

SEX-SPECIFIC GROWTH AND PRE-AND POST-
HATCHING PATTERNS OF SEX ALLOCATION IN
MURRES (URIA SPP.) AND ATLANTIC PUFFINS
(FRATERCULA ARCTICA)

CENTRE FOR NEWFOUNDLAND STUDIES

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MAUREEN L. CAMERON



SEX-SPECIFIC GROWTH AND PRE-AND POST-HATCHING PATTERNS OF SEX
ALLOCATION IN MURRES (*URIA* SPP.) AND ATLANTIC PUFFINS (*FRATERCULA*
ARCTICA)

by

© Maureen L. Cameron

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ABSTRACT

Patterns of pre- and post-hatching sex allocation were explored in the Common Murre *Uria aalge*, Thick-billed Murre *Uria lomvia*, and Atlantic Puffin *Fratercula arctica*. Chicks from each species were sexed using the CHD gene. Growth rates of male and female chicks were compared, as were parental feeding rates and time spent at the nest site. The sex ratios produced with respect to parental age, size and body condition, as well as annual mean feeding rate at the site, were examined.

While males and females gained mass at a similar rate, wing growth was faster for female chicks. In Thick-billed Murres, wing growth in males, but not females, was positively correlated with parent quality. In the latter part of the chick-feeding period at the nest site, Common Murre parents fed their sons at a higher rate than their daughters. There was no sex difference in time to fledging. In years where parents provisioned their chicks less than usual, the sex ratio at the Common Murre study site showed a female bias. Parents that were larger or in better condition were no more likely to produce a son, and there was little support for an effect of parental age, though very young parents tended to produce daughters.

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CO-AUTHORSHIP STATEMENT

This work incorporates data from studies on three alcid species. I contributed in research design and collection of field data from the two Great Island studies, on Atlantic Puffins and Common Murres, in 2000 to 2002. Data from previous years of the long-term Common Murre study and the Thick-billed Murre work on Coats Island that are used here were collected by other graduate students of Dr. Anne Storey's lab (Carolyn Walsh, Sabina Wilhelm and Mark Hipfner). I performed all of the molecular sexing of chicks for this thesis, as well as most of the DNA extractions. DNA was extracted from most of the pre-2000 Common Murre chick feather samples by Carolyn Walsh. Data analysis and manuscript preparation were largely done by myself, with help and input from my supervisory committee.

Chapter 1 Introduction

1.1 Background of Study

The theory of sex allocation was first formalized by Fisher (1930), who reasoned that frequency-dependent selection is why populations tend to have a sex ratio of approximately 50:50. He argued that if a population contained a surplus of males, then the average genetic return per unit investment would be greater for an individual producing female offspring, and vice versa, resulting in an equal sex ratio in the population. Fisher's theory applies to populations, and makes no prediction about individual allocation strategies. This theory relies on the assumption that mating is panmictic (population-wide), and that offspring success is directly proportional to the amount of parental investment received.

Hamilton (1967) noted that very different predictions are warranted when competition for mates is local, rather than population-wide. The extreme example he cited was that of certain parasitic arthropods, in which mothers lay several eggs in a host, and produce an overwhelming majority of females. Because mating is limited to siblings in these species, parents maximise genetic returns by maximising the number of offspring of the limiting sex. Local competition for mates is higher among males than females in such cases; this idea has been extended to sex differences in kin competition for other resources, such as food or breeding sites. Often, one sex has a higher rate of dispersal than the other, and selection favours greater allocation of parental effort toward production of the dispersing sex, thus minimizing local resource competition with

offspring. This is particularly evident when the resources in question are scarce (Emlen, 1997). Besides local mate competition and local resource competition, a third explanation of sex ratio variation due to sexually different dispersal has recently been developed (Hardy, 1997). Local resource enhancement is a special case in which the non-dispersing sex helps the parents to rear their siblings, and so the benefits of producing that sex outweigh the costs of kin competition in all but the poorest territories (Emlen *et al.*, 1986; Komdeur *et al.*, 1997).

One of the earliest suggestions that cost and benefits of raising a son or a daughter differ among individuals came from Trivers & Willard (1973). They considered the effects of maternal condition on parental investment in offspring of each sex, invoking the following three assumptions. First, there is a correlation between the condition of the mother during the period of parental investment and the condition of the offspring upon reaching independence. Second, the relative condition of an individual in adulthood is similar to its condition at the termination of parental care. Third, because their reproductive success is highly variable, males have a disproportionately large increase in success with a slight advantage in condition over competitors for mates; this is in contrast to the second assumption of Fisher's theory, namely that reproductive success is proportional to the amount of parental care received. Thus, Trivers & Willard's theory predicts that females in good condition would do well to invest more in sons.

It is important to note that Trivers & Willard's theory refers to sex biases in resource allocation, rather than in the ratio of offspring produced. However, selective

resource allocation can cause greater mortality in the larger sex (typically males), leading to a biased sex ratio at independence (Trivers & Willard, 1973). This point was clarified by Clutton-Brock *et al.* (1985), who provided evidence that sex-biased mortality was a result of sex differences in nutritional requirements due to higher growth rates of the larger sex, rather than biased parental care.

Trivers & Willard's model has since been extended, and is now used to predict greater investment in the sex that provides higher genetic returns in the local environment (including, but not limited to, maternal condition) in which it was raised (Hardy, 1997; Julliard, 2000). For example, the timing of reproduction may have different consequences on sons and daughters. Often, young produced early in the breeding season or in the sequence of birth have a considerable advantage over their later-arriving counterparts in survival and subsequent social status or reproductive success, and this effect is especially pronounced in males (e.g., Dijkstra *et al.*, 1990; Velando, 2000). Paternal quality, if heritable, should also influence sex allocation; females mated to high-quality males would do well to invest heavily in sons, the sex that would benefit most from its local environment (Ellegren *et al.*, 1996).

As shown here, there is no shortage of adaptive explanations for facultative sex ratio manipulation by individuals. Perhaps Emlen (1997) put it best when he wrote, "No one can fault evolutionary theorists for a lack of creativity when it comes to devising hypotheses of adaptive sex ratio variation." However, each theory falls into one of the two broad categories described above: differential resource allocation due to sex

differences in dispersal, and differential resource allocation due to environmental effects (Hardy, 1997).

Most early sex allocation work was done on species with environmental sex determination or haplodiploidy, because chromosomal sex determination was thought to be a constraint on variability of the sex ratio at conception (the primary sex ratio). Work on mammals focussed on sex allocation after conception and its consequences on the secondary sex ratio; sex-biased mortality may occur *in utero* or after birth (e.g., Trivers & Willard, 1973; Clutton-Brock *et al.*, 1985; Frank, 1990). Avian sex allocation studies were particularly late in developing, due to the difficulties in determining offspring sex. The few studies that did exist either relied upon post-mortem gonadal inspection or difficult and invasive laparoscopic sexing techniques, or they involved species that were dimorphic at fledging and so could make no conclusions on sex-biased mortality of eggs or younger chicks (e.g., Howe, 1977; Ryder, 1983; Slagsvold *et al.*, 1986; Frank, 1990; Heinsohn *et al.*, 1997; Torres & Drummond, 1999). However, with the advent of reliable and nearly universal molecular sexing techniques in the last decade, studies of sex ratio and sex allocation in birds are becoming more and more common (Ellegren & Sheldon, 1997). The tremendous diversity of mating and breeding strategies, as well as the relative ease of observation, makes birds particularly well suited for studies of adaptive sex allocation.

Besides providing additional support for many of the current theories for adaptive sex allocation, recent studies are providing convincing evidence that the primary sex ratio

in birds is not as constrained by chromosomal sex determination as was previously thought (Oddie, 1998; Sheldon, 1999). Emlen (1997) postulated that post-ovulation manipulation mechanisms, such as resorption or dump-laying of eggs of the “wrong” sex, were the likely cause of avian sex ratio variation. Such tactics would be fairly costly due to delayed laying and gaps in the laying sequence in broods with more than one egg. However, Emlen proposed that parents would minimize these costs by manipulating only the sex of the first egg of a clutch, leaving the sex of the rest of the offspring to chance. Further, he pointed to the fact that the most striking example of biased sex ratio was in a species that laid a single-egg clutch; in the Seychelles Warbler, parents on high-quality territories almost invariably produced females, the helping sex, while those on poorer territories produced males, the dispersing sex (Komdeur *et al.*, 1997). However, a recent experimental study on the Seychelles Warbler has shown that birds are not only able to detect the sex of their eggs but can control the sex before ovulation (Komdeur *et al.*, 2002). When birds were placed in high-quality territories, they were induced to lay two-egg clutches. There was a clear female bias in the sex ratio of second eggs, despite no delay between the laying of first and second eggs, indicating that the skew was present before ovulation.

Mechanisms for adjusting the primary sex ratio may only evolve if there are substantial benefits to having this ability (Komdeur *et al.*, 2002). In particular, if altering the sex ratio is costly, parents may do better to manipulate post-hatching sex allocation instead (Oddie, 1998; Komdeur & Pen 2002). Although sex ratio is the most easily

obtained and frequently used measure of avian sex allocation (Dijkstra *et al.*, 1990; Ellegren *et al.*, 1996; Komdeur *et al.*, 1997; Sheldon *et al.*, 1998), it does not necessarily correspond to parental division of resources toward sons and daughters (Sheldon, 1998). Growth rates and/or body condition of male and female chicks can be measured and compared as a more precise measure of sex allocation (Bradbury & Griffiths, 1999; Weimerskirch *et al.*, 2000; Hipkiss *et al.*, 2002). Also, because many birds have an extended period of parental care after hatching, and feeding events tend to be quite visible to the observer, sex-biased parental behaviour can be quantified with relative ease (Anderson *et al.*, 1993; Sæther *et al.*, 1997; Krijgsveld *et al.*, 1998).

1.2 Purpose of Study

This work examined various aspects of sex allocation in three alcid species, the Thick-billed Murre *Uria lomvia*, Common Murre *Uria aalge*, and Atlantic Puffin *Fratercula arctica*. First, egg size, as well as growth rates in mass, wing length, and body size of male and female chicks were compared. This allowed me to detect the emergence of the sexual size dimorphism that is evident in adults of these species, as well as determine how sex-specific growth rates might make one sex costlier to produce than the other (Stamps, 1990). Then, I compared parental feeding rates and the duration of the period of chick feeding for sons and daughters at the nest site, to show the relative amount of parental effort expended on rearing each. Finally, factors affecting the most fundamental expression of sex allocation -- the sex ratio -- were explored. I investigated whether parental body size, condition and quality, as well as food availability, affected the

chances of producing a son or a daughter.

Each of these studies had different methodological constraints; thus, different data were obtained for each species. For example, the Thick-billed Murre study took place in a single breeding season, eliminating the effects of interannual variation. Each chick was banded and measured at the same age (14 d), and because parents do not tend to desert the site readily while incubating (unlike the other two species), egg sizes could be obtained without risk of site abandonment or egg predation. There were no behavioural observations, so parental effort directed toward male and female chicks could not be compared.

In contrast, the Common Murre study provided a wealth of behavioural data including chick feeds, and values of adult mass and body size could be obtained, so differences between parents of sons and daughters could be explored. Throughout the five years of the Common Murre study considered here, food availability showed marked variation. Chick catching was opportunistic and took place only a few days each season to minimize disturbance, so age at capture varied from 9 d to more than 20 d. As with Common Murres, regular observations at the Atlantic Puffin study site allowed determination of chick feeding rates. However, adult weight data over the chick-rearing period was not available. Unlike both murre species, each puffin chick was captured twice between 10 d and 22 d, within the period of linear growth (Harris, 1984), and so the growth rate for each chick was used for comparison. Because the data sets are so different, not all of the features of sex allocation listed above were explored for each

species. However, general comparisons between the species could be made.

1.3 Significance of Study

This work is significant in that it incorporates parental behaviour, chick growth, and environmental factors into a thorough, comprehensive examination of sex allocation in three alcid species. Few studies have looked at sex allocation biases both before and after conception. Also, one of the greatest problems in studying sex allocation in birds has been making accurate predictions about the direction of bias in the absence of detailed life history information (Sheldon *et al.*, 1998). The life history of puffins and murres is relatively well known, making them particularly well suited for study (see, for example, Harris, 1984; Gaston & Nettleship, 1981; Ainley *et al.*, 2002).

Most of the research on sex allocation to date has concentrated on species with a high degree of sexual dimorphism, while species with similar sexes are assumed to have unbiased parental care. Although this assumption has been proven wrong in the past (Stamps *et al.*, 1987; Stamps, 1990; Velando, 2000), there remains a dearth of sex allocation research on species with little or no sexual dimorphism such as alcids. Male murres are 2-4% larger than females by mass (Threlfall & Mahoney, 1980; Gaston & Nettleship, 1981); Atlantic Puffins are somewhat more dimorphic, with a mass difference of 10% (Nettleship, 1972). As well, avian sex allocation studies have seldom focussed on long-lived species with small brood sizes such as seabirds (but see Torres & Drummond, 1999; Weimerskirch *et al.*, 2000; Velando, 2002). Indeed, this is believed to be the first study of sex allocation in the Alcidae. In particular, the long-term nature of the study on

Common Murres, which raise a single offspring in a season, allows a unique opportunity to examine strategies used by the same pairs for rearing sons and daughters in the absence of sibling competition.

1.4 References

- Ainley, D.G., Nettleship, D.N., Carter, H.R. and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*, No. 666 (A. Poole and F.Gill, eds.) The Birds of North America Inc., Philadelphia, PA.
- Anderson, D.J., Reeve, J., Martinez Gomez, J.E., Weathers, W.W., Hutson, S., Cunningham, H.V. and Bird, D.M. 1993. Sexual size dimorphism and food requirements of nestling birds. *Canadian Journal of Zoology*, **71**: 2541-2545.
- Bradbury, R.B. and Griffiths, R. 1999. Sex-biased nestling mortality is influenced by hatching asynchrony in the Lesser Black-backed Gull *Larus fuscus*. *Journal of Avian Biology*, **30**: 316-322.
- Clutton-Brock, T.H., Albon, S.D. and F.F. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**: 131-133.
- Dijkstra, C., Daan, S. and Buker, J.B. 1990. Adaptive seasonal variation in the sex ratio of kestrel broods. *Functional Ecology*, **4**: 143-147.
- Ellegren, H., Gustafsson, L. and Sheldon, B.C. 1996. Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proceedings of the National Academy of Science, USA*, **93**: 11723-11728.
- Ellegren, H. and Sheldon, B.C. 1997. New tools for sex identification and the study of sex allocation in birds. *Trends in Ecology and Evolution*, **12**: 255-259.
- Emlen, S.T. 1997. When mothers prefer daughters over sons. *Trends in Ecology and Evolution*, **12**: 291-292.
- Emlen, S.T., Emlen, J.M. and Levin, S.A. 1986. Sex-ratio selection in species with helpers-at-the-nest. *American Naturalist*, **127**: 1-8.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford, Clarendon.

- Frank, S.A. 1990. Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics*, **21**: 13-55.
- Gaston, A.J. and Nettleship, D.N. 1981. *The Thick-billed Murres of Prince Leopold Island: A study of the breeding ecology of a colonial high arctic seabird*. Canadian Wildlife Service Monograph Series No. 6.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science*, **156**: 477-488.
- Hardy, I.C.W. 1997. Possible factors influencing vertebrate sex ratios: an introductory overview. *Applied Animal Behaviour Science*, **51**: 217-241.
- Harris, M.P. 1984. *The Puffin*. Poyser, Calton, U.K.
- Heinsohn, R., Legge, S. and Barry, S. 1997. Extreme bias in sex allocation in *Eclectus* parrots. *Proceedings of the Royal Society of London B*, **264**: 1325-1329.
- Hipkiss, T., Hörnfeldt, B., Eklund, U. and Berlin, S. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's Owl nestlings. *Journal of Animal Ecology*, **71**: 693-699.
- Howe, H.F. 1977. Sex-ratio adjustment in the Common Grackle. *Science*, **198**: 744-746.
- Julliard, R. 2000. Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionarily stable offspring sex ratios. *Behavioral Ecology*, **11**: 421-428.
- Komdeur, J., Daan, S., Tinbergen, J. and Mateman, C. 1997. Extreme adaptive modification in sex ratio of the Seychelles Warbler's eggs. *Nature*, **385**: 523-525.
- Komdeur, J., Magrath, M.J.L. and Krackow, S. 2002. Pre-ovulation control of hatchling sex ratio in the Seychelles Warbler. *Proceedings of the Royal Society of London B*, **369**: 1067-1072.
- Komdeur, J. and Pen, I. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philosophical Transactions of the Royal Society of London B*, **357**: 373-380.
- Krijgsveld, K.L., Dijkstra, C., Visser, G.H. and Daan, S. 1998. Energy requirements for growth in relation to sexual size dimorphism in Marsh Harrier *Circus aeruginosus* nestlings. *Physiological Zoology*, **71**: 693-702.

- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**: 239-268.
- Oddie, K.R. 1998. Sex discrimination before birth. *Trends in Ecology and Evolution*, **13**: 130-131.
- Ryder, J.P. 1983. Sex ratio and egg sequence in Ring-billed Gulls. *Auk*, **100**: 726-729.
- Sæther, B.-E., Lorentsen, S.-H., Tveraa, T., Andersen, R. and Pedersen, H.C. 1997. Size-dependent variation in reproductive success of a long-lived seabird, the Antarctic Petrel (*Thalassoica antarctica*). *Auk*, **114**: 333-340.
- Sheldon, B.C. 1998. Recent studies of avian sex ratios. *Heredity*, **80**: 397-402.
- Sheldon, B.C. 1999. Sex allocation: at the females' whim. *Current Biology*, **9**: R487-R489.
- Sheldon, B.C., Merilä, J., Lindgren, G. and Ellegren, H. 1998. Gender and environmental sensitivity in nestling Collared Flycatchers. *Ecology*, **79**: 1939-1948.
- Slagsvold, T., Røskft, E. and Engen, S. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica*, **17**: 117-125.
- Stamps, J.A. 1990. When should avian parents differentially provision sons and daughters? *American Naturalist*, **135**: 671-685.
- Stamps, J., Clark, A., Arrowood, P. and Kus, B. 1987. The effects of parent and offspring gender on food allocation in Budgerigars. *Behaviour*, **101**: 177-199.
- Threlfall, W. and Mahoney, S.P. 1980. The use of measurements in sexing Common Murres from Newfoundland. *Wilson Bulletin*, **92**: 266-268.
- Torres, R. and Drummond, H. 1999. Does large size make daughters of the Blue-footed Booby more expensive than sons? *Journal of Animal Ecology*, **68**: 1133-1141.
- Trivers, R.L. and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**: 90-92.

Velando, A. 2000. The importance of hatching date for dominance in young shags. *Animal Behaviour*, **60**: 181-185.

Velando, A. 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the Blue-footed Booby. *Behavioral Ecology*, **13**: 443-449.

Weimerskirch, H., Barbraud, C., and Lys, P. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology*, **81**: 309-318.

Chapter 2 Egg size dimorphism and sex-specific growth patterns of alcid chicks

2.1 Introduction

Sexual size dimorphism (SSD) has been reported in several species of alcids, including murres *Uria* spp. (Threlfall & Mahoney, 1980; Gaston & Nettleship, 1981; Stewart, 1993) and Atlantic Puffins *Fratercula arctica* (Nettleship, 1972). Though mass varies throughout the year for both sexes, males are slightly heavier than females on average, by about 2-4% in murres (Threlfall & Mahoney, 1980; Gaston & Nettleship, 1981), and by 10% in puffins (Nettleship, 1972). Sexual size dimorphism in adult Thick-billed Murres has been explored in detail by Stewart (1993), who concluded that sexual selection was the predominant force in shaping the observed patterns of dimorphism. Head and bill measurements of males were significantly greater than those of females; this is consistent with advantages in agonistic behaviours such as bill fencing, used by males in territory defense and mate guarding at colonies. Similarly, a number of studies have found that male Common Murres have greater culmen lengths and bill depths than females (Ainley *et al.*, 2002). SSD in puffins may also be explained by sexual selection, as Nettleship (1972) found that males breeding at better quality sites (i.e., burrows situated on grassy slopes) were heavier than those breeding on poor quality sites (burrows in flat areas), while there was no such difference for females. Presumably, greater mass provides an advantage in burrow defence, which is a predominantly male activity (Creelman & Storey, 1991).

While adult SSD has been studied in depth, there has been relatively little study of

SSD in chicks. Many studies have suggested that chicks that are larger or in better condition are more likely to survive and reproduce (Cooke *et al.*, 1984; Magrath, 1991; Erikstad *et al.*, 1997; Green, 2002), but few have looked at factors affecting survival of sons and daughters separately. Evidence from another sexually dimorphic seabird, the Wandering Albatross *Diomedea exulans*, indicates that male chicks that were larger at fledging were more likely to survive to adulthood, while for female chicks, body condition rather than size predicted subsequent survival and recruitment (Weimerskirch *et al.*, 2000).

