BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF BREEDING COMMON MURRES (URIA AALGE): EXPLORING INTER-ANNUAL VARIABILITY WITHIN INDIVIDUALS

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BEHAVIOURAL AND PHYSIOLOGICAL RESPONSES OF BREEDING COMMON MURRES (*URIA AALGE*): EXPLORING INTER-ANNUAL VARIABILITY WITHIN INDIVIDUALS

by

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This thesis was written in memory of
Chick 11

ABSTRACT

Most avian studies investigating variation in parental behaviour have focused on differences between species, populations, or the sexes. Despite the importance of understanding variation at multiple levels, few have investigated parental care at the individual level. The same pairs of individually marked Common Murres (*Uria aalge*) breeding on Great Island, Witless Bay, showed variable behavioural and physiological responses across three consecutive breeding seasons (1998-2000). Despite high foraging effort, chick-feeding rates were low in the early chick rearing period of 2000. Low chick feeding rates in 2000 were related to the late arrival of inshore spawning capelin (*Mallotus villosus*). In contrast, high chick feeding rates in 1999 may have resulted from chicks hatching later and well after capelin had arrived in the vicinity of the breeding colonies. Hatching was delayed in 1999 because more chicks hatched from re-laid eggs. Female pre-lay attendance in that year was low, which resulted in less synchronous breeding and higher predation during early incubation. Frequency of feeding rates was positively correlated with chick body mass but no relationship was found with wing length. However, chicks had longer wings in 2000 compared to 1998 and 1999. Chick diet did not differ between these two years, with chicks being fed primarily capelin supplemented with sand lance (*Ammodytes* spp.).

Collectively, females showed higher foraging effort and exhibited overall more direct parental care. At the pair level, however, both sexes tended to engage equally in behaviours related to chick rearing. It is possible that role partitioning between the sexes, in which one sex does most of the brooding while the other does most of the provisioning, may not be an adaptive strategy for Common Murres due to the high energetic costs associated with flying.

Overall, males and females showed similar physiological responses to breeding. Both sexes had comparable haematocrit and corticosterone levels during chick rearing. In all years, body condition of males and females increased during incubation, dropped immediately after chick hatching and continued to decrease during chick rearing. Females maintained lowered body condition after their chick had departed the colony. Body condition of murres does not appear to decrease during chick rearing solely in response to reproductive stress. Rather, mass loss may reduce energetic costs associated with flying. In 2000, murres had lower body condition during the first week of chick rearing and showed elevated corticosterone levels compared to 1998 and 1999. These results suggest that murres were stressed during early chick rearing in 2000, supporting the view that breeding conditions were less favourable in that year.

Because the same breeding pairs were monitored across years, the observed inter-annual differences were likely due to varying environmental conditions rather than individual variation. These results are consistent with other studies suggesting that seabirds relying on capelin in the Northwest Atlantic are experiencing highly variable breeding conditions as a result of delayed spawning and changes in the distribution of capelin. Including long-term behavioural and physiological information of marked individuals provides additional insight on the health of a population and may help further assess the quality of the breeding environment.

ACKNOWLEDGEMENTS

I am very grateful to my supervisor, Dr. Anne Storey, for introducing me to seabird research. Anne has been an inspiring advisor. Her dedicated support in all forms has been constant throughout the years. I also sincerely thank my co-supervisor, Dr. Donald McKay, for his patience and expertise. Don's first task was to teach me how to pipette. Needless to say, he has taught me everything I know related to working in an endocrinology lab. Special thanks to my committee members, Anne, Don, and Dr. Ian Jones, for always providing thoughtful comments and sharing their time and knowledge. I am also grateful to Dr. Carolyn Walsh, who initiated this project with Anne in the mid-1990s. Carolyn did much of the ground (and back) breaking work involved in the set-up of this multi-year project. Sharing an office with Carolyn is no less than stimulating and she has shown me the true meaning of multi-tasking. Many thoughts and ideas presented throughout this thesis have resulted from thinking aloud in her presence.

Data collection from 1997-2000 would have been impossible without the help of hearty souls getting up at wee hours of the morning, spending way too much time in the blind, yet maintaining their sense of humour. Thank you Amy, Anne, Carolyn, Chris, Kelly, and Maureen. Special thanks to Joel Heath and Allison Moody who showed above-average data collection and cooking skills, and dedicated two consecutive summers to this research. Thanks to Brianna, Carla, Don, Iain, Julie, Lynn, Mark, and Rachel for providing additional help with field work over the years. I am grateful to Tommy Reddick and family, as well as Sean Power, for transport to and from the island

and for upper body strength to help unload the gear. The Canadian Wildlife Service provided additional logistic support (Greg, Peter, the Pauls – thanks!). Special thanks to Dr. Greg Robertson and Paul Taylor for replacing the murre blind on Great Island in 2002.

Numerous people over the years have helped the completion of this journey. Mom, Dad, Stephen, thanks for all your love and support. Dave, thanks for your love and encouragement, for providing a creative atmosphere, and restraining to ask the dreaded question: "Aren't you done yet?". Tech Services staff's creativity and ingenuity produced the scales described in Chapter 5 and helped create other devices over the years. Craig Barnes, Peter Earl, Roy Ficken, Maureen Howard, and Brenda Noftle were always available to provide valuable technical and administrative assistance. Krista, Carla, Mackenzie, thanks for making the lab a better place. Drs. Atef Mansour, Joe Brown, Bill Montevecchi, John Piatt, and Greg Robertson gave constructive feedback on chapters. Greg was also helpful with statistical analyses as were Dr. Dave Schneider and Scott Gilliland. Thanks to Glenn and Suzanne for dog-sitting while I was in the field and to Theresa for formatting the table of contents and saving me hours of frustration. Thanks Mom for helping with the data entry! Finally, I thank all the wonderful people in the Biopsychology (now CABE) Programme for their friendship. See you at Bitters.

Canadian Wildlife Service and Newfoundland Parks and Natural Areas Division (Department of Tourism, Culture and Recreation) kindly gave us permission to work on the island. This research was funded by the National Sciences and Engineering Research Council of Canada (NSERC) and by Memorial University of Newfoundland.

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CHAPTER 1 Introduction and co-authorship statement

1.1 INTRODUCTION

> "... parental behavior is one of the most variable traits known: variation exists at all levels – among taxa, populations, the sexes and individuals. How can we understand this variation?"
>
> (Westneat and Sargent, 1996, p. 87)

The above-mentioned quote acknowledges the importance of understanding variation at multiple levels. However, most avian studies examining variation in parental behaviour have focused on differences between species, populations, or the sexes. Few have investigated parental care at the individual level.

Within the last decade, studies monitoring individuals, rather than populations or sub-populations, have shown that including long-term information from marked individuals provides additional insight into the health of a population (Weimerskirch et al. 1994; Weimerskirch et al. 1997; Wendeln and Becker 1999) and helps in the modeling of population trends (Cobley et al. 1998). Documenting parental behaviour of individuals across multiple years yields a more sensitive design, which can increase the accuracy of population parameter estimates and provide insight into the quality of the breeding environment (Granadeiro et al. 1999; Hedd et al. 2002).

This thesis examines behavioural and physiological changes within the same set of banded Common Murres (*Uria aalge*) across multiple successive breeding seasons.

Data were collected across four breeding seasons (1997-2000) from a murre sub-colony breeding on Great Island in Witless Bay, Newfoundland and Labrador, Canada. At this location, a wooden blind has been in place since the 1980s. The birds' behaviour appears to be unaffected by its presence, with some breeding within two feet of the base of the blind. Murres have been colour-banded at the Great Island study site since 1996, facilitating individual recognition. In fact, some adults had been previously marked with a Canadian Wildlife Service metal band in the 1980s (D. Cairns, pers. comm.) and were observed to be rearing chicks up to 2003. At this site, the proportion of birds raising a chick successfully to colony departure is generally high. Hence, this site was viewed as being well established and most likely included many experienced, older birds. The close proximity of the observation blind to the murres, coupled with dawn-to-dusk observation watches, has generated a database with a wealth of detailed behavioural observations dating back to 1996.

Behavioural observations have been restricted to 30 pairs of murres breeding at nest sites easily viewed from the blind, allowing for the unambiguous identification of individuals. Restricting observations to approximately 60 individuals also permits one observer to reliably record most events such as arrivals, departures, nest reliefs, and prey identification. Although this restriction yields small sample sizes, particularly when analyses include only the same individuals across multiple years, data obtained from such a focal study allows exploration at a scale which is not frequently examined: individual changes across multiple years.

Common Murres are long-lived seabirds and return in subsequent years to breed at the same nest site. They are socially monogamous (Walsh 2001) and usually re-pair with the same mate if both return to the colony in the spring (Moody 2001). Murres lay a single egg per season, although a second egg is laid if the first is lost (Hatchwell 1991). Chick rearing at the colony is brief (15-25 days) with the chick departing to sea at 15-30% of adult mass (Ydenberg 1989). While at the colony, parents provision their chicks at high rates, which maximizes growth and facilitates colony departure (Morbey and Ydenberg 1997). However, frequency and size of chick meals are constrained by at least two factors: 1) murres have an extremely high wing load (Pennycuick 1987), making flying energetically expensive and 2) they carry only one fish at a time in their bill. Although both parents are required to rear a chick successfully, males and females may show differential investment at different stages of breeding. Females have been shown to exhibit higher chick feeding rates (Wanless and Harris 1986) during the chick-rearing period at the colony, whereas males accompany the chick to sea where they continue to provide care for several weeks (Harris and Birkhead 1985).

Common Murres breeding off the island of Newfoundland rely on capelin to feed their chicks (Piatt 1987; Davoren and Montevecchi 2003) and themselves (Piatt 1987; Wilhelm et al. 2003). In the Northwest Atlantic, capelin distribution and spawning times have shifted since the 1990s (reviewed in Carscadden et al. 2002). Consequently, some seabirds breeding in the Northwest Atlantic have experienced shifts in diet and reduced reproductive success (reviewed in Carscadden et al. 2002).

One aspect of this thesis describes the variability that Common Murres display in response to breeding on a short-term time scale: within and between four breeding seasons (1997-2000). Behavioural (Chapters 2 and 3) and physiological (Chapter 5) responses are examined, as are their consequences on chick growth (Chapter 4). I also investigated whether males and females respond differently to varying breeding demands within the breeding season and across years in terms of behavioural (Chapters 2 and 3) and physiological (Chapter 5) responses. A second aspect of this thesis examines if changes in Common Murre breeding responses have occurred on a long-term scale, i.e., across decades. Time budgets (Chapter 3) and chick growth parameters (Chapter 4) of murres from Great Island during 1998-2000 are compared to those of murres from Gull Island, a nearby island in Witless Bay, during the late 1970s to mid 1980s.

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1.3 CO-AUTHORSHIP STATEMENT

With the guidance of my supervisor, Dr. Anne Storey, I was responsible for proposing and designing the research questions presented in this thesis. Field data (1997-2000) and blood samples (1997-2000 and 2002) were primarily collected by myself or under my supervision. I carried out all of the hormonal analyses in the laboratory, under the supervision of Dr. Donald McKay. I was solely responsible for analyzing the data, developing and writing all of the chapters. Subsequently, my committee members (Drs. Anne Storey, Donald McKay, and Ian Jones) provided comments on these chapters, which were incorporated prior to submitting the thesis. Dr. Anne Storey is a co-author on all of the data chapters due to her various contributions, including fieldwork and financial support. Dr. Donald McKay is co-author on Chapter 6 as he was a key person in the development of the radioimmunoassay procedure described.

Chapter 2 of this thesis has been published as: Wilhelm, S.I. and Storey, A.E. 2002. Influence of cyclic pre-lay attendance on synchronous breeding in Common Murres. Waterbirds 25: 156-163.

CHAPTER 2 Influence of cyclic pre-lay attendance on synchronous breeding in Common Murres

2.1 ABSTRACT

Social stimulation in concert with environmental factors may influence the degree of reproductive synchrony among colonial breeders. Synchronous breeding has been shown to enhance reproductive success by decreasing predation. Although Common Murres (*Uria aalge*) typically have a cyclic pre-lay attendance pattern, I observed one acyclic pre-lay period (1999) during four consecutive breeding seasons (1997-2000). The present study investigated how differences in pre-lay attendance patterns may influence breeding synchrony and reproductive success in a Common Murre sub-colony on Great Island, Newfoundland and Labrador. Compared to the cyclic pre-lay period (2000), the acyclic pre-lay period showed: 1) less synchronous egg-laying, 2) pairs spent less time together at their site due to the overall lower attendance by both sexes, but particularly by females, and 3) higher susceptibility to predation during early and first half of peak egg-laying, although overall reproductive success did not differ between years due to high re-laying rates. These results suggest that cyclic attendance during the pre-lay period of Common Murres may influence breeding synchrony within a sub-colony, which may reduce predation during early incubation and late chick rearing.

2.2 INTRODUCTION

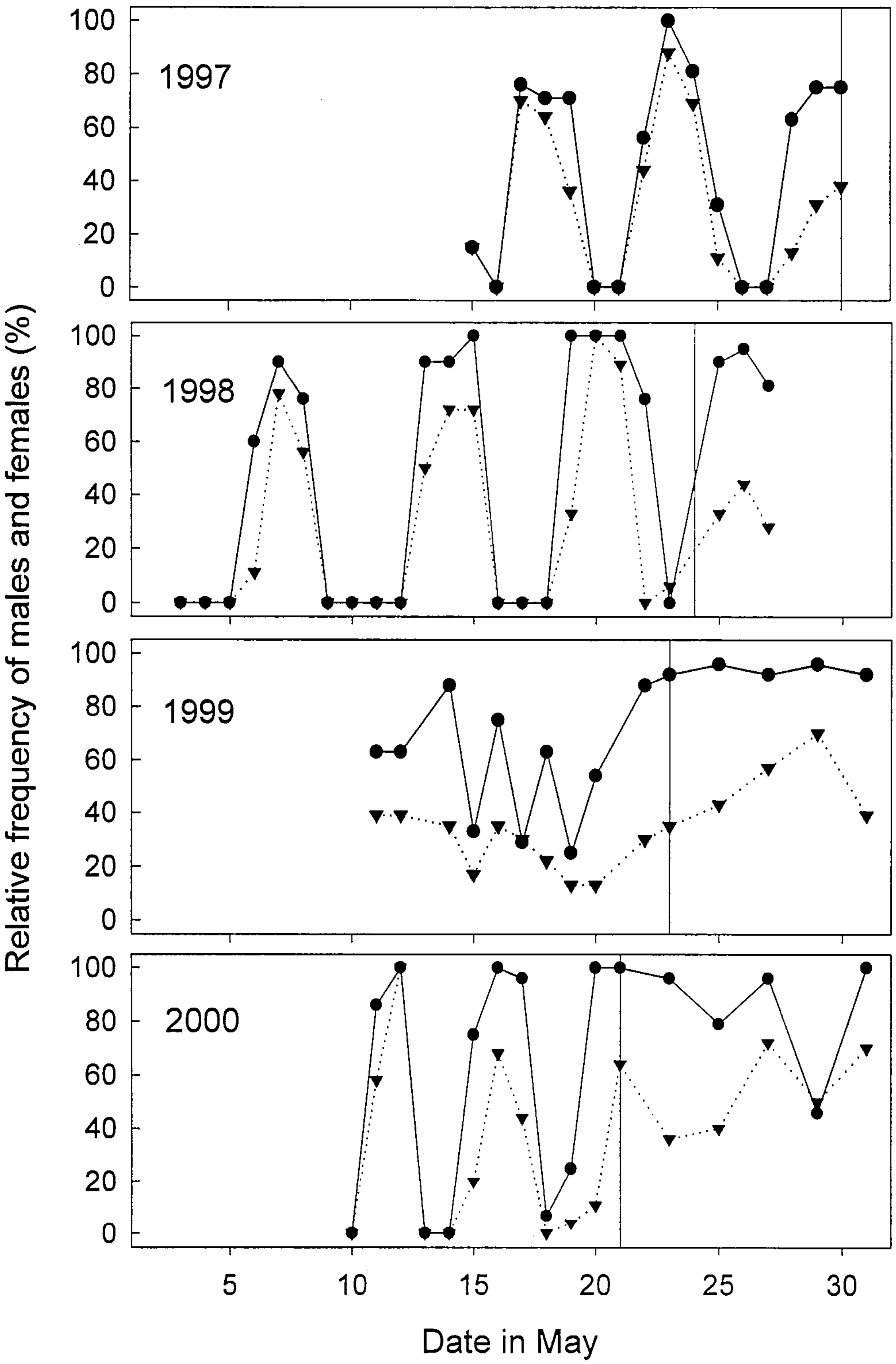
Most marine bird species gather with conspecifics in large colonies (Lack 1968) and may exhibit a high degree of reproductive synchrony. Temporal clustering of reproduction is thought to have evolved so that chicks will be reared during maximum food availability and/or to reduce predation (reviewed in Gochfeld 1980). Experimental studies in seabirds where hatching dates of early breeders were artificially delayed have shown that lower reproductive success in late-laying pairs is not always due to declining food sources (Parsons 1975; Hatchwell 1991). Rather, the seasonal decline in productivity reflects individual quality, usually related to age and/or experience: older females tend to lay earlier (Coulson and White 1956; Hipfner et al. 1997) and are more successful than younger females, even when forced to lay a late, second egg (De Forest and Gaston 1996). As synchronous breeding reduces predation (Findlay and Cooke 1982a; but see Ims 1990), breeding early may be less important than breeding at the same time as other individuals (Parsons 1975; Hatchwell 1991).

Darling (1938) proposed that the breeding colony provides a setting in which social stimulation should lead to more synchronous egg laying. There is evidence that social stimulation can act as a proximate mechanism to synchronize reproductive events among neighbouring conspecifics. Hailman (1964) suggested that behavioural displays of neighbouring Equatorial Swallow-tailed Gulls (*Larus furcatus*) accelerate their reproductive cycle and synchronize their breeding. Among Spotted-backed Weavers (*Ploceus cucullatus*), where nest-building and breeding are highly synchronized within colonies, Victoria and Collias (1973) observed that female presence stimulated male pre-breeding behaviour, which in turn stimulated females to lay their eggs. Barfield (1971) found that female Ring Doves (*Streptopelia risoria*) with the most exposure to male courtship behaviour showed the shortest latency to ovulation. Observations such as these suggest the importance of studying both social and ecological factors when investigating mechanisms influencing reproductive synchrony and its function.

Common Murres (*Uria aalge*), known as Common Guillemots in some areas, are socially monogamous long-lived seabirds that maintain pair bonds across years (Hatchwell 1988). At Witless Bay, Newfoundland and Labrador (NL), murres return to their breeding sites in April, approximately four to eight weeks prior to egg-laying (pers. obs.). During the pre-lay period, they aggregate on cliffs where they defend their sites and engage in pair and extra-pair copulations (Birkhead et al. 1985; Hatchwell 1988; Walsh 2001). Each female lays a single egg, but if this is lost, she will often lay a replacement egg (Hatchwell 1991). Common Murres tend to be especially flighty during the pre-lay period and leave the cliff as part of a group several times a day when disturbed by avian predators or humans (e.g., boat, plane, pers. obs.). The first few eggs on the site lost to Herring Gull (*Larus argentatus*) or Great Black-backed Gull (*L. marinus*) predation each year typically occurred when the incubating adult left the nest site with the rest of the sub-colony due to disturbance. Hatchwell (1991) also reported that early laying individuals alone at the colony experienced egg loss to predation.

Common Murres experienced lower predation and higher reproductive success when they were reproductively synchronous with their neighbours (Wanless and Harris 1988; Hatchwell 1991; Murphy and Schauer 1996). Although the adaptive value of synchronous breeding is typically reported on a colony basis, breeding synchrony within small social units or groups of neighbouring individuals may be more important (Wissel and Brandl 1988; Murphy and Schauer 1996), as collective defence against avian predators within local aggregations of synchronously breeding neighbours reduces predation (e.g., Murphy and Schauer 1996). Although these studies demonstrate the adaptive value of synchronous breeding within groups of Common Murres, proximate mechanisms leading to local synchrony have remained unreported.

The pre-lay attendance pattern of Common Murres at the nest site is typically cyclic (Corkhill 1971; Birkhead 1978; Hatchwell 1988): periods when many are present are followed by periods of complete absence (Fig. 2.1). The pre-lay period in 1999 differed and lacked the oscillating pattern of high and low attendance (Fig. 2.1), and was termed "acyclic". This observation led to the investigation of how the temporal pattern of Common Murre pre-lay attendance may influence the reproductive synchrony of a sub-population and how variation in synchrony, in turn, may affect individual reproductive success. The following hypotheses were tested: i) Common Murres will spend more time at their site during the pre-lay period in the cyclic years compared to the acyclic year, ii) reproductive synchrony of the years where a cyclic pre-lay attendance pattern was observed will be higher compared to the acyclic pre-lay period, iii) individuals will experience lower predation during a synchronous breeding period compared to an asynchronous breeding period, and iv) individuals will experience higher reproductive success during a synchronous breeding season compared to a less synchronous breeding season.



1997
1998
1999
2000
Relative frequency of males and females (%)
Date in May
0
20
40
60
80
100
5
10
15
20
25
30

2.3 METHODS

Common Murres nesting at high density on a broad ledge (1.6 m x 2.5 m area containing 30 breeding pairs) were observed at Great Island, NL, Canada (47^0 11'N, 52^0 49'W). At the time of this study, 28 males and 25 females were colour-banded.

2.3.1 Temporal pattern of pre-lay attendance

Proportions of males and females present at the site during the pre-breeding season were recorded from 1997-2000. The sex of all birds had been determined by observation of copulation. These results were confirmed in ten individuals using DNA analysis (M. Cameron and C. Walsh, pers. comm.). For 1998-2000, arrival and departure times of murres were recorded during each observation day prior to egg laying and the following proportions were calculated: i) total time an individual spent at its site over the total observation time and ii) total time pairs spent together at the site over the total observation time. Continuous observations were made, beginning at dawn (05.00 h), ranging from 180 min (3 hr) to 960 min (16 hr) on 19 days in 1998 (164 hr total), 14 days in 1999 (144 hr total) and 16 days in 2000 (174 hr total). If no murres landed on our study site within the first three hours on an observation day, it was categorized as a "no murre day" and observations were terminated. Spot checks in the afternoon of such days confirmed that no murres were in attendance throughout the day.

2.3.2 Breeding synchrony

Local breeding synchrony of the sub-colony was determined by the relative timing of egg laying and chick departure, categorized as early, peak, or late. Because predation pressures are most apparent in early and late breeders (Murphy and Schauer 1996), the benefits of synchronous breeding should be reflected during the early and late periods of the breeding season. Laying and departure dates were assigned to a category depending on the number of days before or after they occurred based on the median lay and fledge dates of the sub-colony (median value=0). Groups were defined as: 1) early: up to day -4, 2) peak: day –3 to day +4, and 3) late: after day +4 (Hatchwell 1991).

2.3.2.1 Egg-laying synchrony

Egg laying synchrony was determined by the laying dates of first eggs only. Although murres often lay a second egg if the first egg is lost, second eggs were not considered because the date on which re-lay occurs is largely dependent on when the first egg was lost. In 1998, the observation period focused on the period prior to egg laying and observations ceased at the onset of egg laying. In 1999 and 2000, observations continued past the median lay date (1999: 28 May, 2000: 26 May). Hence, egg laying dates of first eggs for all active breeding pairs are available only for these two years. The laying date of an egg was determined by: i) observing the actual laying of the egg, ii) seeing an egg at a site where there had not been an egg on the previous observation day or iii) counting back the mean incubation period (33 days, pers. obs.) from the chick's hatching date. The actual lay dates of three eggs in 1999 and one egg in 2000 could not be determined but were categorized as "late"; these eggs were laid after the last observation day during the incubation period (1999: 4 June; 2000: 2 June) but did not hatch despite being incubated well into the normal chick-rearing period. For this reason, median dates were calculated rather than mean dates. To control for individual factors such as genetic predisposition (Findlay and Cooke 1982b; Barbraud et al. 2000) or parental age (De Forest and Gaston 1996; Hipfner et al. 1997), only eggs of same pairs laid in both 1999 and 2000 were included in the analyses (N = 27). The fate of each egg was monitored as the breeding season progressed.

2.3.2.2 Chick departure synchrony

Chick departure dates were recorded when a chick and its male parent were observed to have departed to sea successfully or when the first day a chick > 16 days old was no longer at its nest site that had been present on the last observation day. A nest departure was deemed a success when parent and chick reunited on the water at the base of the cliff. To control for nest site characteristics, which may influence the survival rate of eggs and chicks (Gaston and Nettleship 1981), only nest sites where a successful departure occurred in both 1999 and 2000 were included in the analyses (N = 18). For all nest sites, I recorded whether the chick hatched from a first or re-laid egg, as well as the fate of the chick if it failed to successfully fledge.

2.3.3 Data Analysis

All "time at site" proportions were square root and arcsine transformed to meet the assumptions of normality for parametric statistics (Sokal and Rohlf 1995). Because the cyclic pre-lay attendance pattern changes with the laying of the first egg in the sub-colony (Fig. 2.1), behavioural analyses were done only on the 11-day period prior to the laying of the first egg of the sub-colony (1998: 24 May, 1999: 23 May, 2000: 21 May). This period was the longest observed pre-lay period common to all three years. The mean time individuals spent at their respective sites in relation to the total observation time during the 11-day interval was calculated for each year. A mixed within-subjects ANOVA with individuals as the repeated measure was used to investigate the relationship between the proportion of time males and females spent at their site prior to the laying of the first egg, across years (1998-2000). To control for individual variability across years, the same, banded individuals in all three years were included in the analyses (males: N = 17, females: N = 18). A within-subjects ANOVA with nest site as the repeated measure was used to determine yearly differences (1998-2000) in the proportion of time pairs spent together, quantified as the amount of time both pairs were seen together at their nest site in relation to the total observation time on days that murres were present. Post-hoc comparisons were conducted using the Dunnett test (Keppel 1991), suitable to contrast time spent at site by pairs in the acyclic year to each of the two cyclic years. Only pairs where both mated males and females were banded in all three years were included in the analyses (N = 12), to control for individual variability across years. Values are reported as means ± SE.

Chi-squared tests were used to investigate differences in egg laying and departure synchrony by comparing the occurrences of early, peak, and late eggs or departed chicks between years. To test for yearly differences in timing of first egg laying and departure, calendar dates were transformed into Julian dates, and the same nests in both years were compared using a Wilcoxon signed-ranks test. Chi-squared tests, applied with the Yates's correction for 2 X 2 tables and small sample sizes (Sokal and Rohlf 1995), were used to investigate differences in predation pressure, quantified as the number of first eggs and chicks lost to predation by Herring Gulls or Great Black-backed Gulls. Statistical significance for all tests was set at $\alpha = 0.05$.

2.4 RESULTS

2.4.1 Male and female attendance patterns

Male and female attendance patterns at the study site during the pre-breeding period varied across years (Fig. 2.1). In 1997, 1998, and 2000, males and females had synchronized attendance with clear cycles of presence and absence, up to the last cycle in May, after which the proportion of males remained high. However, in 1999, attendance lacked the alternating periods of presence and absence, with only a small proportion of females being present at the colony on each day. Most males visited the colony on a daily basis only after the first egg of the study was laid. Furthermore, no periods of total absence were observed in 1999 in contrast to other years. Time spent at site differed for males and females across years (sex x years: $F_{2,66} = 6.54$, $P = 0.003$), with the significant interaction due to females' low attendance in 1999 (Fig. 2.2). The amount of time pairs

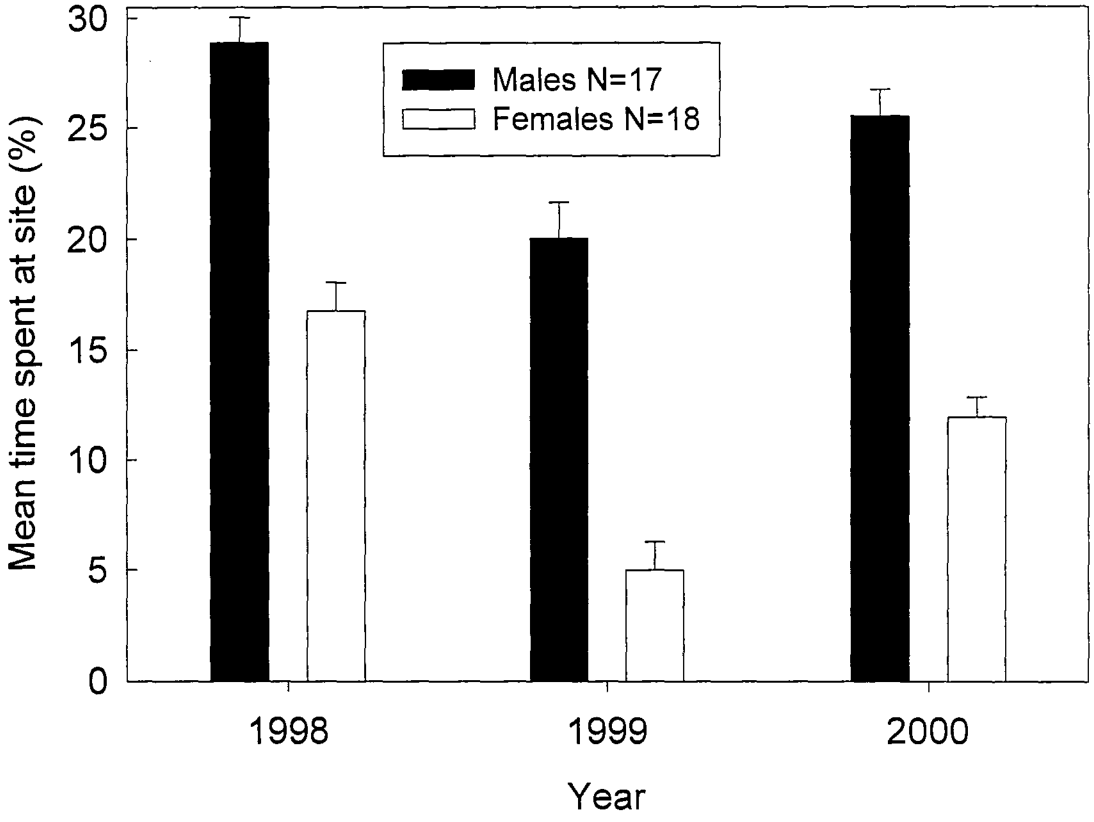


Figure 2.2. Mean percentage of time (± SE) spent by male and female Common Murres during the 11-day period prior to the laying of the first egg at the study site in three years (1998-2000).

spent together at their sites differed across years (year: $F_{2,33} = 85.71$, $P < 0.001$; Fig. 2.3). Compared to 1999, pairs were together 5.1 times more in 1998 (Dunnett test = 18.75, $P < 0.01$) and 3.5 times more in 2000 (Dunnett test = 11.67, $P < 0.01$).

