Male chicks are more costly to rear than females in a monogamous seabird, the Common Murre

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Feeding rates and mass loss during chick rearing were compared for individually marked parents of male and female Common Murre (*Uria aalge*) chicks at Great Island, Newfoundland, Canada, from 1997–2001. Both parents in this socially monogamous seabird species share parental care duties until colony departure, after which the single chick is fed only by its father. Because murres provision their single chicks with one clearly visible fish per trip, it is possible to accurately determine whether parents differentially feed male and female chicks. Based on slightly greater mass of males in adulthood, possibly favored by sex differences in breeding roles, we predicted that male nestlings would be fed more than females. Fathers' feeding rate to sons, but not daughters, increased with chick age, whereas maternal feeding rate increased with chick age for both sexes. When year-corrected feeding rates of pairs rearing both sexes were compared, both mothers and fathers fed their sons significantly more than their daughters in the later part of the chick-rearing period. Moreover, parents rearing male chicks lost mass at a significantly higher rate than those rearing females. There was no difference in fledging age for sons and daughters. These results indicate that differential parental allocation occurs and has measurable costs even in a species with only slight adult sexual dimorphism. *Key words:* Common Murre, feeding rate, parental care, sex differences, sexual size dimorphism, *Uria aalge*. [Behav Ecol 18:81–85 (2007)]

Raising offspring is costly, both in terms of parental energy expenditure and risks to adult survival (Gabrielson 1996; Jönsson et al. 1998). To maximize lifetime reproductive success, parents must balance current investment in young against future reproductive potential (Williams 1966; Frank 1990; Webb et al. 2002). Parents may adjust the amount of effort that they invest according to available resources and their own body condition, as well as to the demands and fitness value of particular offspring (Erikstad et al. 1997).

The relationship between an offspring's fitness value and the conditions under which it is reared may depend on its sex. In sexually size-dimorphic species, offspring of the larger sex may require more parental resources, as they are often more susceptible to death from starvation in poor conditions (Howe 1977; Clutton-Brock et al. 1985; Stamps 1990; Anderson et al. 1993; Torres and Drummond 1999). Thus, depending on resource availability and parental body condition, parents may benefit from biased sex allocation. Recently, however, altered sex ratios or differentially provisioned eggs have also been reported in species with moderate or minimal size dimorphism, such that more males are produced or males receive more resources under optimal conditions (Albrecht and Johnson 2002; Andersson et al. 2003; Müller et al. 2005). These studies suggest that because high-quality males are better at competing reproductively, parents in good enough condition or with sufficient resources to produce high-quality offspring should bias the sex ratio or parental allocation toward males.

Common Murres are long-lived, socially monogamous alcids. Male Common Murres generally weigh more than females, depending on time of year (a difference of approximately 5%; Threlfall and Mahoney 1980; Harris et al. 2000). There are two breeding phases where high-quality (heavier) male murres may hold a competitive advantage over lower quality ones. Male murres vary considerably in the time they spend on the breeding cliffs prior to egg laying (Wanless and Harris 1986; Hatchwell 1988; Wilhelm and Storey 2002). Males that stay on the ledge longer lose body mass, and individual males spend relatively more time on the ledge in years when their body mass is greater (Storey et al. 2004). High ledge attendance increases the chance that a male will be present when his mate arrives to court and copulate, whereas low attendance is correlated with subsequent low chick provisioning, and to divorce and delayed repairing (Moody et al. 2005).

Although males and females share the prefledging care of chicks (Ainley et al. 2002), male murres take their single fledging chicks to sea when the chicks are approximately 25% of adult body weight (alcid intermediate fledging strategy: Sealy 1973; Ydenberg 1989). Fathers are the sole chick provisioners for several weeks after colony departure (Ainley et al. 2002). Both male and female murres decline in body mass during the chick-rearing period at the nest site (Harris et al. 2000; Ainley et al. 2002). Chicks may be more likely to survive if their fathers are in relatively good body condition at the start of this period and at the onset of the flightless molt that follows (a period when males are heavier than females; Harris et al. 2000).