Sexual size dimorphism appears at different stages of life, egg to adult, in different avian taxa. Sexually dimorphic eggs have been found in some studies (e.g., Anderson *et al.*, 1997; Cordero *et al.*, 2000), and size dimorphic hatchlings from eggs that are similar in size have also been reported (Rutkowska & Cichoń, 2002), suggesting that mothers are able to detect or even dictate the sex of their offspring and provision the eggs accordingly. Alternately, male and female embryos may differ in patterns of resource allocation. More often, differences in chick size do not appear until days or even weeks after hatching, during the period of parental feeding, and correspond to a higher growth rate of the larger sex (e.g., Slavsgold *et al.*, 1986; Bradbury & Griffiths, 1999; Hipkiss *et al.*, 2002). Finally, sexes may be monomorphic at fledging, but due to selection against larger or smaller members of one of the sexes, show sexual size dimorphism as adults (Merilä *et al.*, 1997).

This study examines if and when sexual size dimorphism appears in early life

stages of Atlantic Puffins and Common and Thick-billed Murres by comparing growth rates in mass as well as wing length and tarsus length, and egg volume of males and females. While murre and puffin parents cannot manipulate clutch size as in many other avian species, they are able to adjust the amount of parental effort allocated toward their single offspring. Because males are more variable in their reproductive success than females, putting extra effort into raising a large son should yield greater relative returns (Trivers & Willard, 1973). Even in alcids, which are socially monogamous, males are occasionally successful in securing extra-pair fertilizations (Gaston & Hipfner, 2000; Walsh, 2001). Parents are predicted to invest more cautiously in their female offspring, perhaps avoiding “excess” parental effort in order to maximise their future reproductive output. Therefore, it is expected that males will be larger in mass and in skeletal characteristics (tarsus length) from an early age.

Wing length is an important determinant of fledging success in murres, who must glide from their nest site on rocky cliff faces to the ocean below (Hipfner & Gaston, 1999a). Similarly, puffins are more likely to avoid predation when they fly rather than stumble from their burrows to the sea (Øyan & Anker-Nilssen, 1996). Richner (1991) noted that in many sexually dimorphic birds, members of the smaller sex fledge earlier on average than the larger sex due to faster plumage development. Thus it is expected that females, the smaller sex, will show faster wing growth than males, allowing them to fledge sooner and reducing the total amount of parental care that pairs must allocate to daughters at the breeding site. Although egg size may be correlated with chick mass at

hatching, it is not related to the rate of mass increase of chicks (Amundsen & Stokland, 1990; Williams, 1994; Hipfner & Gaston, 1999a). However, wing length at 14 days is positively correlated with egg volume (Hipfner & Gaston, 1999a). Thus, egg volume is expected to be larger for females, corresponding to faster wing growth.

2.2 Methods

2.2.1 Field Methods

2.2.1.1 Thick-billed Murres

This study was conducted on Coats Island, Nunavut (62°57'N, 82°00'W) in 1998. Breeding sites on two plots (SP and Z) were mapped and numbered, and the length and maximum breadth of the egg at each site was measured to the nearest 0.1 mm using vernier calipers. An egg volume index (EVI; $\text{length} \times \text{maximum breadth}^2$) was used as a measure of egg size; this index is highly correlated with egg mass in the species ($R = 0.95$; Birkhead & Nettleship, 1982). The plots were observed at 2-day intervals to obtain estimated hatch dates (± 2 d) at each site. Chick mass at hatching was estimated from egg volume using the following formula: $\text{Hatching Mass} = 5.33 + 0.32 * \text{EVI}$. This relationship was derived from chicks at Coats Island, and was found to be fairly reliable, with egg volume index explaining 72% of the variation in hatch mass (Hipfner & Gaston, 2002).

At 14 days of age, just prior to the minimum observed fledging age of Thick-billed Murres (15 days; Gaston & Nettleship, 1981), chicks were captured, banded with an individually numbered metal band, and weighed to the nearest gram using a spring

balance. Wing length was measured to the nearest millimetre using a wing ruler. Two growing coverts were plucked and stored in ethanol for later genetic analysis. Chick growth from hatching to day 14 was calculated by subtracting the estimated hatch mass from mass at 14 days.

2.2.1.2 Common Murres

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 behaviour watches were conducted on approximately 30 known breeding pairs, every two to three days throughout the chick-rearing period. The number of pairs studied tended to increase slightly over the years, as the number of colour-banded individuals has increased since the beginning of the study. Hatching and fledging dates of chicks were recorded when possible, within ± 2 days. If a chick had hatched before the study season began, the hatch date was assumed to be 33 days after the lay date of the egg at that site (Ainley *et al.*, 2002); since observations were also conducted during the pre-breeding and early egg laying period of early May to early June, the lay date was known for most early breeders.

When chicks were able to thermoregulate, at least ten 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 five study years. Mass was measured to the nearest gram with a 500 g Pesola scale, and unflattened wing chord length was measured

to the nearest millimetre with a wing ruler. Three growing primary feathers were taken for genetic analysis and stored in 70% ethanol before the chick was released. The parent was almost invariably at the site calling to the chick upon its release, and in all instances the parent and chick successfully reunited soon after handling.

2.2.1.3 Atlantic Puffins

The first objective for the Atlantic Puffins in 2001 was to establish a study site on Great Island, with forty marked burrows. The site was located on a grassy slope, where puffins tend to have higher breeding success than those occupying burrows on flat areas (Nettleship, 1972), thus maximising the sample size. A canvas blind was erected about 30 m from the study site, and in 2002 was replaced with a wooden blind. Burrows whose entrances were visible from the blind and that contained an egg within an arm's length were selected, and all 40 burrows could be watched simultaneously with the unaided eye.

The site was observed in 2001 and 2002 during peak feeding times (05:00 to 09:00 and 16:00 to 20:00; Harris, 1984) every two or three days from late June to early August. Observations of adults bringing food to marked burrows were made with binoculars, as described by Rodway & Montevecchi (1996), to determine chick hatching dates. Chicks are not fed until the day after they hatch (Harris, 1984), so hatch date was taken to be halfway between the previous observation day and the day prior to the first observed chick feed and so were accurate to within ± 2 days. If an adult was observed leaving the burrow two minutes or less after entering, it was considered a chick feed even if bill contents could not be seen. As adults were not observed making such short visits without food

(pers. obs.), this was considered a valid assumption.

Chicks were temporarily removed (“grubbed”) from their burrows on two separate occasions between 10 and 22 days of age, within the linear phase of growth (Harris, 1984). They were banded and measured in the same manner as Common Murre chicks upon first catching. Additionally, tarsus length was measured to the nearest 0.1 mm with dial calipers. A second set of measurements was taken when the chicks were recaptured, so that the growth rate in mass, wing chord, and tarsus length could be calculated. Tissue samples to be used for sexing were taken during the first catching, unless the primary feathers were considered to be too small to obtain an appreciable amount of DNA (approximately 5 mm or less in length); in these cases, feathers were obtained when the chick was recaptured.

2.2.2 Lab Methods

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 hours. The contents of the buffers used are detailed in Appendix 1; the protocol was modified in 2001, as a new buffer described in Bello *et al.* (2001) increased the yield of DNA in the final product. This was followed by a standard phenol: chloroform: isoamyl alcohol extraction, and the DNA was 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 TE.

The product was sexed using the 2550F/2718R primer pair, which flanks introns

on the CHD-Z and CHD-W genes (Fridolfsson & Ellegren, 1999). The PCR protocol is detailed in Appendix 2. These homologous genes are located on the W and Z sex chromosomes of all non-ratite birds, and are highly conserved (Griffiths *et al.*, 1996). The intron flanked by the primers differs in length on the two genes, resulting in the amplification of a 600 bp segment on CHD-Z, and a 450 bp segment on CHD-W. Heterogametic (WZ) females were identified by the presence of two bands when the PCR product was run on an agarose gel, whereas homogametic (ZZ) males showed only one band.

2.2.3 Statistical Methods

2.2.3.1 Thick-billed Murres

All statistics were performed using SPSS 11.0 for Windows (SPSS Inc., 2001). A significance level (α) of 0.05 was used in all analyses. For Thick-billed Murres, the effect of sex on egg volume index, chick mass at 14 days, and chick growth rate from hatching to 14 days were examined. A univariate GLM was performed on each of these dependent variables, with sex as a fixed factor. Hatch date was included as a covariate because date of egg laying is negatively correlated with parental age, a reliable indicator of parental quality in Thick-billed Murres, and presumably in other intermediate and semi-precocial alcids (Hipfner, 1997; Hipfner & Gaston, 1999b). A sex by hatch date interaction was also included in the initial model. For analysis of wing length at 14 days, egg volume was added as a factor to account for the positive relationship between egg size and 14 d wing length (Hipfner & Gaston, 1999a), as were sex by egg volume, hatch date by egg volume,

and sex by egg volume by hatch date interaction terms.

2.2.3.2 Common Murres

Only chicks sampled during the linear growth phase, up to 16 d (Ainley *et al.*, 2002), were included in the analyses. Since chicks were captured at different ages, general linear model analyses were done using the residuals of regressions of mass and wing length on age. While the use of residuals as a response variable under certain circumstances has been criticized, such as in studies of animal body condition, it has been acknowledged that statistical conclusions are usually equivalent to those obtained using the more widely used ANCOVA (Garcia-Berthou, 2001). Further, a number of studies have used this statistical method (e.g., Jakob *et al.*, 1996; Lourdais *et al.*, 2002). In this case, it was felt that the relative simplicity and intuitiveness of this method made it an appropriate choice here. Chicks from all years were pooled to calculate growth rates, and year was included as a parameter in the models to account for interannual growth rate variation. Wing length and mass were examined, with sex and year as fixed factors, and lay date of first egg as a covariate. Sex by year, sex by lay date, and sex by year by lay date interactions were included in the initial model.

Lay date of the first egg was used as a measure of parental quality instead of hatch date, because many of the chicks came from second eggs laid after loss of the original egg. Evidence from the Thick-billed Murre indicates that parental quality, not hatch date itself, is an important determinant of breeding success (Hipfner, 1997).

2.2.3.3 Atlantic Puffins

Rates of mass increase (g/day), tarsus growth (mm/day) and wing growth (mm/day) in male and female Atlantic Puffin chicks were compared using a general linear model, with sex as a fixed factor. Hatch date was expressed in days relative to the annual median and included as a covariate, so that data from both years could be combined. Year of study was also included in the model, to account for the interannual variation in growth rates due to the variable nature of the food supply (Gaston *et al.*, 1983). Sex by hatch date and sex by year interactions were also incorporated in the model.

2.3 Results

2.3.1 Thick-billed Murres

Of the 67 chick samples obtained (59 from first eggs, 8 from replacement eggs), 46 were sexed successfully (23 male, 23 female; all from first egg chicks). The remaining samples, which were distributed randomly with respect to hatch date (excluding the replacement chick samples, which were laid later), did not yield DNA; this failure was attributed to problems with storage of the feathers. The ethanol had leached out of the plastic containers in which the feathers had been stored, leaving them desiccated for an unknown length of time between collection in 1998 and their use in the lab in 2001.

Eggs containing female embryos tended to be larger than male eggs. Controlling for the effects of hatch date, however, egg volume did not vary significantly between sons and daughters (Table 2.1). Egg volume decreased significantly with later hatch dates, consistent with previous studies of the species (Hipfner *et al.*, 1997). Mass at 14 d and growth from hatching to 14 d were similar for male and female chicks, and neither varied

with hatch date (Table 2.1). The sex by hatch date interaction was non-significant and was dropped from the final model in each of these analyses.

As predicted, females had longer wings at 14 d than males (Table 2.1). However, the effect of egg volume on wing length at 14 days differed significantly for male and female chicks (Table 2.2). A closer inspection of this interaction found that male wing growth was positively correlated with egg volume, while there was no such correlation for females. That is, males hatching from small eggs had shorter wings than females, while males hatching from large eggs had longer wings than females (Table 2.3; Figure 2.1a). There was also a significant interaction of hatch date and sex on 14 d wing length. However, both male and female wing length were independent of time of hatching (Figure 2.1b), and mean 14 d wing length of females was somewhat longer than that of males hatching both before and after the median hatch date (Table 2.3). Thus, the appearance of this sex by hatch date interaction is surprising.

2.3.2 Common Murres

Seventy-six chicks captured between 1997 and 2001 were sexed, and 49 of these (21 males, 28 females) were captured within 16 d after hatching. Five chicks from which feather samples were taken could not be sexed, likely due to degradation of the stored DNA (all failures were from chicks captured in 1997 and 1998).

From the remaining 49 chicks, linear growth rates in wing length and mass were calculated. Mean growth in wing length was 1.46 mm/day ($R^2 = 0.260$, $p < 0.001$), and rate of mass increase was 7.44 g/day ($R^2 = 0.313$, $p < 0.001$). Males tended to be heavier

than females at a given age, while females had slightly longer wings (Table 2.4). The residuals were compared using the general linear model; the sex by year, sex by lay date, and sex by year by lay date interaction terms were not significant and so were dropped from the final model in both analyses. The sex difference in residuals was not significant for either mass or wing length; effects of first egg lay date and year of study were non-significant as well (Table 2.4).

2.3.3 Atlantic Puffins

Of the 40 marked burrows on the study site, 26 produced chicks in 2001 and 18 in 2002. However, sample size was severely reduced due to chick mortality (5 in 2001, 2 in 2002), inability to reach chicks in their burrows (5 in 2001 and 4 in 2002), and obvious inaccuracy of chick age estimation, i.e., chicks taken from their burrows ten days after the first observed chick feed which were closer in size 20-day-old chicks (2 in 2001, 6 in 2002). Thus, in total, 21 chicks of known age were sexed: 6 females, 8 males in 2001; 0 females, 6 males in 2002. Because there was no way to assess growth in females in 2002, only the 14 chicks from 2001 were used, and the year and sex by year terms were dropped from the general linear model. The non-significant sex by hatch date interaction was also dropped from the final model.

There were no sex differences in mass, tarsus or wing growth (Table 2.5). Later-hatching chicks gained mass more slowly, but no such effect was seen for tarsus or wing growth (Table 2.5; Figure 2.2). Figure 2.3 shows the value of each measurement plotted against the age of the chick (two measurements for each chick are included in the figures;

because data were not independent, regression analyses were not considered appropriate). While sample sizes were too small to draw firm, statistical conclusions, note that males tended to have relatively long tarsi at a given age (Figure 2.3b; 10 of 16 points fall above the fit line, versus only 4 of 12 female measurements). There was no such trend for mass (Figure 2.3a), with roughly equal distribution of both sexes above and below the fit line. Figure 2.3c shows that for wing length, all of the female measurements fell very close to the fit line, while male wing length at a given age was more variable.

2.4 Discussion

As predicted, female Thick-billed Murre chicks hatched from larger eggs and had longer wings than males on average. However, the positive correlation between egg volume and wing length reported in Hipfner & Gaston (1999a) was shown here to be specific to male chicks only, while female 14 d wing length was independent of egg size, so that males hatching from large eggs had faster-growing wings than females and males hatching from small eggs had slower-growing wings than females. As well, male 14 d wing length decreased with hatch date, while female wing length did not. Still, mean wing length of females was higher than that of males hatching both before and after the median hatch date.

The observation that only male wing growth is affected by hatch date and by egg volume may be explained by success of males being more dependent on parental quality than success of females. Sons hatching from smaller eggs tend to have younger, less experienced parents (Hipfner, 1997). The slower wing growth associated with hatching

from a smaller egg may be an adaptation to prevent the chick from fledging too soon, before reaching a mass that would ensure a greater possibility of survival to breeding age. Females, being less “expensive” for poorer-quality parents to rear (see Chapter 3), would reach fledging condition sooner than males. Males hatching from larger eggs have better, more experienced breeders as parents and will likely grow faster. They would be able to go to sea sooner, where the father can provision the chick at a much higher rate, further increasing the growth rate so that the chick is much larger by the time winter arrives (Ydenberg, 1989). The probability of an alcid chick surviving to breed is believed to be positively related to its mass at the onset of its first winter (Ydenberg, 1989).

Wing length data from Atlantic Puffins, though scant, appears to provide further support to the pattern seen in Thick-billed Murres. While average wing growth rate was similar between the sexes, male wing length is more variable than female wing length, and this may similarly reflect the greater effect of parent quality on growth of sons. While there was no significant effect of hatch date (or interaction between sex and hatch date) on wing growth, egg volume might in fact be a more sensitive indicator of parental quality, and this was not measured to minimize risk of burrow abandonment (Rodway *et al.*, 1996).

Common Murres also showed a trend in the expected direction, females having longer than average wings for their age (Figure 2.2). However, the analysis showed that the sex difference in wing length was not significant, nor did year of study or lay date of the first egg at the site explain the variation seen. Perhaps if egg volume information

were available, patterns similar to those seen in the congeneric Thick-billed Murre might emerge in the data. Unfortunately, it is not possible to remove and measure eggs without causing adults at the site to flush and leave other eggs in the area vulnerable to predation.

Mass growth in Common Murre chicks showed little intersexual variation, possibly due to interannual variation in food supply (Kitaysky, 1999; Øyan & Anker-Nilssen, 1996). However, results from the Thick-billed Murre data, which had no interannual variation to consider, were even less supportive of the initial hypothesis that male chicks would be more massive than females. There was no difference in either 14 d mass or chick growth from hatching to 14 d. The uncertainty of the hatch mass used in calculating growth rate was taken into consideration, as hatch mass is not always closely correlated with egg volume (Rutkowska & Cichoń, 2002). Birkhead & Nettleship (1982) found that in the Thick-billed Murre, egg size was indeed a reliable indicator of chick mass at hatching, but according to Hipfner & Gaston (2002), less than three quarters of the variation in hatch mass was explained by egg volume. There may be sex differences in hatch mass that would not have been detected, leading to systematic errors in the calculated growth rates. Male and female Atlantic Puffin chicks had very similar growth rates, and both sexes showed a marked decline in growth rate with later hatch dates. As with Thick-billed Murres, this was likely an effect of parental age rather than decreased food availability (Hipfner & Gaston, 2002), as feeding rates of earlier-breeding puffins on Great Island were fairly consistent over the entire chick-rearing period (pers. obs.).

While males tended to have longer tarsi at a given age, due to small sample size,

the skeletal growth rate of male and female puffin chicks was not detectably different. In puffins, the tarsus does not continue to grow after fledging (Kitaysky, 1999), thus it was expected that males would grow larger during the chick-rearing period and so would become larger adults. A larger sample of sexed chicks of known age would give a clearer idea of whether puffins do in fact show this sexual size dimorphism from an early age.

In summary, the available evidence indicates that male and female alcid chicks gain mass at similar rates. Skeletal growth rate did not differ between the sexes in this study, although sample sizes were small. However, females tended to have faster-growing wings on average, and so were capable of fledging sooner (Hipfner & Gaston, 1999b). This is consistent with studies of many other sexually dimorphic species, in which the smaller sex fledges 5-13% earlier and reaches asymptotic mass at the same time (Richner, 1991). Males, being the larger and more expensive sex to produce, are more vulnerable in adverse conditions such as being cared for by young, inexperienced parents. Male wing growth was positively correlated with egg volume, while female wing growth was not. Egg volume in turn is positively correlated with adult age and quality (Hipfner *et al.*, 1997). As an apparent adaptation to prolong the period of parental care at the nest site, males with poor quality parents (those hatching from small eggs) have slower wing growth, allowing them more time to accrue fat reserves before leaving the natal colony.

2.5 References

Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*, No. 666 (A. Poole and F. Gill, eds.) The Birds of North America Inc., Philadelphia, PA.

- Amundsen, T. and Stokland, J.N. 1990. Egg size and parent quality influence nestling growth in the Shag. *Auk*, **107**: 410-413.
- Anderson, D.J., Reeve, J. and Bird, D.M. 1997. Sexually dimorphic eggs, nestling growth and sibling competition in American Kestrels *Falco sparverius*. *Functional Ecology*, **11**: 331-335.
- Bello, N., Francino, O. and Sánchez, A. 2001. Isolation of genomic DNA from feathers. *Journal of Veterinary Diagnostic Investigations*, **13**: 162-164.
- Birkhead, T.R. and Nettleship, D.N. 1982. Adaptive significance of egg size and laying date in Thick-billed Murres. *Ecology*, **63**: 300-306.
- Bradbury, R.B. and Griffiths, R. 1999. Sex-biased nestling mortality is influenced by hatching asynchrony in the Lesser Black-backed Gull *Larus fuscus*. *Journal of Avian Biology*, **30**: 316-322.
- Cooke, F., Findlay, C.S. and Rockwell, R.F. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk*, **101**: 451-458.
- Cordero, P.J., Griffith, S.C., Aparicio, J.M. and Parkin, D.T. 2000. Sexual dimorphism in House Sparrow eggs. *Behavioural Ecology and Sociobiology*, **48**: 353-357.
- Creelman, E. and Storey, A.E. 1991. Sex differences in reproductive behavior of Atlantic Puffins. *Condor*, **93**: 390-398.
- Erikstad, K.E., Ashiem, M., Fauchald, P., Dahlhaug, L. and Tveraa, T. 1997. Adjustment of parental effort in the Puffin; the roles of adult body condition and chick size. *Behavioural Ecology and Sociobiology*, **40**: 95-100.
- Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**: 116-121.
- Garcia-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology*, **70**: 708-711.
- Gaston, A.J., Chapdelaine, G. and Noble, D.G. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. *Canadian Journal of Zoology*, **61**: 2465-2475.