2.4.2 Breeding synchrony

The distribution of first-egg lay dates differed between 1999 and 2000 ($\chi^2_2 = 6.46$, $P < 0.05$, $N = 27$; Table 2.1) and more eggs were laid during the peak period in 2000 compared to 1999, suggesting that the laying of first eggs was more synchronous in 2000. The median lay dates (1999, May 28; 2000, May 26) did not differ between years (Wilcoxon signed-ranks test: $z = -1.79$, $P > 0.05$).

No significant difference was found between years for chick departure ($\chi^2_2 = 2.74$, $P > 0.05$; Table 2.1), with most departures occurring during the early and peak periods. The median departure date was earlier in 2000 (21 July) compared to 1999 (29 July; Wilcoxon signed-ranks test: $z = -2.68$, $P < 0.01$ Fig. 2.4). Although the overall mean age at departure did not differ between years (1999: 20.7 ± 0.4 d, $N = 18$; 2000: 21.8 ± 0.6 d, $N = 18$; $t_{34} = 1.48$, $P = 0.15$), in 1999, chicks that departed from July 29-31 left at an earlier age (19.8 ± 0.3 d, $N = 10$) than chicks that departed from July 17-25 (21.8 ± 0.8 d, $N = 8$; $t_{16} = 2.86$, $P = 0.011$).

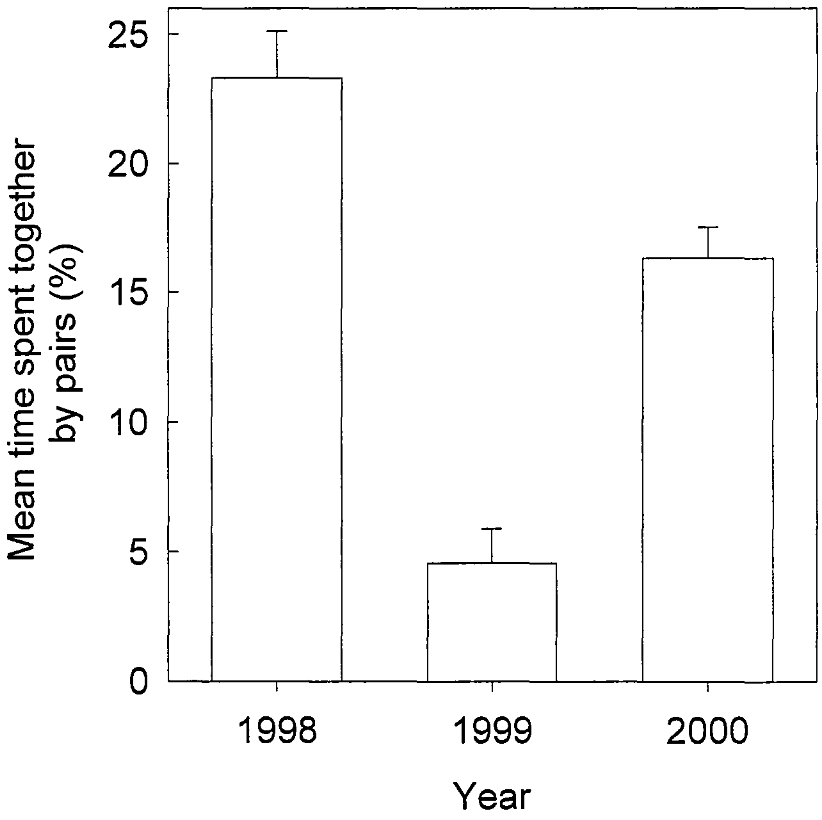


Figure 2.3. Mean percentage of time (± SE) mated Common Murre pairs (N = 12) spent together at site during the 11-day period prior to the laying of the first egg at the study site in three years (1998-2000).

Table 2.1. Relative egg-laying and chick departure frequencies of a Common Murre sub-colony on Great Island, NL. Although more first eggs were laid during the peak laying period in the cyclic year (2000) compared to the acyclic year (1999), most chicks left the colony during early and peak departure periods in both years.

	Relative time of egg-laying		Relative time of departure	
	1999	2000	1999	2000
Early	6	3	8	5
Peak	12	21	10	11
Late	9	3	0	2
N	27	27	18	18

Note: The laying and departure dates were assigned to a category depending on the number of days before or after they occurred in relation to the laying and departure dates of the sub-colony. Early = up to day –4, peak = day –3 to day +4, and late = after day +4 (Hatchwell 1991).

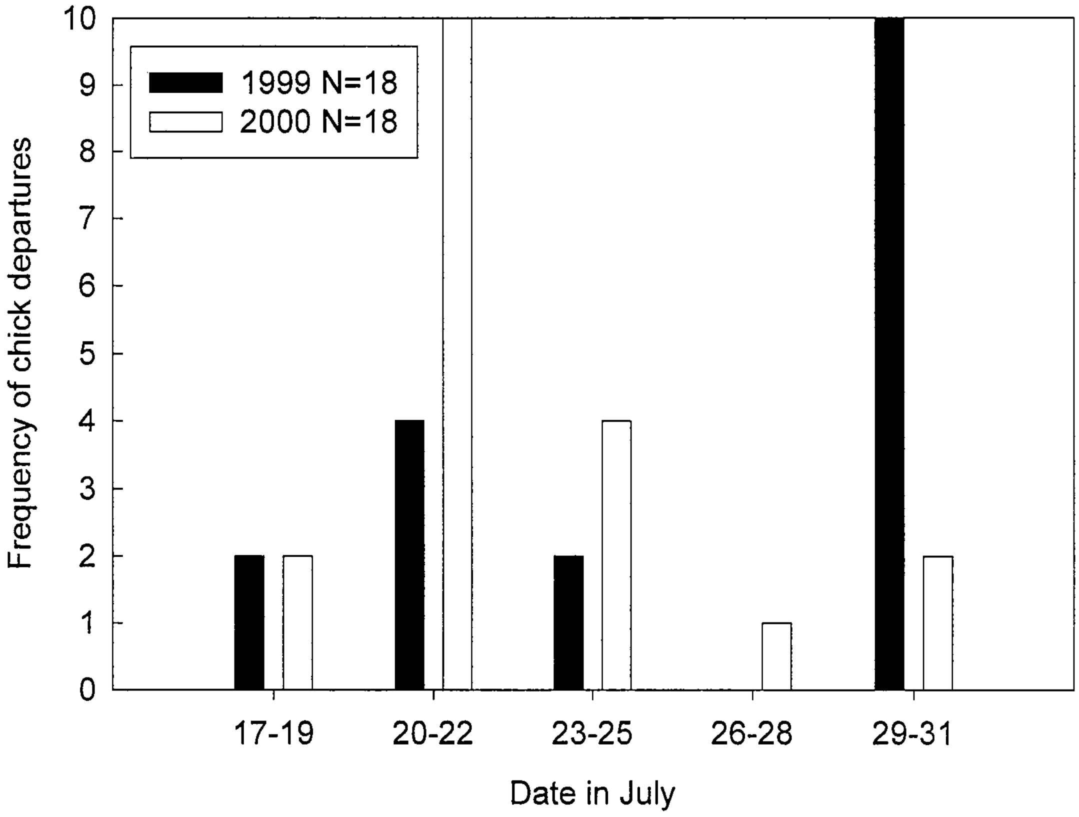


Figure 2.4. Chick departure frequencies during the 1999 (median departure date: 29 July) and 2000 (median departure date: 21 July) departure periods in a Common Murre sub-colony on Great Island, NL.

2.4.2 Predation

In 1999, eggs were more susceptible to predation during early and first half of peak egg-laying and 57% (8/14) of eggs laid prior to the median lay date were lost, whereas in 2000, only 7% (1/14.5) were lost prior to the median lay date ($\chi^2_1 = 6.17$, $P < 0.05$). The number of first eggs lost to gulls (predated eggs/total number of eggs) during the entire incubation period did not significantly differ between years (1999: 11/28, 39%; 2000: 6/29, 21%; $\chi^2_1 = 1.55$, $P > 0.05$). When combining the number of eggs and chicks lost to gulls (predated eggs and chicks combined/total number of eggs), predation was nonetheless twice as high in the asynchronous year (1999: 12/28, 43%) than the synchronous year (2000: 6/29, 21%), although this was not significant ($\chi^2_1 = 2.30$, $P > 0.05$). The chick lost to predation in 1999 was the only chick remaining at the study site after all other chicks had departed. This chick was taken by a Great Black-backed Gull when no adult murres were present. The re-laying rate for all lost eggs was 82% (9/11) in 1999 and 50% (3/6) in 2000. No second eggs were observed being lost to predation in any year. The overall reproductive success (departed chicks/eggs laid), including first and second eggs, for the sub-colony was 75% (21/28) in 1999 and 79% (23/29) in 2000 ($\chi^2_1 < 0.01$, $P > 0.05$).

2.5 DISCUSSION

The occurrence of an apparently unusual event, namely the acyclic pre-lay attendance in 1999, provided the opportunity to study the effects of cyclic pre-lay attendance. The frequency of such a year is unknown but is likely low, thereby making it difficult to investigate its impact on breeding.

2.5.1 Importance of cyclic pre-lay attendance

Male and female Common Murres spent less time at the colony in the acyclic year compared to a year when pre-lay attendance was cyclic. In addition, the laying of first eggs was less synchronous among female murres in the acyclic year, suggesting that the typical cyclic pattern may enhance synchronous reproduction. Thus, one function of cyclic attendance may be to increase egg-laying synchrony within groups by maximizing the time neighbours and mates spend together at their sites during the pre-lay period. There is evidence that low attendance may have decreased social stimulation between individuals: during the cyclic pre-lay years, pairs experienced higher rates of copulation (Walsh 2001). Hence, the observed asynchronous egg-laying in 1999 may have been influenced by reduced social stimulation which in turn resulted from low colony attendance.

Overall low attendance of male and female Common Murres during the pre-lay period may be due to low food availability in the surrounding areas of the breeding colony (Boekelheide et al. 1990). Great Skuas (*Catharacta skua*) have also been reported to reduce adult territorial defence by 50% in order to increase their foraging efforts as a response to declining food sources (Hamer et al. 1991). The unusually low female attendance in 1999 may further reflect possible difficulties associated with self-provisioning in the vicinity of the colony in that year. During the two-week period of egg formation, females begin to decrease their attendance time at the colony and are completely absent up to four days prior to laying, during which they are thought to be spending most of their time foraging to meet the higher nutritional demands associated with yolk formation (Birkhead and del Nevo 1987). If murres were flying long distances in 1999 to locate foraging areas, the extra energy spent flying these long distances may have been too demanding for females to visit the colony as frequently during egg formation as in other years.

Weather conditions have been reported to influence colony attendance of Common Murres, where non-breeders and off-duty mates spent less time in the colony on warmer days (Murphy and Schauer 1994; Thayer et al. 1999). Although warmer temperatures were observed during the latter half of the pre-lay period in 1999, temperature variation did not appear to account for low attendance throughout the entire observed pre-lay period (pers. obs.). Slater (1977, 1980) observed a daily rhythm in Common Murre pre-lay attendance, with numbers being greatest during high tide. It was proposed that a low or rising tide increased prey availability and that murres returned to the cliffs during high tide when fish were more difficult to find. Wind-induced upwelling has also been found to increase the concentration of fish (Ings et al. 1997), thereby providing birds and other predators a predictable food source (Schneider and Methven 1988). Interestingly, in the Witless Bay Ecological Reserve and surrounding areas, upwelling occurs in a cyclical fashion every 3-6 d (Schneider and Methven 1988), similar to the cyclic attendance of murres in this study. Murres were perhaps absent from the cliffs following an upwelling to take advantage of the high fish concentrations, and returned to the colonies between these events.

Cyclic attendance during the pre-lay period occurs in several other auk species including Thick-billed Murres (*Uria lomvia*; Gaston and Nettleship 1981), Atlantic Puffins (*Fratercula arctica*; Corkhill 1971), Razorbills (*Alca torda*; Corkhill 1971), and Ancient Murrelets (*Synthliboramphus antiquus*; Jones et al. 1989). Although Common Murre pairs spend time together at the breeding colony during the pre-lay period, much of their non-land time during this period is spent in aggregated groups on the waters surrounding the breeding colonies. Rates of body mass loss throughout the pre-lay period suggest that it is energetically demanding for murres to be present and engaging in social interactions at the colony (Hatchwell 1988; Chapter 5). Furthermore, males typically arrive earlier in the day than females (Wanless and Harris 1986; pers. obs.). To minimize energy expenditure during the egg-formation by reducing the amount of time they spend at the site, females may fly to the colony only when there is a high probability that their mate or other potential partner is present.

2.5.2 Predation and egg-laying synchrony

More eggs were lost to predation during the early and first half of peak egg-laying in the asynchronous year compared to the synchronous year, suggesting that synchrony reduces predation. Synchronous breeding has been associated with higher breeding success in previous studies of Common Murres (Wanless and Harris 1988; Hatchwell 1991, Murphy and Schauer 1996). One reason for this high reproductive success may be that when birds breed synchronously, there are more individuals in early egg laying to contribute to group defence. However, the overall reproductive success of the sub-colony did not differ between years, probably due to the high re-laying rate of females.

Other Common Murre colonies breeding in the Atlantic also typically experience high reproductive success (71-85%; Hedgren 1980; Birkhead and Nettleship 1987; Harris and Wanless 1988), with most failures occurring during the incubation period. At the Isle of May, predators took very few eggs; most egg loss was due to eggs rolling off narrow ledges (Harris and Wanless 1988). The sub-colony of Common Murres observed on Great Island is located on a broad flat ledge where eggs are rarely observed rolling off the ledge. Rather, the main cause of egg loss is predation during early incubation. It appears that the asynchronous egg-laying observed in 1999 may have been a contributing factor to the higher predation rates.

2.5.3 Predation and departure synchrony

The finding that chick departure was not extended in the year with an asynchronous egg-laying period, due to late-hatching chicks departing at a younger age, supports the suggested importance of synchronized chick departures within a sub-colony (Williams 1975). Chicks leaving before or during the peak departure period may experience less predation risk since collaborative defensive behaviour in the colony decrease as the departure period progresses due to the decreasing number of breeding pairs left in the colony (pers. obs.). The age of chick departure is quite variable (16-30 days; Harris and Birkhead 1985), suggesting that timing of departure may be modified by the parents or the chick. Given that body condition at departure does not predict a chick's likelihood to survive its first winter at sea (Harris et al. 1992), chicks leaving the colony at a younger age (and presumably in poorer condition), but timed to coincide with neighbouring birds, may have a higher chance of survival than if they left later, but at a higher body mass.

In conclusion, Common Murres and other high-density nesters may benefit by engaging in a cyclic pre-lay attendance pattern as this allows pairs to maximize the time they spend together at their site to engage in important pre-breeding behaviours, such as copulations and maintenance of the pair bond. Furthermore, peaks in female attendance at the site may allow for a higher degree of social stimulation between neighbours, which in turn may increase egg-laying synchrony. Late nesting pairs were observed to perform more nest-related courtship behaviours than early laying pairs, suggesting that females of these late pairs may require more social stimulation (A. Storey, unpub. data). Thus, individuals of colonial species may have evolved particular hormonal responsiveness to social cues that promote early and synchronous breeding, which in turn function to reduce predation.

Ultimate factors, such as seasonality, may stimulate Common Murres to return to their breeding colonies. However, the daily decision to fly to their nest site may be further influenced by the location of food sources and effective communication between and within the sexes. Studying murres' communication system and social interaction at sea would provide further insight on the underlying mechanisms influencing colonial breeding. Finally, location and abundance of food sources during the pre-lay period may have important consequences on individual reproductive success and deserves greater attention when studying factors affecting the breeding success of colonial breeders.

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CHAPTER 3 Inter-annual time budget comparisons of male and female Common Murres breeding in Witless Bay, Newfoundland

3.1 ABSTRACT

Since the 1990s, seabirds inhabiting the Northwest Atlantic have experienced variable breeding conditions due to changes in breeding biology of their main prey, capelin (*Mallotus villosus*). Common Murres (*Uria aalge*) can show flexible time budgets during chick rearing by increasing or decreasing their co-attendance time, allowing them to provision their chick at similar rates despite changes in prey availability. Using the same established pairs, time budgets of male and female Common Murres were investigated in Witless Bay, Newfoundland, during three consecutive chick-rearing periods (1998-2000). Chick feeding rates, co-attendance time and length of provisioning trips were highly variable within and across years. In all years, provisioning rates increased from the end of June to mid-July and subsequently declined. Despite high foraging effort (longer provisioning trips and lower co-attendance time), chick feeding rates were low during early chick rearing in 2000 compared to 1998 and 1999. Low chick feeding rates were attributed to the late arrival of inshore spawning capelin. Although chick feeding rates have not changed since the 1980s, murres currently breeding in Witless Bay are exhibiting higher foraging effort as shown by a decrease in co-attendance time and increase in length of provisioning trips.

At the group level, females spent more time brooding and provisioned the chick more frequently compared to males. At the pair level, however, there was no evidence of

role partitioning; only 7-14% of pairs showed role partitioning in any given year. Role partitioning has been proposed to reduce the energetic demands of chick rearing, particularly during stressful breeding conditions. For Common Murres, role partitioning may not be advantageous due to the high costs associated with flying.

INTRODUCTION

Over the past two decades, seabirds inhabiting the Northwest Atlantic have been experiencing highly variable breeding conditions, primarily as a result of changes in the biology of their main prey, the capelin (*Mallotus villosus*). Compared to the 1980s, size of capelin have decreased and their inshore spawning times are delayed by one month (reviewed in Carscadden et al. 2002), sometimes resulting in a mismatch between chick hatching and capelin availability (e.g., Massaro et al. 2000). Consequently, surface feeders such as Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) have experienced lower reproductive success (Regehr and Rodway 1999). Black-legged Kittiwakes (*Rissa tridactyla*) and Leach's Storm-petrels (*Oceanodroma leucorhoa*) have been further affected by changes in capelin availability as a result of increased predation by gulls. Predation rates on kittiwakes and storm-petrels (eggs, chicks, and adults) decrease following the inshore arrival of spawning capelin as a result of gulls switching from bird to fish prey. Delayed capelin arrival prolongues this period of high predation (Stenhouse and Montevecchi 1999; Massaro et al. 2000). In contrast, the reproductive success of Common Murres (*Uria aalge*) and other pursuit diving birds appear to be more resilient to prey availability fluctuations (Monaghan et al. 1996; Regehr and Rodway 1999) because of their ability to exploit the water column at a greater depth (Piatt and Nettleship 1985) and are less prone to predation due to their size and breeding biology.

Although the reproductive success of pursuit divers has been less affected by reduced prey availability (Monaghan et al. 1996; Regehr and Rodway 1999), individuals may be experiencing higher breeding demands through increased foraging effort. Common Murres have flexible time budgets during chick rearing. When foraging, murres spend most of their time on the sea surface and time spent pursuing prey may be increased or decreased depending on prey availability (Monaghan et al. 1994; Burger and Piatt 1990). Chick provisioning rates will only be affected when food availability is extremely low and adults cannot locate prey despite increased foraging effort (Uttley et al. 1994; Monaghan et al. 1994). An inverse relationship exists between food availability and foraging effort: as food supply increases, time spent foraging decreases. Conversely, as food supply increases, birds spend more time co-attending their brooding mate (reviewed in Cairns 1987). Hence, murres are able to compensate for reduced prey availability by decreasing time spent at colony when not brooding (co-attendance time), thereby continuing to provision the chicks at healthy rates, which ultimately results in less variable reproductive success.

Cooperation between mates becomes important in such a variable environment as reduced co-attendance time presumably means more time spent engaged in parental activities and less time for self-maintenance. Murre chicks are continuously brooded and parents take turns between brooding and provisioning. When both parents must participate for young to be raised successfully, males and females show a certain "complementarity" in parental roles they assume (Trivers 1972), where the most efficient parents are those showing the most cooperation. However, conflict can arise within pairs as a result of one mate minimizing its own investment and thereby forcing the partner to maximize its contribution (e.g., Sandell et al. 1996). Unfavourable breeding conditions may also lead to differential allocation (Nol 1985), where both mates may be stressed and therefore minimize their contribution in order to ensure their own survival and future reproductive success. Effective role partitioning between the sexes may therefore minimize conflict and increase the likelihood of successful fledging of young.

Within the Alcidae family, males and females of several species show some level of role differentiation during the chick-rearing period. These species include: Atlantic Puffins (*Fratercula arctica*; Creelman and Storey 1991), Common Murres (Wanless and Harris 1986), Thick-billed Murres (*Uria lomvia*; Jones et al. 2002), Razorbills (*Alca torda*; Wanless and Harris 1986), Crested Auklets (*Aethia cristatella*; Fraser et al. 2002), and Marbled Murrelets (*Brachyramphus marmoratus*; Bradley et al. 2002). The pattern emerging from these studies is that females feed the chick more and males spend more time with the chick (at the colony and/or at sea). Marbled Murrelets are the exception as males provision the chick more during late chick rearing (Bradley et al. 2002). Role partitioning is expected in long-lived species that provide extensive biparental care and maintain stable pair bonds (Trivers 1972; Nol 1985), characteristics that apply to all of the auk species in which sex differences in parental roles have been observed.

This study investigated if Common Murres breeding on Great Island in Witless Bay, showed sex differences in time budgets (chick provisioning rates, foraging effort, and activities related to brooding and role switching), and how variable these were over time (within and across seasons). Provisioning rates and foraging effort of these murres were then compared to other murre colonies in the Northwest Atlantic and if changes occurred since the 1980s. Finally, role partitioning was examined at the pair level, and the following questions were explored: i) what proportion of pairs engaged in role partitioning, and ii) did role partitioning occurrence vary across years?

3.2 METHODS

Time budgets and role partitioning were investigated in Common Murres nesting at high density on a broad ledge (1.6 m x 2.5 m area) on Great Island (47° 11'N, 52° 49'W), Newfoundland and Labrador (NL), Canada, from June to August 1998-2000. Continuous observations were made, beginning at dawn (first light after 04.30 h) and finishing at dusk (last light before 21.30 h), on 11 days in July and August 1998 (175.8 hr total), 15 days in July and August 1999 (238 hr total), and 12 days in July 2000 (196 hr total). To assess daily time budgets for both sexes accurately, it was important to be able to account for nocturnal activities as well as diurnal ones. Although chicks are not fed during the night (Harris and Wanless 1985; pers. obs.), one parent spends the night at the colony (Wanless and Harris 1986; pers. obs.). Common Murres of either sex spend the night with the chick (Wanless and Harris 1986; Verspoor et al. 1987). Observations were done during two nights (6-7 July and 8-9 July 1999). There was very little activity overall and no birds were heard flying in or out of the colony or giving the characteristic greeting call of reuniting mates. Attendance was taken at dusk and again the following morning at dawn. Two nest reliefs had been missed from 6-7 of July (N = 21 sites) and zero nest reliefs from 8-9 of July (N = 21 sites), suggesting that birds infrequently changed over at night. The missed nest reliefs most probably occurred at dusk, when visibility through the tinted blind window was very poor and the band colours of the departing individual were not observable. For the purpose of this study, individuals present at dawn were credited with having spent the night at the colony and individuals present at dusk were assumed to be staying throughout the following night. This created individual time budgets from midnight to midnight.

Nine breeding behaviours related to Common Murre time budgets were examined. The first six behaviours relate to chick provisioning and foraging effort and include: a) number of provisioning trips/day, defined as an individual arriving at the breeding site with a fish, b) length of provisioning trips (min), defined as the time between an individual's departure from the colony and its return with a fish, c) number of chick feeds within a provisioning bout, defined as the number of feeds that occurred between the end of an individual's brooding shift to the beginning of its next brooding shift and in which at least one provisioning trip was observed (therein after referred to as a provisioning bout), d) time spent at sea over a 24-hr period (%), e) latency to depart (min), a measure of motivation to forage (Nol 1985), defined as the time between the end of an individual's brooding shift and its departure from the colony, and f) time spent co-attending brooding mate (min). The other three behaviours relate to brooding and role switching, and include: a) time spent brooding chick over a 24-hr period (%), b) latency to brood (min), defined as the time between an individual's arrival at the colony and the beginning of its brooding shift, and c) number of times that mates switched parental roles during the day (from brooder to provisioner or provisioner to brooder).

3.2.1 Data analysis

3.2.1.1 Male and female time budgets

Time budgets were analyzed for 17 pairs in 1998, 19 pairs in 1999, and 19 pairs in 2000. Only pairs that successfully reared a chick to colony departure in at least two years were included in the analyses. Fourteen pairs were included in the analyses in all three years and 7 pairs in two years (N = 21).

To test for possible effects due to age of chick, all response variables were grouped into five chick age categories: 1-4 d, 5-8 d, 9-12 d, 13-16 d, and 17-20 d. To test for possible date effects, calendar dates were transformed into Julian dates and grouped into 7-d categories according to date: Julian date 178-184, 185-191, 192-198, 199-205, and 206-212. Only two chicks at our study site hatched prior to 3 July in 1998, therefore the first date category (178-184) was not included in that year. Similarly, only two chicks of nest sites included in the analyses remained at the site after 25 July in 2000, so the date category of 206-212 was not included in that year.

Because time spent brooding chick by one sex is dependent on the other sex (chicks are continuously brooded by one parent and only one parent can brood at a time), a within-subjects analysis of variance (ANOVA) was used on one sex (males were arbitrarily chosen) to test for brooding differences across years and between the sexes. To meet the assumptions of normality for parametric statistics, “time spent brooding” and “time spent at sea” proportions were square root and arcsine-transformed and lengths of provisioning trips were log-transformed (Sokal and Rohlf 1995). On the rest of the variables, with the exception of number of provisioning trips within a provisioning bout and frequency of role switching (see below), main effects for year (3 levels: 1998, 1999, and 2000), Julian date (5 levels: 178-184, 185-191, 192-198, 199-205, and 206-212), sex (2 levels: males and females) and age of chick (5 levels: 1-4, 5-8, 9-12, 13-16, and 17-20 d) were examined using a mixed within-subjects ANOVA with individual as the subject variable.

Data for number of provisioning trips within a provisioning bout followed a Poisson distribution, therefore, year, date, and sex effects were analyzed using the generalized linear model with individuals as the repeated measures. A within-subjects ANOVA with nest site as the repeated measures was used to test for differences in frequency of role switching across years and Julian date. Interactions were examined in all relevant analyses, however, only significant ones were reported. The Tukey-Kramer Method (Sokal and Rohlf 1995) was applied to make post-hoc comparisons for significant ANOVAs. Pearson's correlations were applied to investigate the relationship between chick age and Julian date, and to correlate frequency of total provisioning trips per day (mates combined) with frequency of daily nest reliefs.

Daily chick feeding rates per hour per pair from dawn to dusk (total daily chick feeds per site divided by 17 hr) were calculated across Julian date for each year. The proportion of time pairs spent together at the site from dawn to dusk (the summed co-attendance time of paired males and females divided by 1020 min and multiplied by 100) was also calculated. This allowed for comparisons with other Common Murre time budget studies conducted in Newfoundland and Labrador (Burger and Piatt 1990; Bryant et al. 1999; Davoren and Montevecchi 2003).

3.2.1.2 Role partitioning within pairs across years

Role partitioning in 14 pairs of murres that successfully reared a chick in all three years (1998 to 2000) was examined. Means for overall daily chick feeding rates and proportion of time spent brooding over 24 hrs were calculated for each individual in each year across the entire chick-rearing period. Role partitioning was said to occur if one mate brooded more while the other mate fed the chick more. To assess if pairs showed role partitioning within years and if the occurrence varied across years, it was determined if pairs were engaging in even or uneven brooding and even or uneven chick provisioning. Mates were said to be even brooders if their brooding time differed less than 7% (one SD of overall brooding all years combined, N = 42). Similarly, mates were said to be even provisioners if their mean daily chick provisioning trips differed less than one SD. Because chick provisioning rates differed across years, the SD was calculated for each separately (1998: 0.75, N = 34; 1999: 0.71, N = 38; 2000: 0.60, N = 38). For all analyses, statistical significance was set at $\alpha = 0.05$ and values are reported as means ± 1 SE.

3.3 RESULTS

3.3.1 Age, Julian date and inter-annual effects on murre time budgets

3.3.1.1 Relationship between age of chick and Julian date

Within a murre colony, chick hatching is usually synchronous, particularly among neighbouring birds (Murphy and Schauer 1996). Consequently, chick age and Julian date were significantly correlated in each year (1998: $r = 0.59$, $P < 0.001$, $N = 115$; 1999: $r = 0.67$, $P < 0.001$, $N = 175$; 2000: $r = 0.83$, $P < 0.001$, $N = 183$).

3.3.1.2 Chick provisioning and foraging effort

Rates of provisioning trips per day varied across age of chick differently in each year (year x age: $F_{8,186} = 3.59$, $P < 0.001$; Fig. 3.1). This significant interaction was due to provisioning trips peaking at different ages in each year (1998: 9-12 d; 1999: 5-8 d; 2000: 13-16 d) but all years showed a subsequent decline (Fig. 3.1). Rates of provisioning trips varied across Julian date (date: $F_{4,140} = 5.97$, $P < 0.001$) and across years (years: $F_{2,66} = 7.12$, $P = 0.002$; Fig. 3.2). Post-hoc analyses showed that individuals returned less frequently with a fish between Julian dates 178-184 compared to the other 4 date categories and that parents brought overall less fish in 2000 compared to the other two years (Tukey-Kramer Method, $P < 0.05$; Fig. 3.2).

Length of provisioning trips varied across age of chick differently in each year (year x age: date: $F_{8,131} = 2.70$, $P = 0.009$; Fig. 3.3). This interaction was due to individuals decreasing the length of their provisioning trips from 256 min at age 1-4 d to 136 min by age 13-16 d in 2000, whereas mean length of provisioning trips remained between 108-181 min across all ages in 1998 and 1999 (Fig. 3.3). Length of provisioning trips also varied across Julian date (date: $F_{4,120} = 2.98$, $P = 0.02$) with provisioning trips decreasing in length from Day 178-198 and thereafter remaining constant (Fig. 3.4).

