawn from parameters estimated from the logistic regression of sex on year. Years in which the sample confidence interval is intersected by the regression line did not differ significantly from expected values calculated from the regression model (z-test, α = 0.05).

Fig. 2. Long-term variation in sex ratio of goslings captured at fledging at LPB, 1969–91, as a function of age of parental female. The sex ratio is expressed as the proportion of male goslings in the overall sample. Sample sizes and error bars are omitted for clarity of presentation. Regression lines for each age class were drawn from parameters estimated from the logistic regression of sex on year.

Increasing the sample size by including birds for which only the minimum adult age was known did not change the general result of a difference in sex ratio between older and younger birds (n = 4808; χ² = 4.73, P = 0.030), although the rate of the decline in sex ratio among younger birds was reduced by approximately half (−0.68%/year; χ² = 5.46, P = 0.020).

However, the rate of the decrease in male goslings at the population-level (≈−0.15%/year) probably
reflects the age structure of the ringing sample. Under constant conditions, 70% of all breeding adults in this population will be ≥5 years old (Brault et al. 1994).

If we make this assumption, then given the age-specific regressions of sex ratio on year (Fig. 2), an overall decline in the average percentage male goslings of c. −0.13%/year would be predicted, which is very close to the observed overall value (−0.15%/year; Fig. 1). While the assumption of constant proportions of adults of each age class over years is unlikely to be valid (in fact, the average age of the ringing sample is likely to have increased), our purpose here is simply to demonstrate the effect of age structure on our population level estimates of sex ratio.

The pattern of variation in fledging sex ratio over years and between age classes may reflect (i) variation from a 1:1 sex ratio at hatching, (ii) sex-specific differences in growth and survival between hatching and fledging, or (iii) systematic sampling bias. We will consider each of these in turn.

HATCHING SEX RATIO
Among 2008 broods (1973–87) for which sex ratio at hatching was known, there was no heterogeneity in sex ratio among years (χ² = 15.5, P = 0.35), and no evidence of any trend over years (χ² = 0.0005, P > 0.5). Thus, at the population level, there appeared to be no evidence of systematic changes in hatching sex ratio overall.

To test for possible age differences, we first used the direct hatching sex-ratio data available for 1982–86. Within this sample, birds were classified as either ‘young’ (age = 2–4 years) or ‘old’ (age = 5+ years). To maximize our sample size, we included birds for which only the minimum age was known. Among 307 birds (64 young, 243 old), there was no significant difference overall in the proportion of male goslings at hatching between young (mean = 0.53, SE = 0.03) and old females (mean = 0.49, SE = 0.02), pooled over years (F = 0.91, P > 0.3). Superseding this data set by including data from females where all goslings in the brood were known to survive to fledging more than doubled the sample size (n = 648 birds; 185 young, 463 old), and greatly increased the range of years included in the sample (1973–86). Controlling for year, there was no significant difference in hatching sex ratio overall (F = 0.07, P > 0.5) between young (mean = 0.51, SE = 0.03) and old females (mean = 0.50, SE = 0.02), and no significant interaction of age and year (F = 0.52, P > 0.5).

However, among younger birds (age <5 years) there was marginally significant heterogeneity among age classes in hatching sex ratio: 2-year-old females had a higher proportion of male goslings at hatch (mean = 0.63, SE = 0.06, N = 22) than did the pooled sample of 3- and 4-year-old females (mean = 0.50, SE = 0.03, n = 95; t = 1.81, P = 0.073). There was insufficient data to test for trend with respect to age class, especially among younger birds.

SEX-SPECIFIC DIFFERENCES IN GOSLING SIZE AND SURVIVAL
Both body mass and structural size of male and female goslings measured at fledging declined significantly over time. However, male body mass declined proportionately faster than female body mass (c. 4 g year⁻¹ difference in rate of the decline; F[1,103] = 5.44, P = 0.020); among goslings from early years (pre-1978), female goslings were 100–120 g lighter on average than male goslings (c. a 7–8% difference), whereas in later years (post-1984) this difference had declined to 50–55 g (c. a 4–5% difference; Fig. 3). The rate of change in the difference in body mass between male and female goslings did not differ significantly as a function of parental age (year × sex × age; F[2,50] = 0.68, P > 0.5). In contrast, there was no difference between male and female goslings in the rate of the decline in either culmen or tarsus length (culmen: F[1,251] = 0.59, P = 0.443; tarsus: F[1,190] = 0.50, P = 0.482). Female goslings were structurally smaller (c. 2–4%) in all years (Fig. 3). If physiological condition is approximately scaled as the ratio of body mass to culmen length, then there was a significant difference among years in changes in condition of male goslings; in recent years, males were in proportionately worse physiological condition than females.