- Gaston, A.J. and Hipfner, J.M. 2000. Thick-billed Murre (*Uria lomvia*). In *The Birds of North America*, No.497 (A. Poole and F. Gill, eds.) The Birds of North America Inc., Philadelphia, PA.
- Gaston, A.J. and Nettleship, D.N. 1981. *The Thick-billed Murres of Prince Leopold Island: A study of the breeding ecology of a colonial high arctic seabird*. Canadian Wildlife Service Monograph Series No. 6.
- Green, D.J. 2002. Pair bond duration influences paternal provisioning and the primary sex ratio of Brown Thornbill broods. *Animal Behaviour*, **64**: 791-800.
- Griffiths, R., Daan, S. and Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London B*, **263**: 1251-1256.
- Harris, M.P. 1984. *The Puffin*. Poyser, Calton, U.K.
- Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. *Condor*, **99**: 353-360.
- Hipfner, J.M. and Gaston, A.J. 2002. Growth of nestling Thick-billed Murres (*Uria lomvia*) in relation to parental experience and hatching date. *Auk*, **119**: 827-832.
- Hipfner, J.M. and Gaston, A.J. 1999a. The relationship between egg size and posthatching development in the Thick-billed Murre. *Ecology*, **80**: 1289-1297.
- Hipfner, J.M. and Gaston, A.J. 1999b. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology*, **80**: 587-596.
- Hipfner, J.M., Gaston, A.J. and DeForest, L.N. 1997. The role of female age in determining egg size and laying date of Thick-billed Murres. *Journal of Avian Biology*, **29**: 271-278.
- Hipkiss, T., Hörnfeldt, B., Eklund, U. and Berlin, S. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's Owl nestlings. *Journal of Animal Ecology*, **71**: 693-699.
- Jakob, E.M., Marshall, S.D. and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**: 61-67.
- Kitaysky, A.S. 1999. Metabolic and developmental responses of alcid chicks to experimental variation in food intake. *Physiological and Biochemical Zoology*,

72: 462-473.

- Lourdais, O., Bonnet, X., Shine, R., DeNardo, D., Naulleau, G. and Guillon, M. 2002. Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *Journal of Animal Ecology*, **71**: 470-479.
- Magrath, R.D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. *Journal of Animal Ecology*, **60**: 335-351.
- Merilä, J., Sheldon, B.C. and Ellegren, H. 1997. Antagonistic natural selection revealed by molecular sex identification of nestling Collared Flycatchers. *Molecular Ecology*, **6**: 1167-1175.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**: 239-268.
- Øyan, H.S. and Anker-Nilssen, T. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. *Auk*, **113**: 830-841.
- Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex-specific growth contribute to balanced sex ratios? *Functional Ecology*, **5**: 19-28.
- Rodway, M.S. and Montevecchi, W.A. 1996. Sampling methods for assessing the diets of Atlantic Puffin chicks. *Marine Ecology Progress Series*, **144**: 41-55.
- Rodway, M.S., Montevecchi, W.A. and Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic Puffins *Fratercula arctica*. *Biological Conservation*, **76**: 311-319.
- Rutkowska, J. and Cichoń, M. 2002. Maternal investment during egg laying and offspring sex: an experimental study of Zebra Finches. *Animal Behaviour*, **64**: 817-822.
- Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits *Parus major*. *Ibis*, **115**: 549-558.
- Slagsvold, T., Røskft, E. and Engen, S. 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. *Ornis Scandinavica*, **17**: 117-125.

- SPSS Inc. 2001. SPSS for Windows version 11.0. SPSS Inc., Chicago.
- Stewart, D.T. 1993. Sexual dimorphism in Thick-billed Murres, *Uria lomvia*. *Canadian Journal of Zoology*, **71**: 346-351.
- Threlfall, W. and Mahoney, S.P. 1980. The use of measurements in sexing Common Murres from Newfoundland. *Wilson Bulletin*, **92**: 266-268.
- Trivers, R.L. and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**: 90-92.
- Walsh, C.J. 2001. Copulation behaviour, parentage analysis and genetic relatedness in Common Murres (*Uria aalge*). Ph.D. dissertation, Memorial University of Newfoundland, St. John's.
- Weimerskirch, H., Barbraud, C., and Lys, P. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology*, **81**: 309-318.
- Williams, T.D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews*, **68**: 35-59.
- Ydenberg, R.C. 1989. Growth-mortality tradeoffs and the evolution of juvenile life-histories in the Alcidae. *Ecology*, **70**: 1494-1506.

Table 2.1. Egg size and chick growth of male and female Thick-billed Murre at Coats Island, Nunavut.

Variable	Mean \pm SD		Between-sex Comparisons <i>F</i> (<i>p</i>)	Hatch Date Effect <i>F</i> (<i>p</i>)
	Males (<i>n</i> = 23)	Females (<i>n</i> = 23)		
Egg Volume (cm ³)	200.8 \pm 19.3	207.1 \pm 19.4	2.151 (0.150)	5.591 (0.023)*
14 d Mass (g)	186.5 \pm 18.9	191.1 \pm 20.8	0.616 (0.437)	0.040 (0.843)
Mass Growth (g)	117.0 \pm 19.5	119.5 \pm 21.4	0.118 (0.733)	0.233 (0.632)
14 d Wing (mm)	54.7 \pm 3.8	55.1 \pm 4.2	— ^a	— ^a

^a See Table 2.2 for results of general linear model

Table 2.2. Analysis of factors affecting 14 d wing length of Thick-billed Murres at Coats Island, Nunavut.

Source	d.f.	MS	<i>F</i> (<i>p</i>)
Sex	1	71.671	4.938 (0.032)*
Hatch Date	1	3.875	0.267 (0.608)
Egg Volume	1	10.335	0.712 (0.404)
Sex*Hatch Date	1	78.809	5.430 (0.025)*
Sex*Egg Volume	1	67.112	4.624 (0.038)*
Sex*Hatch Date*Egg Volume	2	39.241	2.704 (0.080)
Error	38	14.514	

Table 2.3. Mean wing length at 14 d (\pm SD) of Thick-billed Murre chicks hatching from eggs that are larger and smaller than average, and before and after the median hatch date at Coats Island, Nunavut.

	Egg Volume		Hatch Date	
	Large	Small	Early	Late
Males	55.86 \pm 2.12	53.75 \pm 4.80	54.88 \pm 2.76	54.63 \pm 4.90
Females	55.05 \pm 5.03	55.21 \pm 3.54	55.46 \pm 3.22	54.77 \pm 5.24

Table 2.4. Analysis of factors affecting growth of Common Murre chicks at Great Island, NL.

Variable	Mean \pm SD		Between-sex Comparisons <i>F</i> (<i>p</i>)	Lay Date Effect <i>F</i> (<i>p</i>)	Year Effect <i>F</i> (<i>p</i>)
	Males (<i>n</i> = 22 ^a)	Females (<i>n</i> = 28)			
Mass (g)	3.46 \pm 22.12	-0.94 \pm 23.64	0.281 (0.599)	0.896 (0.349)	1.629 (0.184)
Wing Length (mm)	-1.85 \pm 3.15	1.60 \pm 6.03	0.400 (0.530)	1.161 (0.287)	1.139 (0.351)

^aWing length was not recorded for one male chick in 1999, so *n* = 21 for wing length.

Table 2.5. Growth rates of male and female Atlantic Puffin chicks at Great Island, NL.

Variable	Mean \pm SD		Between-sex Comparisons <i>F</i> (<i>p</i>)	Hatch Date Effect <i>F</i> (<i>p</i>)
	Males (<i>n</i> = 8)	Females (<i>n</i> = 6)		
Mass (g/day)	8.3 \pm 4.7	7.9 \pm 4.1	0.012 (0.916)	9.373 (0.011)*
Tarsus (mm/day)	0.17 \pm 0.13	0.08 \pm 0.19	0.869 (0.371)	0.038 (0.849)
Wing (mm/day)	3.2 \pm 1.1	3.3 \pm 0.6	0.112 (0.744)	0.424 (0.528)

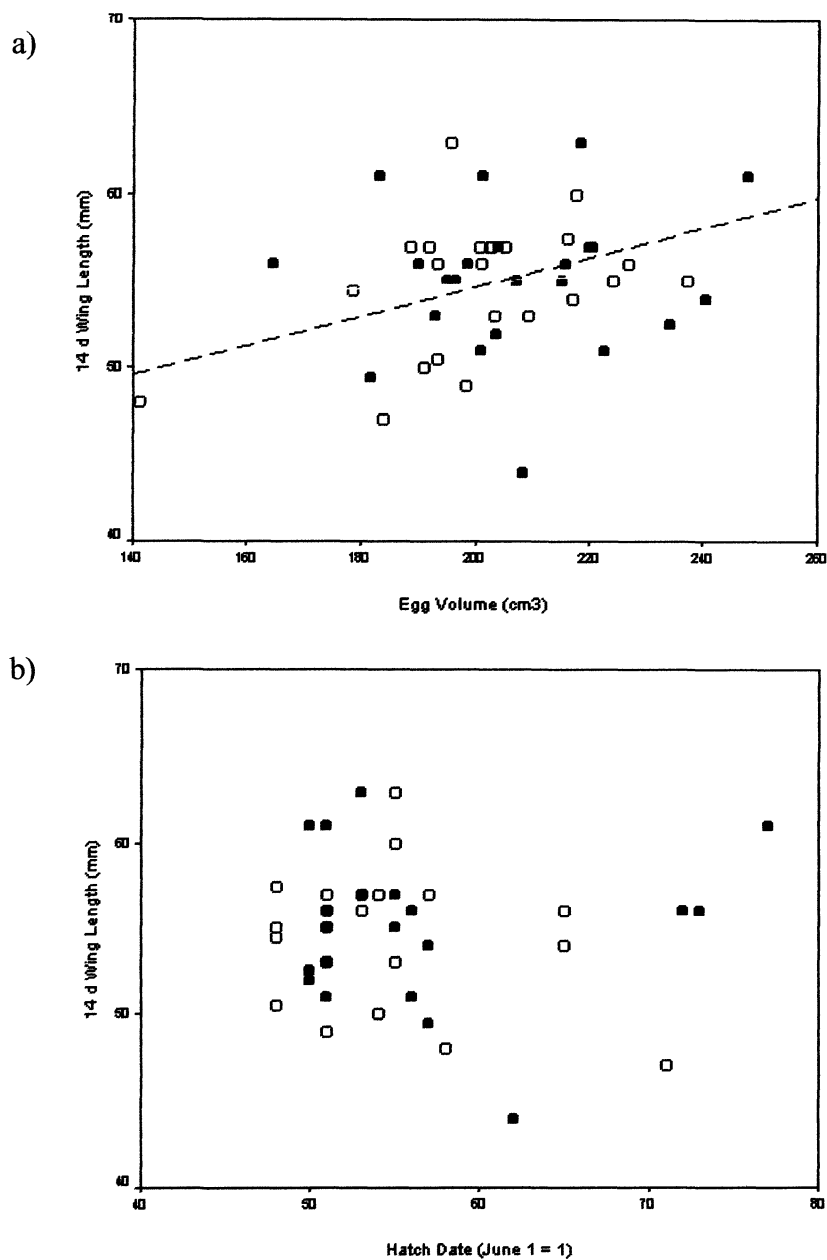


Figure 2.1 a) Relationship between egg volume and 14 d wing length for male and female Thick-billed Murre chicks on Coats Island, Nunavut. Regression is significant for males (dashed line; $R^2 = 0.182$; $p = 0.042$), but not females ($R^2 = 0.009$; $p = 0.668$). b) Relationship between hatch date and 14 d wing length for male and female Thick-billed Murre chicks. Regressions are not significant for either males ($R^2 = 0.069$; $p = 0.224$) or females ($R^2 = 0.003$; $p = 0.798$). Males: open circles, females: filled circles.

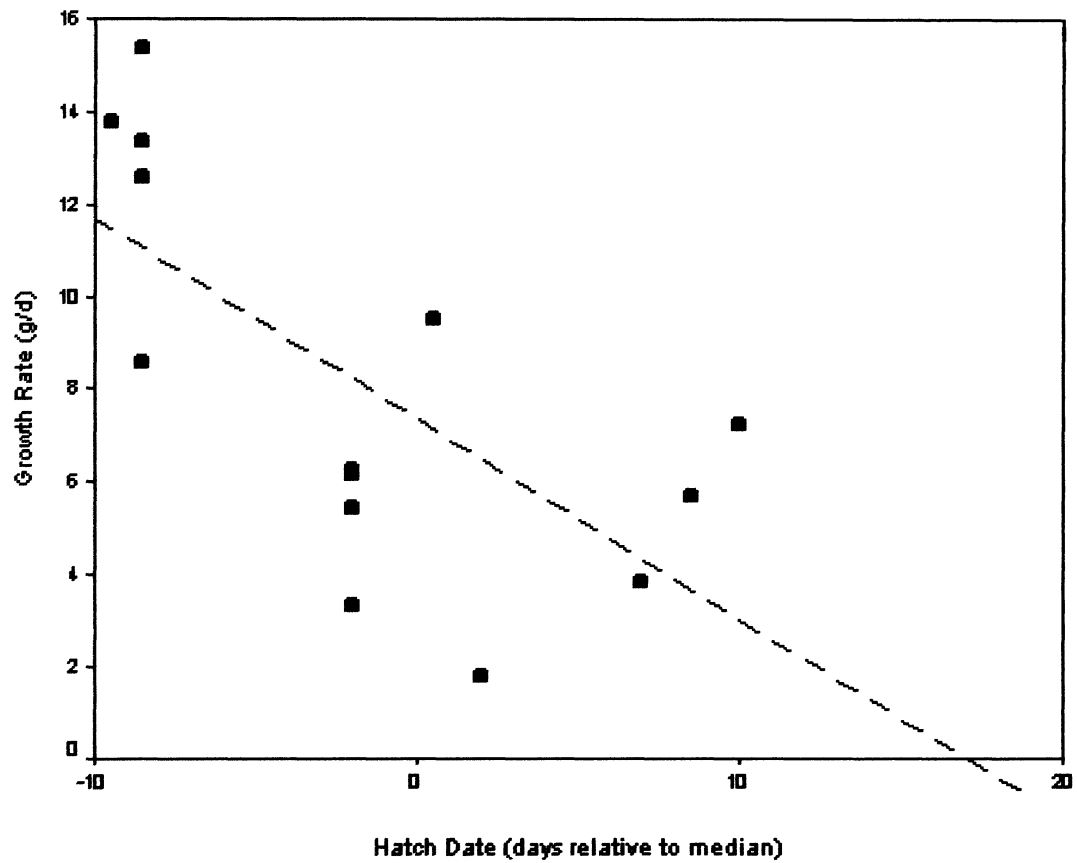


Figure 2.2. Relationship between hatch date and rate of mass gain in Atlantic Puffin chicks on Great Island, NL ($R^2 = 0.461$; $p = 0.008$).

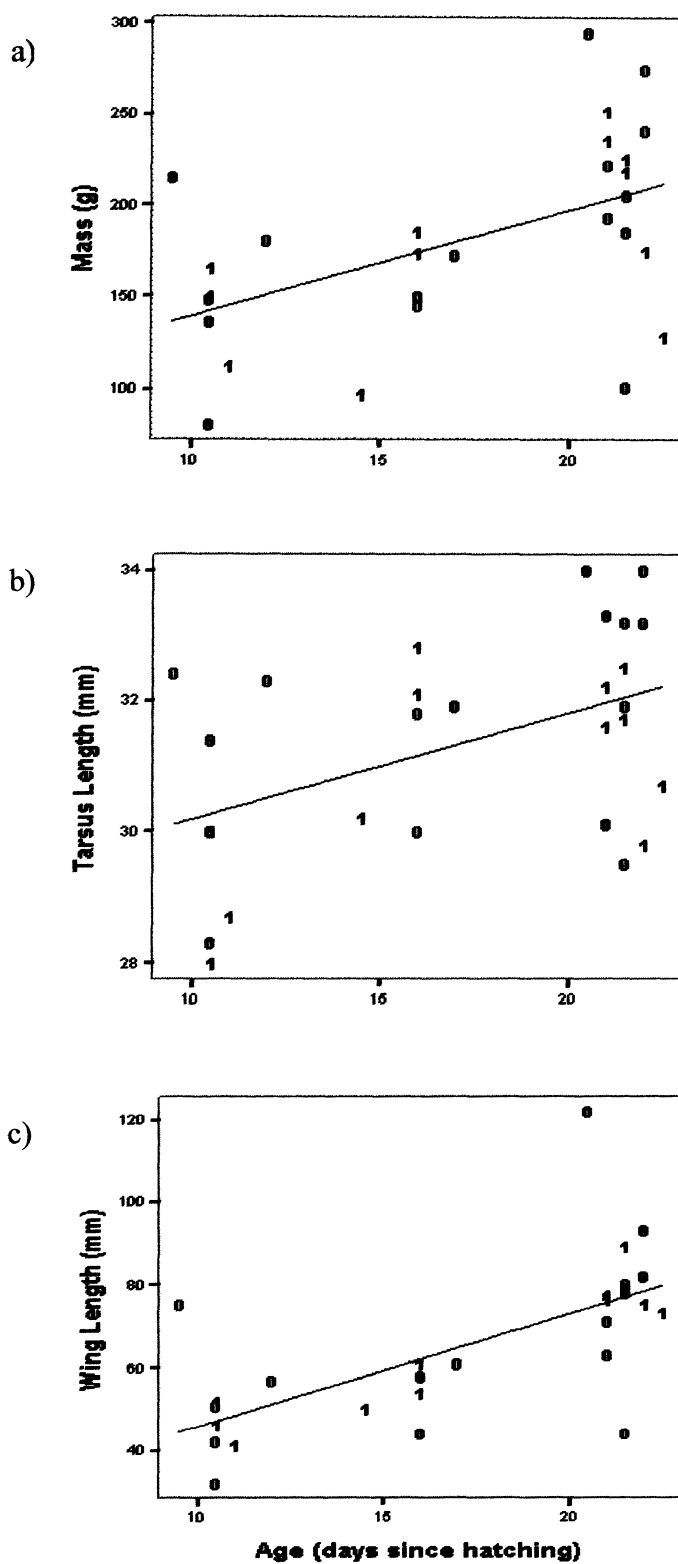


Figure 2.3. Growth of male (0) and female (1) Atlantic Puffin chicks on Great Island, NL. Line represents best fit for all data points. a) Mass growth, b) Tarsus growth, c) Wing growth.

Chapter 3 Sex-biased parental care in Common Murres and Atlantic Puffins

3.1 Introduction

Common Murres *Uria aalge* and Atlantic Puffins *Fratercula arctica* are long-lived, socially monogamous seabirds of the alcid family. Breeding pairs raise one chick each year, and both sexes contribute more or less equally in parental care activities at the nest site (Creelman & Storey, 1991; Wilhelm, 2001). Colony departure of chicks differs in the two species. Semiprecocial puffin chicks fledge in the traditional sense; they leave the burrow independently of the parents and can forage for themselves at 39-83 days (Nettleship, 1972). In contrast, murres and Razorbills employ a unique “intermediate” strategy (Sealy, 1973; Ydenberg, 1989). In these species, chicks are accompanied to sea by the father a few weeks after hatching, when they are roughly 25% of their adult mass. Chicks remain with their fathers for several weeks before reaching independence.

Raising offspring is costly, in terms of both parental energy expense and risks to adult survival (Gabrielsen, 1996; Jönsson *et al.*, 1998). To maximise 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 they invest according to available resources, their own body condition, and/or the demands of the offspring (Erikstad *et al.*, 1997). Seabirds in particular endure high environmental stochasticity, and the future reproductive value of offspring may depend on the conditions of the breeding season in which it was reared (Harris, 1983; Erikstad *et al.*, 1998). Puffins and murres, like some other seabirds, have

flexible parental investment levels and may adjust resource allocation in relation to the fitness value of their offspring (Burger & Piatt, 1990; Johnsen *et al.*, 1994; Erikstad *et al.*, 1997; Velando, 2002). An example of this flexibility in parental behaviour can be seen in the time budgets of Common Murres. When food is plentiful, parents spend more time loafing at the breeding site, but when food availability is low, more time is spent foraging at sea. This variability in resting time allows murres to feed their chicks at a relatively constant rate across years, so chick growth is not severely compromised by poor food availability (Burger & Piatt, 1990; Zador & Piatt, 1999; but see Wilhelm, 2001).