Differential costs of rearing males and females, and thus adaptive explanations for sex ratio manipulation, have been difficult to determine in species with less marked sexual dimorphism. Common Murres raise a single chick per year, and parents provision chicks with a clearly visible single fish per provisioning trip, making it a useful species for examining these issues. In contrast, for species rearing more than 1 chick per brood, it is often difficult to determine which chicks in variably sized broods are fed and how much each chick gets per parental visit (Anderson et al. 1993; Saino et al. 2002). Sex

and size differences in energetic expenditures among chicks competing with siblings for food (as in Anderson et al. 1993) also do not have to be taken into account when only 1 chick is produced. We can therefore compare provisioning rates, as well as costs measured by adult mass loss, for parents rearing male and female chicks. Further, we can compare chick provisioning in the same individually marked pairs in different years when they produce male and female offspring.

This study examines feeding rates and mass loss for parents of male and female Common Murre chicks. Adult murres at this study site are individually color-banded and their sexes are known, providing a rare opportunity to examine sex allocation strategies of mothers and fathers separately (Lessells et al. 1998). We predicted that sons would be fed more than daughters because differences in feeding rate are associated with higher chick growth rate and with quality and size dimorphism in adulthood (Anderson et al. 1993; Sæther et al. 1997; Krijgsveld et al. 1998). Accordingly, it is expected that parents rearing a son would experience a higher rate of mass loss over the chick-rearing period than those rearing a daughter. Finally, fledging ages will be compared for male and female murre chicks. Richner (1991) reported that females in several avian species fledge 5–13% sooner than males on average. If daughters require and receive less parental care than sons, we predict that female murre chicks will leave the nesting site at a relatively young age, whereas male chicks should remain at the nest site receiving feeds from both parents for a longer period.

MATERIALS AND METHODS

Field methods

Research was conducted on Great Island, Newfoundland, (47°11′N, 52°46′W) from 1997 to 2001. The study plot was located at the periphery of a colony on the southeast end of the island. Dawn-to-dusk blind watches lasting approximately 16 h were conducted on approximately 30 known breeding pairs, every 2–3 days throughout the chick-rearing period of late June to early August. Two observers alternated shifts of 2–4 h in a wooden blind, which had a window of one-way glass through which the murres were watched and a canvas extension where the off-duty observer would remain. An average of 11 all-day blind watches were conducted each year, with a minimum of 5 complete days (in the first year of the study) and a maximum of 15 days. Most of these "known" murres were color-banded (over 90%); the rest were mated to color-banded individuals. Four Ohaus CS-2000 weighing scales cemented to rocks on the murre plot provided opportunistic mass measurements of adults that stood on or walked over them (scales were accurate to ±1 g and modified so that they could be read and tared from the blind; design by I.L. Jones). Mass measurements were also obtained when adults were caught for banding and blood sampling.

Observers noted the arrival and departure of known birds, and when birds brought food items to the site, the species and relative size of the prey were recorded in most instances. Female capelin comprised about 90% of the chick diet at this colony during our study. A capelin was coded as small if only the tail could be seen in the parent's bill, medium if less than 2 cm of fish body and tail were visible, and large if more than 2 cm and the tail were visible. Direct measurement of prey items could not be undertaken without causing unacceptable disturbance of the study plot; however, in a few cases, weights of adults were obtained just before and after delivering a fish to a chick. From these events, we estimate that small capelin weigh approximately 15 g, medium capelin about 18 g, and large capelin about 23 g.

Dates of egg lay and hatching were recorded when possible to within ±2 days. Observations were conducted during the prebreeding and early egg-laying period of early May to early June as well as during the chick-rearing period, so the lay date was known for early breeders; if a chick had hatched before the watches were resumed at the site, the hatch date was assumed to be 33 days after the lay date of the egg at that nest site (Ainley et al. 2002). Fledging dates were also recorded from 1999 to 2001.