While a reduction in size and condition of males relative to females may reflect increasing mortality of larger males, it might also reflect a simple reduction in average growth of all males. However, if the hatching sex ratio is 1:1, or at least constant, over the years (see above), then differences in sex ratio at the time of fledging reflect either sex-specific changes in pre-fledging survival or non-random sampling. In this section, we consider the former.

If sex at hatch is known, then relative survival of male and female goslings from hatch to fledging can be assessed directly by comparing the proportions of males and females seen at hatching that were seen again at fledging. However, such data were available for 1982–86 only (clearly, broods where all individuals were known to survive cannot be used in this analysis). Given the relatively small magnitude of the overall change in sex ratio (c. 3% over 23 years), the number of years in this subset of our data (5) was insufficient to allow direct testing of systematic changes in sex-specific mortality. Thus, we could use only indirect tests for differences in survival.

If male goslings suffer proportionately greater mortality under food restriction than females, then there should be an association between fledging sex ratio and variation in habitat quality (i.e. food abundance). We tested this hypothesis by comparing gosling sex ratios between two different brood-rearing sites: LPB
and Cape Churchill (CC; ≈10–15 km east of LPB). The CC site has been shown previously to have significantly more food than the LPB site (Cooch et al. 1993). Using all goslings, regardless of whether or not they were web-tagged (LPB, \( n = 8798 \); CC, \( n = 4573 \)), there was a significantly greater proportion of male goslings in the CC sample than in the LPB sample (Fig. 4; \( \chi^2 = 19.7, P = 0.033 \); likelihood ratio test against model with year-dependence only; \( \chi^2 = 4.50, P = 0.034 \)). After excluding data from 1985 (preliminary analysis showed it to be a significant outlier; 45% male, all other years > 50%), the sex ratio at CC was 51:4% male, which is significantly deviant from a 1:1 expectation (\( z = 2.36, P < 0.02 \)). In contrast, the LPB sample was significantly female biased (48.3% male; \( z = 4.52, P < 0.001 \)). These results contrast with those of Cooch et al. (1993), who showed no significant difference in sex ratio among goslings hatched at LPB but reared at either LPB or CC. However, in this study, we used a significantly larger sample, using all goslings regardless of where they were hatched.

While the female-biased sex ratio at LPB is consistent with expectations given the hypothesis of increased male mortality under food restriction, the male-biased broods at CC are more difficult to explain. A similarly male-biased fledgling sex ratio was also observed in the early years of our study at LPB, also when food was most abundant (Fig. 1). Presum-
Offspring sex-ratio changes in snow geese

Fig. 4. Annual variation in the difference in fledging sex ratio as a function of location of sample (LPB, La Pérouse Bay; CC, Cape Churchill). Sex ratio is expressed as the proportion of male goslings in the overall sample. Sample size and standard errors are omitted for clarity of presentation. Open symbols represent year/site combinations in which the sex ratio deviated significantly (α = 0.05) from 1:1 (significance estimated using the normal approximation of the binomial distribution).

ably, when food is abundant, growth and survival of both sexes should be optimal. A male-biased sex ratio at fledging, in the absence of a biased hatching sex ratio, implies that female goslings suffer proportionately greater mortality than males under good conditions, whereas the opposite is true under food limitation. How could such a difference arise?

Even under optimal foraging conditions, partial brood loss in this population is significant (10–20% proportional brood loss), with most of the loss due to predation. Males, on average, are larger than females at fledging, and the magnitude of this difference (at least for mass) is greatest under optimal feeding conditions (Fig. 3). Further, Black & Owen (1987) showed that male goslings of the barnacle goose Branta leucopsis were dominant to female goslings, although these differences were not significant until the second month after hatching. Dominant goslings within a brood may receive greater parental care. If predators preferentially select the smallest (or least protected) gosling in a brood then, under good conditions, size-specific predation could lead to a male-biased brood.