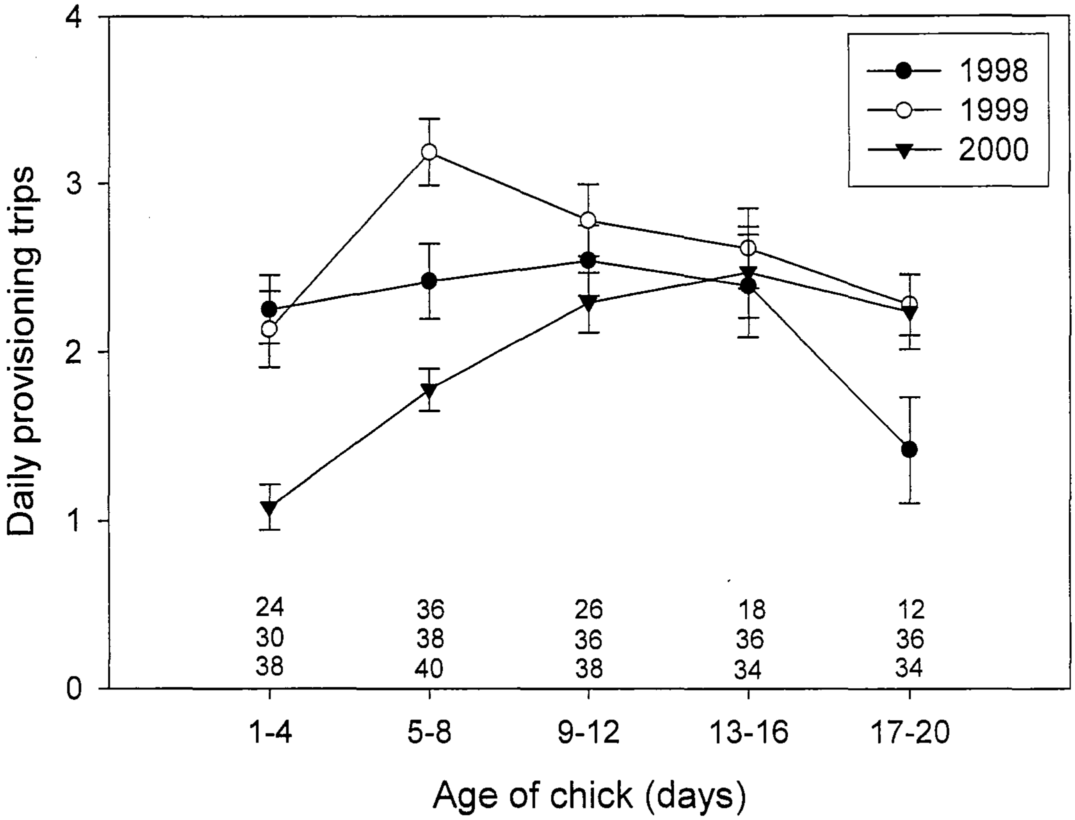

Figure 3.1. Mean (± SE) number of daily provisioning trips made by individual Common Murres (sexes combined) across age of chick (days) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

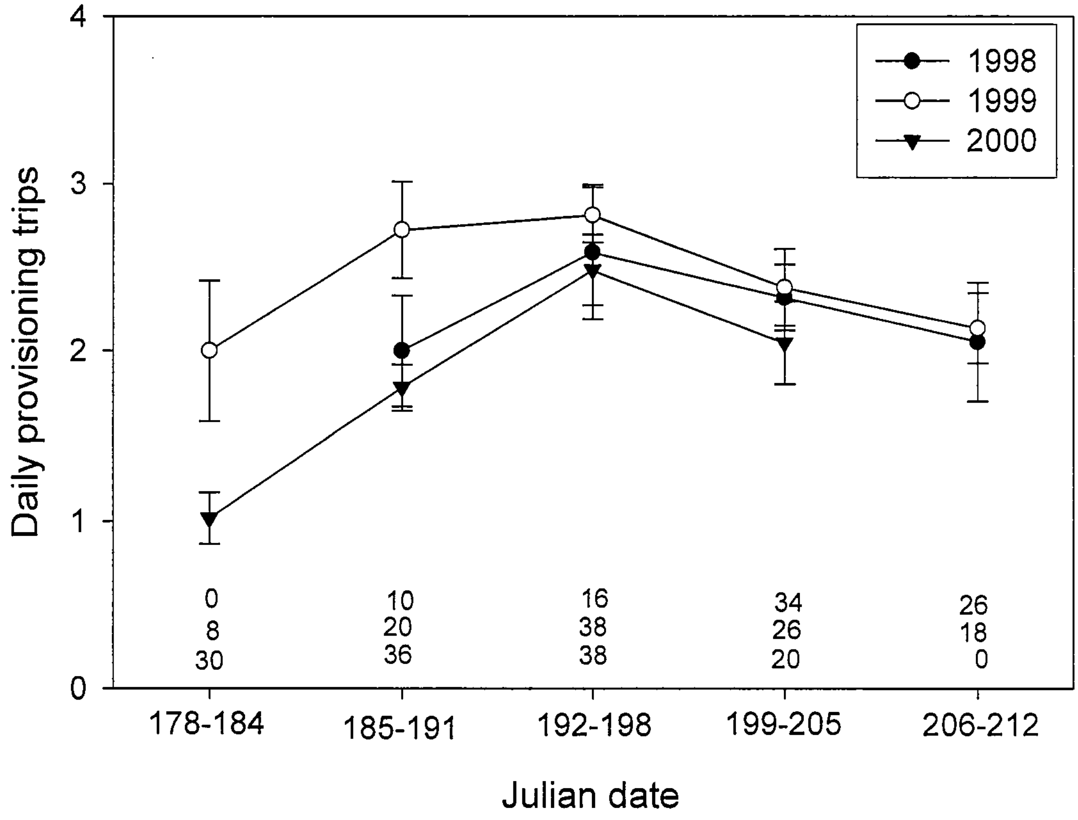

Figure 3.2. Mean (± SE) number of daily provisioning trips made by individual Common Murres (sexes combined) across Julian date from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each date category (top row = 1998; middle row = 1999; bottom row = 2000).

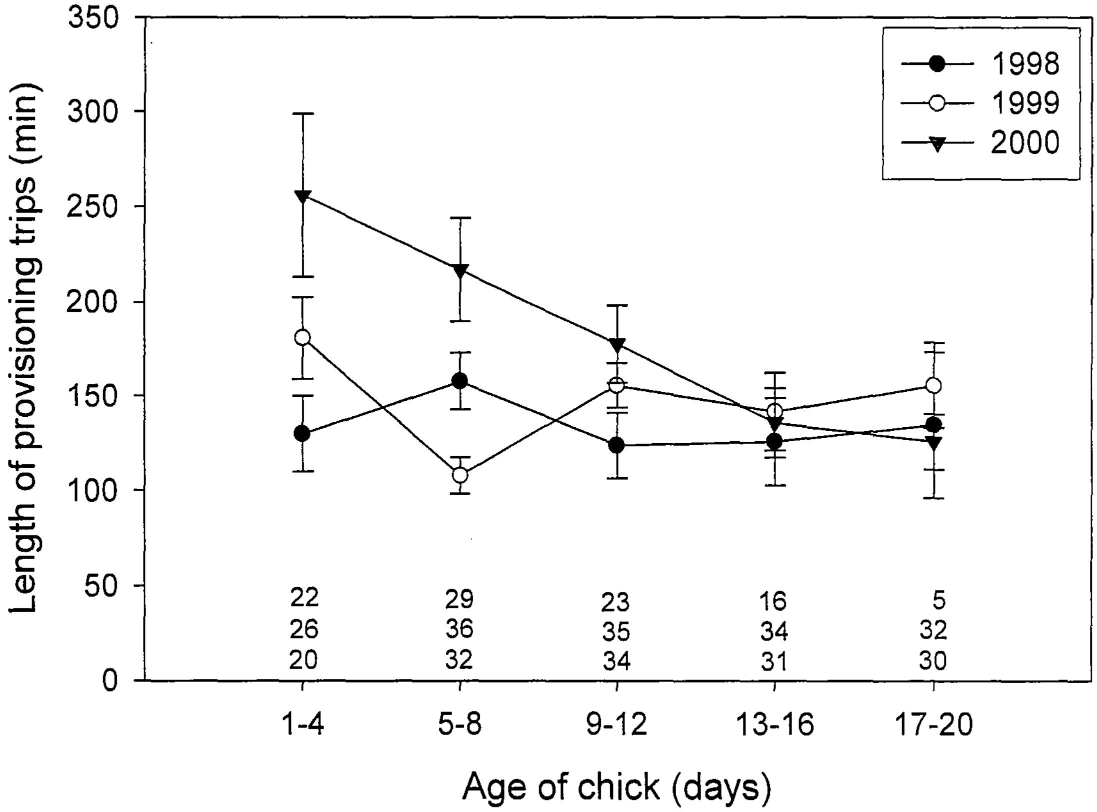

Figure 3.3. Mean (± SE) length of provisioning trips (min) across age of chick (days) by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

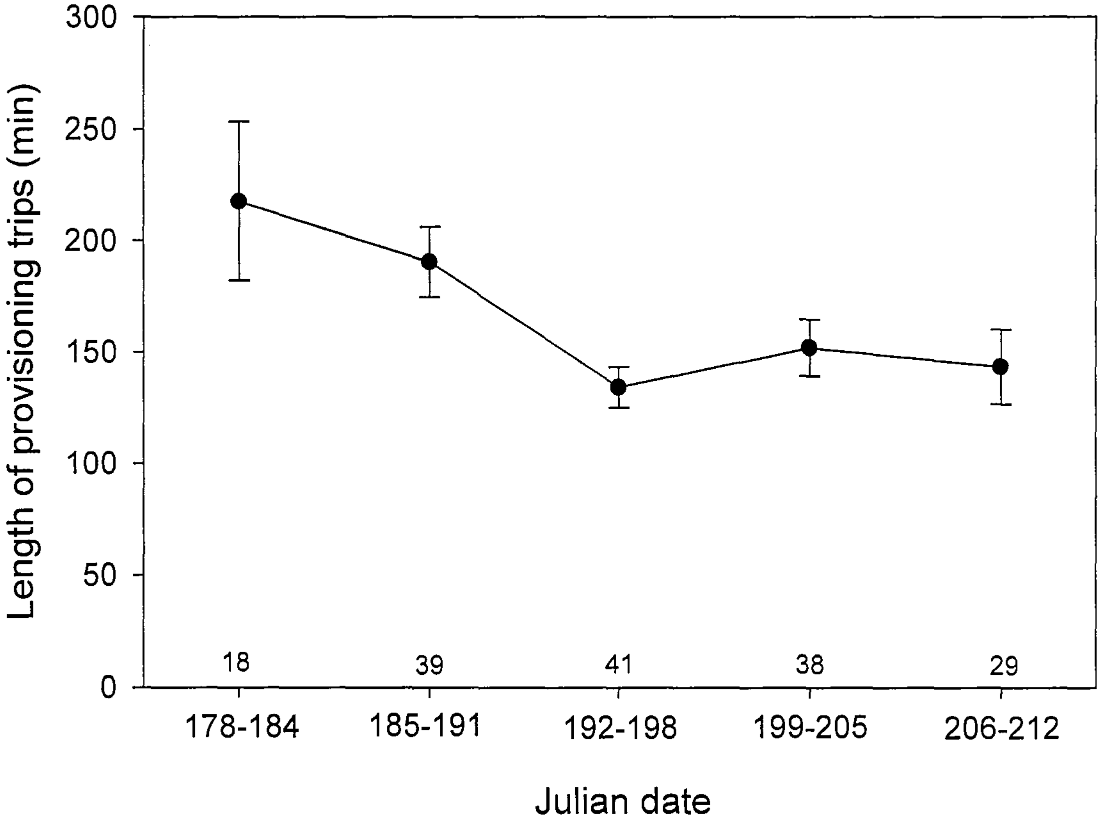

Figure 3.4. Mean (± SE) length of provisioning trips (min) across Julian date by individual Common Murres (sexes and years combined) on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes.

Number of chick feeds within a chick-provisioning bout did not vary across years (generalized linear model: $\chi^2 = 1.86$, d.f. = 2, P = 0.394), date (generalized linear model: $\chi^2 = 4.29$, d.f. = 4, P = 0.369), or age (generalized linear model: $\chi^2 = 4.79$, d.f. = 4, P = 0.310). However sex differences were found (see below). Similarly, time at sea was not affected by date ($F_{4,138} = 1.85$, P = 0.122), age ($F_{4,160} = 0.30$, P = 0.877) or year ($F_{2,66} = 0.33$, P = 0.718). However, males and females differed in mean time spent at sea (see below).

Latency to depart varied across age of chick differently in each year (year x age: $F_{8,162} = 3.05$, P = 0.003; Fig. 3.5) This interaction was due to murres departing the nest site sooner after a brooding shift when chicks were older compared to when chicks were younger, whereas the opposite was true in 2000 (Fig. 3.5). Latency to depart also varied differently in each year across Julian date (year x date: $F_{6,54} = 5.86$, P < 0.001); in 1999, birds consistently departed sooner as the season progressed, whereas latency to depart increased across date in 2000 (Fig. 3.6).

There was a significant interaction between year and age of chick in the amount of time murres spent co-attending their brooding mate ($F_{8,175} = 9.31$, P < 0.001; Fig. 3.7). In 1998 and 1999, co-attendance time decreased as chicks aged; in 2000, however, the opposite trend occurred where co-attendance time was low compared to the other two years until age 9-12 d and suddenly increased two-fold at age 13-16 d (Fig. 3.7). Co-attendance of individuals also varied among years across Julian date (year x date: $F_{6,59} = 12.66$, P < 0.001; Fig. 3.8). In 1999, co-attendance decreased as a function of Julian date,

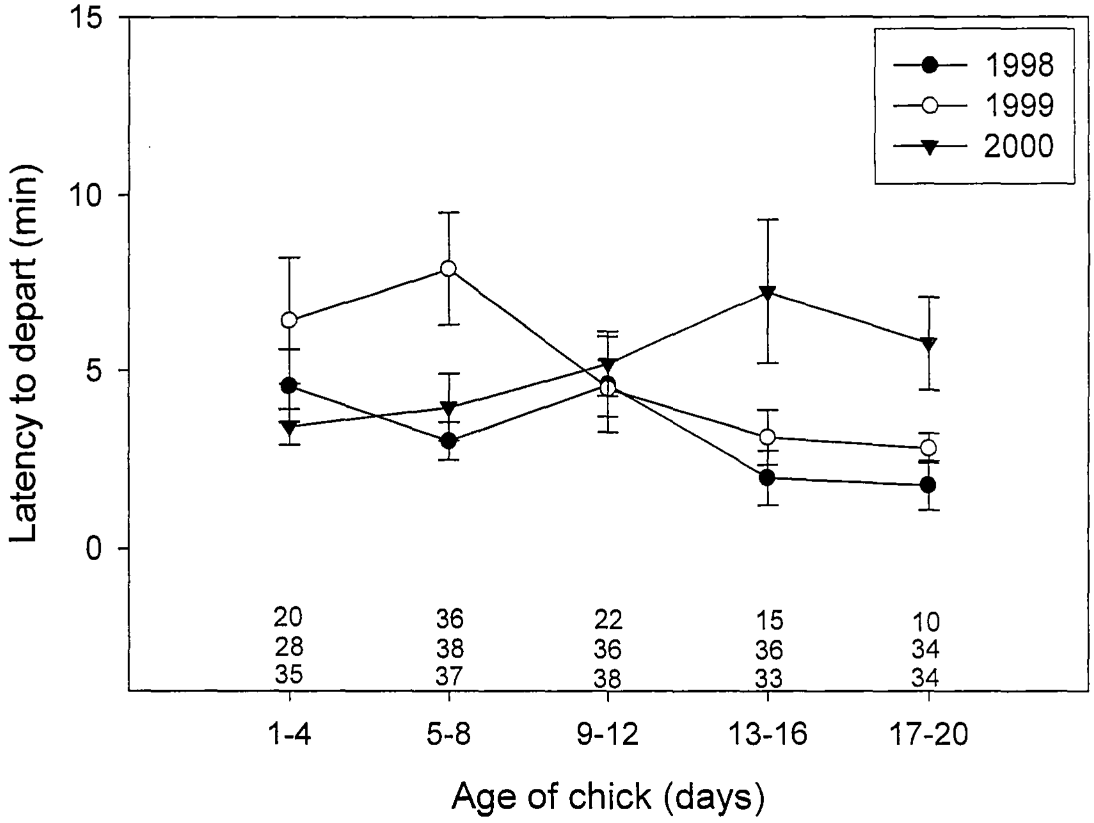

Figure 3.5. Mean (± SE) latency to depart (min) across age of chick (days) by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

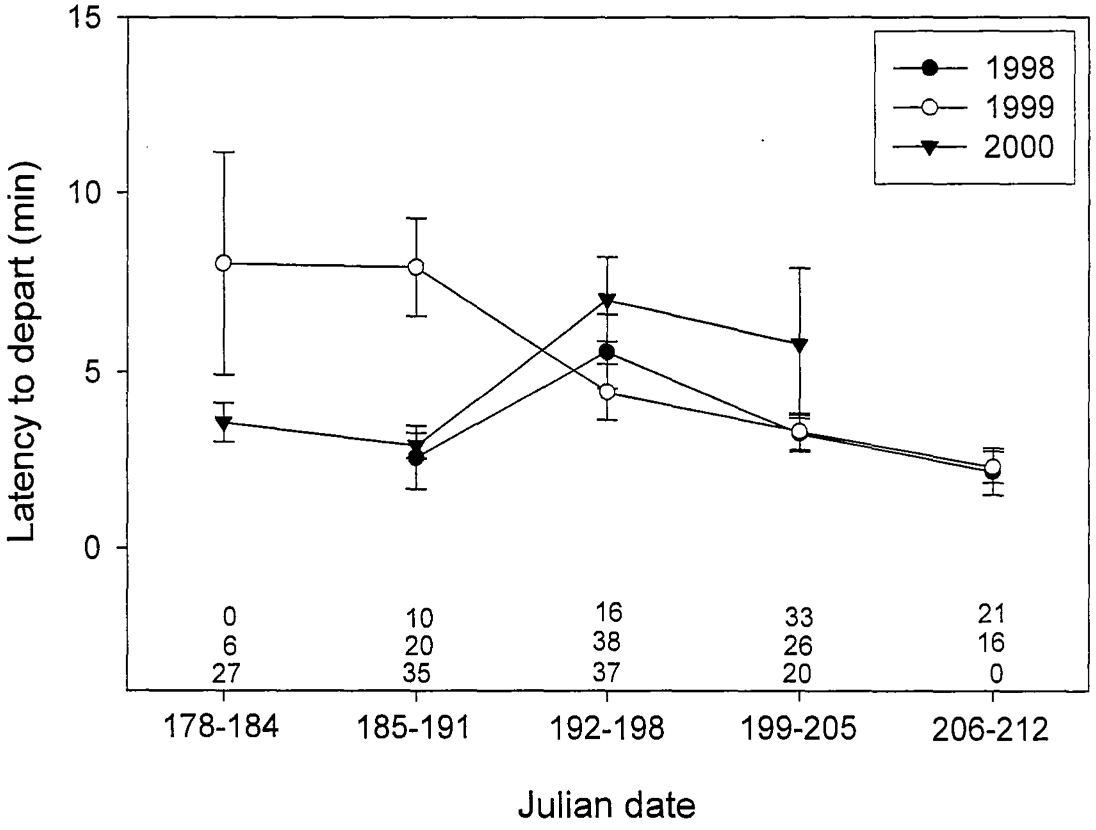

Figure 3.6. Mean (± SE) latency to depart across Julian date by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each date category (top row = 1998; middle row = 1999; bottom row = 2000).

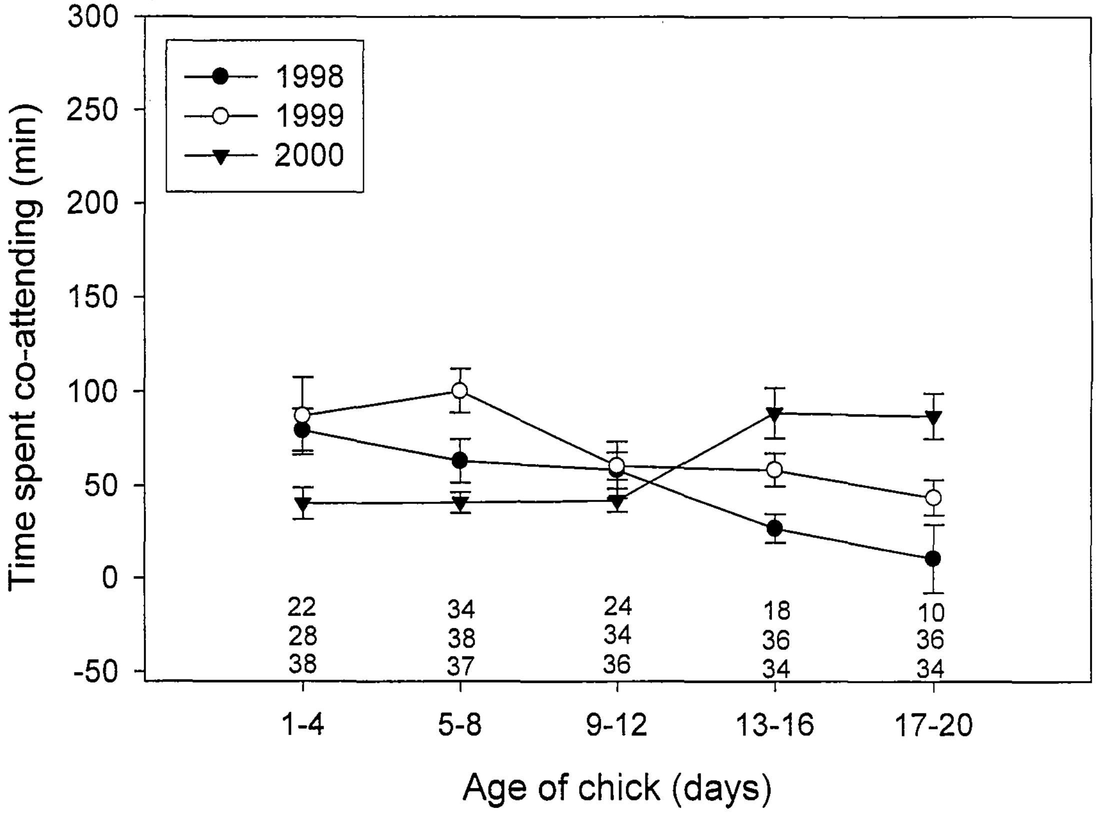

Figure 3.7. Mean (± SE) daily time spent co-attending brooding mate (min) across age of chick (days) by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

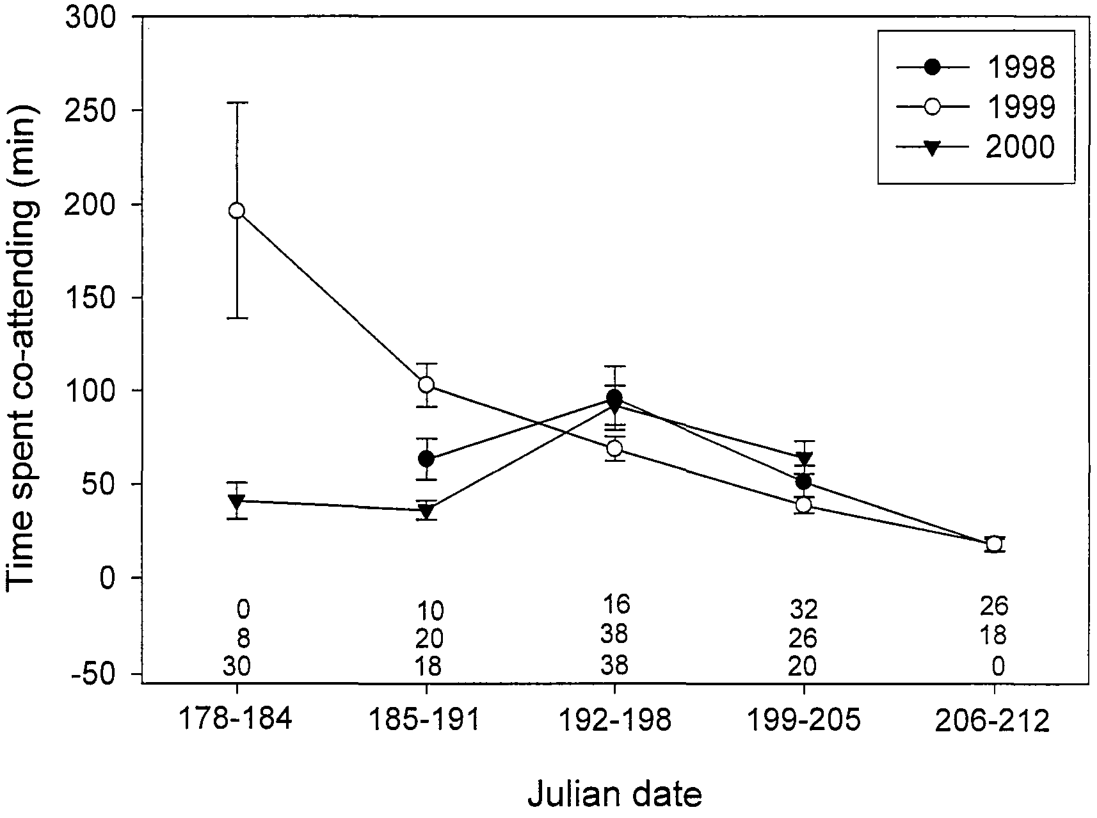

Figure 3.8. Mean (± SE) daily time spent co-attending brooding mate (min) across Julian date by individual Common Murres (sexes combined) from 1998-200 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each date category (top row = 1998; middle row = 1999; bottom row = 2000).

whereas co-attendance in 1998 and 2000 peaked during mid-chick rearing at date 192-198 and subsequently declined (Fig. 3.8).

3.3.1.3 Brooding and role switching

Brooding time was not influenced by date ($F_{4,77} = 0.74$, $P = 0.567$), age ($F_{4,96} = 0.49$, $P = 0.742$) or year ($F_{2,31} = 0.79$, $P = 0.462$). However, sex differences were found (see below).

A year by age of chick interaction was found for time between the arrival of an incoming murre and the occurrence of a role switch with their brooding mate (year x age: $F_{8,16} = 2.08$, $P = 0.04$; Fig. 3.9). In 1998 and 1999, latency to brood decreased from 17 min to approximately 3 min, whereas in 2000, latency to brood peaked at 17 min when chicks were aged 13-16 d (Fig. 3.9). A year x date interaction was also found ($F_{6,54} = 6.05$, $P < 0.001$), with 1998 and 1999 showing a decline in latency to brood as the chick rearing period progressed, whereas 2000 showed an increase across date (Fig. 3.10).

How often mates switched roles within a day varied differently across age of chick for each year (year x age: $F_{8,87} = 7.48$, $P < 0.001$). In 2000, role switching frequency increased as chicks grew whereas in 1998 and 1999, role switching tended to decrease as chicks got older (Fig. 3.11). Role switching also varied across Julian date differently in each year: in 2000, role switching frequency increased as the chick rearing period progressed, whereas in 1998 and 1999, role switching remained constant or decreased (year x date: $F_{6,27} = 4.37$, $P = 0.003$; Fig. 3.12). A positive correlation was

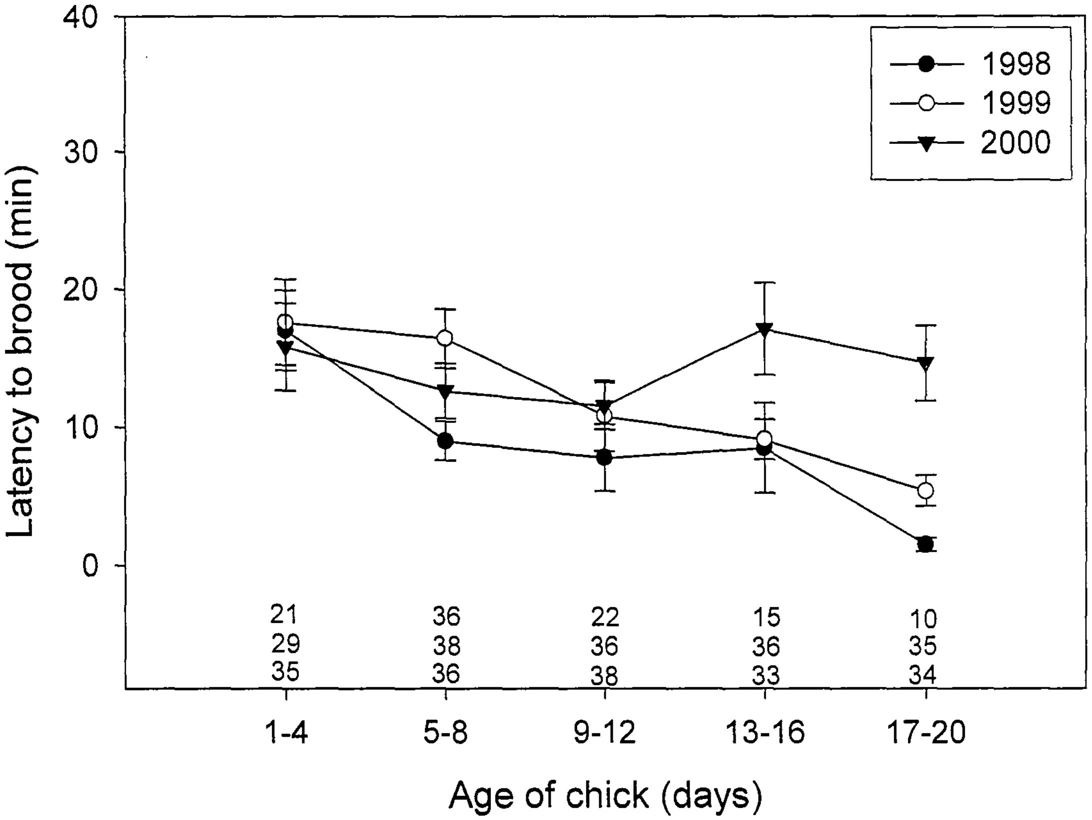

Figure 3.9. Mean (± SE) latency to brood (min) across age of chick (days) by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

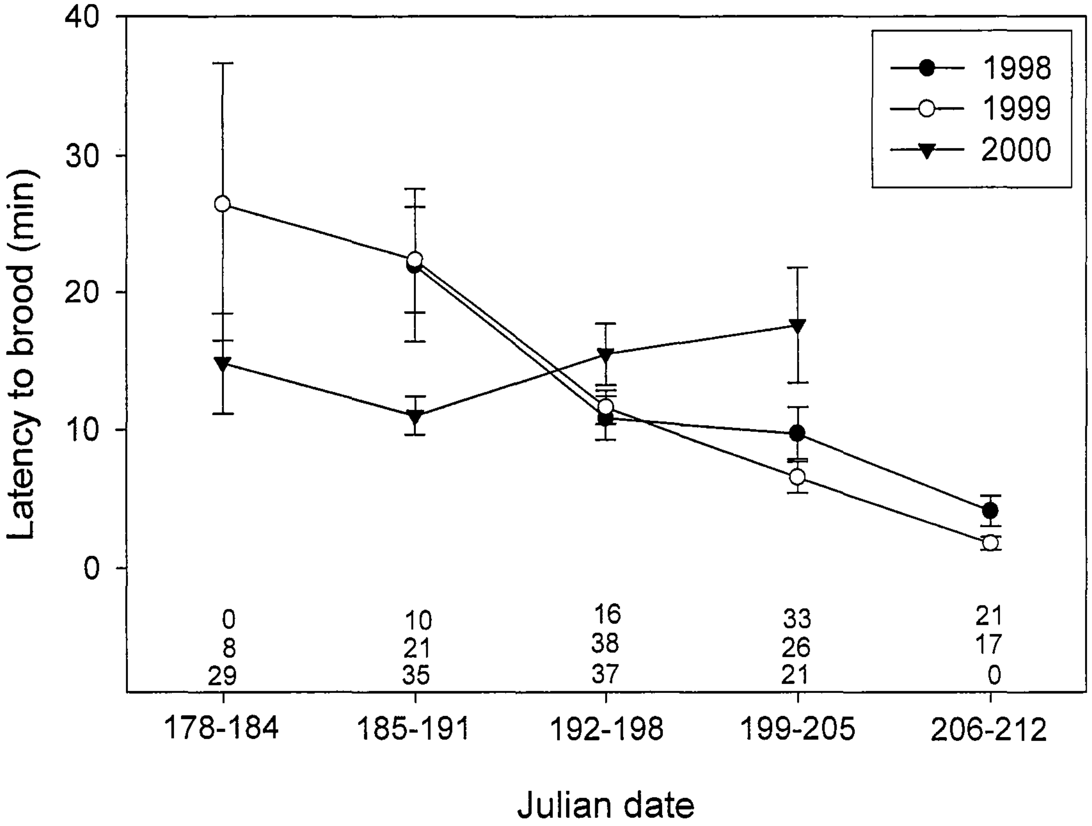

Figure 3.10. Mean (± SE) latency to brood across Julian date by individual Common Murres (sexes combined) from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each date category (top row = 1998; middle row = 1999; bottom row = 2000).