When chicks were able to thermoregulate, at least 10 days after hatching (Ainley et al. 2002), they were captured with a noose pole and banded. Catching was opportunistic; only chicks within reach of the noose pole were sampled, and this was typically around 15 chicks in each of the 5 years. Three growing primary feathers were taken for genetic analysis and stored in 70% ethanol, and the chick was weighed with a spring balance before it was released. In all instances, the parent and chick successfully reunited soon after handling.

Molecular sex identification

Chick sexing was performed after the field season was completed, so researchers were blind to the sex of the chicks throughout the observations. Each chick feather shaft containing pulp was cut into small pieces using a sterile blade and placed in extraction buffer and a proteolytic enzyme (pronase E or proteinase K) for 24–48 h. This was followed by a phenol:chloroform:isoamyl alcohol extraction, and the DNA was then left to precipitate overnight at −20 °C in 95% ethanol. The resulting DNA pellet was rinsed in 70% ethanol and left to dry overnight, then resuspended in 25–100 μl Tris–EDTA.

The product was sexed using the 2550F/2718R primer pair, which flanks an intron found on the CHD-Z and CHD-W genes (Fridolfsson and Ellegren 1999). This intron differs in length on the 2 genes, resulting in the amplification of a 600-bp segment on CHD-Z and a 450-bp segment on CHD-W. Molecular sexing using this primer pair has also been performed on blood samples from 28 adults of known sex at this study site, validating the use of this sexing method for Common Murres (Cameron-MacMillan ML, unpublished data).

Statistical analyses

Statistics were performed using SPSS 13.0 for Windows (SPSS Inc. 2004). A significance level (α) of 0.05 was used in all analyses. Feeding rates by mothers and fathers were compared using a multivariate general linear model (GLM). Explanatory variables included in the model were chick sex and study year, with chick age and hatch date as covariates. Chick age was included because chick feeding rate is not constant throughout the period of parental feeding at the site; young chicks are fed less frequently than older chicks (Gabrielsen 1996). A chick sex by chick age interaction term was included in the model to determine whether this increased rate of feed7ing of older chicks was similar for sons and daughters. The statistical significance of differences between mothers' and fathers' feeding patterns was assessed using Pillai's trace.

To compare rates of feeding to sons and daughters within pairs, individual pairs that were known to have raised both male and female chicks were analyzed further. Maternal and paternal feeding rates were compared for the period from 13 days onward, during the period of increased provisioning of older chicks when sex differences would be more likely detected. Individual pairs rear only 1 chick each year, so to facilitate comparison of feeding rates to sons and daughters, interannual effects were removed by calculating the residuals of mean annual feeding rates of mothers and fathers at the study site relative to all other males and females at the study

site. Mean residual feeding rates to sons and daughters were compared using paired *t*-tests; for pairs rearing more than 1 son or daughter, the average of the residual feeding rates for all chicks of that sex was calculated.

For many of the observed chick feeds, species and relative size of the prey had been noted. Using these data, the proportions of small, medium, and large capelin fed by mothers and fathers to offspring of each sex were compared using a chi-squared analysis to determine whether there were differences in the size of prey delivered to male and female chicks.

Mass changes were compared for adults rearing male and female chicks. Mass data were included for each adult rearing a maximum of 1 chick of each sex. To avoid pseudoreplication, 1 set of data was randomly omitted for each of the 2 adults for which mass data were available that had reared 2 chicks of the same sex. The 2 mass measurements used to calculate the rate of mass loss were taken an average of 8 days apart (8.0 ± 0.5 days standard error [SE]), starting on average when the chicks were a week old (mean chick age of 7.0 ± 0.8 days). This timing coincided with the onset of the increased provisioning of older chicks and avoided both very early chick rearing (because large mass decreases have been reported at hatching in murres; Gaston and Hipfner 2000) and the last few days before fledging. Rate of mass loss (g/day) was analyzed using a univariate GLM, with parent sex, chick sex, and year as explanatory variables. A parent sex by chick sex interaction term was included in the model to determine whether mothers and fathers showed differing chick sex effects.

The fledging ages of male and female murre chicks were compared using a univariate GLM. Explanatory variables in the model were chick sex, year, and hatch date. Because the duration of the breeding season is constrained by food availability, late-hatched chicks and their fathers may be forced to leave the cliff sooner to swim to the food supply. Moreover, chicks remaining late in the season after most pairs have left the breeding site are more susceptible to predation.