The relationship between a chick's reproductive value and the conditions in which it was reared may depend on its sex. In sexually size dimorphic species, offspring of the larger sex are often more susceptible to death from starvation in poor conditions (Howe, 1977; Stamps, 1990; Torres & Drummond, 1999), and require significantly more parental resources to survive to recruitment (Howe, 1977; Clutton-Brock *et al.*, 1985; Anderson *et al.*, 1993). However, the benefit in terms of number of grandchildren produced may be higher for a high-quality son than for a high-quality daughter, because males have a possibility of siring extra-pair offspring (Frank, 1990). Therefore, parents should invest in sons or daughters according to the fitness returns per unit investment for each sex (Leonard *et al.*, 1994). Sons and daughters may also differ in their costs to parents due to sex differences in philopatry. If one sex tends to disperse while the other returns to the natal colony, local resource competition with offspring of the non-dispersing sex may be costly to parents in future seasons. Therefore, parents may do better to bias allocation to

the dispersing sex (Lessells, 2002; Magrath *et al.*, 2002). Local resource competition often explains biased sex allocation in species with little or no sexual size dimorphism (Stamps *et al.*, 1987; Stamps, 1990).

Birds often have an extended period of parental care, with adults tending to their offspring long after hatching. This gives parents ample opportunity to bias allocation toward sons and daughters without altering the sex ratio (Frank, 1990; Sheldon, 1998). Post-hatching sex allocation is advantageous, because altering the primary sex ratio is potentially quite costly to parents, particularly if the sex ratio cannot be manipulated before ovulation (Sheldon, 1998).

This study examines parental feeding rates to male and female Common Murre and Atlantic Puffin chicks. Murres at the study site are individually colour-banded and their sexes known, providing a rare opportunity to examine sex allocation strategies of mothers and fathers separately (Lessells *et al.*, 1998). It was predicted that sons would be fed more than daughters, because both murres and puffins are sexually dimorphic in mass, and differences in feeding rate are associated with both chick growth rate and sexual size dimorphism (SSD) in adulthood (Anderson *et al.*, 1993; Sæther *et al.*, 1997; Krijgsveld *et al.*, 1998). Because differences in feeding rate are correlated with the degree of SSD (Anderson *et al.*, 1993), puffins are expected to show a more pronounced bias in sex allocation as size dimorphism is greater in puffins than in murres (Nettleship, 1972; Threlfall & Mahoney, 1980). While seabirds tend to be highly philopatric (Harris, 1984; Ainley *et al.*, 2002), there is no data on sex differences in dispersal; thus no prediction can

be made about whether local resource competition from either sex will affect sex allocation.

Further, because both hatching and cliff departure dates are known for murre chicks, the duration of parental feeding at the nest site will be compared for male and female chicks. Because daughters are thought to require and receive less parental care than sons, females are expected to leave the nesting site at a relatively young age, while male chicks should remain at the nest site receiving feeds from both parents for a longer period. Indeed, Richner (1991) reported that females in several avian species fledge 5-13% sooner than males on average. While there is no information from nest site departure to chick independence in this study, other studies have suggested that early parental investment is the most important determinant of chick survival and success (Clutton-Brock *et al.* 1985). Thus, it is very likely that if there are sex biases in resource allocation in Common Murres and Atlantic Puffins, they should be detected during the first weeks after hatching.

3.2 Methods

3.2.1 Field Methods

3.2.1.1 Common Murres

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. Two observers alternated shifts of typically 2-4 hours 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. Dawn-to-dusk watches were conducted on approximately 30 known breeding pairs from a blind every two to three days throughout the chick-rearing period. The number of pairs studied tended to increase slightly over the years, as the number of colour-banded individuals increased over the years of the study. Some unbanded murres were also included in the study, as the identity of some individuals was often quite certain; for example, if it was mated to a banded bird or was consistently seen at a particular breeding site, it was considered a “known” murre.

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 was noted. Hatching and fledging dates of chicks were recorded when possible, within ± 2 days. If a chick had hatched before the study season began, the hatch date was assumed to be 33 days after the lay date of the egg at that site (Ainley *et al.*, 2002); since observations were also conducted during the pre-breeding and early egg laying period of early May to early June, the lay date was usually known for early breeders. In most years, the research was concluded before all chicks at the site had left because of fears that the birds still at the site would be highly sensitive to possible observer disturbance, so the fledging date of these chicks was simply recorded as “unknown.” However, chicks surviving to 15 d were assumed to have fledged successfully.

When chicks were able to thermoregulate, at least ten 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 five years. Mass was measured to the nearest gram with a 500 g Pesola scale, and unflattened wing chord length was measured to the nearest millimetre with a wing ruler. Three growing primary feathers were taken for genetic analysis and stored in 70% ethanol before the chick was released. The parent was almost invariably at the site calling to the chick upon its release, and in all instances the parent and chick successfully reunited soon after handling.

3.2.1.2 Atlantic Puffins

The first objective for Atlantic Puffins in 2001 was to establish a study site of forty marked burrows on Great Island. The site was located on a grassy slope, where puffins tend to have higher breeding success than those occupying burrows on flat areas (Nettleship, 1972), thus maximising the sample size. A canvas blind was erected about 30 m from the study site, and in 2002 was replaced with a wooden blind. Burrows whose entrances were visible from the blind and that contained an egg within an arm's length were selected, and all 40 burrows could be watched simultaneously with the unaided eye.

The site was observed in 2001 and 2002 during peak feeding times (05:00 to 09:00 and 16:00 to 20:00; Harris, 1984) every two or three days from late June to early August. Observations of adults returning to marked burrows were made with binoculars, as described by Rodway & Montevecchi (1996). Species and number of prey items brought to the chick were recorded when possible. However, seeing the bill contents was often difficult because puffins entered the burrows very rapidly, particularly if a Herring Gull

Larus argentatus was nearby. If an adult was observed leaving the burrow two minutes or less after entering, then it was considered a chick feed even when bill contents could not be seen. As adults were not observed making such short visits without food (pers. obs.), this was considered a valid assumption.

The hatch date was assumed to be halfway between the previous observation day and the day prior to the first observed chick feed, as the chick is not fed in the first day of life, and so were accurate to within ± 2 days (Harris, 1984; Rodway *et al.*, 1996). Chicks were temporarily removed (“grubbed”) from their burrows between 10 and 22 days after the estimated hatching date, and banded and measured in the same manner as the murre chicks. Three primary feathers were taken for subsequent sexing.

3.2.2 Lab Methods

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 hours. The contents of the buffers used are detailed in Appendix 1; the protocol was modified in 2001, as a new buffer described in Bello *et al.* (2001) increased the yield of DNA in the final product. This was followed by a standard phenol: chloroform: isoamyl alcohol extraction, and the DNA was 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 μ L TE.

The product was sexed using the 2550F/2718R primer pair, which flanks introns on the CHD-Z and CHD-W genes (Fridolfsson & Ellegren, 1999). The PCR protocol is

detailed in Appendix 2. These homologous genes are located on the W and Z sex chromosomes of all non-ratite birds, and are highly conserved (Griffiths *et al.*, 1996). The intron flanked by the primers differs in length on the two genes, resulting in the amplification of a 600 bp segment on CHD-Z, and a 450 bp segment on CHD-W. Heterogametic (WZ) females were identified by the presence of two bands when the PCR product was run on an agarose gel, whereas homogametic (ZZ) males showed only one band.

3.2.3 Statistical Methods

3.2.3.1 Common Murres

All statistics were performed using SPSS 11.0 for Windows (SPSS Inc., 2001). Feeding rates by mothers and fathers were compared using general linear models; a significance level (α) of 0.05 was used in all analyses. To eliminate interannual variation in feeding rate, residuals from annual mean feeding rates of males and females were used as the dependent variables. Explanatory variables included in the initial model were sex, lay date and the sex by lay date interaction term. Lay date (number of days relative to the annual median lay date) refers to the date that the first egg at the site was laid, regardless of whether the chick in question hatched from this egg or a replacement egg laid after the loss of a first egg. Date of first egg lay is a reliable indicator of parental quality in the congeneric Thick-billed Murre (Hipfner, 1997). Older, more experienced murres tend to lay earlier in the season than younger breeders, and it has been shown that parental experience is a more reliable predictor of breeding success than the conditions at the time

of hatching (Hipfner, 1997; Hipfner & Gaston, 2002). Chick feeding rate is not constant throughout the period of parental feeding at the site; young chicks are fed less than older chicks (Gabrielsen, 1996). Thus, separate analyses were conducted on early and late chick rearing (hatching to 12 d, and 13 d to cliff departure, respectively). Total parental feeding rates were compared in the same manner, to determine if one parent may be compensating for a lower feeding rate toward chicks of one sex by increasing his or her own feeding rate.

To compare rates of feeding to sons and daughters within pairs, pairs that raised both male and female chicks were analysed further. The means of the residuals of annual feeding rates to sons and daughters were compared using a paired *t*-test; because sons were predicted to have a higher feeding rate than daughters, a one-tailed test was used. As with the analysis of all pairs, both maternal and paternal feeding rates were compared, and early and late chick rearing were explored.

The amount of time spent at the nest site by murre chicks, from hatching to cliff departure, was compared using a general linear model. As with feeding rates, interannual variation was eliminated by comparing residuals from the mean cliff time for each year. Explanatory variables in the initial model were sex, hatch date and sex by hatch date. Because the duration of the breeding season is constrained by food availability (mainly Capelin *Mallotus villosus*; Piatt, 1990), late-hatched chicks and their fathers may be forced to leave the cliff sooner, regardless of parental quality, to swim to the food supply. As well, chicks remaining late in the season after most pairs have left the breeding site are

more susceptible to predation (A. Storey, pers. comm.).

3.2.3.2 Atlantic Puffins

Analysis of feeding rates to male and female Atlantic Puffin chicks were similar to that used for Common Murres. Because not all of the individuals at the study site were colour-banded, feeds by mother and fathers could not be distinguished in many of the pairs. Therefore, total parental feeding rate was compared for sons and daughters. Residual of annual mean feeding rate was the dependent variable, with sex, hatch date, and a sex by hatch date interaction as explanatory variables. Early and late chick rearing were analysed separately, as with the murres. One parent remains with the chick in the burrow until the chick is able to thermoregulate at 10 d (Harris, 1983), while both parents are able to forage simultaneously after this time. Thus, hatching to 10 d was considered early chick rearing, while 11 d to 30 d, when chicks begin to reduce their food intake voluntarily (Harris, 1984; Johnsen *et al.*, 1994), was considered late chick rearing.

3.3 Results

3.3.1 Common Murres

From 1997 to 2001, 76 chicks were captured and sexed. Because some of the breeding pairs were unmarked in 1997 and 1998, feeding data was unavailable for certain chicks in these years. Further, although most chicks were observed throughout their time at the site, data from late chick rearing was not obtained for some late-hatched chicks because the study period ended while these chicks were still quite young. Ultimately, the sample size was 66 for early chick rearing (27 males, 39 females), and reduced to 57 for

late chick rearing (22 males, 35 females).

As found in previous studies of the Common Murre (Wanless & Harris, 1986; Wilhelm, 2001), mothers fed the chick at a greater rate on average than fathers (Table 3.1; Table 3.2). Over the period of parental feeding at the nest site, the ratio of feeds to sons to feeds to daughters was 1.1:1. This is somewhat higher than the male mass to female mass ratio of about 1.04:1 (Threlfall & Mahoney, 1980). In the general linear models including all breeding pairs, none of the analyses had significant sex by lay date interactions, so the final models contained only the main effects. Neither parent had a significant sex bias in feeding during early chick-rearing, but fathers had a significant lay date effect (Table 3.1). Fathers' feeding rate declined with lay date relative to the annual median, while there was no such relationship for mothers (Figure 3.1a). Later in the chick-rearing period, fathers fed sons significantly more than they fed daughters, while for mothers, the difference in feeding rate was non-significant (Table 3.1). There was no significant relationship between lay date and parental feeding, although fathers showed a trend in the same direction as in early chick rearing (Figure 3.1b). Total feeding rates by both parents showed a similar trend, suggesting that parents of one sex are consistently compensating for the other in feeding either their sons or their daughters (Table 3.1).

Thirteen pairs were known to have produced both male and female chicks during the five years of the study. Mean residual feeding rates by mothers and fathers were calculated for each pair, from between one and three chicks of each sex. The sample size was reduced to 12 pairs for late chick rearing, because data were not available for one

late-hatched chick. While there were no significant sex differences in early chick rearing, both fathers and mothers fed sons significantly more than daughters in late chick rearing (Table 3.2).

Male and female chicks spent an equal amount of time at the breeding site. Mean number of days from hatching to fledging for sons was 21.1 ± 1.8 ($n = 14$), while females spent 21.9 ± 2.8 days at the nest site ($n = 27$). Results of the general linear model are shown in Table 3.3; the sex by hatch date interaction term was not significant, so was dropped from the analysis. While the sex difference did not approach significance, hatch date did affect the amount of time spent at the cliff (Table 3.3). Chicks hatching before the median hatch date spent more time at the nest site than later-hatched chicks (Figure 3.2).

3.3.2 Atlantic Puffins

In 2001 and 2002, a total of 23 chicks of known age were captured and sexed (16 males, 7 females). For five of these chicks, data on feeding rates were insufficient for early chick rearing; if there were fewer than three days of observations in the first 10 d after the estimated hatch date, the chick was excluded from analysis. Of the 18 chicks included in early chick rearing, 13 were male and 5 were female. Throughout the observation period, the ratio of feeds to sons over feeds to daughters was 1.28:1. As with the murrelets, this was greater than the observed SSD in adulthood (a ratio of approximately 1.1:1; Nettleship, 1972).

Feeding rates were analysed with general linear models; the sex by hatch date

interaction terms were non-significant in both early and late chick rearing and so were dropped from the final models. Neither sex nor hatch date had a significant effect on parental feeding rates (Table 3.4).

3.4 Discussion

Four main findings were of interest in this study, and these will be addressed in turn. Common Murre parents fed their sons more than their daughters in the latter part of the chick-rearing period. Paternal (but not maternal) feeding rate declined with lay date in murre, which itself is an indicator of female quality. In both murre and puffins, the ratio of chick feeds to sons and daughters exceeded the ratio of adult male mass to female mass. Finally, male and female murre chicks spent a similar amount of time at the natal colony.

In the late chick rearing period, from 13 days after hatching until cliff departure, Common Murre sons received more parental feeds than daughters. This difference was significant when total feeding rates were compared, as well as for fathers in the analysis of all breeding pairs; when within-pair differences in sex allocation were explored, it was significant for both mothers and fathers. Because adult males benefit more than females from slight advantages in condition that may arise from receiving greater parental care early in life, parents should expend more parental effort when raising a son than a daughter (Trivers & Willard, 1973). For puffins, sex differences in feeding rates during late chick rearing were not significant. However, the sample size was small, and further study is needed to address fully whether or not puffins bias parental care toward their

sons.

Sons and daughters were fed equally in early chick rearing, presumably because the food requirements of such young chicks are less than those of older chicks (Gabrielsen, 1996). It may be well within the capacity of parents to fulfill the nutritional requirements of a young chick regardless of its sex; only when the chick grows bigger and requires more effort to feed do the differences between the sexes emerge.

One surprising aspect of the Common Murre data was that paternal feeding rate, but not maternal feeding rate, was related to the lay date of the first egg at the site (even if the chick hatched from a replacement egg). Fathers fed chicks at a higher rate if mothers laid their first egg early in the season. There are at least three possible explanations for this observation, none of which are mutually exclusive. First, males may respond to female experience and quality, as indicated by lay date (Hipfner, 1997), by investing proportionally more or less in their offspring. Second, females, who work equally hard to feed their chick regardless of lay date, would presumably prefer a mate that contributes more than an average male in terms of chick feeding. A high-quality (early laying) female should be more likely to attract a high-quality (high feeding rate) mate. Third, males may feed their chicks more as they become older and more experienced, and if age within pairs is correlated, one would expect to see the pattern observed here.

Another case of males and females using different cues to determine their chick feeding rate was found in an experimental study of the Brown Thornbill *Acanthiza pusilla* (Green, 2002). In this species, female provisioning rate was determined by brood sex

ratio (male-biased broods were fed more), while males fed more when they were in a pair that had previously reared young together at least once. In a natural setting, these strategies complemented each other, because females in established pairs tended to produce male-biased broods. Male Brown Thornbills invest more in offspring when mated to a female with whom he knows he can produce viable offspring; this is suggestive of a decision rule similar to one that may be employed by male Common Murres. In both species, a male feeds at a higher rate when mated to a female who is capable of producing viable offspring. When a male murre knows that a female is of poorer quality because she lays later, or when a male thornbill has no knowledge of a female's prior breeding success because he has not bred with her before, he will feed the offspring at a lower rate. Further study of sex-biased provisioning in birds, including information on both mothers and fathers, is warranted. The few examples that have been published to date (Leonard *et al.*, 1994; Lessells *et al.*, 1998; Green, 2002) have provided interesting and intriguing glimpses of emerging patterns in avian sex allocation.

The ratio of mean chick feeding rate to sons and daughters was greater for puffins than for murres, as was predicted due to the greater adult size dimorphism observed in puffins (Nettleship, 1972; Threlfall & Mahoney, 1980). However, in both species, the mean difference in feeding rate to male and female chicks was considerably larger than would be predicted based on differences in adult size alone (Krijgsveld *et al.*, 1998). Adult sexual size dimorphism has not been the sole reason for observed patterns of sex allocation in many avian taxa (Stamps, 1990). Indeed, while sex-biased feeding has been

observed in some sexually monomorphic species, other species with sexual size dimorphism are fed equally by parents, and even grow at different rates when hand-fed the same amount of food (Stamps *et al.*, 1987; Stamps, 1990; Lessells *et al.*, 1998; Torres & Drummond, 1999). Incomplete knowledge of alcid life histories, such as a dearth of information on relative dispersal rates of the sexes, leaves us unable to explain why sex-biased feeding is even more pronounced than expected, because sex allocation theory relies on knowledge of the relative costs and benefits of producing each sex (Leonard *et al.*, 1994; Komdeur & Pen, 2002).

Consistent with previous studies on alcids, early-hatching Common Murre chicks spent a longer time at the colony than those hatching late in the breeding season (Murphy, 1995; Hipfner & Gaston, 1999). However, the time from hatching to cliff departure did not differ between male and female chicks. This was in contrast to Richner (1991), who reported that in many sexually dimorphic passerine and raptor species, members of the smaller sex fledge earlier. These results suggest 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 parental care (specifically, paternal care) in murre does not end at colony departure, and there may be a difference in the amount of time it takes a son or a daughter to reach independence. Similarly, the duration of parental feeding of Atlantic Puffin chicks could not be assessed here. Because parents often return to the burrow with chick feeds days after the chick departs (Harris, 1984), it is impossible to determine fledging date without reaching into the burrow, and this disturbance may

have serious negative consequences for the chick (Rodway *et al.*, 1996). While the duration of parental feeding could not be fully addressed by this study, the intensity of feeding during the chicks' first weeks of life has been well explored, and parental care at this stage is highly correlated with chick survival and future reproductive success (Clutton-Brock *et al.*, 1985).

3.5 References

- Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In The Birds of North America, No. 666 (A. Poole and F. Gill, eds.) The Birds of North America Inc., Philadelphia, PA.
- Anderson, D.J., Reeve, J., Martinez Gomez, J.E., Weathers, W.W., Hutson, S., Cunningham, H.V. and Bird, D.M. 1993. Sexual size dimorphism and food requirements of nestling birds. *Canadian Journal of Zoology*, **71**: 2541-2545.
- Bello, N., Francino, O. and Sánchez, A. 2001. Isolation of genomic DNA from feathers. *Journal of Veterinary Diagnostic Investigations*, **13**: 162-164.
- Burger, A.E. and Piatt, J.F. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. *Studies in Avian Biology* **14**: 71-83.
- Clutton-Brock, T.H., Albon, S.D. and F.F. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**: 131-133.
- Creelman, E. and Storey, A.E. 1991. Sex differences in reproductive behavior of Atlantic Puffins. *Condor*, **93**: 390-398.
- Erikstad, K.E., Ashiem, M., Fauchald, P., Dahlhaug, L. and Tveraa, T. 1997. Adjustment of parental effort in the Puffin; the roles of adult body condition and chick size. *Behavioural Ecology and Sociobiology*, **40**: 95-100.
- Erikstad, K.E., Fauchald, P., Tveraa, T. and Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, **79**: 1781-1788.
- Frank, S.A. 1990. Sex allocation theory for birds and mammals. *Annual Review of*

Ecology and Systematics, **21**: 13-55.

- Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**: 116-121.
- Gabrielsen, G.W. 1996. Energy expenditures of breeding Common Murres. In Montevecchi, W.A. Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Canadian Wildlife Service occasional paper, **91**: 49-58.
- Green, D.J. 2002. Pair bond duration influences paternal provisioning and the primary sex ratio of Brown Thornbill broods. *Animal Behaviour*, **64**: 791-800.
- Griffiths, R., Daan, S. and Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London B*, **263**: 1251-1256.
- Harris, M.P. 1984. The Puffin. Poyser, Calton, U.K.
- Harris, M.P. 1983. Parent-young communication in the Puffin *Fratercula arctica*. *Ibis*, **125**: 109-114.
- Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. *Condor*, **99**: 353-360.
- Hipfner, J.M. and Gaston, A.J. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology*, **80**: 587-596.
- Hipfner, J.M. and Gaston, A.J. 2002. Growth of nestling Thick-billed Murres (*Uria lomvia*) in relation to parental experience and hatching date. *Auk*, **119**: 827-832.
- Howe, H.F. 1977. Sex-ratio adjustment in the Common Grackle. *Science*, **198**: 744-746.
- Johnsen, I., Erikstad, K.E. and Saether, B.E. 1994. Regulation of parental investment in a long-lived seabird, the Puffin *Fratercula arctica*. *Oikos*, **71**: 273-278.
- Jönsson, K.L., Tuomi, J. and Järemo, J. 1998. Pre- and postbreeding costs of parental investment. *Oikos*, **83**: 424-431.
- Krijgsveld, K.L., Dijkstra, C., Visser, G.H. and Daan, S. 1998. Energy requirements for growth in relation to sexual size dimorphism in Marsh Harrier *Circus aeruginosus* nestlings. *Physiological Zoology*, **71**: 693-702.

- Komdeur, J. and Pen, I. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philosophical Transactions of the Royal Society of London B*, **357**: 373-380.
- Lessells, C.M. 2002. Parentally biased favouritism: why should parents specialize in caring for different offspring? *Philosophical Transactions of the Royal Society of London B*, **357**: 381-403.
- Lessells, C.M., Oddie, K.R. and Mateman, A.C. 1998. Parental behaviour is unrelated to experimentally manipulated Great Tit brood sex ratio. *Animal Behaviour*, **56**: 385-393.
- Leonard, M.L., Teather, K.L., Horn, A.G., Koenig, W.D. and Dickinson, J.L. 1994. Provisioning in Western Bluebirds is not related to offspring sex. *Behavioural Ecology*, **5**: 455-459.
- Magrath, M.J.L., Green, D.J. and Komdeur, J. 2002. Sex allocation in the sexually monomorphic Fairy Martin. *Journal of Avian Biology*, **33**: 260-268.
- Murphy, E.C. 1995. Seasonal declines in duration of incubation and chick periods of Common Murres at Bluff, Alaska in 1987-1991. *Auk*, **112**: 982-993.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**: 239-268.
- Piatt, J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Studies in Avian Biology*, **14**: 36-51.
- Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex-specific growth contribute to balanced sex ratios? *Functional Ecology*, **5**: 19-28.
- Rodway, M.S. and Montevecchi, W.A. 1996. Sampling methods for assessing the diets of Atlantic Puffin chicks. *Marine Ecology Progress Series*, **144**: 41-55.
- Rodway, M.S., Montevecchi, W.A. and Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic Puffins *Fratercula arctica*. *Biological Conservation*, **76**: 311-319.
- Sæther, B.-E., Lorentsen, S.-H., Tveraa, T., Andersen, R. and Pedersen, H.C. 1997. Size-

- dependent variation in reproductive success of a long-lived seabird, the Antarctic Petrel (*Thalassoica antarctica*). *Auk*, **114**: 333-340.
- Sealy, S.G. 1973. The adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. *Ornis Scandinavica*, **4**: 113-121.
- Sheldon, B.C. 1998. Recent studies of avian sex ratios. *Heredity*, **80**: 397-402.
- SPSS Inc. 2001. SPSS for Windows version 11.0. SPSS Inc., Chicago.
- Stamps, J.A. 1990. When should avian parents differentially provision sons and daughters? *American Naturalist*, **135**: 671-685.
- Stamps, J., Clark, A., Arrowood, P. and Kus, B. 1987. The effects of parent and offspring gender on food allocation in Budgerigars. *Behaviour*, **101**: 177-199.
- Threlfall, W. and Mahoney, S.P. 1980. The use of measurements in sexing Common Murres from Newfoundland. *Wilson Bulletin*, **92**: 266-268.
- Torres, R. and Drummond, H. 1999. Does large size make daughters of the Blue-footed Booby more expensive than sons? *Journal of Animal Ecology*, **68**: 1133-1141.
- Trivers, R.L. and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**: 90-92.
- Velando, A. 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the Blue-footed Booby. *Behavioral Ecology*, **13**: 443-449.
- Wanless, S. and Harris, M.P. 1986. Time spent at a colony by male and female Guillemots *Uria aalge* and Razorbills *Alca torda*. *Bird Study*, **33**: 168-176.
- Webb, J.N., Székely, T., Houston, A.I. and McNamara, J.M. 2002. A theoretical analysis of the energetic costs and consequences of parental care decisions. *Proceedings of the Royal Society of London B*, **269**: 331-340.
- Wilhelm, S.I. 2001. Variation in parental roles among Common Murres: Effect of food availability. Abstracts: American Ornithologists' Union, Annual Meeting, Seattle, WA.
- Williams, G.C. 1966. Natural selection, the cost of reproduction, and a refinement of

Lack's principle. *American Naturalist*, **100**: 687-690.

Ydenberg, R.C. 1989. Growth-mortality tradeoffs and the evolution of juvenile life-histories in the Alcidae. *Ecology*, **70**: 1494-1506.

Zador, S.G. and Piatt, J.F. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. *Condor*, **101**: 149-152.

Table 3.1. Analysis of mean parental feeding rate to sons and daughters in early chick rearing (hatching to 12 days; 27 sons and 39 daughters) and late chick rearing (13 days until cliff departure; 22 sons and 35 daughters) for Common Murres at Great Island, NL.

		Feeding Rate (\pm SD)		Sex Difference <i>F</i> (<i>p</i>)	Lay Date Effect <i>F</i> (<i>p</i>)
		Sons	Daughters		
Early	Mothers	2.20 \pm 0.81	2.30 \pm 1.23	1.540 (0.219)	0.229 (0.634)
	Fathers	1.95 \pm 0.87	1.85 \pm 0.88	0.001 (0.980)	12.643 (0.001)*
	Total	4.15 \pm 1.08	4.15 \pm 1.41	0.089 (0.767)	0.576 (0.933)
Late	Mothers	2.30 \pm 0.95	2.06 \pm 0.93	1.645 (0.205)	0.205 (0.653)
	Fathers	2.34 \pm 1.12	1.81 \pm 0.91	5.996 (0.018)*	3.540 (0.065)
	Total	4.64 \pm 1.43	4.18 \pm 1.35	7.171 (0.012)*	1.461 (0.158)

Table 3.2. Results of paired *t*-tests showing within-pair biases in Common Murre feeding rates to sons and daughters in early (hatching to 12 d; n = 13) and late (13 d to fledging; n = 12) chick rearing at Great Island, NL.

		Feeding Rate (\pm SD)		<i>t</i> (<i>p</i>)
		Sons	Daughters	
Early	Mothers	2.44 \pm 0.71	2.27 \pm 0.67	0.663 (0.260)
	Fathers	1.84 \pm 0.70	2.03 \pm 0.61	-1.583 (0.070)
Late	Mothers	2.59 \pm 0.73	2.06 \pm 0.71	2.650 (0.012)*
	Fathers	2.30 \pm 1.05	1.84 \pm 0.59	1.817 (0.049)*

Table 3.3. Analysis of time spent at the nest site by sons (n = 14) and daughters (n = 27) for Common Murres at Great Island, NL from 1999 to 2001.

Source	d.f.	MS	<i>F</i> (<i>p</i>)
Sex	1	1.780	0.419 (0.521)
Hatch Date	1	69.386	16.346 (0.000)*
Error	38	4.245	

Table 3.4. Analysis of mean parental feeding rate to sons and daughters in early (hatching to 10 days; n = 18) and late (11 to 30 days; n = 23) chick rearing for Atlantic Puffins at Great Island, NL.

	Feeding Rate (\pm SD)		Sex Difference <i>F</i> (<i>p</i>)	Hatch Date Effect <i>F</i> (<i>p</i>)
	Sons	Daughters		
Early	1.17 \pm 0.21	1.28 \pm 0.35	0.480 (0.499)	3.581 (0.078)
Late	1.36 \pm 0.42	1.04 \pm 0.22	1.440 (0.244)	0.158 (0.696)

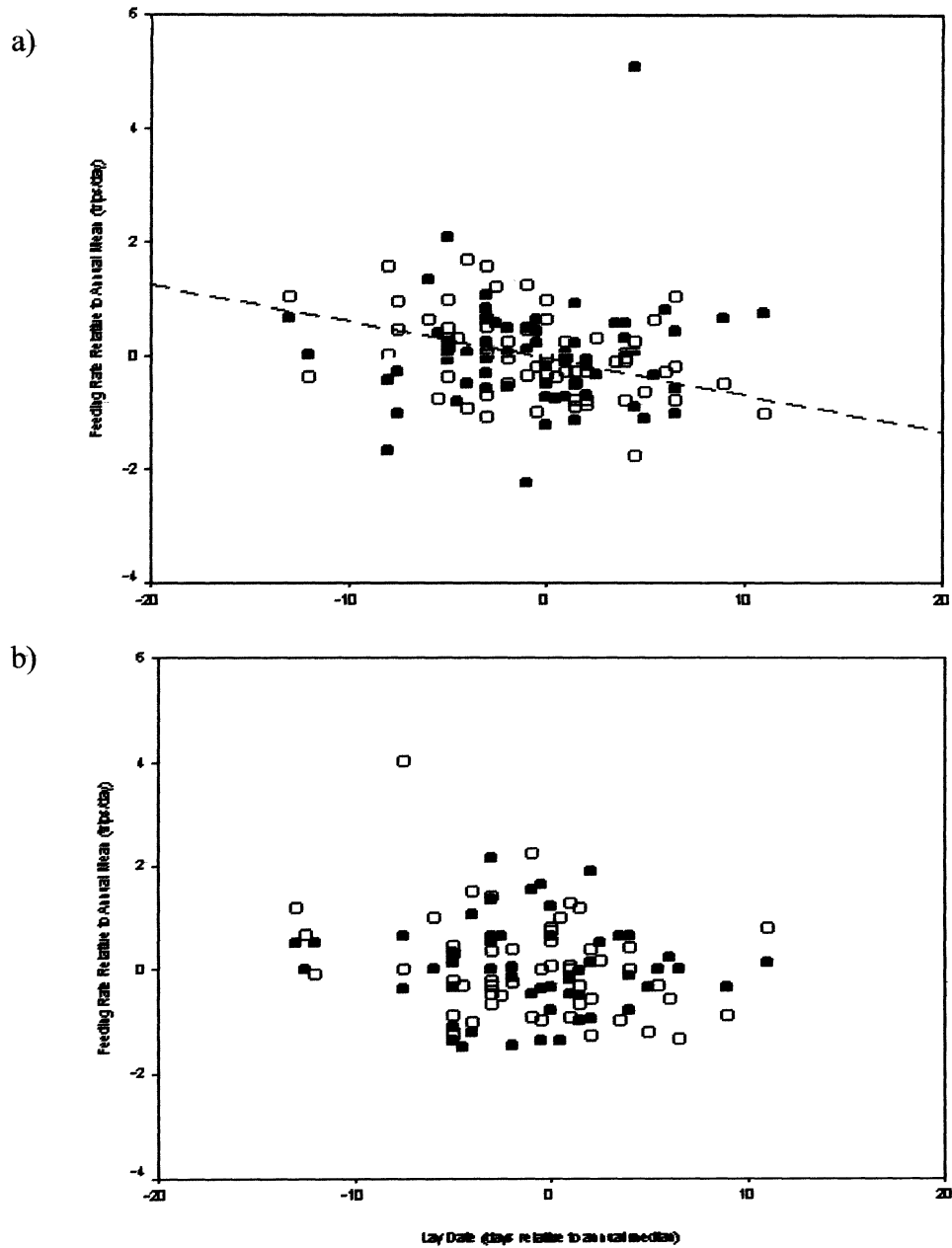


Figure 3.1. Relationship between lay date and feeding rate by mothers (filled circles) and fathers (open circles), relative to annual mean values for Common Murres. a) Early chick rearing. Relationship is significant for fathers (dashed line; $R^2 = 0.167$; $p = 0.001$), but not mothers ($R^2 = 0.004$; $p = 0.620$). b) Late chick rearing. Relationship approaches significance for fathers ($R^2 = 0.053$; $p = 0.085$) but not mothers ($R^2 = 0.003$; $p = 0.673$).

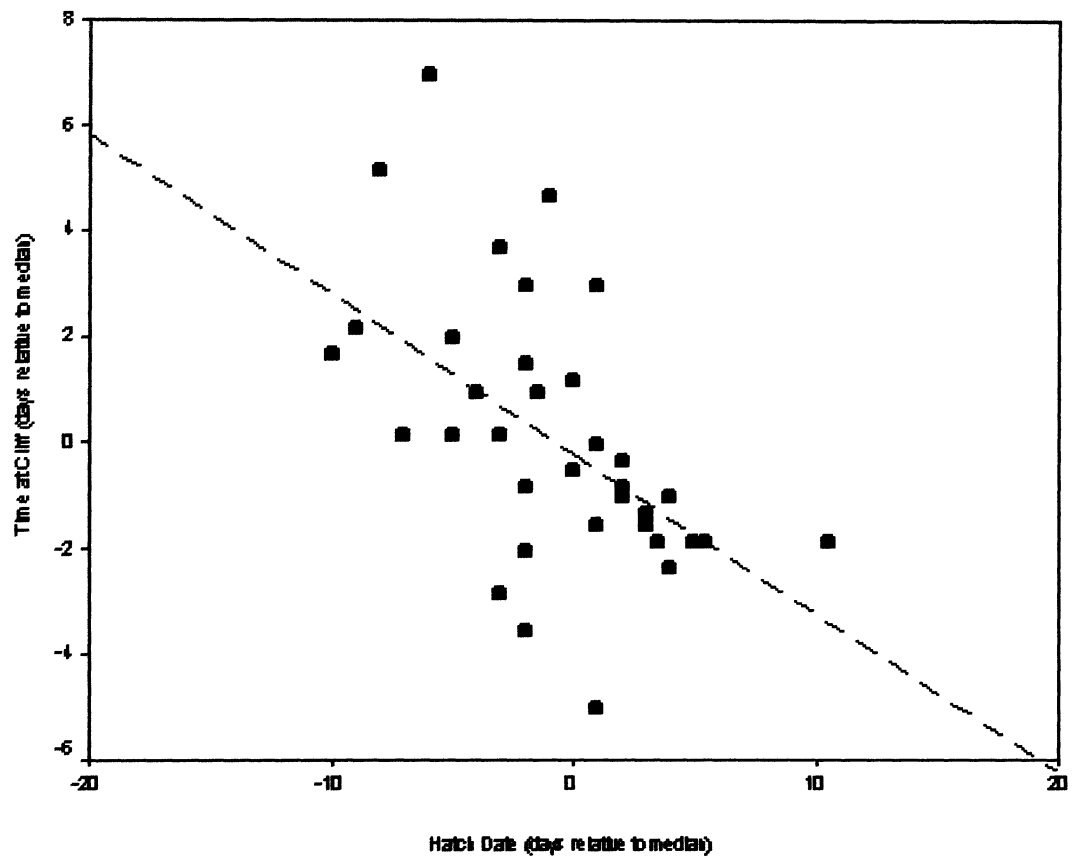


Figure 3.2. Relationship between hatch date and days from hatching to cliff departure, relative to the annual mean, for Common Murre chicks. Fledging age declines significantly with hatch date ($R^2 = 0.299$; $p < 0.001$).

Chapter 4 Effects of environment and parent quality on sex ratio of alcids

4.1 Introduction

Brood sex ratio variation is the most easily measured and well-studied area of sex allocation (West *et al.*, 2002). Contrary to Charnov (1982), chromosomal sex determination is not an insurmountable constraint on sex ratio variation (Heinsohn *et al.*, 1997; Komdeur & Pen, 2002). In fact, parents of several species have been shown to adjust the sex ratio of their offspring in response to a variety of factors, including habitat quality (Komdeur *et al.*, 1997), maternal condition (Nager *et al.*, 1999; Kalmbach *et al.*, 2001), parental age (Blank & Nolan, 1983; Heg *et al.*, 2000), pair bond duration (Green, 2002) and perceived mate quality or attractiveness (Velando *et al.*, 2002; Sheldon *et al.*, 1999).

The question of how birds are able to skew the sex ratio at hatching remains largely unanswered (Sheldon, 1999). Dump laying or selective resorption of eggs of the “wrong” sex has been hypothesised, and is particularly feasible for species laying a single egg, because brood asynchrony or gaps in the laying sequence are not of concern (Emlen, 1997). However, there is evidence that biases may be present at the time of ovulation (Sheldon, 1998; Oddie, 1998; Komdeur *et al.*, 2002).

Optimising the sex ratio can have large fitness benefits to parents, in both the short and long term (Komdeur, 1998). Parents can maximise fitness returns by producing offspring of the sex that they can produce well. There is evidence that high quality offspring typically become high quality adults, live longer on average, and have greater

lifetime reproductive success (Trivers & Willard, 1973; Weimerskirch, 1992; Wendeln & Becker, 1999). High quality individuals are less likely to desert a breeding attempt in adverse conditions (Webb *et al.*, 2002), and are more likely to relay following egg loss (Hipfner *et al.*, 1999), than poor quality breeders. Thus, if parents have limited resources to invest in offspring, they should produce offspring of the cheaper sex. This is especially true of species that cannot manipulate clutch size, such as those birds that produce only a single chick in a season.

Having a good understanding of the life history of a species is important in order to identify the variables in the environment that may be pertinent in determining the optimal sex ratio (Gowaty, 1990; Ellegren & Sheldon, 1997). Among organisms with complex life histories, several factors may affect the optimal sex ratio in different ways. The predicted optimum will depend on only the factors that are considered by the researcher, while the observed optimum is determined by the organism (Oddie, 1998; Sheldon, 1999). Difficulty in assessing what determines optimal sex allocation, such as mate quality and environmental stochasticity, may explain why skewed vertebrate sex ratios are not seen more frequently (West *et al.*, 2000). Also, sex ratio manipulation should only occur if the expected fitness gain of doing so outweighs the cost, which depends largely on the mechanism of sex determination (Komduer & Pen, 2002; West *et al.*, 2002).

Body condition is a measure of mass relative to an individual's structural body size. In certain seabirds, adult condition is often quite stable across years, but there is

considerable variation between individuals (Weimerskirch, 1992; Wendeln, 1997; Wendeln & Becker, 1999). Maternal condition has long been known to be a determinant of optimal sex ratio (Trivers & Willard, 1973). Females in good condition often produce more of the larger and more expensive sex, usually males (Trivers & Willard, 1973; Nager *et al.*, 1999; Korpimäki *et al.*, 2000; Whittingham & Dunn, 2000; Whittingham *et al.*, 2002). More recently, in species with biparental care, it has been shown that paternal condition may also affect the sex ratio (Sheldon, 1998).

Parental condition influences parental care decisions such as whether or not to desert one's offspring (Webb *et al.*, 2002). Reproductive success and growth rate of chicks are both positively correlated with parental condition in the Atlantic Puffin (Barrett & Rikardsen, 1992; Erikstad *et al.*, 1997). Parental body condition declines throughout chick rearing, likely because of a decrease in stored fat (Gaston, 1985; Barrett & Rikardsen, 1992). The rate of decline in condition is similar, regardless of condition at the onset of breeding (Barrett & Rikardsen, 1992). Parents in poor condition at the start of the chick rearing period risk falling below a threshold condition, where continuing to provide parental care might endanger survival to an extent that would outweigh the potential fitness benefit of the current chick. As smaller females are believed to be less costly to produce, this threshold condition would be lower.

Reproductive performance in birds tends to increase with parental age (Curio, 1983; Forslund & Pärt, 1995). In long-lived species such as alcids, this is thought to be due to an age-related increase in competence through previous breeding experience and

improved foraging ability (Forslund & Pärt, 1995). In Thick-billed Murres, fledging mass is significantly higher for chicks reared by older, more experienced parents (Hipfner & Gaston, 1999). Also, older females are more likely to relay following egg loss, and the chicks produced are just as likely to fledge and be recruited into the breeding population as their earlier-hatched counterparts (Hipfner, 1997; Hipfner *et al.*, 1999; Hipfner, 2001). The optimal sex ratio has been predicted to vary with parental age (Daunt *et al.*, 2001). This has in fact been shown in some avian species, in which older and more experienced parents produced more of the costlier sex on average than younger breeders (Blank & Nolan, 1983; Heg *et al.*, 2000).