We tested this hypothesis by regressing the fledging sex ratio on the proportion of a brood surviving to fledging among older (age > 4 years) and younger (age = 2–4 years) adults. Our results show male-biased broods only among younger adults (Fig. 2). To maximize our sample, we included birds where only minimum age was known, subject to conditions used in previous analyses. If predators preferentially select the smaller, female goslings, then we would expect that the sex ratio would be closest to 1:1 when proportional brood survival was at or near 100%, becoming progressively male-biased with increasing brood loss. To indirectly control for SSD, we used only data from early years (<1980), where offspring SSD was largest. Among 557 adults (223 young, 334 old), there was no evidence of any variation among old and young adults in the relationship of sex ratio and the proportion of the brood surviving to fledging (χ² = 0.33, P > 0.5). There was also no difference when birds were classified as 'complete brood' (i.e. all goslings in a brood surviving to fledging) or 'partial brood' (i.e. at least one but not all goslings in a brood surviving to fledging); sex ratio did not differ between complete or partial broods for either young (χ² = 0.04, P > 0.5) or old birds (χ² = 0.47, P > 0.4). Thus, there is little evidence to suggest increasing mortality of female goslings with increasing brood loss.

SAMPLING HETEROGENEITY

If the sex ratio of goslings in broods that locally disperse from LPB after hatch are a non-random sample of the population, this could potentially bias some of our analyses. We tested this possibility by categorizing all broods for which hatching sex ratio was known on the basis of whether or not the parent was seen later that same year during ringing at LPB. The probability of seeing one or more members of a family group at ringing is, in fact, a product of the probability that it has not left the sampling region, and the probability that if in the sampling region it will be captured at ringing. Our sample consisted of 465 adult females (1982–86). While use of individually identifiable mothers only in this analysis restricted our sample size (for example, we could have used the presence of one or more hatching goslings at ringing), using adults rather than goslings eliminated confounding by mortality and dispersal, since adult mortality from hatching to ringing is essentially 0. Thus, assuming that the probability of capturing a brood, given that it is in
the sampling region, is independent of sex ratio, then
differences in encounter rates among adults reflect true
differences in the dispersal rate. Pooling over the years,
there was no evidence that the probability of recapturing
an individual adult female at ringing was
related to the sex ratio of her brood (χ² = 0.089,
P > 0.5).

We also tested for systematic changes in fledging
sex ratio within individual adult females, using data
from 168 females for which offspring sex ratio at
fledging was recorded in 2 or more years at LPB
(excluding Cape Churchill). Within-individual changes
are robust to sampling bias, provided the sample of
individuals is itself an unbiased sample of the popula-
tion (see above).

Since > 50% of the individuals in our sample had
their first and last measurements at 5 or more years
of age (no trend in fledging sex ratio was detected
among older birds; Fig 2), we considered young (2–5
years) and old (5–11 years) birds separately. Because
of the sparseness of the data set of known-aged indi-
viduals for which repeated measures were available,
we included birds for which only the minimum age
was known. Further, since there was annual variation
in the direction and magnitude of the difference in sex
ratio between young and old birds over time (Fig 2),
we further partitioned the data into four subsets, each
consisting of 3 consecutive years in which some
females were seen for the first time (first-observation
years), with ≤ 5 years difference between first and last
observation (relative to the first year). The range of
first-observation years for each data set were: 1973–
75, 1976–78, 1979–81 and 1982–84, respectively. Only
females within a given age group seen at least twice
within a 5-year block (conditional on the first year
of observation) were included. Each year-block was
treated as a classification level in a single-factor analy-
sis of covariance, with number of years between ob-
servations as the covariate.