RESULTS

From 1997 to 2001, 76 chicks were captured and sexed. However, the sample size was reduced to 67; because some of the breeding pairs were unbanded in 1997 and 1998, feeding data were unavailable for 9 of the chicks.

Overall, mothers and fathers fed their male and female chicks equally (Table 1). Average maternal feeding rate was 2.16 ± 0.10 trips/day for sons and 2.19 ± 0.10 trips/day for daughters (mean $\pm$ SE). For fathers, average feeding rate was 2.01 ± 0.10 trips/day for sons and 1.92 ± 0.09 trips/day for daughters. However, although both parents showed an overall increase in

chick feeding rate with chick age, fathers had a significant interaction of chick sex with chick age (Table 1). Fathers' feeding rate to sons increased significantly with chick age, whereas feeding rate to daughters did not (Figure 1), such that although sons and daughters were fed equally in early chick rearing by their fathers, older sons were fed more than older daughters. No such interaction was seen for mothers.

There was significant interannual variation in chick feeding rates for both parents, and year effects differed between mothers and fathers: for fathers, feeding rate in 1999 was significantly higher than in 1998, 2000, and 2001; whereas for mothers, feeding rates in 1998, 1999, and 2000 were all significantly higher than in 2001 ($P < 0.05$). Maternal feeding rate increased significantly with later hatch date ($R^2 = 0.007$, $P = 0.022$), whereas fathers' feeding rate did not (Table 1).

Mean residual feeding rates by mothers and fathers were calculated for each of the 12 pairs that were known to produce both sons and daughters. For these 12 pairs, average feeding rate of mothers was 2.59 ± 0.17 trips/day for sons and 2.06 ± 0.15 trips/day for daughters; average feeding rate of fathers was 2.30 ± 0.25 trips/day for sons and 1.84 ± 0.13 trips/day for daughters. Correcting for year effects, both mothers and fathers fed their sons significantly more than their daughters (fathers: $t_{11} = 1.8$, $P = 0.049$; mothers: $t_{11} = 2.6$, $P = 0.016$; Figure 2).

Contents of chick feeds did not differ for male and female chicks. Chicks of both sexes received approximately 90% capelin and the remaining 10% was almost exclusively sand lance (*Ammodytes* spp.). Analyzed over all years, both parents delivered a similar proportion of small, medium, and large capelin to their male and female chicks (mothers: $\chi^2_2 = 1.52$, not significant [NS]; fathers: $\chi^2_2 = 2.29$, NS).

Rate of mass loss of parents with sons was more than double that of parents with daughters (parents rearing sons: 7.4 ± 1.6 g/day; parents rearing daughters: 2.5 ± 1.6 g/day), a significant difference (Table 2). There was no significant interannual variation in mass loss. Neither the parent sex effect nor chick sex by parent sex interaction was significant; that is, mothers and fathers lost mass at a similar rate overall, and the effect of chick sex was similar for both parents (Table 2, Figure 3).

Fledging ages were similar for male (21.1 ± 1.8 days, $n = 14$) and female chicks (21.9 ± 2.8 days, $n = 27$; Table 3). There were

Table 1

Multivariate GLM analysis of mean parental feeding rate to sons and daughters for Common Murres at Great Island, Newfoundland