Differences in food availability can also play a role in determining the optimal sex ratio. Reproductive success and chick growth rates decline when food availability is low, and offspring of the larger sex tend to be more severely affected, apparently due to their higher food requirements (Clutton-Brock *et al.*, 1985; Cooch *et al.*, 1996; Ellegren & Sheldon, 1997; Sheldon *et al.*, 1998). For many species, the food supply declines predictably over the breeding season, and correspondingly, a higher proportion of the smaller sex is produced by late breeders (Sheldon, 1998). Interannual food supply variation also affects reproductive success; in Atlantic Puffins, fledging success and chick mass decline with capelin *Mallotus villosus* abundance (Pierotti, 1983; Rice, 1985). Capelin abundance is highly variable in the northwest Atlantic (Carscadden 1984). Similarly, small but significant interannual variation in Thick-billed Murre chick growth rates in the Hudson Strait is apparently due to changes in the food supply (Gaston *et al.*,

1983).

The purpose of this study is to determine whether alcids exert control over the sex of the offspring they produce, and under what circumstances. The sex ratio with respect to adult body condition at the onset of breeding will be examined. It is expected that adults in poor condition (those having a low mass to tarsus length ratio) will be more likely to produce females, increasing the likelihood of a successful reproductive attempt by producing the smaller sex. Similarly, using tarsus length as an index, the question of whether adult size affects the sex ratio produced will be explored. However, as there is no evidence that skeletal body size affects reproductive success in alcids, it is expected that there will be no difference in the sex ratio produced by large and small parents.

Variation in sex ratio with respect to adult age, which can be indirectly assessed by lay date (Hipfner *et al.*, 1997), will also be explored. It is expected that older individuals, those laying their first egg early in the breeding season, will produce more males than those laying after the median lay date, as was seen in European Shag *Phalacrocorax aristotelis* broods (Velando *et al.*, 2002). The sex ratio of replacement eggs is expected to be similar to that of early-laid first eggs, because only older, early-laying parents relay following egg loss. Although replacement eggs are laid approximately fourteen days after loss of the original egg (Ainley *et al.*, 2002), and so hatch relatively late in the season, evidence from the Thick-billed Murre suggests that parental age is the reason for poorer performance of late-hatching chicks, not a seasonal decline in food availability (Hipfner, 1997). Finally, the effect of mean annual

provisioning rate on the sex ratio of chicks produced at the study site will be explored.

Feeding rate is thought to reflect food availability at the colony, and it is expected that the sex ratio will be biased toward the smaller sex in years of low capelin abundance.

4.2 Methods

4.2.1 Field Methods

4.2.1.1 Thick-billed Murres

This study was conducted on Coats Island, Nunavut (62°57'N, 82°00'W) in 1998. Breeding sites on two plots (SP and Z) were mapped and numbered. The plots were observed at 2-day intervals to obtain estimated hatch dates (± 2 d) at each site.

At 14 days of age, just prior to the minimum observed fledging age of Thick-billed Murres (15 days; Gaston & Nettleship, 1981), chicks were captured and banded with an individually numbered metal band. Two growing coverts were plucked and stored in ethanol for later genetic analysis.

4.2.1.2 Common Murres

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 watches were conducted on approximately 30 known breeding pairs from a blind every two to three days throughout the chick-rearing period. The number of pairs tended to increase slightly over the years, as the number of colour-banded individuals has increased since the beginning of the study. Some unbanded murres were also included in the study, as the identity of some individuals was often quite

certain; for example, if it was mated to a banded bird or was consistently seen at a particular breeding site, it was considered a “known” murre.

Observers recorded when birds brought food items to the site, and the species and relative size of the prey. Three scales were placed in the study plot in 1998, and when a murre was observed standing on a scale, the mass and identity of the bird (if known) was recorded. Hatching and fledging dates of chicks were recorded when possible, within ± 2 days. If a chick had hatched before the study season began, the hatch date was assumed to be 33 d after the lay date of the egg at that site (Ainley *et al.*, 2002); since observations were also conducted during the pre-breeding and early egg laying period of early May to early June, the lay date was usually known for early breeders. In most years, research was concluded before all chicks at the site had left the nest site because of fears that the birds still at the site would be highly sensitive to possible observer disturbance, so the fledging date of these chicks was simply recorded as “unknown.” However, chicks surviving to 15 d were assumed to have fledged successfully.

When chicks were able to thermoregulate, at least ten 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 five years. Mass was measured to the nearest gram with a 500 g spring scale, and unflattened wing chord length was measured to the nearest millimetre with a wing ruler. Three growing primary feathers were taken for genetic analysis and stored in 70% ethanol before the chick was released. The parent was

almost invariably at the site calling to the chick upon its release, and in all instances the parent and chick successfully reunited soon after handling. Adults were similarly captured and banded; if they were previously banded, missing and worn bands were replaced. The tarsus was measured to the nearest 0.1 mm using dial calipers, and mass was measured to the nearest gram using a 1000 g or 1500 g spring scale. Body condition was calculated by dividing body mass by tarsus length.

4.2.1.3 Atlantic Puffins

The study site was located on a grassy slope, where puffins tend to have higher breeding success than those occupying burrows on flat areas (Nettleship, 1972), thus maximising the sample size. A canvas blind was erected about 30 m from the study site, and in 2002 replaced with a wooden blind. Burrow entrances were visible from the blind, and all 40 could be watched simultaneously with the unaided eye.

The site was observed in 2001 and 2002 during peak feeding times (05:00 to 09:00 and 16:00 to 20:00; Harris, 1984) every second or third day from late June to early August. Observations of adults bringing food to marked burrows were made with binoculars, as described by Rodway & Montevecchi (1996), to determine chick hatching dates. Chicks are not fed until the day after they hatch (Harris, 1984), so hatch date was taken to be halfway between the previous observation day and the day prior to the first observed chick feed and so were accurate to within ± 2 days. If an adult was observed leaving the burrow two minutes or less after entering, it was considered a chick feed even if bill contents could not be seen. As adults were not observed making such short visits

without food (pers. obs.), this was considered a valid assumption. Chicks were temporarily removed (“grubbed”) from their burrows at between ten and 22 days of age, within the linear phase of growth (Harris, 1984). Tissue samples to be used for sexing were taken.

Adult puffins were captured using nooses made from 60 lb fishing line, placed at the burrow entrances. To minimize risk of nest desertion, catching took place at least 10 d after the chick had hatched (Rodway *et al.*, 1996). Adults were individually colour banded, and mass and tarsus length were measured. Additionally, culmen length (from cere to bill tip), maximum bill depth, and gape (from rosette to bill tip) were recorded for morphometric sexing.

4.2.2 Lab Methods

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 hours. The contents of the buffers used are detailed in Appendix 1; the protocol was modified in 2001, as a new buffer described in Bello *et al.* (2001) increased the yield of DNA in the final product. This was followed by a standard phenol: chloroform: isoamyl alcohol extraction, and the DNA was 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 TE.

The product was sexed using the 2550F/2718R primer pair, which flanks introns on the CHD-Z and CHD-W genes (Fridolfsson & Ellegren, 1999). The PCR protocol is

detailed in Appendix 2. These homologous genes are located on the W and Z sex chromosomes of all non-ratite birds, and are highly conserved (Griffiths *et al.*, 1996). The intron flanked by the primers differs in length on the two genes, resulting in the amplification of a 600 bp segment on CHD-Z, and a 450 bp segment on CHD-W. Heterogametic (WZ) females were identified by the presence of two bands when the PCR product was run on an agarose gel, whereas homogametic (ZZ) males showed only one band.

4.2.3 Statistical Methods

4.2.3.1 Thick-billed Murres

All statistics were performed using SPSS 11.0 for Windows (SPSS Inc., 2001). A significance level (α) of 0.05 was used in all analyses. For Thick-billed Murres, the relationship between adult age and probability of producing a son was explored. While age of the parents was not known, it has been shown that maternal age in Thick-billed Murres is inversely related to timing of breeding; that is, older birds lay eggs earlier in the season than younger birds (Hipfner *et al.*, 1997). Although there is within-cohort variation in lay date and so the relationship is not perfect ($r = -0.53$ in one year, -0.35 in the next; $p < 0.05$ for both; Hipfner *et al.*, 1997), the question of whether older birds produce more sons can be addressed indirectly by comparing hatch dates of male and female chicks from first-laid eggs. It is expected that males will hatch earlier than females on average; this prediction will be tested using a one-tailed *t*-test.

4.2.3.2 Common Murres

The relationship between maternal and paternal body size and proportion of males produced was explored for pairs that were followed over several years, and whose chicks were sampled in more than one season. Tarsus length, a skeletal feature that remains constant from the time an individual reaches independence (Kitaysky, 1999), was used as an index of body size. A general linear model, with proportion of males as the dependent variable and tarsus length as a covariate, was conducted. Pre-laying body condition, average mass before egg laying divided by tarsus length, was also compared between parents of male and female chicks. A general linear model, with chick sex, year of study, and a sex by year interaction term, was carried out for both maternal and paternal condition.

Hatching dates of males and females from first-laid eggs were compared in the same way as for Thick-billed Murres. To control for interannual variation in lay dates, the mean residuals from the median hatch date for each year were compared for sons and daughters, using a one-tailed *t*-test. Variation in the sex ratio of chicks from first eggs laid before and after the median lay date, and chicks from replacement eggs were compared using a χ^2 test.

Finally, the effect of food availability on sex ratio of chicks at the site was explored by comparing the proportion of males produced in years of high and low food availability, as determined by mean feeding rates to chicks at the site. A low feeding rate was classified as less than four feeds per chick, per day. A χ^2 test was used to examine deviation of sex ratios from equality in each category of year.

4.2.3.3 Atlantic Puffins

Body size (tarsus length) was compared for parents of male and female chicks using a one-tailed *t*-test, as it was predicted that larger parents would be more likely to produce sons. As with the two murre species, timing of breeding was used to estimate relative parental age. Mean residual hatch date of sons and daughters (relative to the annual median) was compared with a one-tailed *t*-test.

4.3 Results

4.3.1 Thick-billed Murres

Of the 59 chick samples obtained from first-egg chicks, 46 were sexed successfully (23 male, 23 female). The remaining samples, which were distributed randomly with respect to hatch date (excluding the replacement chick samples, which were laid later), did not yield DNA; this failure was attributed to problems with storage of the feathers. The ethanol had leached out of the plastic containers in which the feathers had been stored, leaving them desiccated for an unknown length of time between collection in 1997 and their use in the lab in 2001.

Most of the chicks at the site hatched in late July, with a few late chicks hatching in early- to mid-August (Figure 4.1). Three of the four latest-hatched chicks were females, and the four earliest were males, but there was a similar number of sons and daughters produced before and after the median hatch date. There was no difference in the mean date of hatching (\pm SD) of male chicks (July 24 \pm 5.9 d), and of female chicks (July 26 \pm 7.8 d) (one-tailed *t* = 0.896; *p* = 0.188).

4.3.2 Common Murres

Seventy-six chicks captured between 1997 and 2001 were sexed, and 49 of these (21 males, 28 females) were captured within 16 d after hatching. A further five chicks from which feather samples were taken could not be sexed, likely due to degradation of the stored DNA (all failures were from chicks captured in 1997 and 1998). Tarsus measurements were obtained for 20 male breeders and 16 female breeders at the site. The relationship between body size and proportion of sons was not significant for mothers ($F = 0.348$; $p = 0.565$) or for fathers ($F = 0.180$; $p = 0.676$).

The sample size for pre-laying body condition between 1998 and 2001 was 11 for mothers and 17 for fathers. The chick sex by study year interaction term was non-significant and therefore dropped from the final model for both mothers and fathers. Adult body condition did not vary with either chick sex or year of study (Table 4.1).

Data on whether chicks hatched from first-laid or replacement eggs were available from 1999 to 2001. Twenty-two females and ten males hatched from first eggs (Figure 4.2); mean hatch date relative to the median was not earlier for male chicks (one-tailed $t = 0.442$; $p = 0.330$). Twenty-one early-hatched chicks, 11 chicks from first eggs laid after the median hatch date, and 12 chicks from replacement eggs were sampled from 1999-2001. Late-laid first eggs had a significant female bias ($\chi^2 = 4.45$; $p = 0.035$), while early-laid first eggs ($\chi^2 = 1.19$; $p = 0.275$) and replacement eggs ($\chi^2 = 0$; $p = 1.00$) had no sex bias (Figure 4.3).

In the years 1997 to 1999, chicks were fed at a relatively high rate (4.0-5.4

feeds/day). Feeding rate was considered low in 2000 and 2001 (3.2 and 3.5 feeds/day, respectively). The sex ratio in years of poor food availability was significantly female-biased ($\chi^2 = 4.19$; $p = 0.041$), but in good years, there was no sex bias ($\chi^2 = 0.02$; $p = 0.888$) (Figure 4.4).

4.3.3 Atlantic Puffins

Of the 40 marked burrows on the study site, 26 produced chicks in 2001 and 18 in 2002. However, sample size was reduced due to chick mortality (5 in 2001, 2 in 2002) and inability to reach chicks in their burrows (5 in 2001 and 4 in 2002). Obvious inaccuracy of hatch date estimates, i.e., chicks taken from their burrows ten days after the first observed chick feed which were closer in size 20-day-old chicks, further reduced the sample size for hatch date comparison to 6 females, 8 males in 2001, and 0 females, 6 males in 2002.

Adults that produced sons were no larger on average than those that produced daughters (Table 4.2). While three of the four latest-hatching chicks were female, hatch dates of male chicks were not earlier than female chicks on average (one-tailed $t = 0.525$; $p = 0.303$). Mean females hatch date was 1.3 d before the annual median (± 4.9 d), while mean residual hatch date for males was 0.0 ± 7.1 d (Figure 4.5).

4.4 Discussion

Sex ratio was investigated with respect to feeding conditions (as indicated by mean feeding rate at the site), as well as parent age, body condition, and size. Each of these matters will be addressed in turn, followed by a brief discussion on possible

mechanisms of sex ratio manipulations in these species.

The sex ratio of Common Murres appears to be affected by mean provisioning rate at the site. In years where chicks were fed less than four times a day, the sex ratio was significantly female-biased, while in other years, the sex ratio did not deviate from parity. It seems that murres adjust the sex ratio only when the cost of rearing a son rather than a daughter outweighs the cost of sex ratio manipulation. While differential survival rather than differential production of sons and daughters cannot be entirely ruled out, it seems unlikely because egg and chick mortality is low at the site. Further, the reproductive success in years when parents brought less food to the site was not lower than in other years (Table 4.4).

Mean parental age, as inferred from a hatch date, did not differ between male and female chicks in any of the three study species. In Thick-billed Murres, the decrease in hatch date with parental age is evident only between the ages of three to eight years; in older birds, the mean hatch date remains stable (Hipfner *et al.*, 1997). Unfortunately, the number of very late-laying birds sampled was too small in this study to draw any conclusions about the sex ratio produced by inexperienced breeders; further study is warranted.

In Common Murres, for which data on egg and chick mortality at the study site were available, eggs that failed to hatch were usually laid after the median hatch date. Chicks that died before cliff departure, presumably from predation or starvation except for one case where a chick was knocked off the breeding ledge, were always late-hatched.

Because these eggs and chicks could not be sexed, male-biased mortality may be the reason for the observed female skew in very late-hatching chicks. The sex ratio of late-hatched chicks from replacement eggs was not biased, suggesting that parent age and experience, not a seasonal decline in food availability, is the reason for the female bias in surviving chicks hatching from late-laid first eggs.

Older breeders, while more successful on average than their younger counterparts, do vary in quality (Hipfner, 1997). Thus, although early-laying parents are old and experienced, some of those parents might be of poor quality relative to other breeders of the same age, and would do well to produce females. However, if older parents vary in quality, one would expect to find Common Murre pairs consistently producing one sex depending on their quality; this was not the case in this study. More likely, the fitness differences of producing a son or a daughter would be very small to a capable, older breeder, and the cost of adjusting the sex of the offspring produced may outweigh any fitness benefit of sex ratio manipulation.

While facultative sex ratio manipulation does appear to occur in murrelets, it seems that parents exercise this ability only under very poor conditions (e.g., when low food availability or lack of breeding experience make chick rearing a difficult task). Rearing a daughter under poor conditions is less costly than rearing a son under the same conditions, as female chicks require less food (Chapter 3, Tables 3.1 and 3.2). Also, a poor-quality male may have lower reproductive success, and yield fewer grandchildren, than a poor-quality female, possibly through inability to obtain and defend a good breeding site. In

puffins, territory defence is a predominantly male activity (Creelman & Storey, 1991), while in Common Murres, males arrive at the colony earlier and spend more time at the nest site than their mates during the prelay period (Wilhelm & Storey, 2002). When environmental conditions and parental quality are adequate, parents do not appear to manipulate the sex ratio. The difference in fitness returns of rearing an average- to high-quality son or daughter is probably smaller to these parents, and the mechanism of manipulation of the sex ratio may be too costly for parents to execute when conditions are favourable.

Body condition has been shown to affect the sex ratio in many species; parents in poor condition frequently produce more of the smaller, less expensive sex (Trivers & Willard, 1973; Sheldon, 1998; Nager *et al.*, 1999; Kalmbach *et al.*, 2001). However, in Common Murres, neither maternal nor paternal condition differed between birds rearing sons and those rearing daughters. Notably, although food availability (as inferred from feeding rates) varied considerably across years, the annual mean pre-laying body condition did not vary. In deciding whether or not to breed, individuals must weigh the risks associated with current reproduction against threats to their own survival and future reproductive potential. Murres and other seabirds are long-lived, iteroparous organisms, and each reproductive event contributes relatively little to their lifetime reproductive success (Williams, 1966). Thus, it would be wise for breeding pairs to have body conditions well above the minimum that would be required to rear a chick of either sex, thereby improving their chances of surviving to future breeding seasons.

Not surprisingly, adult size did not affect the proportion of sons produced. In alcids, there are no data indicating that reproductive success is correlated with tarsus length. Male Atlantic Puffins nesting in high-quality sites are heavier than those breeding in poorer habitats (Nettleship, 1972), and large size in head and bill characters are thought to confer an advantage in nest site defence in murres (Stewart, 1993), but skeletal body size seems to be irrelevant to breeding success.

The question of how the sex ratio is manipulated by Common Murres cannot be answered here. However, a trial and error process involving dump laying or selective resorption of eggs of the undesired sex, as suggested by Emlen (1997), is not likely. Murres and puffins, with their single-egg clutches, would seem to be an ideal candidate for such post-ovulatory sex ratio adjusting. Indeed, the observation that young breeders lay later on average and may have a tendency to lay the “right” sex could lead one to speculate that the reason that young birds lay late is because they have had to eliminate one or more embryos of the “wrong” sex. However, it has been suggested that young birds are less likely to relay because of physiological constraints; when young Thick-billed Murres do manage to relay, it takes them 3-4 days longer than it does older individuals (DeForest & Gaston 1996).

Even if young birds were fully capable of selectively eliminating embryos, it would follow that in years of low provisioning rates (when many of the birds at the site are apparently adjusting the sex of their offspring) the median hatch date at the site would be later and egg laying would be spread out over a long period. This would be the case

when pairs try without success once or twice or more before producing the desired female egg, but in fact the opposite is seen in Common Murres. The median hatch dates in 2000 and 2001 were the earliest seen in the five years of the study, and breeding at the site in 2000 was more synchronous than any other year; this implies that females are determining the sex of embryos at conception. Evidence for pre-ovulatory sex determination has recently been found for at least one avian species, the Seychelles Warbler (Komdeur *et al.*, 2002). Although one cannot explain how alcids are able to adjust the primary sex ratio, time-consuming post-ovulatory mechanisms can, for all intents and purposes, be ruled out.

4.5 References

- Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*, No. 666. (A. Poole and F.Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.
- Barrett, R.T. and Rikardsen, F. 1992. Chick growth, fledging periods and adult mass loss of Atlantic Puffins *Fratercula arctica* during years of prolonged food stress. *Colonial Waterbirds*, **15**: 24-32.
- Bello, N., Francino, O. and Sánchez, A. 2001. Isolation of genomic DNA from feathers. *Journal of Veterinary Diagnostic Investigations*, **13**: 162-164.
- Blank, J.L. and Nolan Jr., V. 1983. Offspring sex ratio in Red-winged Blackbirds is dependent on maternal age. *Proceedings of the National Academy of Science, U.S.A.*, **80**: 6141-6145.
- Carscadden, J.E. 1984. Capelin in the northwest Atlantic. Pp. 170-183 in D.N. Nettleship, G.A. Sanger and P.F. Springer (eds.), *Marine birds: their feeding ecology and commercial fisheries relationships*. Canadian Wildlife Services Special Publication, Ottawa.
- Charnov, E.L. 1982. *The Theory of Sex Allocation*. Princeton University Press: Princeton.