There was no heterogeneity among year-blocks in
the regressions of the difference in sex ratio on the
number of years between paired observations (within
female) for younger birds (F[1,132] = 1.39,
P = 0.253),
and only marginal heterogeneity among block-years
for older birds (F[3,137] = 2.24, P = 0.086). Examination
of the individual regressions for older birds showed
that the heterogeneity was due to one year-block
(1973–75). There was no evidence of systematic change
among year-blocks in the magnitude and sign of
the with-block regressions for older birds (t = 0.25,
P > 0.5); however, among younger birds, there was
a near-significant linear decrease in the slopes among
year-blocks (i.e. a decreasing proportion of male
goslings within individuals in recent year-blocks;

\[ t = -1.93, P = 0.053; \text{Fig 5}. \]

In early years (1973–
75), the average sex-ratio difference between first
and last records among younger birds (weighted by
the number of years between records) was close to zero
(i.e. no change within individuals). However, over
time, the average difference between first and last
records became increasingly negative (i.e. fewer males).
No equivalent trend was seen among older birds.

**Discussion**

We have shown a significant long-term change in the
fledging sex ratio of snow goose goslings reared at
LPB. In the early years of our study, when food was
abundant, there was a significant bias towards male
goslings. In recent years, however, when food has been
less abundant, the direction of the bias has changed,
favouring female goslings. Results of within-year
analyses comparing fledging sex ratios between two
different brood-rearing areas were consistent with this
trend; the fledging sex ratio was significantly male-

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Offspring sex-ratio changes in snow geese

biased at the site with abundant food, and female-biased at the site with restricted food supply. We have also shown that this result is not an artifact of sampling bias. To our knowledge, the only other comparable study of long-term sex-ratio variation in a bird with praeococial young is that by Wegge (1980), who showed a systematic decrease in male offspring in a declining grouse population. What are the causes of the sex-ratio changes at LPB, and ultimately, what are the likely consequences?

FACULTATIVE MANIPULATION OR PASSIVE MORTALITY?

Clutton-Brock (1991) suggested that an increased frequency of the smaller sex under poor conditions may be due to a facultative manipulation or may simply reflect the cost of sexual selection for dimorphic growth, or both. However, where good conditions are associated with a bias towards the larger sex, the simplest explanation might be that adaptive manipulation is involved, since there is little reason to expect differential survival of male and female offspring under good conditions. Manipulating sex ratio is adaptive only if there are significant differences in the cost-benefit ratio of rearing male or female goslings. Ignoring the possibility that males and females might differ in survival probabilities (a clear cost), is it possible that producing goslings of either sex is costly in other ways?

In species with self-feeding young, the larger direct costs to producing offspring are in egg formation (e.g. Brunton 1988). In snow geese, male and female goslings hatch from eggs of the same size (Harmsen & Cooke 1983). Thus there is probably no direct cost to adult snow geese in producing offspring of either sex. However, there are several potential sources of indirect costs to producing male or female offspring. In the following, we consider two different possibilities.

Snow geese exhibit strong female philopatry to the natal colony. If returning female goslings compete significantly with their parents for local resources (local resource competition; LRC), then parents should skew the offspring sex ratio to favour the dispersing (and therefore less costly) sex (sensu Clark 1978; Silk 1983, 1984; Chapman et al. 1989; Gowaty 1993). Although the male-biased sex ratio in the early years of our study is consistent with this general prediction, we believe such an interpretation may be premature. Despite some degree of fidelity to specific feeding areas (Cooke & Abraham 1980; Healey, Cooke & Colgan 1980), snow geese are far less gregarious on the breeding grounds than typically observed in large winter flocks. Direct agonistic encounters between family units in general are relatively rare, even under increasingly patchy food availability at LPB (Mulder, Williams & Cooke 1995).

In addition, even if there was significant competition between parents and recruited offspring for some local resource, LRC also predicts that, all other things being equal, as food supply decreases parents should increasingly favour producing more male goslings, the opposite to what we actually observed. Clearly, more data on the degree of competition (at a broader level) with conspecifics on the breeding ground is needed.

Trivers & Willard (1973) proposed that if larger male size increased the chances of reproductive success of male offspring, and if females in good condition reared relatively larger males, then females in good condition could increase their inclusive fitness by producing more males. Females in poorer condition, producing smaller, less competitive males, should produce more females. If, however, females in good condition produce more rather than larger offspring, then no change in sex ratio is predicted. Among Arctic-nesting geese, birds with proportionately larger endogenous reserves of lipids and protein tend to lay more, but not larger, eggs (Ankney & MacInnes 1978; Davies, Rockwell & Cooke 1988; Cooch et al. 1992).