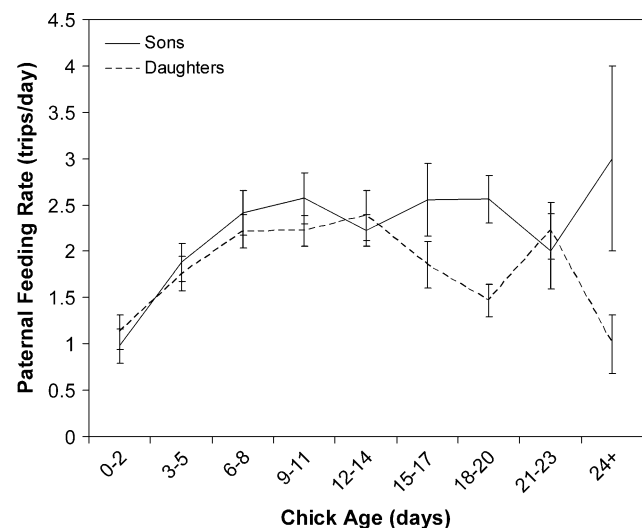| Source	df	Mothers		Fathers		Parent sex differences		
		F	P	F	P	df	F	P
Chick sex	1	0.29	0.59	2.27	0.13	2	1.33	0.26
Year	4	6.56	<0.001	10.34	<0.001	8	8.50	<0.001
Hatch date	1	5.30	0.022	0.000	0.99	2	2.65	0.072
Chick age	1	4.17	0.042	10.15	0.002	2	7.58	0.001
Chick sex × chick age	1	0.23	0.63	7.19	0.008	2	3.80	0.023
Error	439					438		

df = degrees of freedom.

Figure 1
Paternal feeding rate to sons and daughters in relation to chick age. Error bars represent SE values. Relationship is significant for sons ($R^2 = 0.087$, $P < 0.001$) but not daughters ($R^2 = 0.003$, NS).
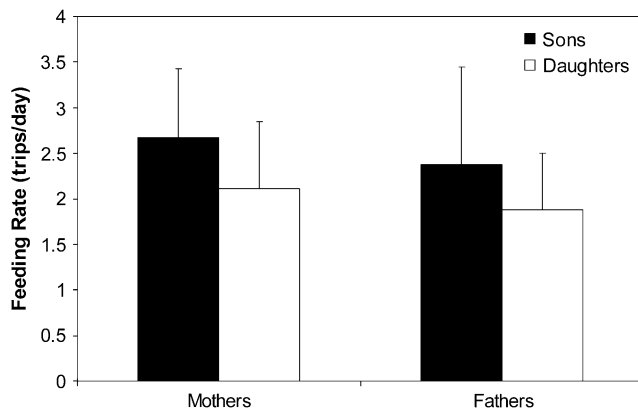
Figure 2
Mean parental feeding rates (±SE) to chicks of each sex in late chick rearing for pairs rearing both sons and daughters in different years. Difference is significant for both mothers and fathers.
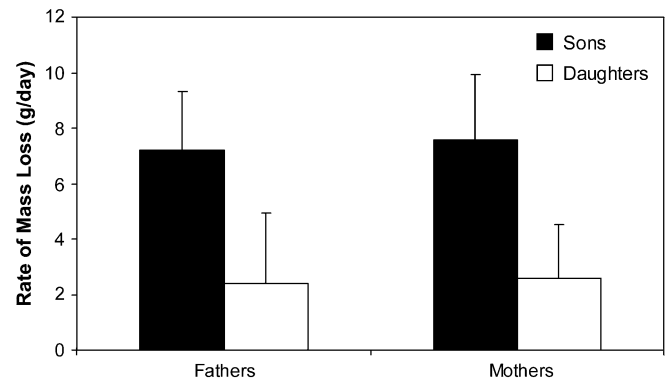

Figure 3
Mean daily mass loss during chick rearing at the site (±SE) for mothers and fathers rearing offspring of each sex. For both mothers and fathers, rate of mass loss is significantly higher while rearing male chicks.

no interannual differences in fledging age, but hatch date had a significant effect (Table 3), later-hatched chicks fledging at a younger age ($R^2 = 0.22$).

DISCUSSION

Common Murre fathers fed their sons more than their daughters in the later part of the chick-rearing period at the nest site, whereas maternal feeding showed no sex bias in increased rate of feeding with chick age. However, when year-corrected feeding rates of pairs rearing both sons and daughters were compared, both mothers and fathers fed their sons significantly more in the later part of the chick-rearing period at the nest site. Parents did not differ in the size of fish they fed their sons and daughters, confirming that provisioning frequency accurately portrays differential parental investment. Parental mass loss during chick feeding was greater for parents rearing sons than those rearing daughters.