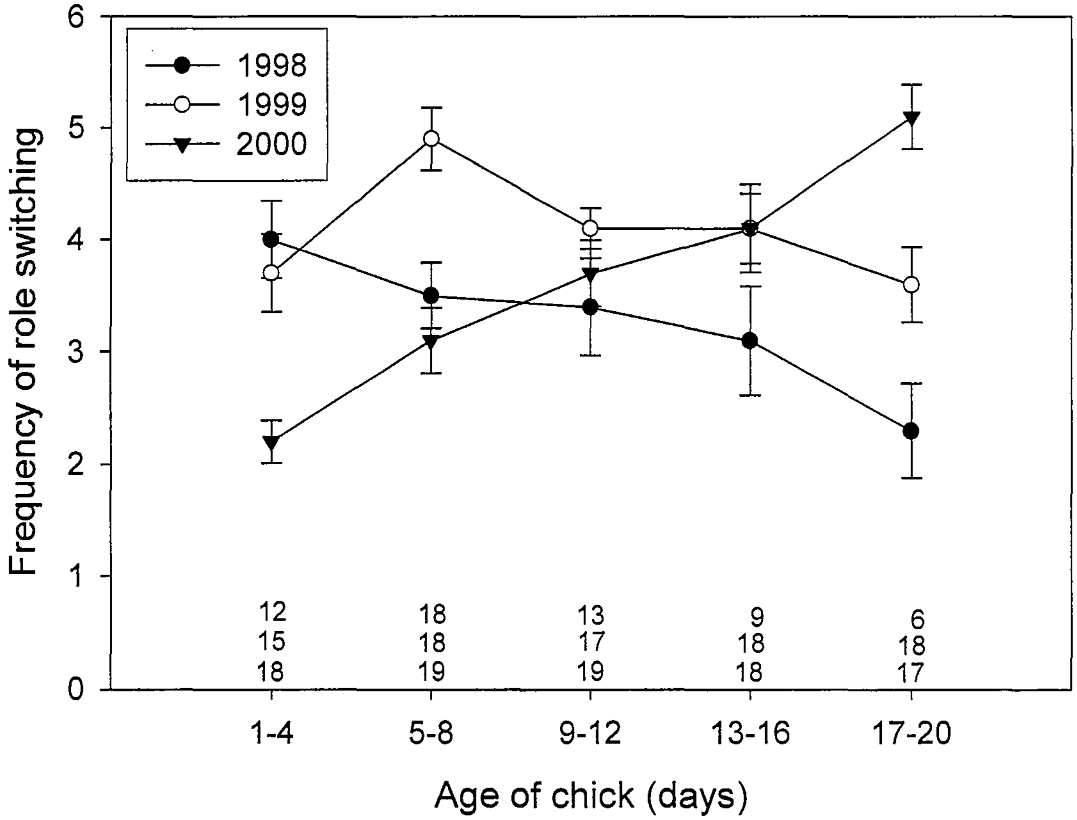

Figure 3.11. Mean (± SE) number of times mates switched roles per day across age of chick (days) by Common Murres from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

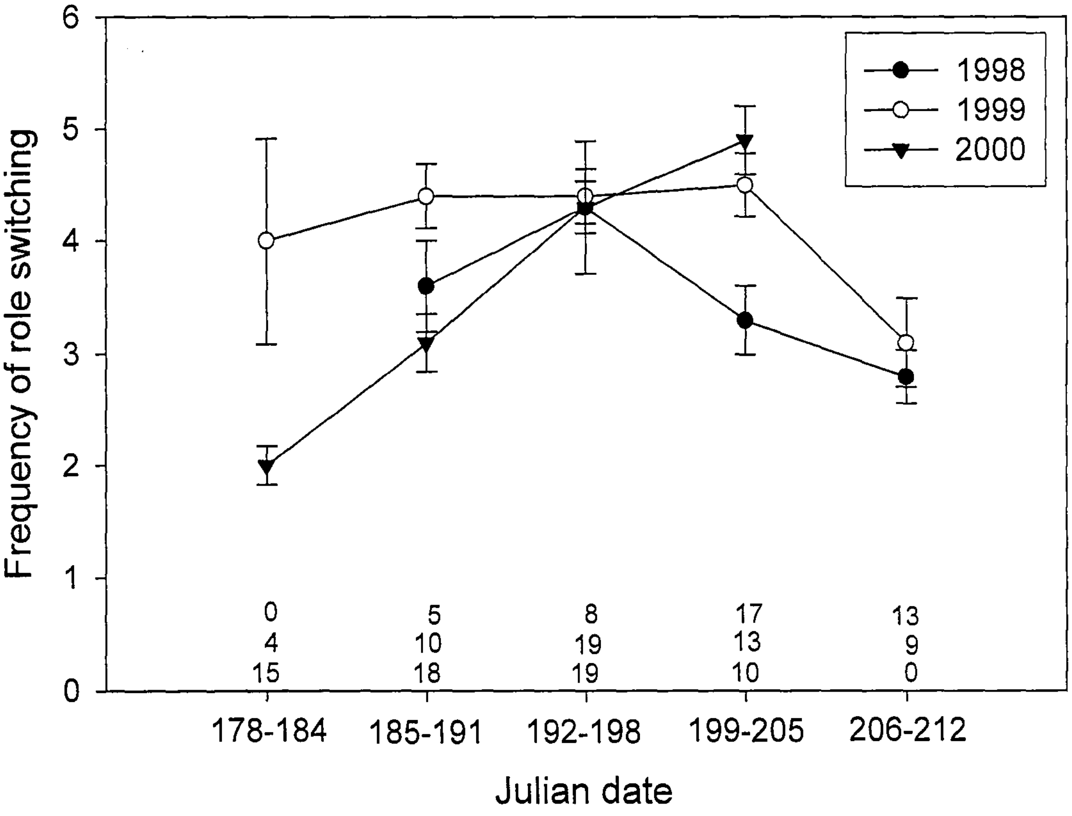

Figure 3.12. Mean (± SE) number of times mates switched roles per day across Julian date by Common Murres from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above x-axis represent sample sizes for each year in each date category (top row = 1998; middle row = 1999; bottom row = 2000).

found between frequency of role switching and total number of provisioning trips per pair (Pearson's correlation: $r = 0.56$, $P < 0.001$, $N = 234$).

3.3.2 Sex differences in murre time budgets

3.3.2.1 Chick provisioning and foraging effort

Across all years, females consistently made more provisioning trips per day than males (sex: $F_{1,40} = 9.17$, $P = 0.004$; Fig. 3.13). Sex differences were also found in length of provisioning trips, however, these varied across years (year x sex: $F_{2,64} = 4.17$, $P = 0.002$), with males showing overall longer provisioning trips in 1998 and females in 2000 (Fig. 3.14).

Females fed the chick more frequently within a provisioning bout compared to males (males: 1.3 ± 0.1 fish/provisioning bout, females: 1.6 ± 0.2 fish/provisioning bout; generalized linear model: $\chi^2 = 9.13$, d.f. = 1, $P = 0.003$). On average, females ($N = 21$) fed the chick twice before a brooding shift whereas males ($N = 21$) typically fed the chick once before switching roles.

Sex differences were also found in time spent at sea ($F_{1,40} = 7.17$, $P = 0.011$) with males spending a higher proportion of their day at sea compared to females (males: 48.7 ± 1.4%, $N = 21$, females: 43.6 ± 1.3%, $N = 21$). However, males and females did not differ in latency to depart to sea after a brooding shift ($F_{1,55} = 1.39$, $P = 0.224$; males: 7 ± 1 min, females: 4 ± 1 min). No difference in co-attendance time was found between the sexes ($F_{1,41} = 0.70$, $P = 0.408$).

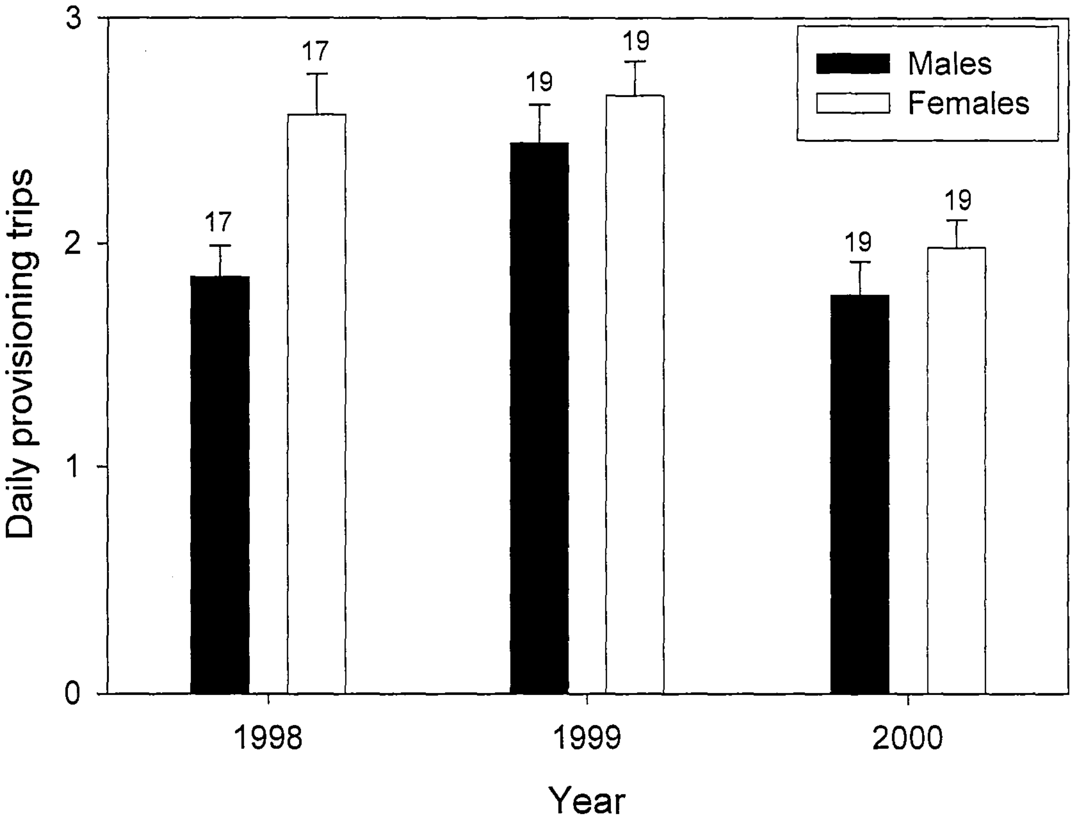

Figure 3.13. Mean (± SE) number of daily provisioning trips made by male and female Common Murres from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above bars represent sample sizes.

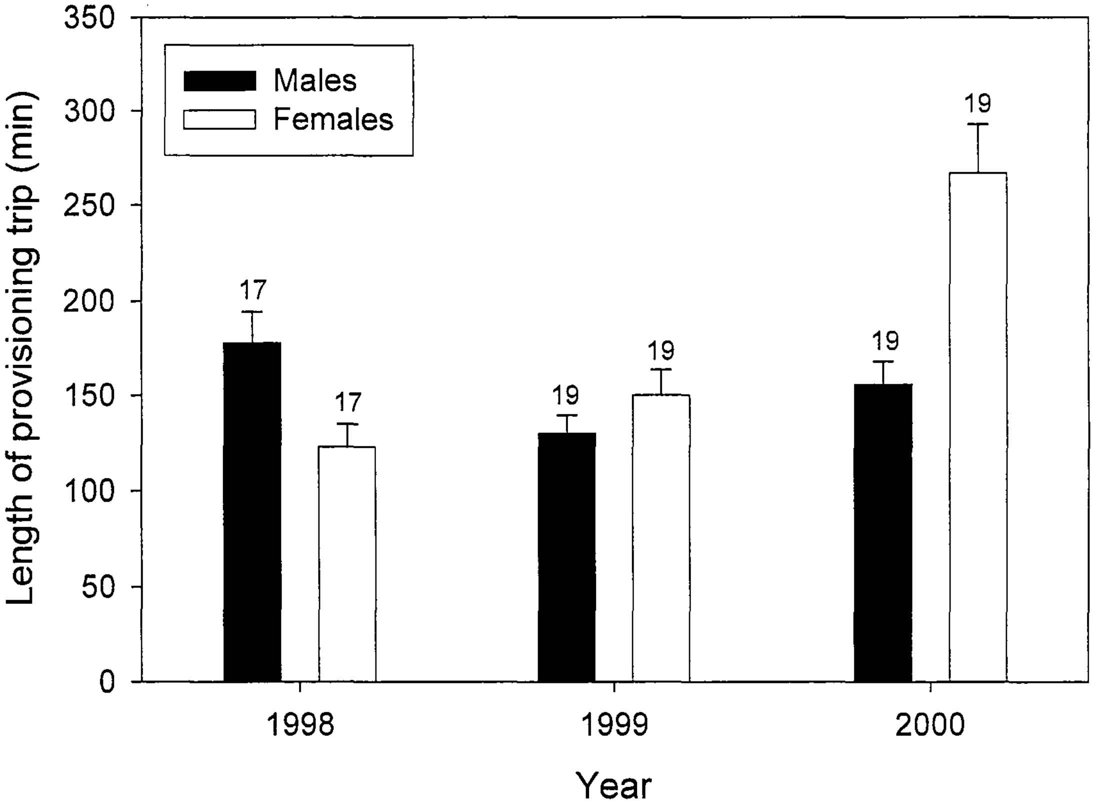

Figure 3.14. Mean (± SE) length of provisioning trips (min) of male and female Common Murres from 1998-2000 on Great Island, Witless Bay, NL, Canada. Numbers above bars represent sample sizes.

3.3.2.2 Brooding

In all years, females spent a higher proportion of their day brooding the chick compared to males (males: 46.9 ± 1.4%, N = 21, females: 52.4 ± 1.4%, N = 21; $F_{1,40}$ = 9.74, P = 0.003). No sex differences were found in latency to brood. Males and females took the same amount of time before beginning a brooding shift upon their return to the site (sex: $F_{1,40}$ = 1.01, P = 0.321).

3.3.3 Role partitioning within pairs

There was no evidence that Common Murres showed individual preference in brooding or provisioning within or across years. Out of 14 pairs, only 1 pair (Site 29) consistently partitioned roles across years, with the male being the primary brooder and the female the primary provisioner (Table 3.1). Site 17 also showed role partitioning in 1999, with the female consistently brooding more and the male bringing one extra fish to the chick per day. More common than role partitioning was the occurrence of one member of the pair brooding <u>and</u> provisioning more than its mate (1998: 1 male and 3 females; 1999: 2 females; 2000: 1 male and 1 female; Table 3.1). Combining years, more females showed higher levels of brooding and provisioning (N = 6) compared to males (N = 2; $\chi^2 = 4.5$, d.f. = 1, $P < 0.05$).

Table 3.1. Differences in brooding and provisioning patterns within 14 pairs of Common Murres breeding on Great Island, Witless Bay, NL, across three years (1998-2000). Number in brackets demonstrates how much more time (%) individual spent brooding or how many more daily chick provisioning trips individual engaged in compared to mate.

Site	1998		1999		2000	
	Brooder	Provisioner	Brooder	Provisioner	Brooder	Provisioner
2	F (23)	S	F (21)	F (1)	F (22)	S
4	S	F (1)	F (16)	S	S	M (1)
5	S	S	M (8)	S	S	M (1)
7	M (18)	S	S	S	S	M (2)
9	M (16)	S	S	S	M (27)	M (1)
10	M (8)	S	S	S	S	S
11	F (27)	S	S	M (1)	F (12)	F (1)
16	S	F (1)	F (8)	F (1)	S	F (1)
17	M (20)	M (1)	F (16)	M (1)	F (17)	S
20	F (39)	F (1)	F (19)	S	S	S
24	S	S	S	F (3)	S	S
25	F (18)	F (2)	F (24)	S	F (18)	S
27	F (29)	F (1)	M (12)	S	S	S
29	M (29)	F (2)	M (27)	F (2)	M (13)	F (2)

M = Male brooded or provisioned more
F = Female brooded or provisioned more
S = Male and female showed same level of brooding or provisioning

3.4 DISCUSSION

3.4.1 Age, Julian date and inter-annual effects on Common Murre time budgets

3.4.1.1 Provisioning trips and foraging effort

Common Murre chick provisioning rates differed with age of chick. Frequency and length of provisioning trips, latency to depart and co-attendance time also varied as a function of chick age. This effect differed across years with the most striking differences occurring between 1999 and 2000 when chicks were aged 1-8 d: although murres exhibited high foraging effort (as shown by faster colony departure after brooding and reduced co-attendance time), adults engaged in fewer and longer provisioning trips in 2000 compared to 1999. When chicks were older than 9 d, provisioning rates increased to "normal" rates, despite reduced foraging effort in 2000.

Some studies of provisioning rates in Common Murres show no significant changes as a function of chick age (Burger and Piatt 1990; Barrett et al. 1997). Others report a quadratic trend with chick feeds increasing as a function of age, peaking at around 6-10 d, and then decreasing (Harris and Wanless 1985; Birkhead and Nettleship 1987; Hatchwell 1991a,b). Chick feeding rates may increase across age of chick to accommodate the energetic requirements of the growing chick, and subsequently decline to promote colony departure. In this study, chick feeding rates peaked at different ages in each year, and particularly late relative to chick age in 2000 (1998: 9-12 d; 1999: 5-8 d; 2000: 13-16 d), suggesting that additional factors to age of chick influenced provisioning rates.

When provisioning rates were plotted as a function of Julian date, all years showed a similar trend: provisioning rates increased from the end of June to mid-July and subsequently declined. Hatchwell (1991a) also found that Common Murre chick feeding rates decreased across calendar date, whereas other studies fail to support such a relationship (Harris and Wanless 1985; Birkhead and Nettleship 1987; Burger and Piatt 1990; Barrett et al. 1997). The general trend of co-attendance decreasing during the last two weeks of chick rearing (July 18-31) compared to mid-season (July 11-18) provides some evidence that murres may have increased their foraging effort later in the breeding season, perhaps in response to a seasonal decline in food supplies. However, the duration of provisioning trips does not support the prey deterioration hypothesis. Long foraging trips can be associated with low prey availability (Monaghan et al. 1994; Davoren and Montevecchi 2003). In this study, trip length remained relatively constant from mid to the end of the chick-rearing period.

3.4.2 Varying provisioning rates, foraging effort and prey availability

This study focused on the same set of established breeding pairs. Therefore, the observed variable provisioning rates and foraging effort within and across years cannot be due to differences in age or experience of individuals. Rather, these differences are most likely attributed to varying prey availability in the vicinity of the breeding colonies. In 1999 and 2000, chicks were fed less during the early part of chick rearing (between 26 June and 3 July), particularly in 2000, compared to later dates.

During the early to mid-1980s, Burger and Piatt (1990) found that capelin abundance in Witless Bay varied across the chick rearing season: capelin abundance was low during early chick rearing, peaked during mid-season and was low again during the fledging period. Although provisioning trips did not differ across the breeding season, parents were able to compensate for low capelin availability by either bringing in more sand lance (*Ammodytes* spp.) or by decreasing their co-attendance time (Burger and Piatt 1990).

In this study, prey abundance also appeared to vary across the season as shown with the low chick provisioning rates despite high foraging effort in 2000. Low chick feeding rates were most likely due to the late arrival of spawning capelin. Inshore spawning capelin were estimated to arrive in Witless Bay on 8 July in 2000 (Julian date 190; G. Robertson, pers. comm.), 9 days after the median hatch date of chicks in this study (29 June, N = 27). Chick feeding rates increased and foraging effort decreased between 3 and 9 July, which coincides with when capelin was estimated to arrive in the vicinity of the breeding colonies. Another contributing factor to the low feeding rates in 2000 may be related to the vertical migration of capelin. Capelin were found in deeper waters (150-400 m) in the spring of 2000 (Mowbray 2002; DFO 2001), behaviour linked to low capelin densities (Mowbray 2002). Although Common Murres have been found caught in fishing gear as deep as 180 m (Piatt and Nettleship 1985), capelin remaining at 200-400 m in the water column are probably too deep for foraging murres to access. Estimates of capelin abundance vary depending on the type of survey used. Catches decreased from 1998-2000 (in thousands of tons: 1998 = 29.8; 1999 = 18.6; 2000 = 16.3;

DFO 2000, DFO 2001), however, so did participation in the capelin fishery (DFO 2001). Acoustic surveys done in May suggest that capelin densities were similar albeit slightly lower in 2000 compared to 1999 (DFO 2001). Inshore acoustic surveys revealed temporal differences in peak capelin densities: capelin density was highest during early July in 1999 whereas capelin concentrations were greatest during late July in 2000 (DFO 2001). Hence, it is likely that capelin distribution and behaviour rather than abundance have led to the observed decrease in capelin availability to murres in 2000.

In contrast, murres appeared to enjoy higher prey availability in 1999, as chick-feeding rates were overall higher despite lower foraging effort. A combination of capelin and sand lance availability may have contributed to this abundance of prey. In 1999, median chick hatching was 7 July (N = 21), 11 days after capelin were estimated to have arrived in Witless Bay (26 June; Massaro et al. 2000). Furthermore, sand lance migrated further north in 1999 and increased their distribution off the east coast of Newfoundland (Anderson 2001). Although sand lance was present in the diet of chicks in 2000 (see Chapter 4), murres were not able to fully compensate for low capelin availability with sand lance as these were perhaps too far south from the breeding grounds for murres to exploit abundantly.

3.4.3 Comparisons of provisioning rates and foraging effort with other colonies in Newfoundland and Labrador

The mean seasonal rates of provisioning trips per pair per day reported in this study are similar to feeding rates reported in other Common Murres colonies in

Newfoundland and Labrador conducted in the 1980s and 1990s (Table 3.2). The only exception being Funk Island, where chicks were fed at low rates due to adults having to travel far distances (~ 45 km) to find capelin (Davoren et al. 2003). The body mass of departing chicks is lowest on Funk Island compared to other colonies in Newfoundland and Labrador (Davoren and Montevecchi 2003). Interestingly, when daily provisioning trips per pair for this study were calculated as a function of weeks into the chick-rearing period, chick-feeding rates for Week 1 (Julian date 178-181) and Week 2 (Julian date 182-191) were 1.0 ± 0.12 feeds per d and 1.8 ± 0.21 feeds per d respectively. These rates are comparable to rates observed on Funk Island. These observations further suggest that adults were having difficulties provisioning their chicks during early chick-rearing in 2000, and were most likely traveling far distances to locate prey.

Murres in this study showed similar trip durations and co-attendance time as another study conducted on Great Island during the same time period (1998-1999), but on different birds from a nearby colony (Davoren and Montevecchi 2003; Table 3.2). However, murres showed considerable variation in foraging effort between islands. Murres breeding on offshore islands (Funk and Gannet) had longer provisioning trips and/or spent less time co-attending their brooding mate compared to murres breeding on inshore islands (Gull and Great) in Witless Bay (Table 3.2). Furthermore, foraging effort appears to have increased since the 1980s: murre co-attendance has decreased by half whereas trip duration appears to have increased (Table 3.2). These behavioural changes concur with the concern that capelin abundance has declined since the 1980s (reviewed in Carscadden et al. 2002).

	Feeds per chick per h	% time pairs spent together at colony	Length of provisioning trips (min)		Source
Great Island					
(47°11'N, 52°49'W)			Mean ± se	Median	
1998	0.26 ± 0.01	9.5 ± 1.3	152.2 ± 13.3	133	This study
1999	0.31 ± 0.01	14.2 ± 1.9	145.2 ± 9.5	135	
2000	0.22 ± 0.01	11.3 ± 1.1	170.1 ± 15.2	154	
1998	0.22 ± 0.02	11.9 ± 1.4	163.3 ± 1.5	120-179[1]	Davoren and Montevecchi (2003)
1999	0.22 ± 0.02	11.4 ± 1.9	147.6 ± 12.1	120-179[1]	
Gull Island					
(47°16'N, 52°46'W)					
1983	0.24 ± 0.02	33.5 ± 10.8	---	100-132[1]	Burger and Piatt (1990)
1984	0.29 ± 0.02	19.4 ± 9.7	---	100-132[1]	
1985	0.26 ± 0.03	28.4 ± 13.0	---	100-132[1]	
Funk Island					
(49°45'N, 53°49'W)					
1998	0.10 ± 0.04	14.6 ± 4.0	244.9 ± 42.5	180-239[1]	Davoren and Montevecchi (2003)
1999	0.17 ± 0.04	10.6 ± 2.0	214.6 ± 21.8	120-179[1]	
Gannet Islands					
(53°57'N, 56°31'W)					
1997	0.25[1]	3.8[1]	---	---	Bryant et al. (1999)

[1] Values estimated from figures.

3.4.4 Sex differences in Common Murre time budgets

At the group level, females showed higher investment during the pre-departure chick-rearing period compared to males. Females spent more time brooding and provisioned the chick more frequently. Females also engaged in longer provisioning trips in 2000, the season when capelin availability appears to have been low. Length of provisioning trip is a good predictor of amount of time spent flying and diving. Individuals engaging in longer trips make more dives within a diving bout (Monaghan et al. 1994; Falk et al. 2000) and fly further from the colony (Falk et al. 2000), two activities which involve high energy expenditure (Gabrielsen 1996). Females were perhaps more persistent in finding prey when capelin was difficult to obtain because of differences in self-maintenance requirements between the sexes. Although there is little sexual dimorphism, males are structurally larger (culmen length, bill depth, and tarsus; Threlfall and Mahoney 1980) and can be heavier in body mass (Harris and Wanless 1988; Threlfall and Mahoney 1980). Overall, males spent more time at sea than females and showed lower chick provisioning effort. It is possible that males require a higher daily caloric intake than females and therefore need more time to forage for themselves, particularly if feeding conditions are poor.

Females typically engaged in two successive provisioning trips before switching roles whereas males on average fed the chick once between two brooding bouts. This difference in chick provisioning strategy may explain how females can provision and brood more, without compromising other time budget activities. Females may be more efficient provisioners by feeding the chick twice before a brooding bout. Common

Murres may use their memory to find predictable areas of prey at sea as shown by the use of regular flight paths to and from the colony to these areas (Davoren et al. 2003). Returning immediately to the foraging site after having fed the chick would increase the likelihood that aggregated fish were still in the same location, thereby reducing the search time to find a capelin.

The conflicting finding that females engaged in longer provisioning trips, fed the chicks more often, spent overall more time at the colony yet spent less time at sea compared to males in 2000 may be reconciled by taking into account trips where a bird returned with no fish (non-provisioning trip). Preliminary analyses show that males are responsible for a higher proportion of non-provisioning trips (69%) compared to females (31%; pers. obs.). Although individuals infrequently returned without a fish (average of 0.33 non-provisioning trips per d in all years; pers. obs.), male provisioning trips would be shortened if they returned to the colony without a fish prior to a chick feed.

3.4.5 Brooding behaviour

The findings that Common Murres spent 47-52% of a 24-hr day brooding the chick, independent of year, are similar to the only other 24-hr study done on the closely related Thick-billed Murre. Falk et al. (2000) reported that birds spent 50% of their daily time budget brooding the chick in a year when food availability was thought to be low. Brooding makes up as much of an individual's time budget as all other activities combined, and does not appear to respond to a variable environment, suggesting that a chick's survival largely depends on how well it is brooded. Chicks aged below 8 days cannot increase their body heat to survive cold weather (Johnson and West 1975) and therefore need to be kept warm and dry under the wing of a parent. In addition, murre nest sites are especially vulnerable to predation and groups of adults must be present to protect the young from avian predators (Hatchwell 1991b; see Chapter 2).