Since gosling size at fledging is positively correlated with egg size (Cooch et al. 1991a; Cooke et al. 1995), there would appear to be little reason to predict the Trivers & Willard (1973) hypothesis to apply directly.

However, the Trivers & Willard hypothesis may operate indirectly if the circumstances that lead to variation in parental condition also influence gosling growth rates (Cooch et al. 1989, 1991b; Ganter 1994). If offspring reared under poor conditions are smaller as adults, and if adult size influences reproductive success, then any sex-specific differences in the relative advantage of larger size will favour a biased sex ratio. This is essentially a special case of the ‘non-adaptive’ mortality hypothesis; in both cases, offspring of one sex show reduced fitness relative to the other. Earlier studies of several related species of geese have shown that poor growth conditions lead to smaller gosling size at both fledging (Cooch et al. 1991a; Sedinger & Flint 1991; Larsson & Forslund 1992) and subsequently as an adult (Cooch et al. 1991b; Larsson & Forslund 1991; Sedinger, Flint & Lindberg 1995). Several recent studies of other species of Arctic-breeding geese have provided good evidence that there may be a significant fitness cost to smaller size, for both male and female goslings (Sedinger et al. 1995; Choudhury, Black & Owen 1996), although evidence for snow geese has been contradictory (Alisauskas & Ankney 1990; Cooch et al. 1992; Cooke et al. 1995).

Black & Owen (1989) also show clear evidence of active parental exclusion of females during family break-up in late winter and early spring in a population of barnacle geese Branta leucopsis. They suggested that males, being larger, conferred greater fitness advantages to family groups in encounters with conspecifics during winter.

While there would appear to be some potential fitness benefits to parental manipulation of sex ratio in

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snow geese, it is unlikely that an adaptive explanation alone can explain our results. Instead, we believe that the most parsimonious explanation for the long-term decline in the frequency of males is increased male-biased mortality between hatch and fledging, especially among broods from younger females. Our reasons are twofold. First, it is unclear how such a manipulation might be achieved in this species. We found no evidence of systematic changes in hatching sex ratio (see also Cooch et al. 1996). The lack of variation in hatching sex ratio from 1:1 in other waterfowl has also been documented recently (Blums & Mednis 1996). This suggests that any manipulation would have to occur post-hatch. Unfortunately, goslings observed remotely during brood rearing are not individually identifiable, and are of unknown sex (sex is determined at fledging), and thus we have no behavioural data on sexual differences in parent–offspring interactions. The only study of sexual differences in gosling behaviour during brood-rearing of which we are aware is a study of a feral barnacle goose population (Black & Owen 1987). However, that study found no evidence of sexual differences in dominance among siblings until the second month after hatching (generally later than the interval of our study), and did not address possible parent–offspring conflict in relation to offspring sex, which would be important if parents are actively manipulating offspring sex ratio. Secondly, and perhaps more importantly, it is not clear how sex ratio changes among younger adults only, either overall (Fig. 2) or within-individual (Fig. 5), reflect adaptations. Neither the LRC hypothesis, nor Trivers & Willard, appear to be consistent with these differences.

While increased mortality of male goslings under food restriction may explain the long-term decrease in the frequency of male goslings at fledging, the causes of the male-biased broods when food is abundant are less clear. If such a bias does not reflect parental manipulation (contra Clutton-Brock 1991), then what is the basis for a male-biased sex ratio under good conditions? Further, why is it apparent only among younger females? Our analyses did not indicate sexual differences in post-hatch gosling survival in good years, implying that the male bias must have occurred at hatching. We found some evidence to suggest that the hatching sex ratio of younger birds may be male biased, although the sample was small (n = 22). Since the adult sample in early years was biased towards younger birds, this would possibly explain the male-biased sex ratio in those years. Both clutch size and egg size are known to increase with age among individual birds (Rockwell et al. 1993; Robertson et al. 1994), and it may be conceivable that very young birds are constrained from producing a 1:1 hatching sex ratio. In contrast, a recent study of several species of ducks by Blums & Mednis (1996) found no evidence for age-specific differences in hatching sex ratio. Clearly, more data are needed.