- Clutton-Brock, T.H., Albon, S.D. and F.F. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**: 131-133.
- Cooch, E.G., Lank, D.B. and Cooke, F. 1996. Intraseasonal variation in the development of sexual size dimorphism in a precocial bird: evidence from the Lesser Snow Goose. *Journal of Animal Ecology*, **65**: 439-450.
- Creelman, E. and Storey, A.E. 1991. Sex differences in reproductive behavior of Atlantic Puffins. *Condor*, **93**: 390-398.
- Curio, E. 1983. Why do young birds reproduce less well? *Ibis*, **125**: 400-404.
- Daunt, F., Monaghan, P., Wanless, S., Harris, M.P. and Griffiths, R. 2001. Sons and daughters: age-specific differences in parental rearing capacities. *Functional Ecology*, **15**: 211-216.
- DeForest, L. N. and Gaston, A.J. 1996. The effect of age on timing of breeding and reproductive success in the Thick-billed Murre. *Ecology*, **77**: 1501-1511.
- Ellegren, H. and Sheldon, B.C. 1997. New tools for sex identification and the study of sex allocation in birds. *Trends in Ecology and Evolution*, **12**: 255-259.
- Emlen, S.T. 1997. When mothers prefer daughters over sons. *Trends in Ecology and Evolution*, **12**: 291-292.
- Erikstad, K.E., Ashiem, M., Fauchald, P., Dahlhaug, L. and Tveraa, T. 1997. Adjustment of parental effort in the Puffin; the roles of adult body condition and chick size. *Behavioural Ecology and Sociobiology*, **40**: 95-100.
- Forslund, P. and Pärt, T. 1995. Age and reproduction in birds - hypotheses and tests. *Trends in Ecology and Evolution*, **19**: 374-378.
- Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**: 116-121.
- Gaston, A.J. 1985. Energy investment in reproduction by Thick-billed Murres (*Uria lomvia*). *Auk*, **102**: 447-458.
- Gaston, A.J., Chapdelaine, G. and Noble, D.G. 1983. The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. *Canadian Journal of Zoology*, **61**: 2465-2475.

- Gaston, A.J. and Nettleship, D.N. 1981. *The Thick-billed Murres of Prince Leopold Island: A study of the breeding ecology of a colonial high arctic seabird*. Canadian Wildlife Service Monograph Series No. 6.
- Gowaty, P.A. 1990. Facultative manipulation of sex ratios in birds: rare or rarely observed? *Current Ornithology*, **8**: 141-171.
- Green, D.J. 2002. Pair bond duration influences paternal provisioning and the primary sex ratio of Brown Thornbill broods. *Animal Behaviour*, **64**: 791-800.
- Griffiths, R., Daan, S. and Dijkstra, C. 1996. Sex identification in birds using two CHD genes. *Proceedings of the Royal Society of London B*, **263**: 1251-1256.
- Harris, M.P. 1984. *The Puffin*. Poyser, Calton, U.K.
- Heg, D., Dingemanse, N.J., Lessells, C.M. and Mateman, A.C. 2000. Parental correlates of offspring sex ratio in Eurasian Oystercatchers. *Auk*, **117**: 980-986.
- Heinsohn, R., Legge, S. and Barry, S. 1997. Extreme bias in sex allocation in *Eclectus* parrots. *Proceedings of the Royal Society of London B*, **264**: 1325-1329.
- Hipfner, J.M. 2001. Fitness-related consequences of relaying in an Arctic seabird: survival of offspring to recruitment age. *Auk*, **118**: 1076-1080.
- Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. *Condor*, **99**: 353-360.
- Hipfner, J.M. and Gaston, A.J. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology*, **80**: 587-596.
- Hipfner, J.M., Gaston, A.J. and DeForest, L.N. 1997. The role of female age in determining egg size and laying date of Thick-billed Murres. *Journal of Avian Biology*, **29**: 271-278.
- Hipfner, J.M., Gaston, A.J., Martin, D.L. and Jones, I.L. 1999. Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *Journal of Animal Ecology*, **68**: 988-998.
- Kalmbach, E., Nager, R.G., Griffiths, R. and Furness, R.W. 2001. Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. *Proceedings of the Royal Society of*

London B, **268**: 2175-2179.

- Kitaysky, A.S. 1999. Metabolic and developmental responses of alcid chicks to experimental variation in food intake. *Physiological and Biochemical Zoology*, **72**: 462-473.
- Komdeur, J. 1998. Long-term fitness benefits of egg sex modification by the Seychelles Warbler. *Ecology Letters*, **1**: 56-62.
- Komdeur, J., Daan, S., Tinbergen, J. and Mateman, C. 1997. Extreme adaptive modification in sex ratio of the Seychelles Warbler's eggs. *Nature*, **385**: 523-525.
- Komdeur, J., Magrath, M.J.L. and Krackow, S. 2002. Pre-ovulation control of hatchling sex ratio in the Seychelles Warbler. *Proceedings of the Royal Society of London B*, **369**: 1067-1072.
- Komdeur, J. and Pen, I. 2002. Adaptive sex allocation in birds: the complexities of linking theory and practice. *Philosophical Transactions of the Royal Society of London B*, **357**: 373-380.
- Korpimäki, E. May, C.A., Parkin, D.T., Wetton, J.H. and Weihl, J. 2000. Environmental- and parental condition-related variation in sex ratio of kestrel broods. *Journal of Avian Biology*, **31**: 128-134.
- Nager, R.G. Monaghan, P., Griffiths, R., Houston, D.C. and Dawson, R. 1999. Experimental determination that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Science, USA*, **96**: 570-573.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**: 239-268.
- Oddie, K.R. 1998. Sex discrimination before birth. *Trends in Ecology and Evolution*, **13**: 130-131.
- Pierotti, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. *Biological Conservation*, **26**: 1-14.
- Rice, J. 1985. Interactions of variation in food supply and kleptoparasitism levels on the reproductive success of Common Puffins (*Fratercula arctica*). *Canadian Journal of Zoology*, **63**: 2743-2747.

- Rodway, M.S. and Montevecchi, W.A. 1996. Sampling methods for assessing the diets of Atlantic Puffin chicks. *Marine Ecology Progress Series*, **144**: 41-55.
- Rodway, M.S., Montevecchi, W.A. and Chardine, J.W. 1996. Effects of investigator disturbance on breeding success of Atlantic Puffins *Fratercula arctica*. *Biological Conservation*, **76**: 311-319.
- Sheldon, B.C. 1998. Recent studies of avian sex ratios. *Heredity*, **80**: 397-402.
- Sheldon, B.C. 1999. Sex allocation: at the females' whim. *Current Biology*, **9**: R487-R489.
- Sheldon, B.C., Andersson, S., Griffith, S.C., Ornborg, J. and Sendecka, J. 1999. Ultraviolet colour variation influences Blue Tit sex ratios. *Nature*, **402**: 874-877.
- Sheldon, B.C., Merilä, J., Lindgren, G. and Ellegren, H. 1998. Gender and environmental sensitivity in nestling Collared Flycatchers. *Ecology*, **79**: 1939-1948.
- SPSS Inc. 2001. SPSS for Windows version 11.0. SPSS Inc., Chicago.
- Stewart, D.T. 1993. Sexual dimorphism in Thick-billed Murres, *Uria lomvia*. *Canadian Journal of Zoology*, **71**: 346-351.
- Trivers, R.L. and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**: 90-92.
- Velando, A., Graves, J. and Ortega-Ruano, J.E. 2002. Sex ratio in relation to timing of breeding, and laying sequence in a dimorphic bird. *Ibis*, **144**: 9-16.
- Verboven, N., Kakela, M. and Orell, M. 2002. Absence of seasonal variation in Great Tit sex ratios. *Journal of Avian Biology*, **33**: 138-142.
- Webb, J.N., Székely, T., Houston, A.I. and McNamara, J.M. 2002. A theoretical analysis of the energetic costs and consequences of parental care decisions. *Proceedings of the Royal Society of London B*, **269**: 331-340.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos*, **64**: 464-473.
- Wendeln, H. 1997. Body mass of female Common Terns *Sterna hirundo* during

courtship: relationships to male quality, egg mass, diet, laying date and age. *Colonial Waterbirds*, **20**: 235-243.

Wendeln, H. and Becker, P.H. 1999. Effects of parental quality and effort on the reproduction of Common Terns. *Journal of Animal Ecology*, **68**: 205-214.

West, S.A., Herre, E.A. and Sheldon, B.C. 2000. The benefits of allocating sex. *Science*, **290**: 288-290.

West, S.A., Reece, S.E. and Sheldon, B.C. 2002. Sex ratios. *Heredity*, **88**: 117-124.

Whittingham, L.A. and Dunn, P.O. 2000. Offspring sex ratios in Tree Swallows: females in better condition produce more sons. *Molecular Ecology*, **9**: 1123-1129.

Whittingham, L.A., Valkenaar, S.M., Poirier, N.E. and Dunn, P.O. 2002. Maternal condition and nestling sex ratio in House Wrens. *Auk*, **119**: 125-131.

Wilhelm, S.I. and Storey, A.E. 2002. Influence of cyclic pre-lay attendance on synchronous breeding in Common Murres. *Waterbirds*, **25**: 156-163.

Williams, G.C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *American Naturalist*, **100**: 687-690.

Table 4.1. Pre-laying body condition of adult Common Murres producing male and female chicks on Great Island, NL from 1998 to 2001.

	Body Condition (g/mm) Mean \pm SD (n)		Between-sex Comparisons <i>F</i> (<i>p</i>)	Year Effect <i>F</i> (<i>p</i>)
	Males	Females		
Mothers	21.7 \pm 1.0 (5)	21.2 \pm 1.4 (6)	0.679 (0.441)	0.815 (0.531)
Fathers	20.9 \pm 0.6 (9)	20.7 \pm 0.7 (8)	0.359 (0.560)	0.225 (0.877)

Table 4.2. Body size of adult Atlantic Puffins producing male and female chicks at Great Island, NL. One-tailed *p* values are reported.

	Tarsus Length (mm)		<i>t</i> (<i>p</i>)
	Mean ± SD (n)		
	Males	Females	
Mothers	34.8 ± 0.9 (5)	34.2 ± 1.0 (6)	1.098 (0.150)
Fathers	35.5 ± 1.1 (11)	36.1 ± 0.8 (7)	-1.167 (0.130)

Table 4.3. Reproductive success of Common Murres at the study site at Great Island, NL. Success is the percentage of chicks fledged from eggs laid at the site.

Year	Eggs	Chicks	Fledglings	Success (%)
1998	27	24	22	81.5
1999	28	21	21	75.0
2000	29	27	24	82.8
2001	28	22	20	71.4

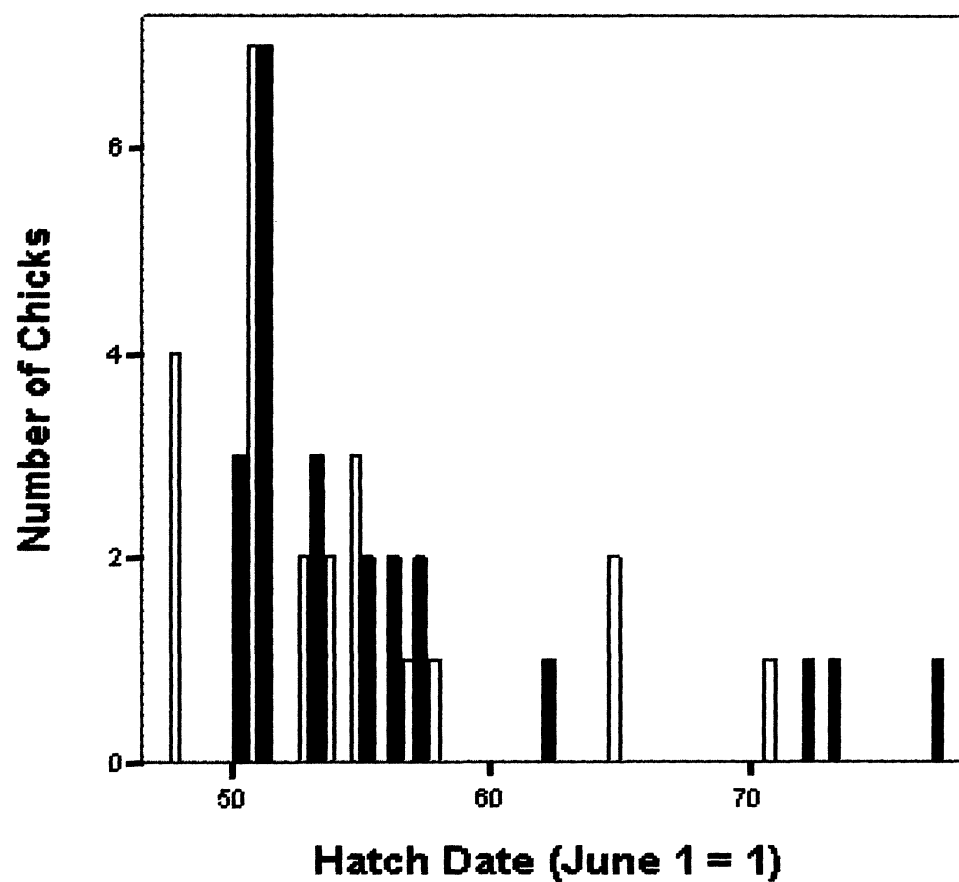


Figure 4.1. Relative frequency of hatch dates of male (open bars) and female (solid bars) Thick-billed Murre chicks on Coats Island, Nunavut.

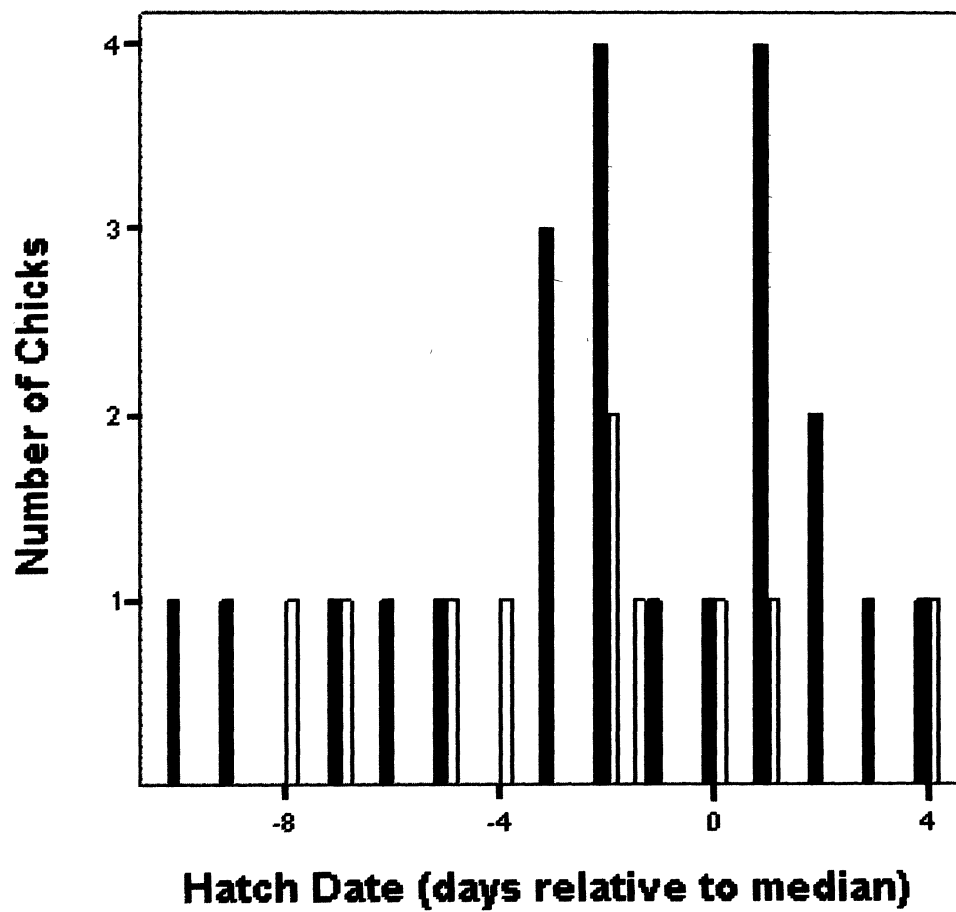


Figure 4.2. Relative frequency of hatch dates of male (open bars) and female (solid bars) Common Murre chicks on Great Island, NL. Only chicks hatching from first eggs are included in the figure.

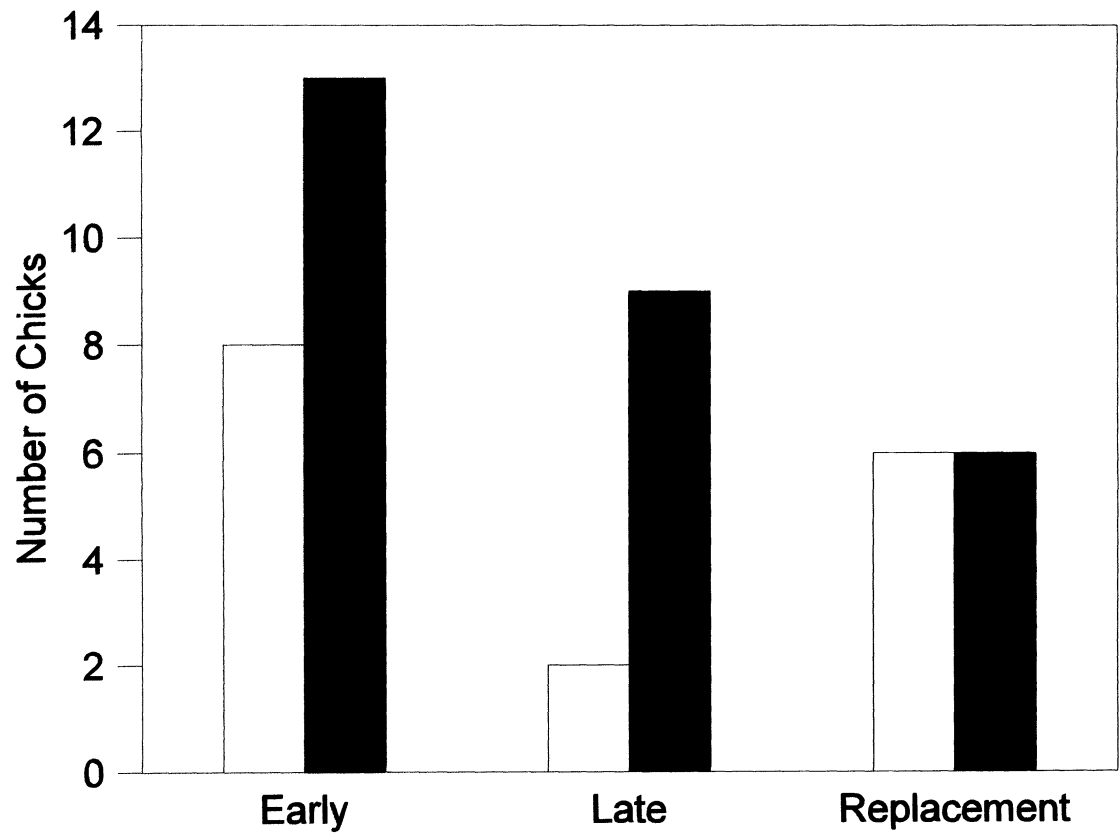


Figure 4.3. Number of males (open bars) and females (solid bars) hatching from early- and late-laid first eggs and replacement eggs by Common Murres on Great Island, NL.