3.4.6 What are non-brooding murres doing at the colony?

Previous studies examining murre co-attendance have used terms such as "resting" (Burger and Piatt 1990; Uttley et al. 1994) or "loafing" (Zador and Piatt 1999) to describe what birds may be doing at the colony when they are present with their brooding mate. Although murres are spending part of this time in a non-active state, these characterizations underestimate the level of interaction between mates. Co-attendance time may have other important functions, including site defense, pair bond maintenance (Davoren and Montevecchi 2003), or role switching. The average time required in switching roles after the arrival of the non-brooder was 13 min. Furthermore, role-switching frequency increased with chick provisioning rates. Therefore, the observed low co-attendance time in 2000 when foraging effort was high, and presumably food conditions were poor, was directly influenced by a decrease in frequency of role switching. This suggests that an important proportion of co-attendance time is spent in the process of role switching. Gaston and Nettleship (1981) also observed that Thick-billed Murres spent more time together at the site when a role switch occurred. However, opposite to findings in this study, role switching was more frequent in Thick-billed Murres during a low food year (Gaston and Nettleship 1981).

3.4.7 Role partitioning at the pair level

Role partitioning (e.g., one adult broods more while the other provisions the chick more) has been proposed to increase the level of cooperation between mates, thereby reducing the energetic demands of chick rearing, particularly during stressful conditions such as low food conditions (Nol 1985). This theory does not appear to apply to Common Murres as only 7-14% of pairs showed role partitioning in any given year. Furthermore, frequency of role partitioning was not higher in 2000, when chick-rearing conditions were presumably more stressful as a result of increased foraging efforts.

In certain bird species, role partitioning during the chick-rearing period may be selective (e.g., Nol 1985). However, in species where chick-rearing activities are uneven energetically (e.g., flying versus brooding), role partitioning may not be advantageous and may cause more desertion. There is evidence that in Common Murres, uneven chick provisioning within pairs may be a symptom of lack of complementarity. Murres sometimes switch partners when provisioning rates are not equal between mates and it is the high provisioning pair-member that initiates the split (Moody et al. 2001).

3.4.8 Conclusion

Common Murre time budgets can be highly variable within and across seasons, as shown by using data on the same established pairs across several years. The close relationship between chick age and Julian date makes it difficult to assess whether it is the varying demands of the growing chick or factors related to seasonal changes (e.g., prey availability) that are linked to the intra-seasonal time budget fluctuations. Most likely, it is a combination of the two. However, low chick provisioning rates and high foraging effort observed in 2000 were most likely due to low capelin availability during early chick rearing. Furthermore, inter-decadal differences in foraging effort also appear to be driven by prey availability. The view that capelin availability has declined since the 1980s (reviewed in Carscadden et al. 2002) concur with the finding that murres currently breeding in Witless Bay are generally working harder to maintain similar chick feeding rates as those reported in the 1980s. This also appears to be the case for birds breeding in the Gannet Islands (Bryant et al. 1999).

At the group level, females showed greater overall investment than males during the chick-rearing period at the colony. However, when investigating role partitioning at the pair level it became apparent that both sexes tend to engage equally in behaviours related to chick rearing, independent of variable breeding conditions. Nonetheless, there is evidence that females may have a more flexible time budget than males. Differences in self-maintenance requirements between the sexes, if these exist, may explain why females tend to feed and brood the chick more when sex differences do occur. Alternatively, females may show a tendency to invest more during the chick-rearing period at the colony to compensate for the additional investment males provide when they take the chick to sea (Harris and Birkhead 1985).

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CHAPTER 4 Temporal comparisons in feeding ecology and growth of Common Murre (*Uria aalge*) chicks

4.1 ABSTRACT

Short and long-term changes in feeding ecology of Common Murres (*Uria aalge*) breeding in Witless Bay, Newfoundland, were investigated across three consecutive breeding seasons (1998-2000). The relationship between feeding rates and two chick growth parameters (mass and wing length) was examined. Chick provisioning rates were highly variable within and across seasons. In all years, provisioning rates were lowest during the first week of chick rearing and peaked during mid-July (Julian date 192-198). During the first week of chick rearing in 2000, chicks were fed at very low rates (2 fish/d). These low rates were attributed to the late arrival of inshore spawning capelin (*Mallotus villosus*). In all years, chicks were fed primarily medium-sized capelin. In 1999 and 2000, their diets were supplemented with sand lance. When capelin availability appeared to be low, a higher proportion of large sand lance appeared in the diet. Chick mass did not differ across years. However, at the individual level, a positive relationship existed between feeding rates and chick mass. Chicks reared in 2000 had longer wings than same aged chicks reared in 1998 and 1999. During unfavorable breeding conditions, wing growth may be prioritized to allow earlier departure. Overall, the diet and condition of Common Murre chicks reared in Witless Bay are similar to those reported in the 1980s, despite important changes in capelin biology and distribution in the Northwest Atlantic.

4.2 INTRODUCTION

In the spring, many seabirds return to land to breed, often in large dense colonies. Off the east coast of the island of Newfoundland, this spatial and temporal clustering of birds is generally timed to coincide with the inshore arrival of spawning capelin (*Mallotus villosus*), the main prey fed to many seabird chicks (e.g., Massaro et al. 2000; Davoren and Montevecchi 2003). Prior to 1990, capelin was also the primary prey item for Common Murres (*Uria aalge*) breeding off the coast of Labrador (Birkhead and Nettleship 1987). Following a sharp decline in capelin abundance in Labrador waters, murre chicks were fed primarily daubed shannies (*Lumpenus maculates*; Bryant et al. 1999). This diet shift had no apparent effect on chick feeding rates and growth, although adults were exhibiting high foraging effort as shown by low co-attendance time at the colony (Bryant et al. 1999).

The impact of changes in capelin biology is also of growing concern on Common Murres and other seabirds breeding off the east coast of Newfoundland. There is some evidence that capelin abundance may have decreased since the 1980s while capelin size and condition continue to decline throughout the 1990s (reviewed in Carscadden et al. 2002). Furthermore, inshore migration and spawning of capelin was delayed by one month in 1991, due to unusually cold sea temperatures (Carscadden et al. 1997). Although sea temperatures have returned to normal, delayed inshore spawning has persisted at least to the 2000 season, presumably because of their smaller size (Carscadden et al. 2002). Spawning times are associated with size of capelin with smaller capelin spawning later (Carscadden et al. 1997).

The Witless Bay Ecological Reserve, located off the south east coast of Newfoundland, supports approximately 100,000 breeding pairs of Common Murres on three islands: Gull, Green and Great Island (Canadian Wildlife Service, unpubl. data). A study conducted on Gull Island from 1982-85 reported that murre chick diet was primarily capelin supplemented by sand lance (*Ammodytes* spp.; Burger and Piatt 1990). Furthermore, hydroacoustic data showed that capelin abundance varied intra-seasonally in two of the four years of the study. Low capelin abundance was related to higher foraging effort and, in at least one year, to lower capelin but higher sand lance proportions in the chicks' diet. Chick feeding rates and fledging success did not vary across years, suggesting that parents were able to compensate for reduced capelin abundance by increasing their foraging effort and/or bringing in more sand lance to the chicks (Burger and Piatt 1990).

Common Murres breeding on Great Island showed variable foraging effort and chick feeding rates within and across three consecutive breeding seasons (1998-2000; Chapter 3). Despite high foraging effort, parents fed the chicks at low rates during early chick rearing in 2000, suggesting that prey availability was low presumably due to the late arrival of spawning capelin (see Chapter 3). In 1999, however, adults fed chicks at high rates with lower foraging effort compared to the other years. It was suggested that the high chick feeding rates might have been due to chick hatching occurring well after the inshore arrival of spawning capelin and/or a higher proportion of sand lance availability around the breeding colonies (see Chapter 3).

This study investigated short and long-term changes in feeding ecology of Common Murres breeding in Witless Bay, Newfoundland. Changes in chick feeding rates and diet (prey type and size) within and across three consecutive years (1998-2000) were examined. In light of the changes in capelin abundance and breeding biology since the 1980s, prey type and size were also compared between decades (early 1980s versus late 1990s and 2000). Because chick growth is directly linked to the amount of food parents bring to their young (e.g., Harris 1978), the relationship between feeding rates and two chick growth parameters (mass and wing length) was examined within and across years, and in comparison to other Common Murre colonies.

4.3 METHODS

This study was conducted on a sub-colony of Common Murres nesting at high density on a broad ledge (1.6 m x 2.5 m area containing 30 breeding pairs) on Great Island (47° 11'N, 52° 49'W), Newfoundland and Labrador (NL), Canada, from June to August 1998-2000. Continuous observations, beginning at dawn (first light after 04.30 h) and finishing at dusk (last light before 21.30 h), were made on 11 days in 1998 (175.8 hr total), 15 days in 1999 (238 hr total) and 12 days in 2000 (190.8 hr total).

4.3.1 Chick provisioning rates and diet composition

Number of daily chick feeds, type and size of prey were determined by direct observation of fish being carried in the bill by adults and delivered to the chick. During 1998, fish species were identified as "capelin" or "other". In 1999 and 2000, fish species were identified as "capelin" or "sand lance". Fish sizes were estimated by the length of fish (including tail) protruding from the bird's bill tip upon its arrival at the nest site and designated to one of three size classes: small (< 3 cm of fish length protruding from bird's bill), medium (3-6 cm) and large (> 6 cm). Diet composition was investigated in relation to age of chick and across Julian date.

4.3.2 Chick body mass and wing length

Body mass (±1 g, with a 300 g Pesola spring scale) and wing length (±1 mm, from the carpal joint to the tip of the longest primary, with a ruler) were obtained from chicks aged 12-20 d in each year (1998: N = 13, 1999: N = 14, 2000: N = 18). To minimize disturbance, chicks were measured only once, when captured for banding. The hatching date of a chick was determined by: i) observing the actual hatching (N = 15), ii) seeing a chick at a site where there had not been a chick on the previous observation day (N = 24) or iii) counting forward the mean incubation period (33 days, pers. obs.; N = 7) from the date the egg was laid.

4.3.3 Data analysis

A mixed within-subjects analysis of variance (ANOVA) with nest site as the subject variable was used to compare mean number of daily chick feeds (total number of fish received by both parents within a day) across age of chick (6 categories: 1-4 d, 5-8 d, 9-12 d, 13-16 d, 17-20 d, 21 d to departure) among years (1998: N = 22; 1999: N = 20; 2000: N = 25). Calendar dates were transformed into Julian dates and grouped into 7-d categories: Julian date 178-184, 185-191, 192-198, 199-205, and 206-212. Provisioning rates were compared across Julian dates among years. The Tukey-Kramer Method (Sokal and Rohlf 1995) was applied to make pair-wise comparisons for significant ANOVAs. All interactions were examined, however, only significant ones were reported.

Chi-squared tests were used to investigate differences in type and size of prey delivered to chicks across years for three age categories separately (1-8 d, 9-16 d and 17 d to departure) and within each year across the three age categories. Chi-squared tests were applied to assess if prey species differed within each year across Julian date. If a significant difference was found, pairwise comparisons were made using the Yates' correction (Sokal and Rohlf 1995).

To quantify differences in chick growth parameters between years, an analysis of covariance (ANCOVA) with age as a covariate was conducted on each growth parameter separately. Chicks were matched by age (N = 10) to ensure that the mean age in each year was the same (15.2 d). Wing lengths were log-transformed to homogenize the variance. Pairwise comparisons were adjusted using the Bonferroni correction.

To assess if provisioning rates were related to chick growth, mean daily chick feeding rates to age of capture was calculated for all chicks and grouped into three age categories: 12-14 d, 15-17 d, and 18-20 d. A Pearson's correlation was subsequently applied to examine the relationship between chick feeding rates with chick mass and wing length. All values are reported as means ± SE. Statistical significance was set at $\alpha = 0.05$.

4.4 RESULTS

4.4.1 Chick provisioning rates

Mean number of daily chick feeds varied differently across age of chick in each year ($F_{8,89} = 4.47$, $P = 0.0001$). The significant interaction was due to chick feeding rates peaking at age 13-16 d in 2000, whereas provisioning rates in 1999 peaked earlier at 5-8 d and subsequently decreased (Fig. 4.1).

When plotted across Julian date, provisioning rates differed across years ($F_{2,32} = 9.52$, $P = 0.0006$) and across date ($F_{4.68} = 9.08$, $P < 0.0001$; Fig. 4.2). Overall, daily chick-feeding rates were significantly lower in 2000 (3.66 ± 0.12 fish per day, $N = 25$) compared to 1999 (4.81 ± 0.15 fish per day, $N = 20$; Tukey-Kramer Method, $P < 0.05$), with chicks being fed on average one extra meal per day in 1999. In all years, provisioning rates were lowest during the first week of chick rearing and peaked between Julian dates 192-198 at approximately five feeds per day (Fig. 4.2).

4.4.2 Species and size of fish fed to chicks

Capelin dominated the diet of Common Murre chicks throughout the chick-rearing period in all years (Fig. 4.3). However, chick diet composition varied significantly among years in all three age groups (1-8 d: $\chi^2_2 = 10.99$, $P < 0.01$; 9-16 d: $\chi^2_2 = 11.17$, $P < 0.01$; 17 d to fledging: $\chi^2_2 = 15.06$, $P < 0.01$). Chicks were fed a higher proportion of sand lance in 2000 compared to 1998, regardless of age of chick (1- 8 d: $\chi^2_1 = 9.40$, $P < 0.01$, Fig. 4.3a; 9-16 d: $\chi^2_1 = 5.80$, $P < 0.05$, Fig. 4.3b; 17 d to departure: $\chi^2_1 = 9.26$, $P < 0.01$, Fig. 4.3c). In 1999, chicks were also fed more sand lance compared to

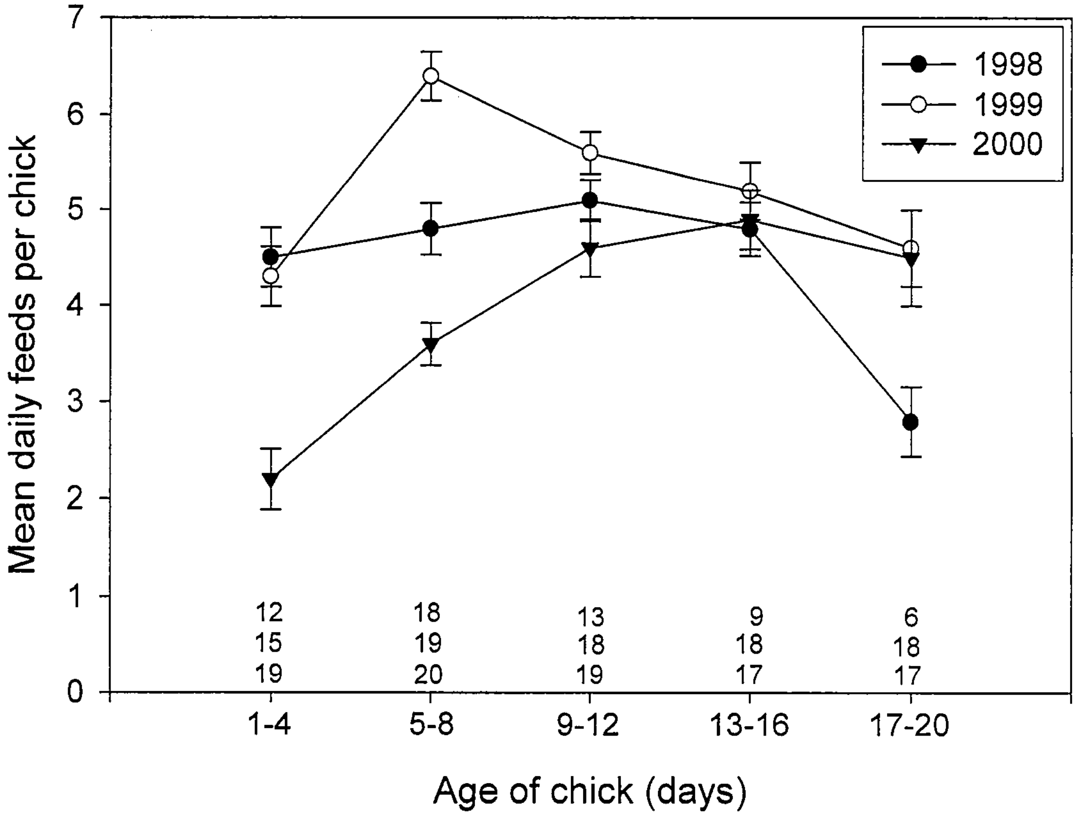


Figure 4.1. Mean (± SE) number of daily feeds received by Common Murre chicks across six age categories (1-4 d, 5-8 d, 9-12 d, 13-16 d, and 17-20 d) during the 1998-2000 chick rearing periods. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

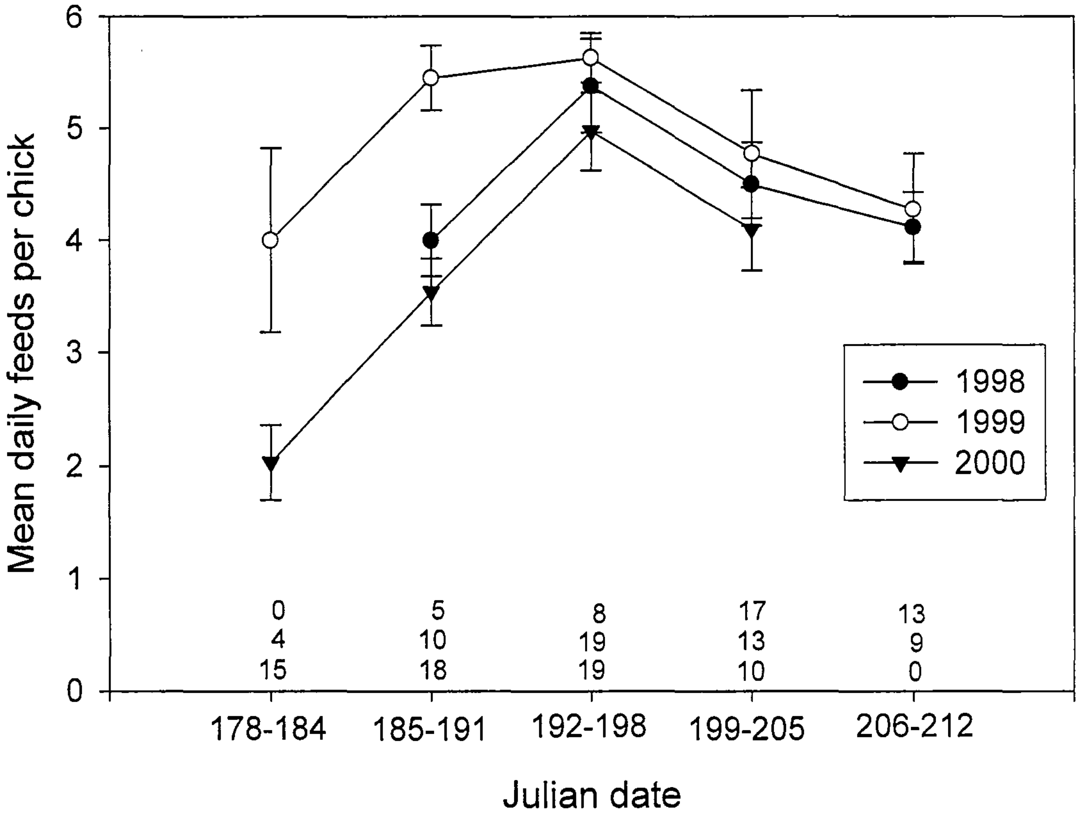
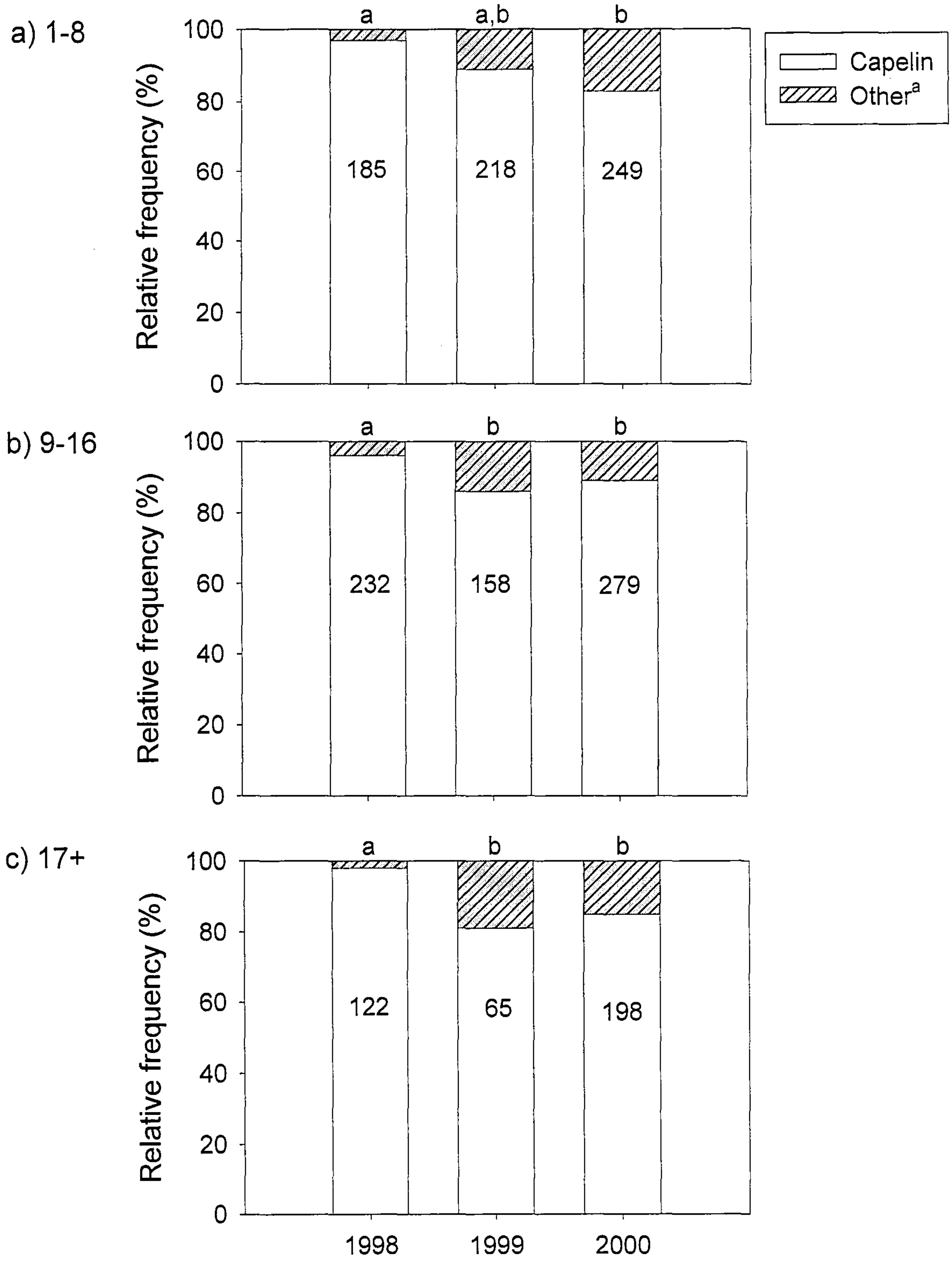


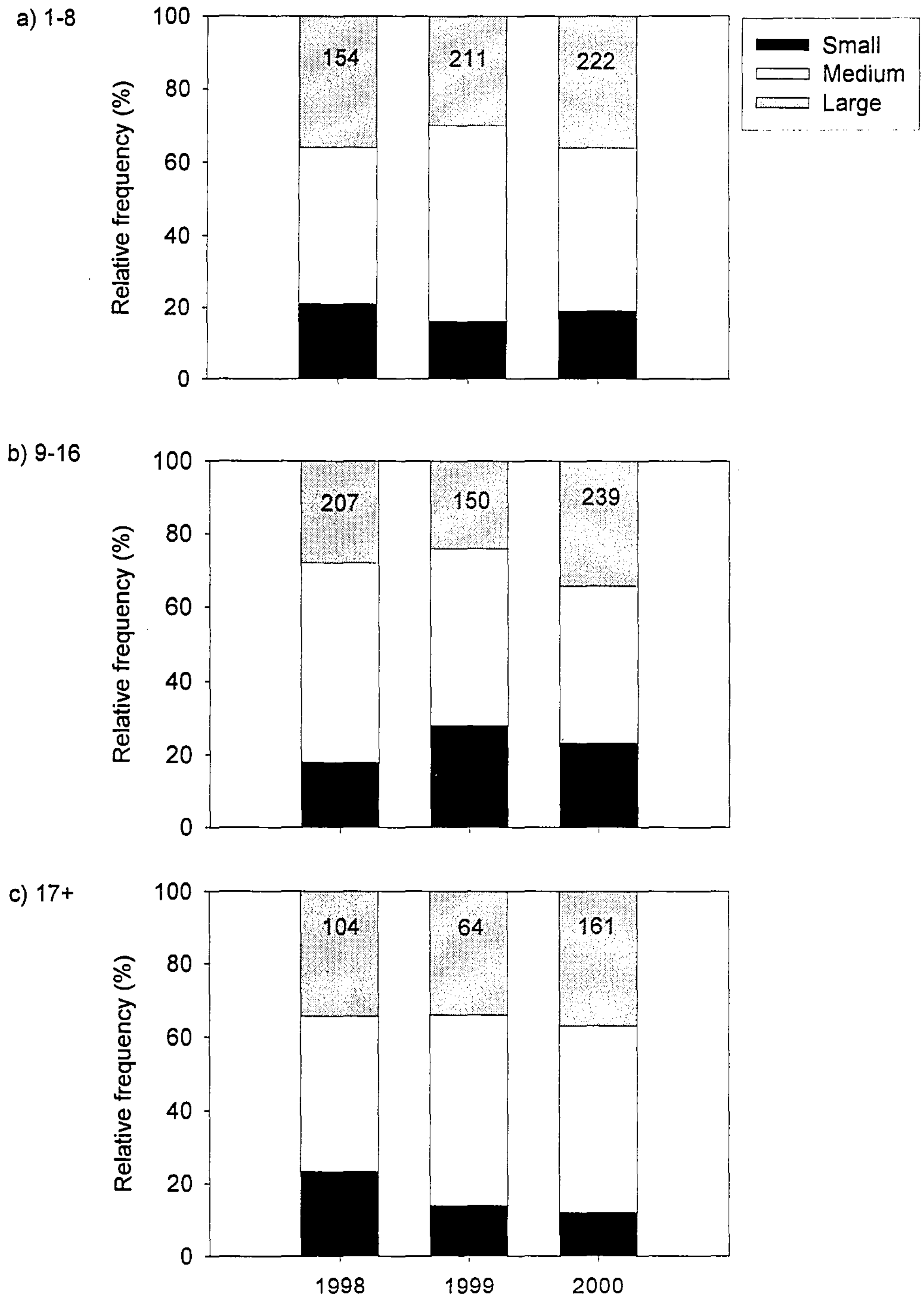
Figure 4.2. Mean (± SE) number of daily feeds received by Common Murre chicks across five Julian date categories (178-184, 185-191, 192-198, 199-205, and 206-212) during the 1998-2000 chick rearing periods. Numbers above x-axis represent sample sizes for each year in each age category (top row = 1998; middle row = 1999; bottom row = 2000).

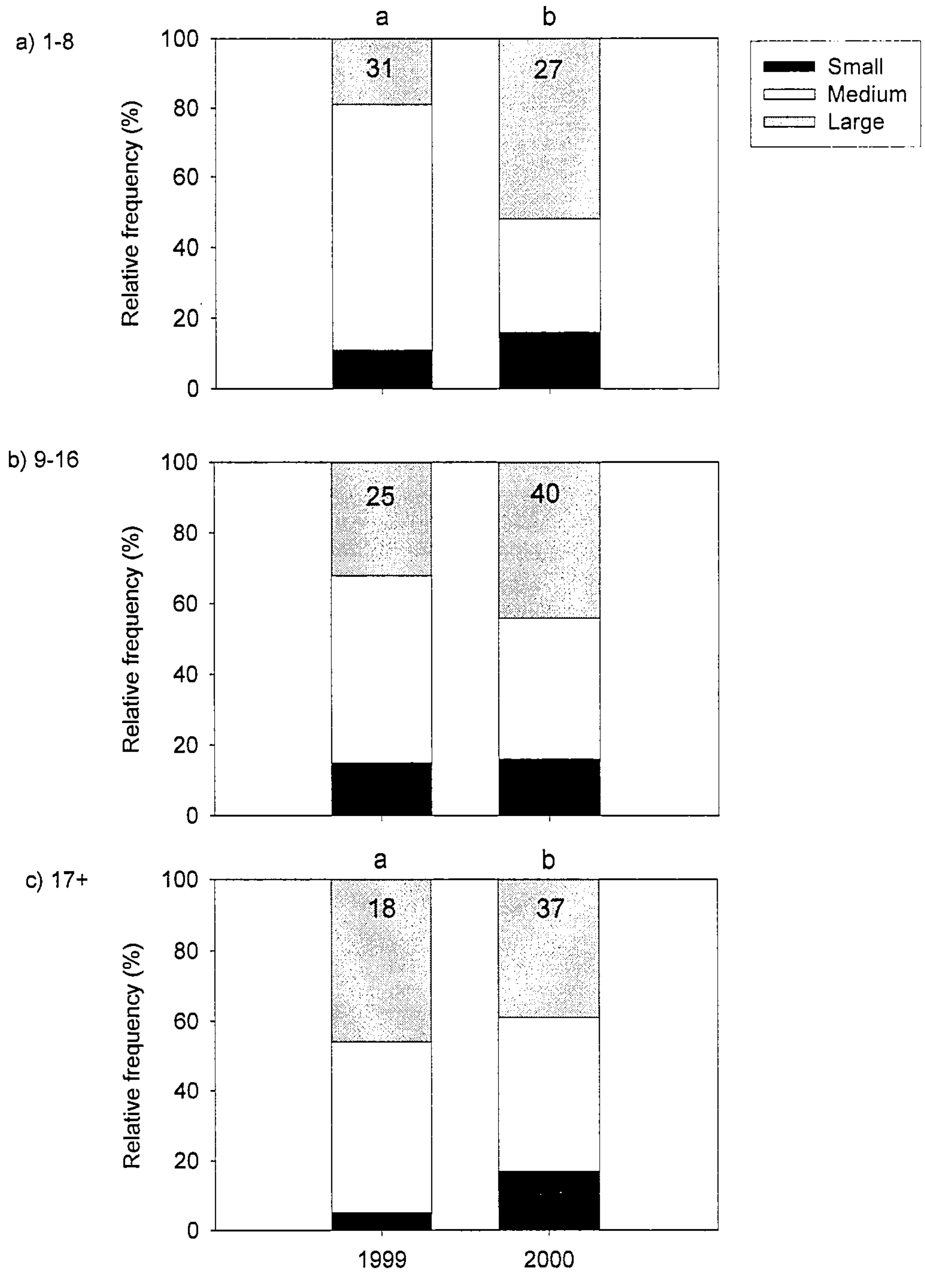

a) 1-8
b) 9-16
c) 17+
Relative frequency (%)
0
20
40
60
80
100
a
a,b
b
185
218
249
a
b
b
232
158
279
a
b
b
122
65
198
1998
1999
2000
Capelin
Other^a

1998 at ages 9-16 d ($\chi^2_1 = 4.94$, $P < 0.05$; Fig. 4.3b) and 17 d to departure ($\chi^2_1 = 13.64$, $P < 0.01$; Fig. 4.3c). Prey composition did not vary within any given year across age of chick (1998: $\chi^2_2 = 0.8$, $P > 0.10$; 1999: $\chi^2_2 = 2.6$, $P > 0.10$; 17 d to departure: $\chi^2_2 = 1.5$, $P > 0.10$; Fig. 4.3). Overall, sand lance made up 3% of a chick's diet in 1998, 15% in 1999 and 14% in 2000.