**Tracking a Changing Environment: The Role of Parental Age**

There was a strong effect of parental age on the long-term change in sex ratio in this study. It is well known that reproductive performance increases with experience in geese (Rockwell et al. 1993; Black & Owen 1995; Black, Choudhury & Owen 1996). The relative advantage of older, typically more experienced breeders would presumably increase when food becomes scarce; offspring of older females should have greater access to remaining patches of food, and thus have maximum growth and survival possible for both sexes. In contrast, inexperienced, young adult females would not be as adept in adapting behaviourally to the reduced food supply, and thus their offspring would have proportionately greater reductions in growth. If males are more susceptible to these reductions (as suggested by the decline in SSD over the years, Fig. 2, and within season; Cooch et al. 1996), this might lead to greater mortality of male goslings.

While we do not have data readily available to assess behavioural differences in foraging as a function of female age, results from our analysis of within-individual changes in fledging sex ratio is consistent with this hypothesis. Among younger birds in the early years, there was no apparent improvement (or variation) in sex ratio with age, whereas as conditions deteriorated, young females showed progressively female-biased broods, despite increasing age and (presumably) experience (Fig. 5a). In contrast, among older birds, there was no evidence of systematic changes with age over the years; old birds seemed able to track changing environmental conditions successfully (Fig. 5b).

It is notable, however, that the rate of change in offspring SSD (Fig. 2) did not differ significantly among old and young adults, either within season (Cooch et al. 1996) or over the years (year × sex × age; \( F_{1,196} = 0.64, P > 0.5 \)). If older females are better able to accommodate the progressive loss of food at LPB, then we might have expected a reduced (or at least different) rate of change in SSD relative to goslings from younger females. No such difference was detected. One explanation may be that the SSD variation among offspring from younger parents is affected by both the long-term decline in food and sex-specific mortality selection, whereas among older birds only the effects of variation in food supply appear to be operating. Unfortunately, we have no direct means of testing this hypothesis.

Cooch et al. (1996) suggested that sexual differences in within-season growth and development may reflect adaptations to minimize increased mortality risk of rapid growth in the presence of predictable seasonal reductions in food supply. Despite significant differences in growth, no seasonal variation in fledging sex ratio was observed. However, in the present study, sexual differences in growth over years have been
accompanied by a significant change in fledging sex ratio. One possible explanation for this difference within and among years is that the same capacity for ‘variable growth’ observed within season is in effect over years, but that the magnitude of the change in food supply over years (c. 18 g year\(^{-1}\); Williams et al. 1993) is sufficiently large (relative to seasonal changes; c. 10–15 g day\(^{-1}\); Cooch et al. 1991a) for male goslings to suffer increased mortality.

**FITNESS CONSEQUENCES**

Although the decrease in the frequency of male goslings among younger adults was substantial (≈20% reduction), the decline at the population level was comparatively small (≈3%). Are changes in fledging sex ratio of this magnitude likely to have any biologically significant consequences? If a population is effectively closed, such that mates are chosen among offspring from the same natal colony, even small changes in the offspring sex ratio may have significant implications on the dynamics of the populations, especially for monogamous species such as the snow goose. In contrast, a small reduction in the frequency of males in a polygynous mating system may have relatively little direct impact on the dynamics of the population (at least in the short run). Further, the presence of even small degrees of sexual size dimorphism implies some level of sexual selection favouring larger male size (Sedinger et al. 1995; Choudhury et al. 1996). Even small skews in the sex ratio of the mate choice pool may have significant consequences for the pattern of selection on body size.

However, predicting the impact of the changes in sex ratio on the LPB population is difficult, for several reasons. First, the LPB population is not closed: females from the LPB population select their mates in wintering areas where birds from several colonies mix. The frequency-dependent consequences of sex-ratio variation at an interdecile level are presently unknown. Secondly, although young adults that remain at LPB may suffer greater proportional brood mortality overall, with increasing selection against male offspring, younger adult females may, in fact, be more likely to disperse locally from the deteriorating traditional feeding areas than older birds (Rockwell et al. 1993). Goslings reared away from LPB are larger and show greater survival (Cooch et al. 1993). To some degree, the decline in sex ratio observed at LPB is an epiphenomenon of sampling in a deteriorating area. Without more detailed information on the rate and pattern of local dispersal during brood rearing, and the frequency distribution of birds from other colonies in winter, it would be premature to do more than speculate at this stage.

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