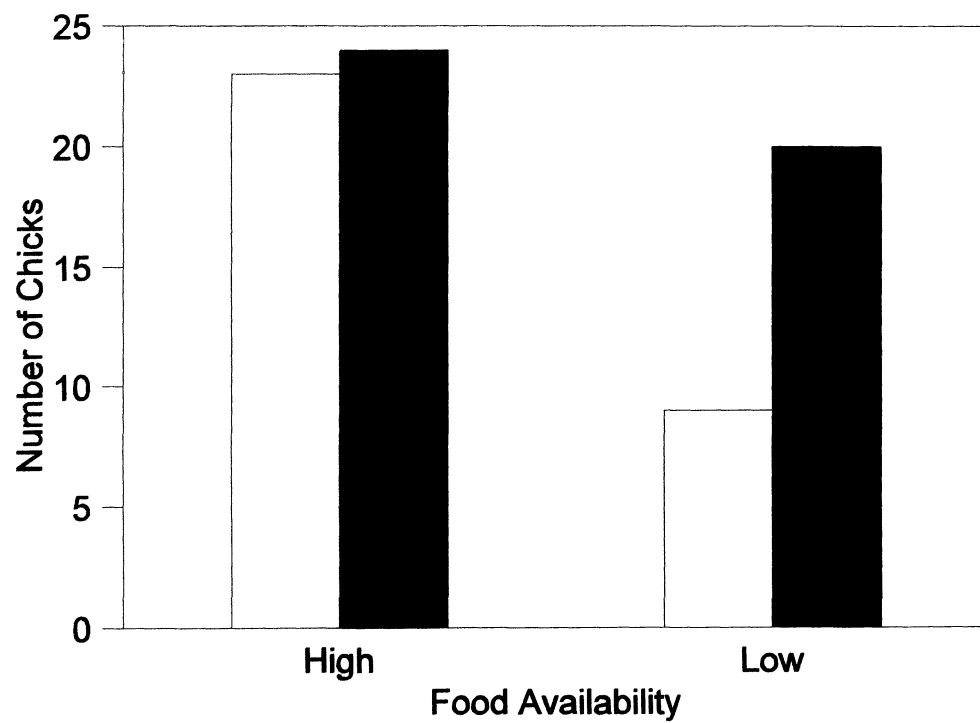


Figure 4.4. Common Murre chick sex ratios in years of high and low food availability at Great Island, NL.

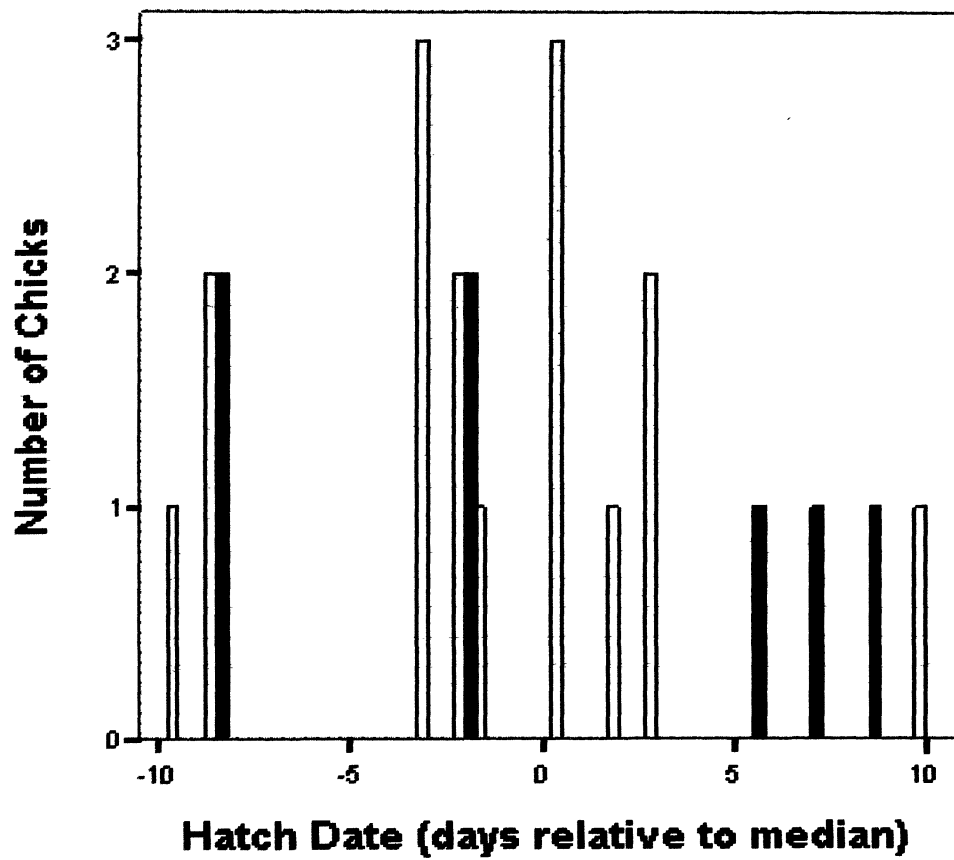


Figure 4.5. Relative frequency of hatch dates of male (open bars) and female (solid bars) Atlantic Puffin chicks on Great Island, NL.

Chapter 5 A review of results and concluding remarks on alcid sex allocation

5.1 Mechanisms of sex allocation biases

Parents may manipulate sex allocation by adjusting the primary sex ratio, or by selectively directing the amount of care given to sons and daughters after conception. Common Murre parents appear to bias sex allocation primarily through differential feeding effort. This was most evident in the later stages of chick-rearing considered in the study, from 12 days after hatching until cliff departure. However, there was also evidence suggesting that Common Murres were able to manipulate the sex of offspring that they produce in response to environmental conditions (food availability) as inferred by provisioning rate at the study site.

Male and female murre and puffin chicks were found to gain mass at a similar rate. There was no detectable difference in wing and skeletal growth rate, though data on puffin chick tarsus lengths were scant (Chapter 2). Based on these results alone, one would conclude that male and female chicks are equally costly to produce. However, observations of Common Murre feeding rates to sons and daughters showed that parents worked harder to raise male offspring (Chapter 3). This difference was not seen in young chicks, but became apparent as they grew larger and their energy demands increased (Table 3.2).

Parents may invest more in sons because sons benefit more from greater parental care. Evidence from the Thick-billed Murre showed that males appeared to be more affected by parental age than females (Figure 2.1a), and older parents do tend to be more

successful in rearing offspring (Curio, 1983; Forslund & Pärt, 1995). Parental age and quality is correlated positively with egg volume in the Thick-billed Murre, and negatively with hatch date (Hipfner *et al.*, 1997). Using egg volume as an indicator, wing length of male Thick-billed Murre chicks at 14 days was positively correlated with parent age/quality, while female wing length showed no such relationship. Because murre chicks do not fledge until a certain threshold wing length has been reached (Hipfner & Gaston, 1999), this may be an adaptation to keep sons of poor quality parents from fledging before they have had enough time to attain a great enough mass to ensure survival after cliff departure. In Atlantic Puffins, male wing growth rate was highly variable, while for females it was quite constant. The variation seen in males could not be attributed to hatch date, but the sample size was too small to rule out parental quality effects conclusively.

The duration of parental care in birds often varies between male and female offspring, with the smaller sex fledging earlier on average than the larger sex (Richner, 1991). The amount of time spent at the nest site by male and female chicks did not differ for Common Murre chicks. However, because murre chicks spend several weeks with their fathers at sea after leaving the nest site, the actual length of the period of parental care could not be determined for the chicks in this study. Puffin chick fledging dates were not obtained, because chicks leave the burrows at night, and parents continue to visit for days after the chick fledges. Thus, sex differences in the duration of parental care could not be detected for either murres or puffins.

One interesting aspect of parental care that emerged in this study was that the feeding rate by Common Murre fathers was lower when the mother laid her first egg late in the season than if she laid earlier, while maternal feeding rate was unaffected by lay date. Late-laying females are typically younger and less experienced than those that lay early in the breeding season (Hipfner *et al.*, 1997). This may be a decision on the part of males to invest more in offspring when the mother is an experienced, high-quality breeder. Conversely, females of good quality may have the privilege to choose to breed with males that are good providers. A third possibility, which is attractive considering that murrelets tend to have long-term pair bonds, is that male feeding rate increases with age, and the correlation between feeding rate and maternal quality is simply a product of within-pair age similarity.

Another manner in which Common Murres were found to selectively allocate resources to the production of a particular sex was by determining the sex of offspring reared. When parents were unable to provide enough resources to produce a viable son due to food shortage, they tended to produce a daughter instead (Figure 4.4). There was no evidence of a bias toward producing males when food availability was adequate, suggesting that the mechanism of sex determination may be too costly for parents to use, unless the costs of producing a chick of the “wrong” sex were even greater (Chapter 4). In socially monogamous species such as alcids, male reproductive success is only slightly more variable than that of females. Although extra-pair fertilizations do occur, at least in Common Murres (Walsh, 2001), they are rare and so very few males sire more than one

chick in a breeding season. Thus, a high-quality male may be no more beneficial to produce than a high-quality female. However, male puffins in poor condition are unlikely to obtain choice breeding sites and therefore suffer higher breeding failure, while female condition does not differ in good and bad nesting habitats (Nettleship, 1972). A poor quality daughter, therefore, should have greater reproductive success than a poor quality son. Further, if conditions are poor in a given season, parents simply may be unable to successfully raise a male, because males require more feeds (Chapter 3) and their growth is more dependent on adult quality (Chapter 2).

There has been much speculation on the mechanisms by which birds adjust the sex ratio of their offspring (Emlen, 1997; Oddie, 1998; Komdeur *et al.*, 2002). A recent study has shown that sex determination in birds can occur before ovulation, through biased release of gametes after meiosis (Komdeur *et al.*, 2002). This is thought to be a far more efficient process than post-ovulation sex ratio adjustment. Dump-laying or resorption of eggs of the undesired sex, as suggested by Emlen (1997), is costly in terms of both time and parental effort. Evidence from the Common Murre supports the hypothesis that avian sex ratio determination occurs at a very early stage, likely before ovulation. In years of low food availability (2000 and 2001), pairs at the study site produced significantly more females than males. If birds used time-consuming mechanisms like those suggested by Emlen (1997), one would predict that the median hatch date would be later than average and hatching dates at the site would be highly asynchronous, because many pairs would delay laying due to one or more failures to produce the “right” sex. Neither of these were

true of the murre study plot in 2000 and 2001.

5.2 Reasons for sex allocation biases

As described in the first chapter, there are two broad categories of adaptive explanations for facultative adjustment of sex allocation (Hardy, 1997). The first category, biased sex allocation due to different dispersal rates of the sexes, could not be addressed here. Although alcids are highly philopatric, there is no information on sex differences in dispersal rates. The second group of reasons for adaptive sex allocation involve factors in the chick-rearing environment, including qualities of the breeding territory, the parents, and the local food supply. This study focussed on the latter two environmental factors. Interannual variation in food supply was found to have an effect on sex allocation in its most fundamental expression, the sex ratio, as described above. Parental body condition, a measure of mass relative to body size, surprisingly did not affect the sex ratio. Many studies have found that mothers in poor condition tend to produce offspring of the smaller sex (Trivers & Willard, 1973; Nager *et al.*, 1999; Korpimäki *et al.*, 2000; Kalmbach *et al.*, 2001). However, long-lived seabirds such as alcids, that can expect to produce a great number of offspring throughout their lifetime, are expected to invest cautiously in any single breeding attempt (Erikstad *et al.*, 1998). Even a small risk to adult survival and future reproduction should be avoided, and so adults should breed only if they are in good condition, not just “adequate” condition to raise a chick. Therefore, threshold breeding condition should exceed the minimum required to rear an offspring of either sex.

Knowledge of the life histories of the study species is invaluable to the study of sex allocation. It is difficult to make and test hypotheses about the existence and direction of sex allocation bias without knowledge of the factors that are important to reproductive success (Sheldon *et al.*, 1998). For example, reproductive success or quality may be a function of size in some species. Larger individuals may have an advantage over smaller ones, such as in competition over breeding territories. In alcids, body size has not been shown to affect reproductive success, and correspondingly, the chances of producing a son or a daughter do not vary with the size of the parents. Alcid parent quality does increase with age; young and inexperienced breeders tend to produce smaller offspring in poorer condition (Hipfner & Gaston, 2002). In this study, very late-laying birds (which are assumed to be new breeders) tended to produce offspring of the smaller, less costly sex, although given the small sample sizes, conclusions could not be drawn. Without knowledge of life history details such as why breeders ought to have a high threshold breeding condition, or exactly what constitutes a “good quality” breeder, one risks overlooking biases in sex allocation because of incomplete information.

5.3 Future Directions

While this work has answered many questions about sex allocation in puffins and murres, further questions have been raised, inviting still more exploration into the parental behaviour of these species. For example, knowledge of the duration of parental care toward male and female chicks is required for a better understanding of the costs of rearing male and female chicks. Murre chicks spend their final weeks of parental

dependence at sea with their fathers, making direct observation impossible. However, father-chick pairs may be captured and fitted with tracking devices, at the same time obtaining feather samples from chicks for sexing. Duration of parental care in puffins might best be studied using cameras placed in burrows, to record the presence of the chick without disturbance. While these studies would be costly, particularly considering the sample sizes that would be necessary to detect any sex differences, the results would be valuable to the study of alcid sex allocation.

Differences in the behaviour of male and female chicks, for example in the intensity and frequency of begging calls, may contribute to parental feeding rate differences observed in Common Murres. Careful observations of chicks-parent interactions would allow us to determine who controls the feeding rate of the chick. For puffins, such observations would again necessitate the use of recording equipment, such as a video camera or tape recorder placed in the burrow. Murre observations could be made directly at the site, but may be easier if recorded on video and studied in detail later.

Larger-scale studies of alcid sex ratio could be used to address some interesting questions. For example, spatial variation in sex ratios could be explored, either on a small scale (e.g., between good and poor habitats), or on a much larger scale (such as comparing colonies that have high and low productivity). The temporal variation in sex ratio seen here in the Common Murre may have interesting implications in population monitoring; researchers may be able to indirectly assess the state of a colony by sexing a sample of the chicks produced. A large female bias may indicate poor chick-rearing conditions at the

colony. In conjunction with any of these studies, sex differences in philopatry could also be explored, to evaluate whether local resource competition between parents and offspring of one sex may be driving biases in sex allocation greater than would be predicted on the basis of sexual size dimorphism alone (Chapter 3). Collecting resightings of birds that were banded and sexed as chicks at the natal colony would take years, as murres and puffins do not breed until at least their third year (Harris, 1984; Gaston *et al.*, 1994; Ainley *et al.*, 2002), but would not be difficult.

More work focussing on new breeders could prove interesting. The number of young breeders in this study, as indicated by lay date, was very low, and so the effect of adult age on sex ratio could not be addressed thoroughly. Because young breeders are frequently unsuccessful in rearing their young (Curio, 1983; Forslund & Pärt, 1995; Hipfner, 1997), determining the sex of chicks that do not survive or eggs that fail to hatch would be very important. For this reason, Thick-billed Murres would be an ideal study species, as collecting dead eggs and chicks could be done without severe colony disturbance.

These are just a few aspects of alcid sex allocation that merit further study. Sex allocation is a broad and fascinating area of parental behaviour, and too few studies have been conducted on long-lived, socially monogamous species. Murres and puffins, being colonial and easily observable species, have both proven to be excellent species for research. Therefore, it is hoped that this is just the beginning of our exploration of sex allocation in the Alcidae.

5.4 References

- Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*, No. 666 (A. Poole and F. Gill, eds.) The Birds of North America Inc., Philadelphia, PA.
- Curio, E. 1983. Why do young birds reproduce less well? *Ibis*, **125**: 400-404.
- Emlen, S.T. 1997. When mothers prefer daughters over sons. *Trends in Ecology and Evolution*, **12**: 291-292.
- Erikstad, K.E., Fauchald, P., Tveraa, T. and Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, **79**: 1781-1788.
- Forslund, P. and Pärt, T. 1995. Age and reproduction in birds - hypotheses and tests. *Trends in Ecology and Evolution*, **19**: 374-378.
- Gaston, A.J., DeForest, L.N., Donaldson, G. and Noble, D.G. 1994. Population parameters of Thick-billed Murres at Coats Island, Northwest Territories, Canada. *Condor*, **96**: 935-948.
- Gaston, A.J. and Hipfner, J.M. 2000. Thick-billed Murre (*Uria lomvia*). In *The Birds of North America*, No.497 (A. Poole and F. Gill, eds.) The Birds of North America Inc., Philadelphia, PA.
- Hardy, I.C.W. 1997. Possible factors influencing vertebrate sex ratios: an introductory overview. *Applied Animal Behaviour Science*, **51**: 217-241.
- Harris, M.P. 1984. The Puffin. Poyser, Calton, U.K.
- Hipfner, J.M. 1997. The effects of parental quality and timing of breeding on the growth of nestling Thick-billed Murres. *Condor*, **99**: 353-360.
- Hipfner, J.M. and Gaston, A.J. 2002. Growth of nestling Thick-billed Murres (*Uria lomvia*) in relation to parental experience and hatching date. *Auk*, **119**: 827-832.
- Hipfner, J.M. and Gaston, A.J. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology*, **80**: 587-596.
- Hipfner, J.M., Gaston, A.J. and DeForest, L.N. 1997. The role of female age in

- determining egg size and laying date of Thick-billed Murres. *Journal of Avian Biology*, **29**: 271-278.
- Kalmbach, E., Nager, R.G., Griffiths, R. and Furness, R.W. 2001. Increased reproductive effort results in male-biased offspring sex ratio: an experimental study in a species with reversed sexual size dimorphism. *Proceedings of the Royal Society of London B*, **268**: 2175-2179.
- Komdeur, J., Magrath, M.J.L. and Krackow, S. 2002. Pre-ovulation control of hatchling sex ratio in the Seychelles Warbler. *Proceedings of the Royal Society of London B*, **369**: 1067-1072.
- Korpiimäki, E. May, C.A., Parkin, D.T., Wetton, J.H. and Weih, J. 2000. Environmental- and parental condition-related variation in sex ratio of kestrel broods. *Journal of Avian Biology*, **31**: 128-134.
- Nager, R.G. Monaghan, P., Griffiths, R., Houston, D.C. and Dawson, R. 1999. Experimental determination that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Science, USA*, **96**: 570-573.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**: 239-268.
- Oddie, K.R. 1998. Sex discrimination before birth. *Trends in Ecology and Evolution*, **13**: 130-131.
- Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: does sex-specific growth contribute to balanced sex ratios? *Functional Ecology*, **5**: 19-28.
- Sheldon, B.C., Merilä, J., Lindgren, G. and Ellegren, H. 1998. Gender and environmental sensitivity in nestling Collared Flycatchers. *Ecology*, **79**: 1939-1948.
- Trivers, R.L. and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**: 90-92.
- Walsh, C.J. 2001. Copulation behaviour, parentage analysis and genetic relatedness in Common Murres (*Uria aalge*). Ph.D. dissertation, Memorial University of Newfoundland, St. John's.

Appendix 1 DNA extraction from alcid chick feathers

Original protocol (pre-2001):

1. Place finely chopped feather tip in 750 μ L extraction buffer (20 mL EDTA [0.5 M], 30mL dH₂O, 0.25g laurylsacrosine). Add 50 μ L pronase E (20 mg/mL) and incubate at 37°C for 24-48 hours.
2. Add 600 μ L phenol (pH 8.0), invert tubes, centrifuge for 10 minutes at high speed.
3. Place aqueous phase in fresh tube, add 600 μ L phenol: chloroform: isoamyl alcohol (25: 24: 1), invert tubes and centrifuge for 10 minutes at high speed.
4. Place aqueous phase in fresh tube, add 600 μ L chloroform: isoamyl alcohol (24: 1), invert tubes and centrifuge for 10 minutes at high speed.
5. Place aqueous phase in fresh tube, add 1200 μ L ethanol (95%). Invert tubes and place in -20°C freezer overnight.
6. Centrifuge at high speed for 20 minutes and pour off ethanol.
7. Add 200 μ L ethanol (70%). Invert tubes and centrifuge for 10 minutes at high speed. Pour off ethanol and leave tubes open to dry overnight.
8. Add 25-100 μ L TE (depending on size of pellet), leave tubes at room temperature for a couple of days, then store in refrigerator.

Modified protocol (recommended):

1. Place finely chopped feather tip in 500 μ L extraction buffer (2.5 mL Tris-HCl pH 8 [1 M], 2 mL EDTA [0.5 M], 10 mL SDS [10%], 35.5 mL dH₂O). Add 3.5 μ L proteinase K (25 mg/mL) and incubate at 37°C for 24-48 hours.

Steps 2-4 as above.

5. Place aqueous phase in fresh tube, add 1200 μ L ethanol (95%) and 50 μ L NaCl (2 M). Invert tubes and place in -20°C freezer overnight.

Steps 6-8 as above.

Appendix 2 PCR-based chick sexing using the CHD gene

For a 25 μ L reaction volume, combine the following in a 0.5 mL Eppendorf tube:

- 17.3 μ L ddH₂O
- 2.5 μ L buffer with MgCl₂ (supplied with Boehringer *Taq*, Roche Pharmaceuticals)
- 2 μ L dNTP (10 mM/ μ L)
- 1 μ L each primer (2550F and 2718R)
- 0.2 μ L *Taq* polymerase
- 1 μ L sample DNA

Cover with mineral oil, about 2 drops. Apply the following temperature cycle:

95°C for 3 minutes of initial denaturation, followed by 40 cycles of:

- 95°C for 1 minute
- 45°C for 45 seconds
- ramp +10°C in 45 seconds
- 55°C for 30 seconds
- ramp +17°C in 45 seconds
- 72°C for 3 minutes

72°C for 10 minutes of final primer extension. Hold at 5°C; place samples in refrigerator until ready to use. Run samples on a 3% agarose gel and visualise under UV light.