There was no significant difference in capelin size between years at any of the age categories (1-8 d: $\chi^2_4 = 5.43$, $P > 0.10$, Fig. 4.4a; 9-16 d: $\chi^2_4 = 3.00$, $P > 0.50$, Fig. 4.4b; 17 d to departure: $\chi^2_4 = 5.49$, $P > 0.10$, Fig. 4.4c) with chicks being fed primarily medium-sized capelin (48%). Within each year, chicks were also fed primarily medium-sized capelin across all age groups (1998: $\chi^2_4 = 3.81$, $P > 0.10$; 1999: $\chi^2_4 = 8.31$, $P > 0.05$; 2000: $\chi^2_4 = 4.56$, $P > 0.10$, Fig. 4.4). In 1998 and 1999, researchers independent of this study collected chick diet at another murre colony on Great Island and reported that chicks were mostly fed capelin measuring 100-150 mm in length, which they classified as medium-sized; no difference in fish sizes were found between years (Davoren and Montevecchi 2003).

Size of sand lance did vary across years with chicks aged 1-8 d being fed a higher proportion of large sand lance and lower proportion of medium sand lance in 2000 compared to 1999 ($\chi^2_2 = 30.42$, $P < 0.01$; Fig. 4.5a). Conversely, chicks aged 17 d or older were fed more small sand lance in 2000 compared to 1999 ($\chi^2_2 = 7.38$, $P < 0.05$; Fig. 4.5c), although most sand lance fed to chicks in both years was medium and large.

a) 1-8
b) 9-16
c) 17+
Relative frequency (%)
0
20
40
60
80
100
154
211
222
207
150
239
104
64
161
1998
1999
2000
Small
Medium
Large


a) 1-8
b) 9-16
c) 17+
a
b
31
27
25
40
18
37
Relative frequency (%)
0
20
40
60
80
100
Small
Medium
Large
1999
2000

Size of sand lance did not differ across years in chicks aged 9-16 d ($\chi^2_2 = 3.54$, $P > 0.10$; Fig. 4.5b). Size of sand lance fed to chicks varied across age in 1999 ($\chi^2_4 = 20.43$, $P < 0.001$) but not in 2000 ($\chi^2_4 = 3.91$, $P > 0.01$; Fig. 4.5). In 1999, older chicks (17 d to departure) were fed a higher proportion of large sand lance compared to younger chicks (1-8 d; $\chi^2_1 = 6.24$, $P < 0.025$; Fig. 4.5).

Type of prey fed to chicks across the chick-rearing period varied differently in each year. In 1998, chicks were fed almost exclusively capelin throughout chick rearing, with the exception of the first week (Table 4.1). In 1999, chicks were fed exclusively capelin during the first week of chick rearing. However, by the end of the season, sand lance made up almost one third of the chicks' diet (Table 4.1). Across the 2000 chick rearing period, chick diet did not vary significantly. Chicks were fed mostly capelin, however, their diets were consistently supplemented with sand lance (Table 4.1).

4.4.3 Chick growth parameters and provisioning rates

Chick body mass did not differ across years ($F_{2,26} = 0.92$, $P = 0.41$). However, inter-annual differences were found in wing length ($F_{2,26} = 9.87$, $P = 0.01$), with chicks reared in 2000 having longer wings compared to the other two years (Fig. 4.6). A significant correlation was found between chick feeding rates and chick mass for chicks aged 12-14 d ($r = 0.49$, $P = 0.05$, $N = 14$). This positive relationship was primarily driven by the low chick mass/low chick feeding rates in 2000 and the high chick mass/high chick feeding rates in 1999 (Fig. 4.7). A similar relationship was found in the other two

Table 4.1. Number (No.) and percentage (%) of fish species fed to Common Murre chicks across Julian dates grouped into 7-d categories (178-184, 185-191, 192-198, 199-205, and 206-212) in three consecutive chick rearing periods (1998, 1999, and 200) on Great Island, NL. Chi-squared analyses examine diet shifts across Julian dates.

	Capelin		Other[1]				
	No.	%	No.	%	Total	χ^2	P
1998							
185-191	20	80	5	20	25	18.81	< 0.001
192-198	145	96	6	4	151		
199-205	153	94	10	6	163		
206-212	135	93	10	7	145		
1999							
178-184	21	100	0	0	21	40.26	< 0.001
185-191	167	87	25	13	192		
192-198	205	92	18	8	223		
199-205	201	82	43	18	219		
206-212	61	71	25	29	86		
2000							
178-184	74	86	12	14	86	4.51	> 0.10
185-191	205	85	36	15	241		
192-198	181	92	16	8	197		
199-205	79	82	17	18	96		

[1] For 1999 and 2000, fish species were identified as sand lance.

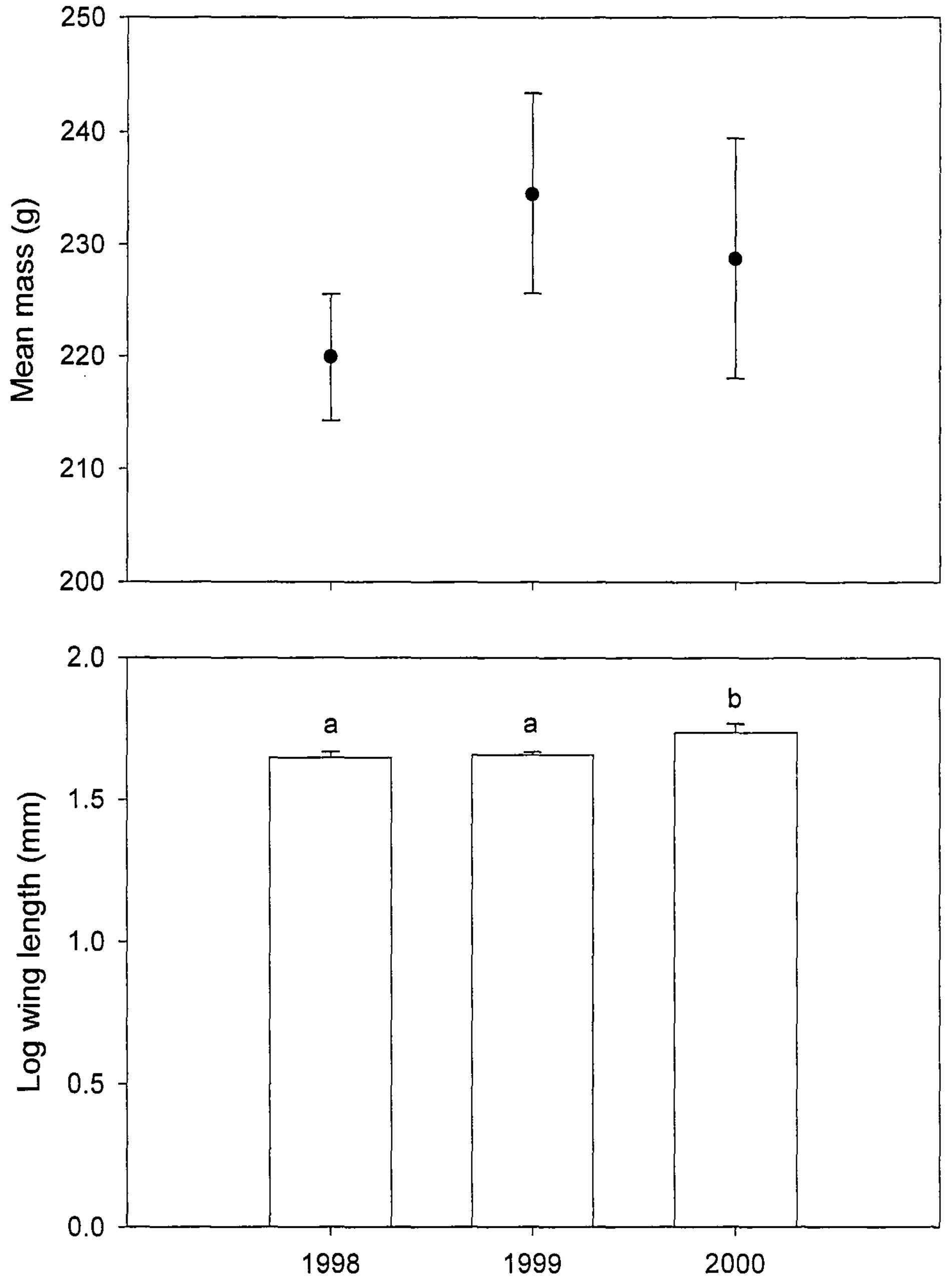
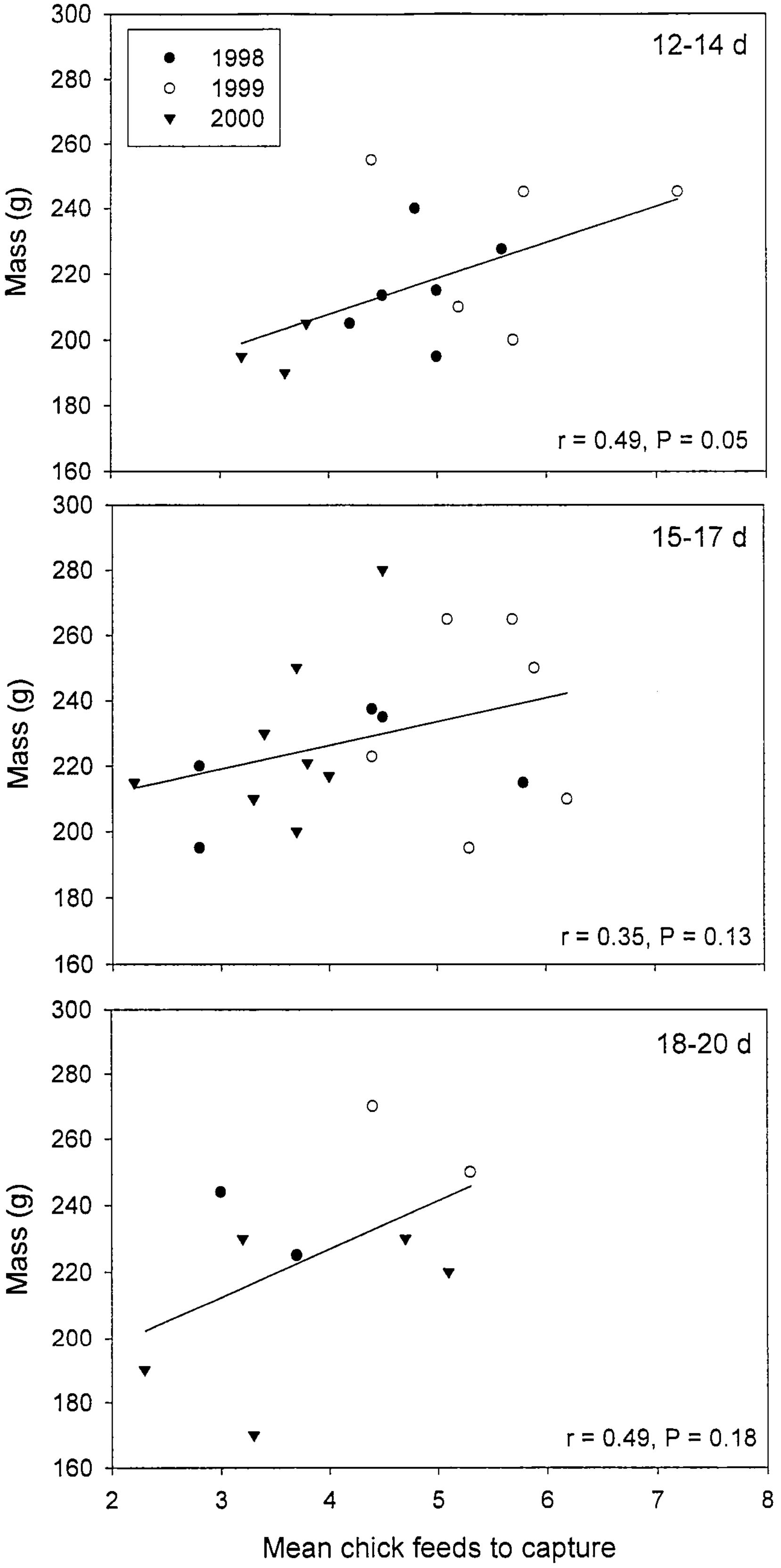


Figure 4.6. Mean (± SE) body mass and mean (± SE) wing length (log-transformed) of Common Murre chicks aged 13 to 20 d during three consecutive chick rearing periods (1998-2000). N = 10 for each group. Letters above bars show significant differences among groups.

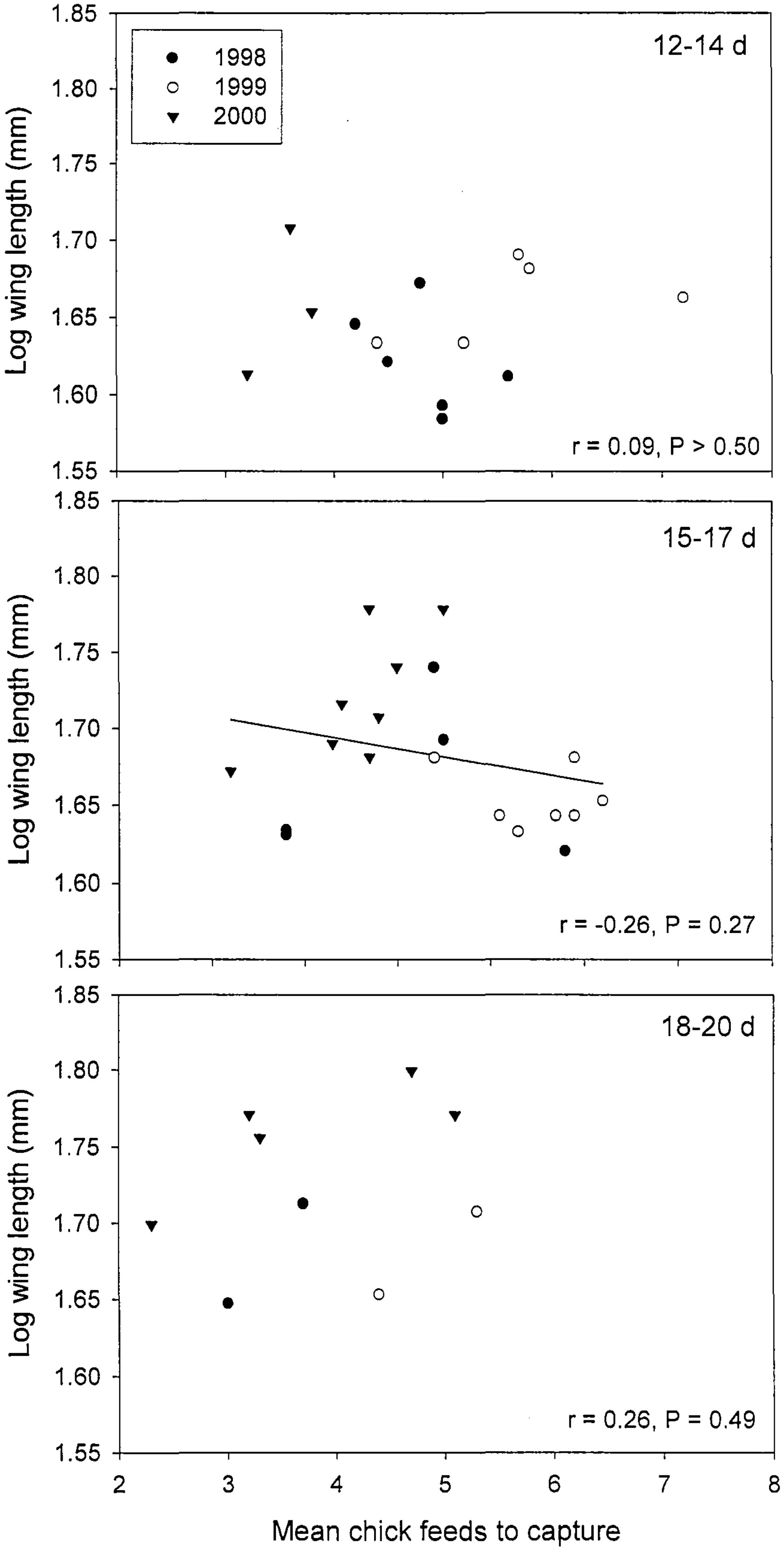

1998
1999
2000
12-14 d
r = 0.49, P = 0.05
15-17 d
r = 0.35, P = 0.13
18-20 d
r = 0.49, P = 0.18
Mass (g)
300
280
260
240
220
200
180
160
2
3
4
5
6
7
8
Mean chick feeds to capture

age categories, although correlations were not statistically significant (Fig. 4.7). No relationship was found between chick feeding rates and wing length, although a negative trend was observed at age 15-17 d ($r = -0.26$, $P = 0.27$, $N = 20$; Fig. 4.8). The low feeding rates and longer wings of chicks in 2000 and higher feeding rates and shorter wings of chicks reared in 1999 mainly influenced this trend.

4.5 DISCUSSION

4.5.1 Inter and intra-annual variation in chick provisioning rates and diet (1998-2000)

Provisioning rates were unusually low during early chick rearing in 2000. During this time, chicks were being fed primarily medium-sized capelin. Adults were presumably foraging at long distances from the breeding colony or allotting longer search times per prey item, reflected in the low chick feeding rates and high foraging effort during early chick rearing (see Chapter 3). Common Murres commute to foraging areas outside of the breeding area in May and early June, but forage in the vicinity of the breeding colonies when spawning capelin arrive inshore (Cairns et al. 1987; Piatt 1990). Hence, the low chick feeding rates during the first half of chick rearing in 2000 was most likely due to a mismatch between capelin arrival and chick hatching. Most chicks hatched prior to the arrival of capelin (see Chapter 3) and parents were presumably still foraging offshore. During this time, however, chick diets were supplemented with a higher proportion of large sand lance compared to other years. Although adults appeared to be partially compensating for potentially low capelin availability by selecting large



1998
1999
2000
12-14 d
r = 0.09, P > 0.50
15-17 d
r = -0.26, P = 0.27
18-20 d
r = 0.26, P = 0.49
Log wing length (mm)
1.85
1.80
1.75
1.70
1.65
1.60
1.55
2
3
4
5
6
7
8
Mean chick feeds to capture

sand lance, feeding rates were still lower compared to other years and other colonies (see Chapter 3). These results suggest that murres breeding in Witless Bay may not have a suitable alternate prey to capelin, as seen elsewhere (Harris and Wanless 1985; Hatchwell 1991; Bryant et al. 1999; but see Burger and Piatt 1990).

Chicks were fed a higher proportion of sand lance during the entire chick rearing periods of 1999 and 2000 compared to 1998. Large increases of juvenile sand lance abundance have been observed over the Grand Banks in 1998 and 1999 (Anderson 2001), which may have contributed to the increase in adult sand lance fed to murre chicks in subsequent years. However, it does not appear that the increase in sand lance abundance was related to the high chick feeding rates observed in 1999. When chick-feeding rates peaked during mid-chick rearing in 1999, chicks were being fed primarily capelin (92%). Sand lance proportions did, however, increase seasonally as chick feeding rates declined, suggesting that capelin became less available as the chick-rearing period progressed.

It is interesting to note that in both instances during apparent low capelin availability (early chick rearing in 2000 and late chick rearing in 1999), birds were returning to the colony with a higher proportion of large sand lance. Sand lance have a higher energy density (7.3 kJ per g) than ovid female capelin (4.6 kJ per g) and adult male capelin (3.8 kJ per g; reviewed in Cairns et al. 1990), thereby making sand lance a higher quality prey for growing chicks. However, sand lance may be more difficult for murres to exploit because of their benthic habit (Scott 1993). When capelin abundance in surrounding waters is low, murres spend more time away from the colony, presumably searching for prey (Burger and Piatt 1990). Therefore, if schools of capelin were not as predictably found or were located far from the colony, and murres were required to increase their foraging time, then it may have been better for them to spend extra time searching for the higher quality large sand lance.

4.5.2 Diet comparison with Gull Island 1982-85

The diets of Common Murre chicks reared in Witless Bay have changed very little since the 1980s. All years combined, Burger and Piatt (1990) reported that chicks were fed 89% capelin, 9% sand lance and 2% other fish. Combining 1998-2000, chick diets on Great Island were comprised of 89% capelin and 11% sand lance. Other fish species were very rarely fed to chicks (pers. obs.). Furthermore, fish sizes also appear to have remained similar since the 1980s. From 1982-85, most fish delivered to chicks measured between 106-141 mm in length (estimated from Burger and Piatt 1990). The majority of fish delivered to chicks in this study (1998-2000) and at another murre colony on Great Island (1998-99) were medium-sized, and estimated to measure 100-150 mm (Davoren and Montevecchi 2003).

4.5.3 Chick mass, wing length, and provisioning rates

Chick mass did not differ across years, although analyses were restricted to a subset of chicks sampled to control for age. However, at the individual level, a positive relationship was found between provisioning rates and chick mass: individuals that were fed more frequently also had higher body mass. This linear relationship between amount of food received and chick mass has been observed in other seabirds, including Atlantic

Puffins (*Fratercula arctica*; Harris 1978; Barrett et al. 1987; Øyan and Anker-Nilssen 1996) and Cassin's Auklets (*Ptychoramphus aleuticus*; Hedd et al. 2002).

Wing length did differ across years, with chicks reared in 2000 having overall longer wings than those reared in 1998 and 1999. Although no relationship was found between provisioning rates and wing length in two of the age groups, a trend toward a negative relationship was found at age 15-17 d. The relationship between wing growth and nutrition has been studied in other Auk chicks, including Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*) and Atlantic Puffins (reviewed in Gaston 1985; Øyan and Anker-Nilssen 1996). Most report no relationship between wing length and food supply (but see Øyan and Anker-Nilssen 1996). The results in this study suggest that during unfavorable breeding conditions, such as low capelin availability, wing growth can perhaps be prioritized in Common Murres. Rapid wing growth can benefit chicks as well as parents by allowing earlier departure, thereby bringing the chick to the food source rather than adults depleting their reserves by bringing the food to the chick (Sealy 1973). This strategy is used by intermediate alcid species, including the Common Murre, where the male parent brings the chick to sea and continues to provide parental care for several weeks (Harris and Birkhead 1985).

4.5.4 Growth parameters of Great Island chicks in comparison to other colonies

Chick mass and wing length from this study and of chicks of similar age from other Common Murre colonies are summarized in Table 4.2. Although growth parameters in this study showed considerable intra-colony variation across years, the

Location	Age of chick (d)	Year	Mean mass ± se (g)	Mean wing ± se (mm)	N	Source
Great Island, NL, Canada	12-14	1998	216.0 ± 6.5	41.9 ± 1.3	6	This study
		1999	231.0 ± 10.9	45.8 ± 1.2	5	
		2000	212.0 ± 10.2	54.2 ± 5.6	5	
	15-17	1998	220.5 ± 7.7	46.4 ± 2.5	5	
		1999	236.9 ± 10.5	45.1 ± 0.8	7	
		2000	227.9 ± 9.1	52.8 ± 1.8	8	
	18-20	1998	234.5 ± 9.5	48.0 ± 3.6	2	
		1999	260.0 ± 10.0	48.0 ± 3.0	2	
		2000	208.0 ± 12.0	57.6 ± 2.1	5	
Gull Island, NL, Canada	13	1977-78	193.3	---	?	Mahoney and Threlfall (1981)
	17		223.0	---	?	
	19		236.0	---	?	
Gannet Islands, NL, Canada	13	1997	205[1]	43[1]	8	Hipfner and Bryant (1999)
	16		215[1]	50[1]	8	
	19		220[1]	58[1]	8	
Hornøya, Norway	12-14	1990	240[1]	46[1]	15	Barrett et al. (1997)
	15-17		250[1]	56[1]	15	
	18-20		250[1]	66[1]	12	
Skomer Island, Wales	12-13	1985-87	180[1]	43[1]	25	Hatchwell (1991)
	16-17		200[1]	53[1]	35	
	18-19		198[1]	57[1]	30	

[1] Values estimated from figures.

weight of chicks reared on Great Island between 1998-2000 fell within the range of chick masses reported at other colonies, and are similar to chicks reared on Gull Island in the late 1970s. Furthermore, relative to other murre colonies, the seemingly low mass of chicks reared on Great Island in 2000 that were close to fledging (18-20 d) were in fact comparable to chick weights on Skomer Island in Wales, and higher than fledging masses of chicks on Funk Island (191.6 ± 4.0 g; Davoren and Montevecchi 2003), an island located approximately 60 km off the east coast of Newfoundland.

Similarly, the apparent long wings of chicks reared in 2000 on Great Island were similar to those reported in Labrador and Wales. However, Great Island chicks reared in 2000 had considerably shorter wings compared to murre chicks reared in Norway and to fledging Funk Island chicks (estimated at 66.1 mm; Davoren and Montevecchi 2003). Chick feeding rates on Funk Island are among the lowest of any reported (Davoren and Montevecchi 2003) as a result of parents travelling approximately 45 km each way to find predictable food sources (Davoren et al. 2003). The low mass and long wings of these chicks are consistent with the view that wing growth may be prioritized when feeding conditions are poor.

4.5.5 Conclusion

Prey type or size does not appear to have changed since the 1980s. Furthermore, there is no indication that fish fed to chicks were of lower quality/condition, as chick growth parameters were similar between the late 1970s and the late 1990s. These results do not corroborate with the view that capelin size have decreased since the 1980s

(Carscadden et al. 1997). However, Common Murres do not sample the ocean randomly (Davoren et al. 2003). Rather, they should selectively choose high quality fish for their chicks.

Mean chick feeding rates prior to capture appeared to be a good predictor of chick mass, although the relationship with wing growth was unclear. During low food availability, Common Murre chicks may prioritize wing growth. Furthermore, wing growth may be more plastic than previously thought: the wing lengths of chicks were highly variable within and between colonies. Caution is warranted when using wing measurement as a single indicator of chick body size or age.

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CHAPTER 5 Physiological changes of male and female Common Murres across three breeding seasons (1998-2000)

5.1 ABSTRACT

Birds may lose mass throughout the breeding season in response to the energetic stresses of reproduction or to decrease wing loading (adaptive mass loss hypothesis). These two hypotheses were tested on the Common Murre (*Uria aalge*), which has one of the highest wing loading among all flying birds. Changes in body condition were examined in males and females breeding in Newfoundland, Canada, across three consecutive breeding seasons (1998-2000). Corticosterone and haematocrit levels were also investigated to assess if males and females showed different physiological responses to breeding during the chick rearing period. Overall, males and females exhibited similar changes in body condition during incubation and chick rearing: body condition increased during incubation, dropped sharply at chick hatching (representing a loss of 6% of their body mass) and continued to decrease during chick rearing. The body condition of females remained low after their chick had departed the colony. These findings support the view that mass loss in birds is not solely a response to reproductive success. Rather, lowered body mass during chick rearing may reduce costs associated with flying. No sex differences were found for corticosterone and haematocrit levels. In 2000, murres had lower body condition during the first week of chick rearing and showed elevated corticosterone levels compared to 1998 and 1999. These results corroborate the view that breeding conditions were unfavourable during early chick-rearing in 2000.

5.2 INTRODUCTION

A relationship exists between a bird's body mass and its activity levels during different periods of the breeding cycle. Body mass normally remains constant or increases during periods when activity levels are low (e.g., incubation) and decreases when activity levels are high (e.g., chick rearing). Birds may lose mass throughout the breeding season in response to the energetic stresses of reproduction (reviewed in Ricklefs 1974), which in turn suggests that it is important for birds to maintain body reserves during incubation in anticipation of the higher energy-demanding period of chick rearing (Moreno 1989). Furthermore, the energy requirements for many seabird species may be greatest during chick rearing, as parents must bring food to the growing chick (Ricklefs 1983). However, foraging abilities of some species are limited because one parent must continuously remain at the site to brood and protect the chick (Ricklefs 1983). An alternative hypothesis is that birds increase in body mass prior or during incubation to act as a buffer against poor feeding opportunities during long incubation shifts (Gaston and Jones 1989; Croll et al. 1991; Jones 1994; Gauthier-Clerc et al. 2001). Once incubation is over and adults have more flexible opportunities to forage while looking for prey for their young, their energy reserves are no longer required and they lose mass. Furthermore, lower mass during chick rearing is thought to be adaptive as this decreases wing loading, which in turn reduces energy expenditure during flight (Norberg 1981).

Fluctuating environmental conditions leading to good or poor breeding conditions can influence mass loss throughout the breeding season. Brief periods of food shortages due to weather (Jones 1987; Jones 1994) and more persistent periods of low food availability due to inaccessible prey (Weimerskirch et al. 2001) can negatively affect the body condition of breeding birds. Other important physiological changes associated with stressful breeding conditions include elevated corticosterone levels. The avian endocrine system responds to short and long-term stressful conditions by releasing higher amounts of corticosterone, the primary glucocorticoid produced by the adrenal glands (Norris 1997). Corticosterone stimulates foraging behaviour (Astheimer et al. 1992), increases locomotor activity (Belthoff and Dufty Jr. 1998), and helps mobilize stored lipids (Norris 1997) and or protein (reviewed in Wingfield et al. 1997). Furthermore, adults breeding when food conditions are poor or unpredictable have a higher stress response than those breeding under more favourable conditions (Kitaysky et al. 1999; Reneerkens et al. 2002).