Common Murre sons received more parental feeds than daughters late in the chick-rearing period. As well, fathers' feeding rate increased with chick age for male but not female offspring. These modest yet significant differences in feeding rate suggest that parents should produce more female than male chicks in resource-poor years, as has been found for this population (Cameron-MacMillan ML, in preparation). Early in the chick-rearing period, sons and daughters were fed equally often. This equality may reflect the lower food requirements of younger chicks (Gabrielsen 1996); alternately, it may reflect the more difficult feeding conditions seen in the early part of some study years, preventing any chicks from being fed very often. Feeding conditions were difficult when capelin, the

main prey fish, arrived inshore to spawn later than the onset of Common Murre hatching in 2000 and 2001 (capelin arrival records; Nakashima B, personal communication).

Common Murre parents lost mass at more than twice the rate when rearing sons than when rearing daughters. This finding further demonstrates a sex bias in parental effort. Murres are known to lose mass during chick rearing (e.g., Harris et al. 2000; Ainley et al. 2002), but few studies have quantified the mass loss in specific individuals of known reproductive status. Paredes et al. (2005) report an approximate 4–5 g/day mass loss for the congeneric, similarly sized, Thick-billed Murre (*Uria lomvia*), values that coincide well with our overall average for both sexes of chicks combined (5.4 g/day).

Male and female murre chicks did not differ in fledging age, which suggests that differences in cost of sons and daughters do not arise from variation in the duration of parental feeding at the nest site. However, it is important to note that paternal care in murres does not end at colony departure, and it would be of interest to determine if there are differences in the amount of time that males spend at sea with their sons and daughters before young become completely independent.

Mothers, but not fathers, appeared to feed their later-hatched chicks at a higher rate than chicks hatching earlier in the season; however, it must be noted that the R^2 value is very low, and it would be speculative to draw conclusions based on this result. Late-hatched chicks depart the nest site with their fathers at a younger age, and if there is increased feeding of late-hatched chicks by mothers, it may be an attempt to ensure that the chicks have sufficient resources at fledging.

Offspring of one sex may receive more care than the other because parents differentially allocate resources and/or

Table 2
Univariate GLM analysis of the effect of chick sex, parent sex, and study year on rate of parental mass loss during chick rearing in Common Murres at Great Island, Newfoundland

Source	df	F	P
Chick sex	1	4.77	0.04
Parent sex	1	0.02	0.90
Year	2	1.24	0.31
Parent sex × chick sex	1	0.00	0.97
Error	17		

df = degrees of freedom.

Table 3
Univariate GLM analysis of the effect of chick sex, hatch date, and study year on fledging ages of Common Murre chicks at Great Island, Newfoundland

Source	df	F	P
Chick sex	1	0.54	0.47
Year	2	2.69	0.082
Hatch date	1	14.61	0.001
Year × chick sex	2	0.28	0.76
Error	34		

df = degrees of freedom.

because offspring show differential skill at extracting resources from their parents (Clutton-Brock 1991). Males in multiple-offspring broods can compete by begging more and positioning themselves closer to incoming parents (e.g., Teather 1992), but even in species rearing a single offspring at a time, males can successfully obtain more resources by making more approaches to solicit provisioning (e.g., in harbor seals, *Phoca vitulina*; Rosen and Renouf 1993). Murre chicks vocalize when their foraging parent returns but they are usually fed immediately and thereafter do not (or cannot) vocalize until they finish swallowing the fish. Parents often "loaf" at the nest site after provisioning, and it is not clear whether cues from chicks contribute to changes in parental foraging behavior (e.g., earlier departure by a parent for the next foraging trip). It remains to be determined whether parents or chicks, or possibly both, are responsible for the higher feeding rate received by older male chicks from their fathers.

In conclusion, Common Murre sons were fed more often than daughters in late chick rearing. Fathers increased their provisioning rate to older sons, but not older daughters, and parents lost more mass while rearing sons than when rearing daughters. These data show that even with minimal sexual dimorphism, there can be greater costs associated with rearing offspring of the larger or more competitive sex.

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