Changes in body condition are related to changes in haematology. Fasting Adelie Penguins (*Pygoscelis adeliae*; Vleck and Vleck 2000) and Chinstrap Penguins (*Pygoscelis antarctica*; Merino and Barbosa 1997) show increases in haematocrit levels. In addition, haematological parameters are indicative of blood oxygen storage capacity with high levels associated with high oxygen storage demands (Costa et al. 1998). Among seabirds, haematocrit levels are higher in breeding birds compared to non-breeders (Wanless et al. 1997; Merino and Barbosa 1997). Breeders may have higher oxygen storage demands as they spend more time underwater pursuing prey for themselves and their chick. Therefore, haematocrit levels may provide additional information on the health of the individual and/or act as an indicator of increased foraging demands.

Murres and other auks have small wings relative to their body size and therefore have one of the highest wing loading among all flying birds (Pennycuick 1987). Although smaller wings increase diving capabilities, flying efficiency is compromised. Adult Thick-billed Murres lose mass rapidly at chick hatching with mass stabilizing for the remainder of the chick-rearing period (Croll et al. 1991). This mass loss may be adaptive as birds engage in more foraging trips to feed their young, thereby spending more time in flight (Croll et al. 1991). Common Murre body mass is highest during incubation, lowest during chick rearing, and intermediate during pre-lay (Belopol'skii 1957; Birkhead and Nettleship 1987; Harris and Wanless 1988a). In addition, adults continue to lose mass throughout the chick-rearing period (Harris and Wanless 1988a). Whether mass loss is due to reproductive stress or is an adaptation to decrease wing loading is unclear (Harris and Wanless 1988a, but see Harris et al. 2000a).

The first objective of this study was to examine how body condition of Common Murres changes across the breeding season. The following hypotheses were tested: i) if mass loss is programmed to coincide with the period when flight demands increase, then Common Murres will show an abrupt decline in body condition at hatching, which then should stabilize, and ii) if mass loss is a result of reproductive stress, Common Murres will show a gradual decline across the chick rearing period.

Common Murre chicks leave the colony accompanied by the male parent who continues to provide for the chick for several weeks (Harris and Birkhead 1985).

Meanwhile, the female may return to the colony for several weeks (Harris and Wanless 2003; pers. obs.) where she continues to defend the nest site and may engage in social interactions with neighbouring birds (pers. obs.). It was further hypothesized that female body condition will stabilize or increase after the chick has gone to sea with the male parent. Because she is no longer provisioning or brooding the chick, lowered mass would no longer be necessary to increase flight efficiency during this time nor should females' body condition continue to decline due to reproductive stress.

The second objective was to test if the sexes showed different patterns in mass loss, corticosterone and haematocrit levels across the season. Throughout the breeding season, males and females assume different roles. During pre-lay, males spend more time attending the nest site while females are spending more time at sea forming the egg (see Chapter 2). During incubation, both parents share duties more or less equally (Verspoor et al. 1987). However, during chick rearing females may provision and/or brood more than males (Wanless and Harris 1986; Chapter 3). Therefore, it was hypothesized that females may show lower body condition, higher corticosterone and higher haematocrit levels compared to males during the chick-rearing period.

5.3 METHODS

Data were collected from a sub-colony of Common Murres nesting at high density on a broad ledge (1.6 m x 2.5 m area) on Great Island (47° 11'N, 52° 49'W), Newfoundland and Labrador (NL), Canada, from June to August 1998-2000. Murres were colour-banded to allow individual recognition.

5.3.1 Body mass and tarsus measurements

Body mass measurements were obtained using three electronic balances (Ohaus CS-2000 accurate to ± 1 g) modified so that they could be powered and tared from inside the observation blind. Balances were placed in wooden bases (17 X 17-cm) and covered with 18 X 18-cm Plexiglas platforms secured with Velcro to the top of the balance. Bases were cemented to flat rocky areas where birds were known to stand or walk around, but not directly on a nest site. Balances were leveled and tested for inter-balance accuracy at the beginning of each breeding season. Measurements were not obtained on days when NE to NW winds were greater than 20 km/h as winds caused the readings to fluctuate. Weights of individuals were recorded, with date and time, manually on data sheets. Measurements were obtained throughout the breeding season over 21 days in 1998, 28 days in 1999 and 26 days in 2000. When measurements of a single individual were obtained several times a day, a mean daily mass was calculated. Only mass of individuals for whom a tarsus measurement had been taken and thus a residual index could be calculated were included in the analyses (see below). Additional mass measurements (± 10 g, with a 1000 g or 1500 g Pesola) were obtained when birds were captured for banding during pre-lay and chick rearing. At this time, total tarsus (± 0.1 mm, with sliding calipers) was measured from the heel joint at the back of the leg to the end of the tarsus on the underside of the foot.

5.3.2 Chick hatching and departure dates

The hatching date of a chick was determined by: i) observing the actual hatching, ii) seeing a chick at a site where there had not been a chick on the previous observation day (observation days were 2-3 days apart) or iii) counting forward the mean incubation period (33 days, pers. obs.) from the egg's laying date. Departure dates were recorded when a chick and its male parent were observed to have departed to sea (18 chick departures were observed and the male parent always accompanied the chick) or when the first day a chick >16 d old and its father were no longer at its nest site that had been present on the last observation day (range of age at chick departure is 16-30 days; Harris and Birkhead 1985).

5.3.3 Blood sampling

During chick rearing, blood was collected from breeding murres on four days in 1998 (20, 22, 27 and 30 July), three days in 1999 (16, 24, 27 July), and three days in 2000 (13, 17 and 20 July). In all years, blood sampling began when most chicks on the site were two weeks of age. Birds were caught with a noose pole, placed in a cotton bag, and approximately 1.5 ml of blood was drawn from the brachial vein, at the height of the ulna joint, within 3 min of capture.

Immediately after collecting each sample, blood was transferred into two heparinized capillary tubes by inserting the needle into the tube and slightly depressing the syringe. Tubes were subsequently sealed at one end with Critoseal. The needle was then removed and blood was dispensed into four preprinted circles on blood collection cards (Sigma Diagnostics, Inc.). Capillary tubes were centrifuged with a manual centrifuge for 10 min. Using a ruler, haematocrit percentages were calculated by dividing the height of the tube containing red blood cells over the height of the tube containing plasma and red blood cells. Blood spot cards were air-dried overnight, placed in individual plastic bags the following morning, and frozen at -20°C upon return to St. John's. Corticosterone concentrations were obtained using the Coat-A-Count Rat Corticosterone ^{125}I radioimmunoassay (Cat. # TKRC1, Inter Medico, Markham, Ontario) with several modifications to the procedure (described in Chapter 6). Briefly, standards were pipetted onto blood collection cards and air-dried overnight. Using a punch (10.5 mm-diameter) and hammer, circles were cut in duplicates from standards and samples. One ml of supplied ^{125}I Rat Corticosterone was added to each tube and tubes were set-aside for 18 hrs at room temperature. Tubes were then thoroughly decanted and counted in a gamma counter. Blood spot values were converted into serum values (see Chapter 6) to allow comparisons with other studies. Intra- and inter-assay coefficients of variation were 5.9% and 10.1% respectively.

5.3.4 Data analysis

A condition index was used to examine body condition of males and females within and across the breeding period. Body mass is not an accurate body condition index because males can be structurally larger and heavier than females (Threlfall and Mahoney 1980; Harris and Wanless 1988a). In this study, body condition is defined as body mass adjusted for body size. Total tarsus length was used to estimate relative body size as tarsus measurements remain constant despite varying environmental conditions. For the sub-population of murres observed in the present study, males (49.55 ± 0.27 mm, N = 24) had significantly longer tarsi than females (48.78 ± 0.35 mm, N = 20; $t_{42} = 1.72$, P = 0.047). Body mass was regressed on tarsus length to calculate a residual index and all analyses were performed on these residuals. Data were homogeneous (visual inspection of body mass regressed on tarsus length showed residuals to be uniformly distributed) and therefore did not require further transformation. The residual index is a reliable body condition index, as it does not fluctuate with body size (Jakob et al. 1996).

Body condition data were examined in two ways to assess changes across the breeding season: 1) by weeks in relation to each individual's chick hatching where day of hatching = day 0 and 2) grouped into four periods: pre-lay, incubation, chick rearing, and post-chick departure. Only males were included in the analyses during pre-lay because of concerns that females increased in mass due to the developing egg and not due to increased fat reserves. Only females were included in the analyses during post-chick departure because of males being at sea with the chick. A mixed within-subject analysis of variance (ANOVA) with individual as the subject variable was used to examine sex effects and year effects (chick rearing period only) within each period separately. Sample sizes were too small to allow for inter-year comparisons for pre-lay, incubation and post-departure periods. A mixed within-subject ANOVA was also used to analyse differences in body condition across the four periods (pre-lay, incubation, chick rearing and post-departure). The Tukey-Kramer Method (Sokal and Rohlf 1995) was used for post-hoc comparisons. To examine the relationship between corticosterone and body condition, a

Pearson's correlation was applied on corticosterone levels of individuals and their matching body condition index.

A mixed within-subjects ANOVA with individual as the subject variable was used to assess if corticosterone and haematocrit levels differed between the sexes and across years. Only individuals that were sampled in two of the three years were included in the analyses. Because the methodology for quantifying corticosterone levels is still under review, only relative corticosterone levels are reported (see Chapter 6). For all analyses, haematocrit proportions were square root and arcsine transformed to meet the assumption of normality for parametric testing (Sokal and Rohlf 1995). Interaction terms were included in all analyses, however only significant ones were reported. All values are reported as means ± SE. Statistical significance was set at $\alpha = 0.05$.

5.4 RESULTS

5.4.1 Changes in body condition across the breeding period

During the pre-lay period, males and females showed different patterns of change in body condition with male body condition declining slightly as the pre-lay period progressed while females showed an increase in mass (Fig. 5.1). After egg laying, both sexes showed similar patterns: breeding adults gradually increased in body condition during the incubation period, decreased immediately after chick hatching and continued to decrease during the remainder of the chick rearing period. With the exception of when females laid the egg, the biggest drop in body condition occurred between incubation and

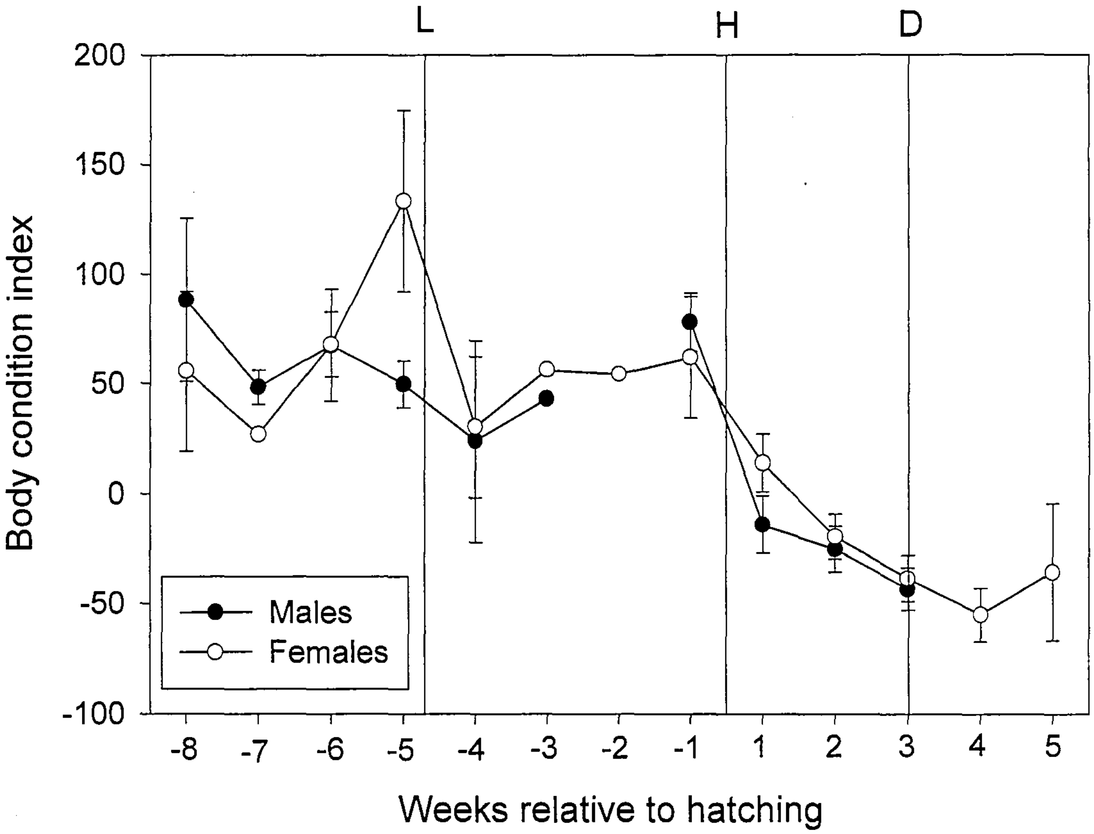

Figure 5.1. Body condition (residual index ± SE) of male and female Common Murres breeding on Great Island, NL (1998-2000 combined). Vertical lines indicate important events during the breeding period (L = egg-laying; H = chick hatching; D = chick departure).

first week of chick hatching. After the male parent left the colony with the chick, female body condition was still low (Fig. 5.1).

When weeks were combined into periods (pre-lay, incubation, chick rearing and post-departure), body condition of breeders decreased significantly as the breeding season progressed (period: $F_{3,27} = 21.05$, $P < 0.0001$). Adults had higher body condition during pre-lay and incubation compared to chick rearing and post-chick departure (Fig. 5.2).

Within the chick-rearing period only, murres showed different patterns of change in body condition across years (week x year: $F_{8,42} = 2.24$, $P = 0.043$). In 1998 and 1999, murres showed a steady decline in body condition across the three weeks of chick rearing. However, in 2000, body condition was atypically low during the first week of chick rearing, increased during the second, and then decreased to levels comparable to the other two years during the final week of chick rearing (Fig. 5.3).

5.4.2 Body condition, corticosterone and haematocrit levels during chick rearing

Both sexes showed similar physiological responses during the chick-rearing period. No sex differences in body condition were found during incubation or chick rearing (Table 5.1). Corticosterone levels did not vary between males ($N = 9$) and females ($N = 10$; $F_{1,17} = 1.60$, $P = 0.224$; mean difference between males and females = 4 ng/ml or 5%). Males ($N = 9$) and females ($N = 10$) also had similar haematocrit levels ($F_{1,4} = 0.90$, $P = 0.396$; males = 48.6 ± 0.8 %, females = 49.2 ± 0.7 %).

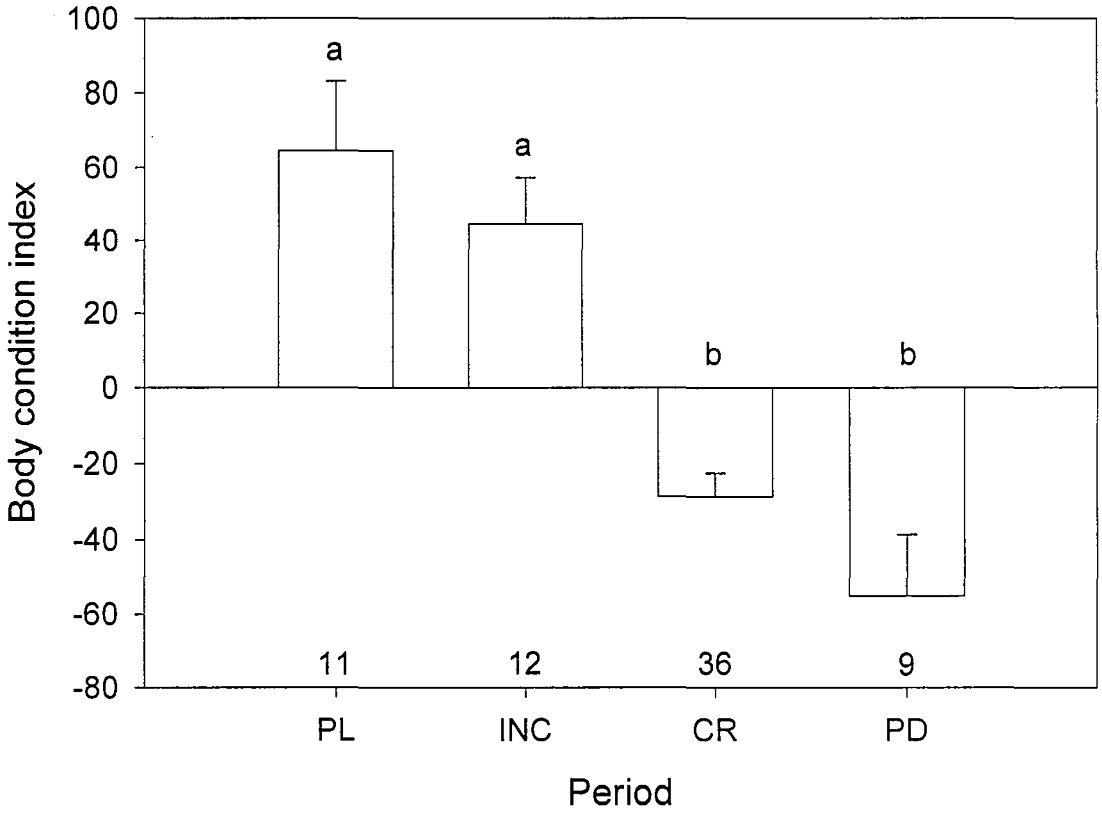

Figure 5.2. Body condition (residual index ± SE) of breeding Common Murres (1998-2000 combined) during pre-lay (PL; males only), incubation (INC; sexes combined), chick rearing (CR; sexes combined), and post-departure (PD; females only). Numbers above x-axis represent sample sizes.

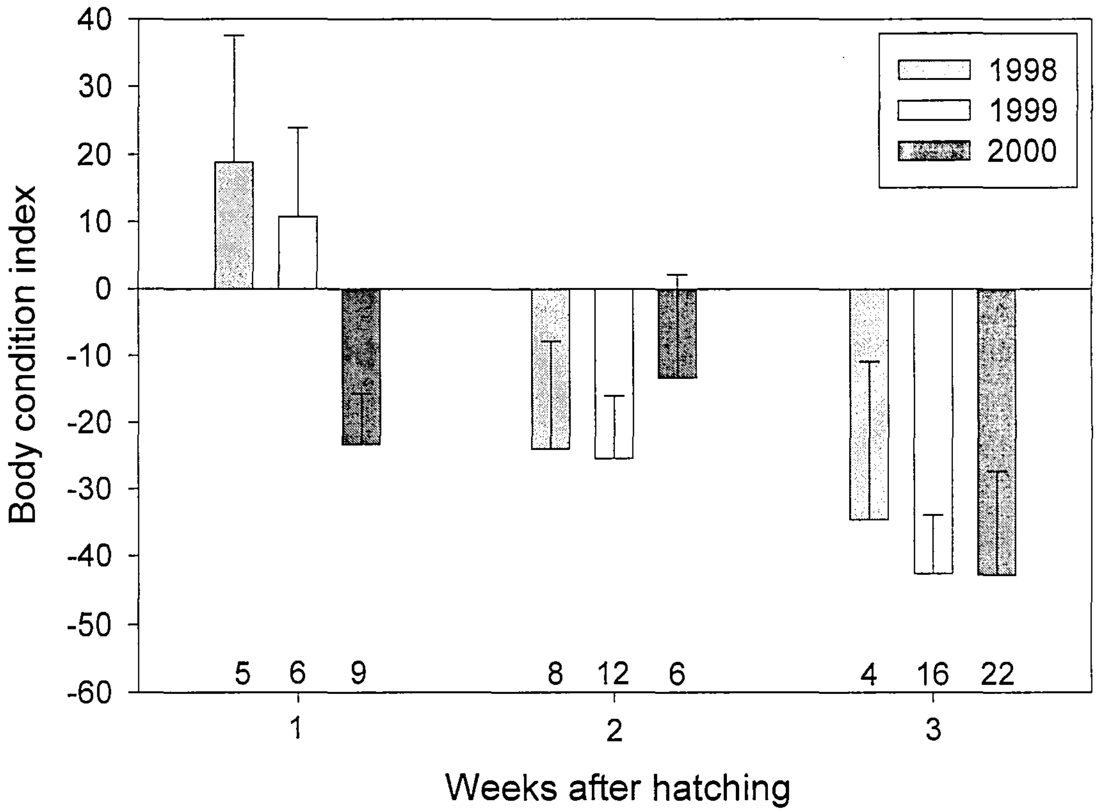

Figure 5.3. Body condition (residual index ± SE) of breeding Common Murres (sexes combined) across weeks after chick hatching, during three consecutive chick rearing periods (1998-2000). Numbers above x-axis represent sample sizes.

Table 5.1. Body condition index (residual index ± SE) of male and female Common Murres during incubation and chick rearing (1998-2000 combined).

Period	Male index ± SE (N)	Female index ± SE (N)	F	P
Incubation	65.09 ± 17.92 (6)	44.22 ± 16.21 (6)	0.75	0.41
Chick rearing	-29.85 ± 6.52 (19)	-24.14 ± 6.52 (17)	0.17	0.84

Haematocrit levels of murres did not vary across years (year: $F_{2,18} = 1.36$, $P = 0.283$). Arcsine-transformed haematocrits levels were 48.2 ± 0.5% (N = 14) in 1998, 49.3 ± 0.6% in 1999 (N = 13), and 49.1 ± 0.6% (N = 16) in 2000. However, a year effect was observed in corticosterone levels (year: $F_{2,17} = 5.94$, $P = 0.011$). This difference was due to the higher levels observed in 2000 compared to the other two years (Tukey-Kramer Method, $P < 0.05$). Levels in 2000 (N = 9) were on average higher by 20 ng/ml (24%) compared to 1998 (N = 14) and higher by 26 ng/ml (31%) compared to 1999 (N = 17).

A negative relationship was found between body condition and corticosterone levels ($r = -0.41$, $N = 37$, $P = 0.01$). Individuals with low body condition tended to have higher corticosterone levels than those with high body condition (Fig. 5.4). No relationship between body condition and haematocrit levels was found ($r = 0.32$, $N = 35$, $P = 0.87$).

DISCUSSION

5.4.3 Changes in body condition across the breeding period

During the pre-lay period, males and females showed different changes in body condition with females increasing and males showing a slight decrease in body condition as egg laying approached. The egg develops over 14 days (Birkhead and del Nevo 1987) and weighs approximately 108 g (Mahoney 1980). Males increase their attendance at the colony as the pre-lay period progresses (Wanless and Harris 1986; Birkhead and del Nevo 1987; Chapter 2), thereby reducing foraging opportunities, which in turn may result

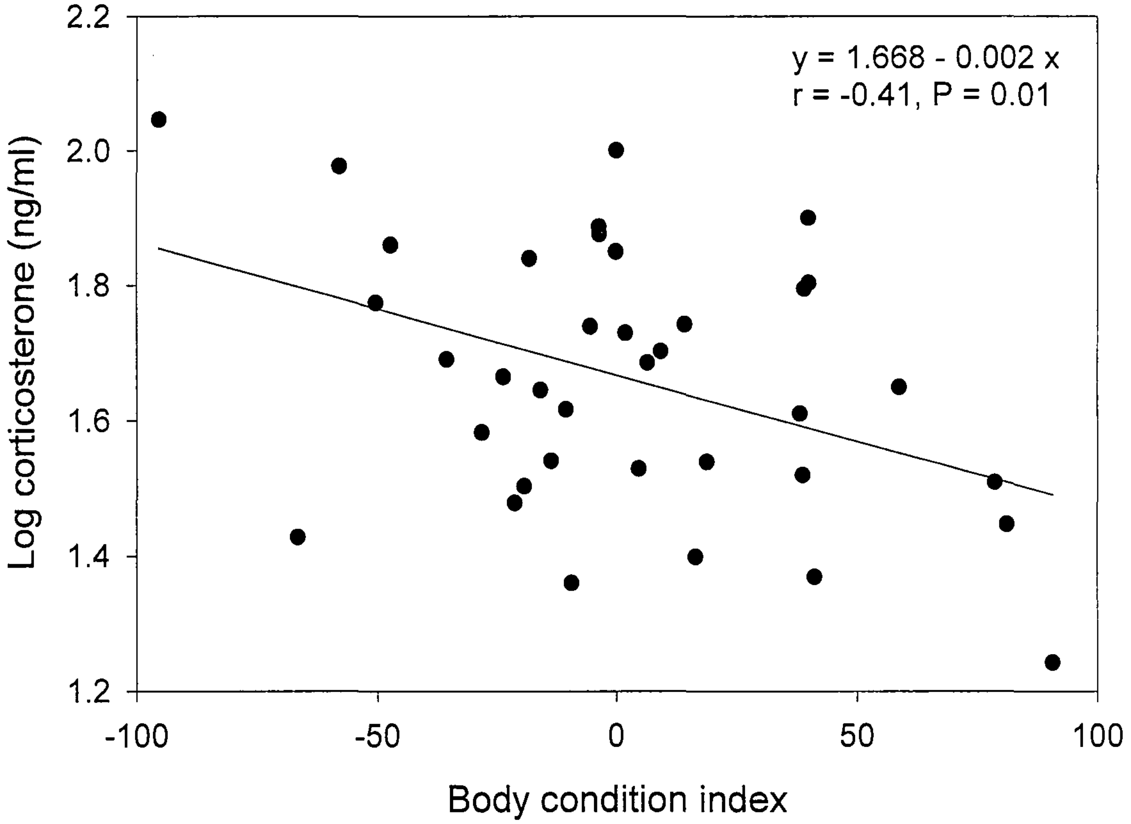

Figure 5.4. Baseline log-transformed corticosterone levels of breeding Common Murres (N = 37) regressed onto their body condition index (residual index).

in lowered body condition. Females may be in better condition than males because of increased body mass due to the developing egg and/or due to increased fat reserves as they have more foraging opportunities. Unlike Harris and Wanless (1988a) who found that females lost more mass than males between incubation and chick rearing, both sexes showed similar patterns of change in body condition during incubation and chick rearing. Body condition increased during incubation, dropped immediately after chick hatching and continued to decrease during chick rearing. Females maintained lowered body condition after chicks had departed the colony although they were no longer exhibiting direct parental care.

The observed decrease in body condition during the 1998 and 1999 chick-rearing periods does not appear to be due to reproductive stress. Rather, it may no longer be economical for murres to be carrying extra mass during this time (Croll et al. 1991). Using equations derived by Norberg (1981), Croll et al. (1991) estimated that Thick-billed Murres reduced their flight cost by up to 10% and saved up to 25% of their daily energy expenditure when decreasing their mass by 3-6% after chick hatching. When examining actual body mass, Common Murres on Great Island lost 67 g between end of incubation and early chick hatching, which is a loss of 6%. However, unlike Thick-billed Murres that showed a stabilization in mass after the initial loss following chick hatching (Croll et al. 1991), body condition of murres in this study continued to decrease throughout chick rearing and into the post chick-departure period, despite demands remaining constant or decreasing. Furthermore, prey was near the breeding colonies as observed by murres foraging within 5 km of the island in 1998 and 1999 (Davoren et al.

2003). Therefore, during late chick rearing, murres may not be in need of carrying extra energy reserves, as they do not risk starvation. The body condition of breeding males during late chick rearing and females during post chick-departure is most likely the lowest of the entire year. Common Murres increase in mass during moult, which occurs after chick rearing, and remain high in mass during the winter (Harris et al. 2000a), perhaps in response to less reliable food sources compared to the summer months, as seen in waterfowl species (Kestenholz 1994; Lovvorn 1994).

5.4.4 Inter-annual variability in body condition

The variable body condition across years was most likely due to variable breeding conditions. Despite high foraging effort in early chick rearing in 2000, murres were not able to provision their young at rates comparable to 1998 and 1999 (see Chapter 3). During the second week of chick rearing, feeding rates increased to those of the other two years, and murres showed lowered foraging effort. Poor breeding conditions during early chick rearing in 2000 most likely resulted from a mismatch between chick hatching and inshore arrival of spawning capelin (see Chapter 3).

Despite their lowered condition during Week 1 of chick rearing, adults did not deplete their reserves beyond the levels reached by Week 3 in years when breeding conditions were more favourable. In the year of delayed capelin arrival, out of 27 sites with chicks, 3 (11%) chicks died within the first week of hatching with no chick feeds observed at two of the sites (pers. obs.). During the eight years (1996-2003) that murres have been observed at this study site, 2000 was the only year in which chicks were seen dead at their nest site. Common Murres are long-lived seabirds with high rates of adult survival (Harris and Wanless 1988b; Harris et al. 2000b). The poorer provisioning conditions of 2000 did not have an effect on adult survival to the 2001 breeding season (0.988 ± 0.019, compared to 0.956 ± 0.030 from 1998 to 1999 and 0.980 ± 0.020 from 1999 to 2000; G. Robertson, A. Storey and S. Wilhelm in prep.). Combined, these observations suggest that when prey is difficult to find, adults will use up to a certain degree their own reserves to feed their young. However, to maintain some critical level of body condition, they will forsake their chick for their own survival. Breeding conditions did improve by the second week of chick rearing (Chapter 3) and overall reproductive success did not differ across the three years (see Chapter 2).

Other studies having investigated the relationship between a variable breeding environment and adult condition report similar findings of lowered adult condition when breeding conditions are poor, with adults adjusting their breeding efforts to ensure their own survival over their chicks' (Chastel et al. 1995; Monaghan et al. 1989; Weimerskirch and Lys 2000; Weimerskirch et al. 2001; but see Kitaysky et al. 2000). However, the threshold at which seabirds abandon their brood varies across species and appears to be influenced by size: smaller species such as puffins and small petrels are more likely to desert under unfavorable conditions compared to albatross (reviewed in Weimerskirch et al. 2001). Larger species may have a higher safety margin allowing them to continue to provision their chicks minimally in case feeding conditions improve (Weimerskirch et al. 2001). Similarly, Common Murres in this study continued to feed their chicks at very low rates rather than desert them, which was a successful strategy for most pairs in 2000.

5.4.5 Physiological responses of males and females during chick rearing

Despite evidence that females may provide more direct parental care during the chick-rearing period at the colony (Wanless and Harris 1986; Chapter 3), females did not show greater physiological responses to breeding compared to males. Males and females had similar body condition indices, corticosterone, and haematocrit levels throughout the chick-rearing period. These findings support the hypothesis that both sexes are working equally hard during chick rearing, as seen at the individual level (Chapter 3), and as predicted for a species where both parents are required to provide parental care for the successful rearing of the single chick.

Individuals showed a negative relationship between body condition and corticosterone. This relationship has been documented in other seabirds, including Magellanic Penguins (*Speniscus magellanicus*; Hood et al. 1998), Harlequin Ducks (*Histrionicus histrionicus*; Perfito et al. 2002), and Black-legged Kittiwakes (*Rissa tridactyla*; Kitaysky et al. 1999). The increase of circulating levels of baseline corticosterone as body condition declines is likely influenced by a combination of factors including increased foraging behaviour and the mobilization of protein (reviewed in Wingfield et al. 1997). Because Common Murres are at their lowest mass and show high levels of activity during chick rearing, it is difficult to assess the causal relationships between these factors in a natural setting. Furthermore, shortages in food supplies may not necessarily affect adult body condition, but can lead to increased baseline corticosterone levels, as seen in a Common Murres breeding in the Bering Sea (Kitaysky et al. 2000). Therefore, it is essential to have insight on the individual's status and breeding environment when interpreting physiological responses. In this study, the higher stress response of murres in 2000 further suggests that breeding conditions were not optimal in that year, likely related to low food availability during early chick rearing. Finally, the lack of relationship between body condition and haematocrit levels suggests that haematocrits may not be a sensitive index to detect short-term changes in health or condition.

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CHAPTER 6 Measurements of Common Murre corticosterone from blood spots: implications for remote field sites

6.1 ABSTRACT

Using a commercially available corticosterone kit, a radioimmunoassay (RIA) procedure was developed and validated to determine corticosterone levels from blood spots in the Common Murre (*Uria aalge*). Serum samples were also analyzed to determine the conversion factor and to further validate the kit for use on an avian species. Blood samples were collected from breeding murres during late chick rearing in Witless Bay, Newfoundland. Samples were taken at 2 min, 6 min, and 11 min after capture. When diluted or spiked with exogenous corticosterone, the assay showed good parallelism and precision in both blood spots and serum. A significant increase in corticosterone levels was observed in blood spots and serum at 11 min, suggesting that the assay was effective in detecting important biological changes due to stressful conditions. Blood spots left at room temperature for a minimum of two weeks did not show signs of degradation. These results suggest that blood spots may provide a practical alternate method for processing and storing blood for subsequent endocrine analyses in remote settings. Mean baseline corticosterone levels reported in this study (26 ng/ml) were considerably higher than baseline levels of the other known study investigating the stress response of Common Murres (6-8 ng/ml). Further investigations are required to determine if these two distinct populations have evolved different baseline levels or if these differences were due to methodology differences.

6.2 INTRODUCTION

Measuring adrenocortical responses can provide useful information on the state of wild populations and may help determine if a given population is healthy or vulnerable to a sudden environmental change because it is chronically stressed (Wingfield et al. 1997). Hormone concentrations are usually measured in serum or plasma from blood samples, although they can also be determined from feces (Wasser et al. 1997; Hirschenhauser et al. 1999; Ludders et al. 2001).

Processing and storing blood samples for endocrine research in the field can be logistically challenging, particularly in remote field sites where electricity is not available and battery power may be limited. In such a setting, blood samples must be centrifuged manually, which can be time consuming as few samples can be spun simultaneously. More problematic, however, is the proper storage of samples. Serum and plasma samples must be frozen within 24 hrs to avoid degradation (Worthman and Stallings 1997). Although samples can be stored on dry ice or in liquid nitrogen, these options have their own limitations. Dry ice sublimates relatively quickly. Liquid nitrogen can last for several weeks, however, transporting a heavy container to a remote field site is not always convenient or safe.

The use of dried blood spots as an alternative to human serum or plasma has gained popularity in the clinical setting, primarily because samples can be obtained less invasively, more quickly, and more safely (Worthman and Stallings 1994). Other advantages include easy storage and transport, as well as allowing sample collection and processing outside of the hospital setting. Furthermore, the hormones within blood spot samples left at room temperature can remain stable for several weeks (Worthman and Stallings 1997). Accurate blood spot hormone measurements have been verified for human steroid hormones, including: prolactin (Bassett et al. 1986), estradiol, progesterone, testosterone (Shirtcliff et al. 2001), and cortisol (Kraiem et al. 1980). The advantages of collecting blood spots over serum or plasma in humans are just as pertinent for researchers interested in the endocrine system of other vertebrates, including birds.

The main objective of this study was to test the use and appropriateness of blood spots for measuring corticosterone levels in the Common Murre (*Uria aalge*). As is the case with many auk species, Common Murres breed in large colonies typically on offshore islands (Harris and Birkhead 1985). Consequently, researchers often live in remote field sites for several weeks or months, as transport to and from the islands is expensive and can take several days. In this study, a commercially available radioimmunoassay (RIA) kit designed to measure corticosterone in rats was validated for use on Common Murre blood spots. Biochemical (dilution and recovery of exogenous corticosterone) and physiological (stress capture protocol) procedures were applied to validate the use of a commercially available kit on an avian species (Washburn et al. 2002).

Other studies have shown a high correlation between blood spots and serum and report a formula to convert blood spot values into serum values to allow comparisons with other studies (Worthman and Stallings 1994; Shirtcliff et al. 2001). Therefore, Common Murre serum samples were also analyzed to determine the conversion factor and to further validate the kit. Finally, preliminary investigations were done on the stability of serum and blood spot samples left at room temperature at different time intervals.

6.3 METHODS

6.3.1 Study areas, blood collection, and storage

Blood samples were collected from breeding Common Murres during late chick rearing on 15 July 2002 on Gull Island (47°15'N, 52°46'W) and on 23 July 2002 and 2 August 2002 on Great Island (47°11'N, 53°49'W), Witless Bay, Newfoundland and Labrador (NL), Canada. Both islands are located only a few km away from the main island of Newfoundland, allowing quick sample removal from the field and subsequent access to proper storage. Birds were caught with a noose pole, placed in a cotton bag, and sampled from the brachial vein within 2 min of capture (considered baseline values; Wingfield et al. 1997) and again after either 6 min or 11 min. For sampling, birds were placed on their side with the wing fully stretched out and 95% ethanol was applied onto the brachial vein at the height of the ulna joint. Approximately 1.5 cc of blood was collected using a 23-gauge butterfly needle and a 3 cc syringe. Immediately after the removal of the needle, a cotton swab was firmly held on the vein until bleeding ceased (usually within a few minutes). The needle was removed from the syringe and blood was dispensed onto blood collection cards (Sigma Diagnostics, Inc.), filling the four preprinted circles and such that the circle was entirely soaked through (as instructed by the manufacturer). The remainder of the blood was transferred into a 2 ml non-heparinized Vacutainer® brand blood collection tube by removing the top of the tube and gently dispensing the blood along the wall of the tube. All blood spots were left to air-dry overnight. Tubes were placed into a small thermal chest containing a hot water bottle and left to clot for 2-4 hrs before centrifugation. When blood samples were left to clot at ambient temperature, particularly on cold days, the serum obtained was often low in quantity and had a gelatinous consistency that made pipetting impossible. Keeping the samples in a warm environment immediately after sampling the bird yielded higher quantities of clear, usable serum.

Serum and blood spot samples were obtained from the same five individuals sampled at 2 min and 11 min. However, baseline samples were not obtained from the five birds that were subjected to the 6 min stress test. All 6 min stress test birds were sampled on 2 August. Veins were difficult to find that day, likely due to cool ambient temperatures.

Blood collected from one murre subjected to the 11 min sampling was entirely dispensed onto blood spot cards. These yielded sufficient spots to validate the assay for blood spots (see Dilution and Recovery sections of blood spot assay below).

Samples from Gull Island (15 July) were transported to the Health Sciences Centre, located in St. John's, NL (approximately 20 km north of Gull Island). Blood samples were centrifuged at 3000 rpm for 15 min. The serum was transferred to a microcentrifuge tube and frozen immediately at -20°C. Blood spot cards were left on a counter to air-dry overnight at ambient temperature. The following morning, all blood spot samples were placed into individual plastic bags after drying, and frozen.

Samples collected on Great Island (23 July and 2 August) were centrifuged on the island for 5-10 min using a manual centrifuge and the serum was transferred to a 1.5 ml Cryovial tube. All serum samples collected on 23 July were put immediately on dry ice. Similarly, after left to air-dry overnight at ambient temperature, blood spots collected on 23 July were put on dry ice. Samples collected on 2 August were either placed immediately on dry ice after proper processing or subjected to different freezing intervals (see Sample stability).

6.3.2 RIA procedure for blood spots

Blood spot corticosterone concentrations were obtained using the Coat-A-Count Rat Corticosterone ^{125}I radioimmunoassay (Cat. # TKRC1, Inter Medico, Markham, Ontario) with several modifications to the procedure. Standards and NSB tubes were prepared by pipetting 30 μl of the standards (0, 20, 50, 100, 200, 500, and 1000 ng/ml) on blood collection cards (Sigma Diagnostics, Inc.) and then allowing the cards to air-dry overnight. For standards, NSB and unknowns, one 10.5 mm-diameter circle was cut using a punch and hammer and cut into three smaller pieces to fit in the supplied tube, with the exception of NSB where plain (uncoated) polypropylene tubes were used. Standards, NSB and unknowns were all prepared in duplicate. One ml of supplied ^{125}I Rat Corticosterone was added to each tube, covered, and set-aside at room temperature. After five hours, tubes were gently shaken so that liquid was mixing but filter paper was not rubbing the wall of the tube. Overall low specific binding were obtained when tubes were vortexed at high speed, suggesting that antibody-bound material was being knocked off the wall of the tube and subsequently lost when decanted. Tubes were then set-aside again at room temperature for an additional 13 hrs. Tubes were thoroughly decanted (with the exception of the total count tubes), let to drain for approximately 5 min and dabbed onto gauze before being set upright in a rack ready for counting in a gamma counter.

6.3.3 RIA procedure for serum

Serum corticosterone concentrations were obtained using the same kit mentioned above and following the kit's normal procedures. The required amount of serum for each sample was 50 μl (100 μl for duplicates). The detection limit of the kit was reported at 5.7 ng/ml and the antiserum used had very low cross-reactivity with other steroids (less than 3% with 11-deoxycorticosterone and less than 1% with five other steroids listed including progesterone; Anon. 1997).

6.3.4 'Dilution' of blood spot assay

To simulate a dilution procedure in blood spots, the '0' standard was dried on filter paper (see RIA procedure for blood spots) and circles from blood and standard cards were cut using a small hole punch (3.3 mm-diameter circle). Blood spots were assayed undiluted (12 blood spot circles/tube), diluted 1:2 (six blood spot circles added to six '0' standard circles/tube), and diluted 1:4 (three blood spot circles added to nine '0' standard circles/tube). All blood spot circles were obtained from the same individual with expected high corticosterone levels (see Study areas, blood collection, and storage).

6.3.5 Dilution of serum assay

The sera of five murres expected to have high levels of corticosterone (birds were subjected to the 11 min handling) were pooled together. Pooled serum was assayed undiluted (50 μl of serum), diluted 1:2 (25 μl of serum added to 25 μl of the '0' standard from the kit) and diluted 1:4 (12.5 μl of serum added to 37.5 μl of the '0' standard).

6.3.6 Recovery of blood spot assay

Exogenous corticosterone was added to blood spots by adding one half of a 10.5 mm-diameter circle of the '0', '100', '200', or '500' standard, dried on filter paper (see RIA procedure for blood spots), to one half of a 10.5 mm-diameter blood spot circle from a single individual. These yielded expected results of 50, 100, or 250 ng/ml in addition to the baseline value, obtained when adding one half of a blood spot circle to one half of a circle containing the '0' standard. All blood spot circles were obtained from the same individual with expected high corticosterone levels (see Study areas, blood collection, and storage).

6.3.7 Recovery of serum assay

The serum of 5 birds was pooled together and 25 μl of serum was assayed with 25 μl of the '0', '100', '200', or '500' standard supplied with the kit. These yielded expected recovery values of 50, 100, or 250 ng/ml in addition to the baseline value, obtained when adding 25 μl of serum to 25 μl of '0' standard.

6.3.8 Sample stability

The serum of five murres collected on 2 August was pipetted into two Cryovial tubes/individual. One vial was frozen immediately while the other was frozen 1 week later. Blood spot cards of eight individuals sampled on 2 August were cut into two, each half containing two spots. One half was frozen immediately and the other half was frozen either 1 week (N = 4) or two weeks (N = 4) later. Samples exposed to different freezing treatments were run in one assay using the radioimmunoassay procedure for blood spots described above.

6.3.9 Statistical analyses

Pearson's correlation was used to correlate serum and blood spot corticosterone values and a linear regression analysis was applied to calculate the equation to convert blood spot values into serum values. Paired t-tests were used to test for differences in corticosterone values between 2 min and 11 min samples for both serum and blood spots. Unpaired t-tests were used to compare values between 6 min with the other two handling conditions for both serum and blood spots.

6.4 RESULTS

6.4.1 Validation of RIA

Serial dilutions (1:2 and 1:4) of Common Murre blood spots showed parallelism with the Coat-A-Count Rat Corticosterone kit standards (Table 6.1). Parallelism was also demonstrated between kit standards and pooled Common Murre serum (Table 6.1).

Recovery of added exogenous corticosterone (50, 100, and 250 ng/ml) further confirmed that the commercially available kit was accurately measuring Common Murre corticosterone when used on both blood spots and serum (Table 6.2). Blood spot and serum values were highly correlated ($r = 0.97$, $N = 20$) with 93% of serum concentration variation explained by blood spot concentrations (Fig. 6.1). Therefore, Common Murre blood spot values obtained using this specific method can be converted into serum values with the following equation obtained from the regression: serum corticosterone = -29.42 + (0.72 x blood spot corticosterone value). Intra-assay variation of low and high blood spot values were 5.2% and 3.8% respectively while variations of low and high serum values were 6.2% and 4.8% respectively. Inter-assay variation for two blood spot and serum assays were 9.0% and 9.4%, respectively.

In both blood spots and serum, corticosterone levels were significantly higher in murres restrained for 11 min compared to 2 min (blood spots: $t_4 = 7.5$, $P = 0.002$; serum: $t_4 = 7.49$, $P = 0.002$) or 6 min (blood spots: $t_8 = 4.89$, $P = 0.002$; serum: $t_8 = 5.53$, $P = 0.002$; Fig. 6.2). No differences in corticosterone levels were found in birds that were restrained and handled for 2 min versus 6 min (blood spots: $t_8 = 0.33$, $P = 0.75$; serum: $t_8 = 1.16$, $P = 0.28$; Fig. 6.2).

Table 6.1. Blood spot and serum samples were assayed undiluted and diluted with the '0' standard (see Methods) to test for parallelism. The mean observed and expected values are presented in ng/ml.

Sample type	Dilution	Observed	Expected	%O/E
Blood spots	undiluted	247.4	---	---
	1:2	120.3	123.7	97
	1:4	53.2	61.8	86
Serum	undiluted	82.9	---	---
	1:2	36.7	41.5	88
	1:4	21.2	20.7	102

Table 6.2. Blood spot and serum samples were assayed spiked with exogenous corticosterone to verify accurate measurement. The spiking solution, observed, and expected values are presented in ng/ml.

Sample type	Spiking solution	Observed	Expected	%O/E
Blood spots	0	105.1	---	---
	50	162.8	155.1	95
	100	214.7	205.1	95
	250	423.4	355.1	119
Serum	0	40.6	---	---
	50	88.9	90.6	98
	100	145.2	140.6	103
	250	314.6	290.6	108

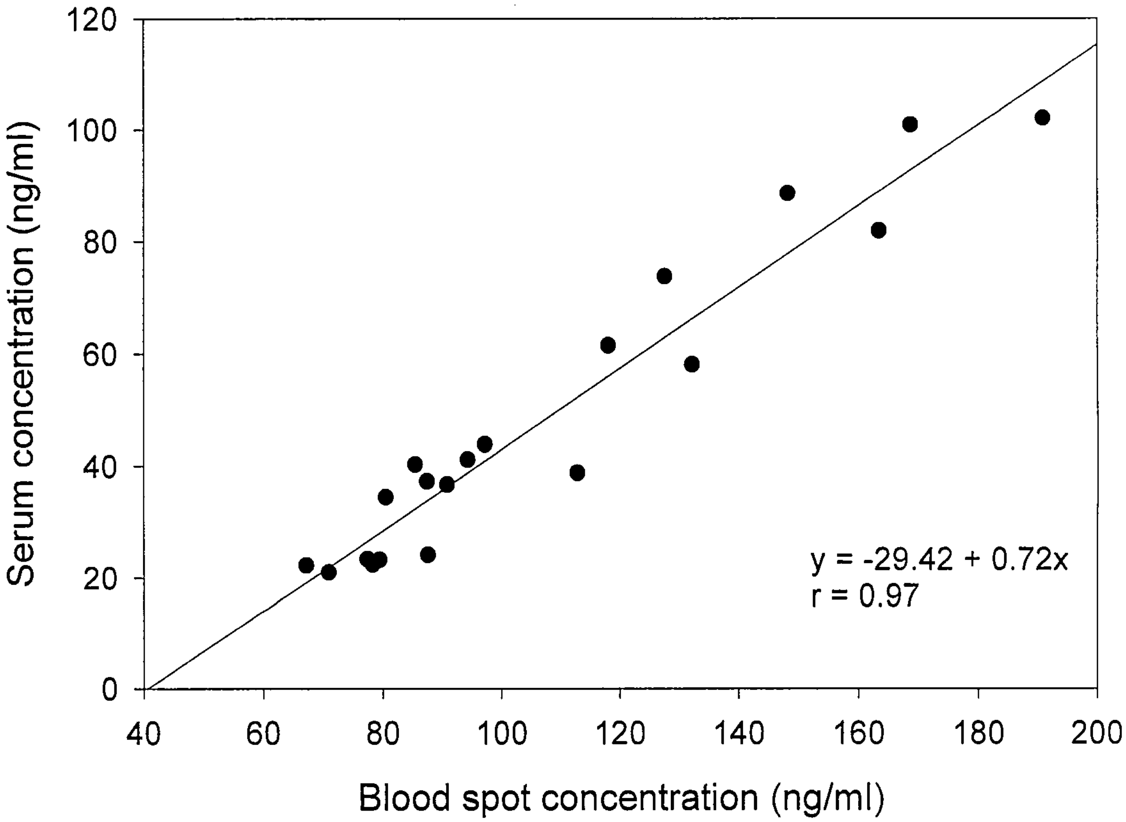

Figure 6.1. Scatter plot and regression line of Common Murre (N = 20) serum and blood spot corticosterone concentrations (ng/ml).

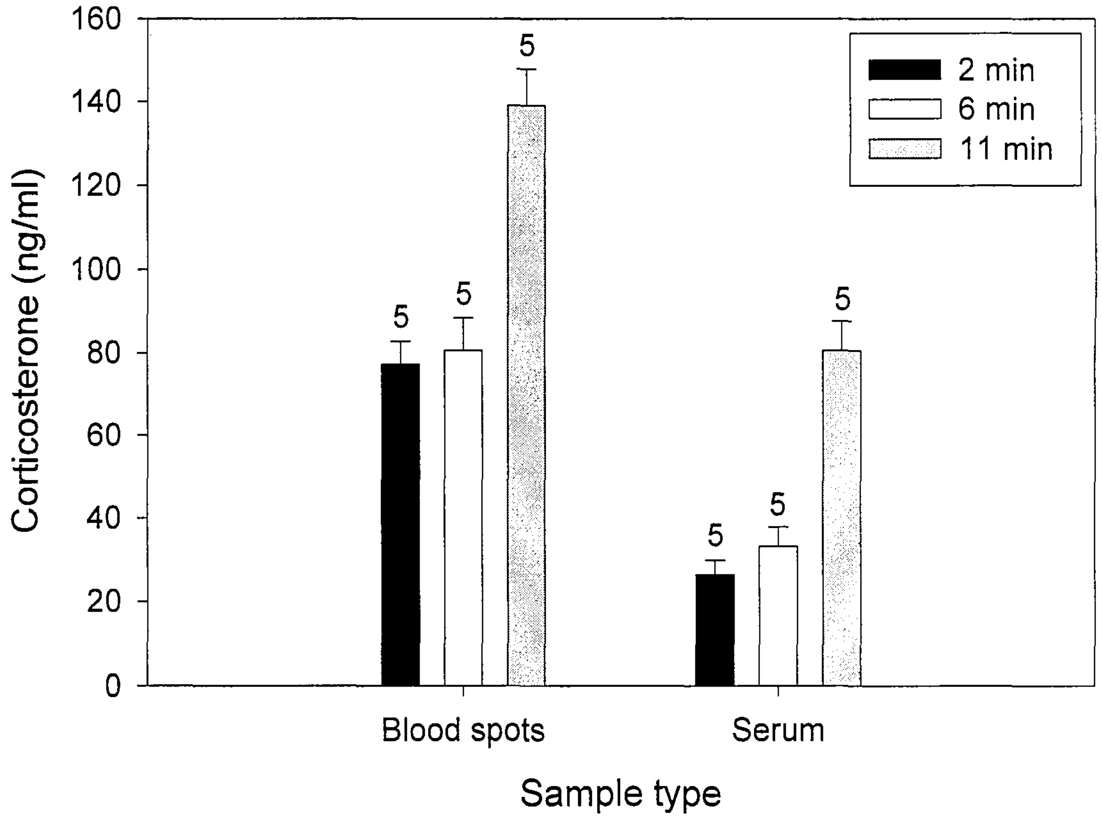

Figure 6.2. Mean (± SE) blood spot and serum corticosterone concentrations (ng/ml) of Common Murres sampled 2 min, 6 min, and 11 min after capture. Note: serum values were obtained from serum samples and not by calculating back from blood spot values.

6.4.2 Sample stability

Compared to corticosterone values of the same serum samples frozen immediately, corticosterone recovery for serum samples stored at room temperature for one week was 93%, consistent with degradation. However, blood spot samples showed no signs of degradation. Corticosterone recovery of blood spot samples frozen 1 and 2 weeks after being spotted on filter paper were not below the levels of the same blood spot samples frozen immediately (1 week: 106%; 2 weeks: 108%).

6.5 DISCUSSION

6.5.1 Validation of blood spot assay

The blood spot assay showed good parallelism and precision when samples were 'diluted' or 'spiked' with exogenous corticosterone. Furthermore, blood spot samples showed an increase in corticosterone levels throughout the stress capture protocol. These increases were similar in magnitude to the serum samples and to the stress response of other avian species (Wingfield et al. 1992; Perfito et al. 2002; Romero and Romero 2002), thereby demonstrating that the assay was effective in detecting important biological changes in corticosterone levels of individuals exposed to stressful conditions. Furthermore, blood spots appeared to remain stable when left at room temperature for two weeks. These results suggest that blood spots provide an alternate method for subsequent endocrine analyses in settings where the collection of serum or plasma is logistically difficult. Other human adrenal hormones in blood spots have shown sample stability for up to four weeks (Worthman and Stallings 1997). The maximum time that corticosterone levels from blood spots of Common Murres remain stable at ambient temperature remains to be tested.

6.5.2 The use of a commercially available RIA on Common Murre blood

Overall, the commercially available rat corticosterone kit appeared to be reliable for use on Common Murre samples. Similar to the blood spot assay, the serum assay also responded as predicted when diluted or spiked with exogenous corticosterone. Both assay types demonstrated overall good repeatability as shown by low intra- and inter-assay variability. The pros and cons of using a commercially available assay over the more commonly reported RIA (as described in Wingfield et al. 1992) are outlined in Washburn et al. (2002). The Coat-A-Count Rat Corticosterone ^{125}I RIA does not require extraction of samples and the procedure is simple. The sensitivity of the assay is adequate for Common Murre corticosterone levels as only one serum sample out of 20 assayed had values below the level of assay sensitivity. Furthermore, relatively little whole blood is required to analyse blood spot samples (less than 100 μl to assay one sample in duplicate). However, this assay may not be sensitive enough for other species with lower baseline levels. Furthermore, slight modifications of the RIA procedure (e.g., vortexing speed or room temperature) may affect the results, particularly for blood spots, in unpredictable ways. There was considerable trial and error before developing this final methodology with relatively low inter-assay variability. It is recommended that laboratories independently determine their own regression line to convert blood spots back to serum values. Otherwise, the use of the reported equation should be limited to relative differences in corticosterone values, rather than absolute levels.

6.5.3 Comparison with the other Common Murre stress study

The serum values reported in this study were considerably higher than those of the only other known study examining the stress response of Common Murres (Kitaysky et al. 2002). Kitaysky et al. (2002) report baseline values of 6-8 ng/ml during late chick rearing, with maximum corticosterone levels (birds held captive for 50 min) close to 40 ng/ml. In general, corticosterone levels in wild birds rise within minutes after initial capture (e.g., Wingfield et al. 1992; Kitaysky et al. 1999) and subsequent changes in levels may be further influenced by how the bird is handled (Romero and Romero 2002). To obtain baseline values that reflect the "natural" stress level of the bird prior to capture and handling, samples must be taken less than 2-3 min after capture (Wingfield et al. 1997). In this study, an average of 1 min 54 sec (range: 1 min 8 sec to 2 min 50 sec) elapsed between capturing the murre and the baseline sample collection. Therefore, the higher corticosterone levels in this study were not due to how the birds were handled.

The Alaskan subspecies of Common Murres (*Uria aalge inornata*) sampled by Kitaysky et al. (2002) are physiologically and genetically distinct from the subspecies of Common Murres breeding in Newfoundland (*Uria aalge aalge*; Ainley et al. 2002). Therefore, one possible explanation for the observed hormonal differences may be that these two populations have evolved different baseline corticosterone levels. However, the magnitude of the difference does warrant concern that the disparity may be due laboratory methods. Samples from Kitaysky et al. (2002) were first extracted in dichloromethane (with recovery values of 80-90%) and subsequently processed using the RIA protocol described in Wingfield and Farner (1975) and Wingfield et al. (1992). Until the two methods are compared, the use of corticosterone values obtained from the methods described in this study should be limited to relative differences rather than absolute levels.

6.5.4 Conclusion

The blood spot method may prove to be a useful tool for assessing and monitoring the health and reproductive state of remote populations across a wide range of vertebrates. The high correlation between Common Murre blood spots and serum values suggests that corticosterone levels from blood spots can be calculated back to serum values for comparisons with other studies. However, further investigations are required for the use of the commercially available kit on Common Murre serum to quantify corticosterone levels. Some hormones, such as testosterone, show more rapid degradation in both serum (pers. obs.) and blood spots (Worthman and Stallings 1997) compared to corticosterone. Field researchers should be aware of the degradation rate of the hormone of interest before sampling in the field.

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CHAPTER 7 General discussion and conclusion

7.1 INTRODUCTION

Individual Common Murres (*Uria aalge*) exhibit much variability in their behavioural and physiological responses within and across successive breeding seasons. Because analyses were restricted to banded individuals that maintained long-term pair bonds and successfully reared a chick, the variability of the murres' responses is not likely due to intrinsic individual characteristics, such as quality or experience. Rather, breeders appeared to be responding to a variable foraging environment.

In each preceding chapter of this thesis, the observed variable responses shown by Common Murres were discussed in light of changes that have occurred in the breeding biology and distribution of their main prey, capelin (*Mallotus villosus*). In this final chapter, the main findings and discussions of the thesis are merged and explored in more depth in the following two sections: a) Breeding behaviour and changes in capelin ecology and b) Common Murre physiology and variable foraging conditions.

7.2 BREEDING BEHAVIOUR AND CHANGES IN CAPELIN ECOLOGY

Since the 1990s, capelin distribution and breeding patterns have undergone important changes due to below normal seawater temperatures (Carscadden et al. 1997). Spawning capelin in Newfoundland have delayed their inshore arrival compared to historical dates (Carscadden et al. 2002). These changes have also been observed in Witless Bay (Regehr and Rodway 1999; Massaro et al. 2000; Chapter 3). During the last decade, capelin has declined in the diet of some seabirds in Newfoundland and Labrador, which may be linked to the observed changes in capelin ecology (Carscadden et al. 2002). Common Murres are generalist seabirds as shown with their diverse diet (Ainley et al. 2002) and can switch prey when availability changes (Bryant et al. 1999). Burger and Piatt (1990) found that Common Murres breeding in Witless Bay compensated for low capelin abundance by bringing in more sand lance (*Ammodytes* spp.) to their chicks. Although murres in this study were feeding sand lance to their chicks prior to capelin arrival, chick diet consisted mainly of capelin (Chapter 4). With the exception of limited availability to sand lance, murres breeding in Witless Bay do not appear to have a reliable alternate food source for their chicks prior to inshore spawning capelin arrival.

In the absence of capelin, Common Murres breeding in Witless Bay may have difficulties finding sufficient sand lance due to sand lance distribution. Similar to capelin, sand lance are diurnal, schooling fish (Auster and Stewart 1986). However, around the island of Newfoundland, sand lance are primarily found on the west and south coasts (Scott 1993). Sand lance schools are also reported on the Southeast Shoal of the Grand Banks (Scott 1993). Murres are either flying long distances from Witless Bay to find sand lance or are perhaps preying on individuals that have ventured further north from the Grand Banks. The interactions between capelin and Common Murres have been well documented for the Northwest Atlantic (Piatt 1990; Schneider et al. 1990; Davoren 2001). However, there is a gap in the literature with respect to the relationship between Common Murres breeding off the coast of Newfoundland and sand lance, the second most important prey item for chicks reared in Witless Bay. Assessing the reliance that

Common Murres have on sand lance may be important to model the sustainability of murres breeding in Witless Bay and other nearby colonies, in the event that capelin stocks should decline further.

On Great Island in 1999, chicks enjoyed high feeding rates in part because they hatched at a later date, well after spawning capelin had arrived in the vicinity of the breeding colony. Female murres laid their eggs less synchronously in 1999, which led to more egg predation during early incubation (Chapter 2). Consequently, more chicks hatched from the re-laid eggs, and thus at a later median date (Chapter 4). With global warming, many species of invertebrates, amphibians, birds and plants are showing signs of earlier breeder (Root et al. 2003). The gap between murre and capelin breeding patterns will most likely persist and deserves continued monitoring.

With the exception of periods of extreme poor food availability, Common Murres continue to adequately provision their chicks under moderate food availability due to their flexible time budgets (Burger and Piatt 1990; Monaghan et al. 1994). When capelin availability was presumed low in 2000, both males and females increased their search efforts to find prey and spent less time at the colony co-attending their brooding mate (Chapter 3). Independent of year, females collectively tended to show higher levels of direct parental care during the chick rearing period. However, when examining the contribution of individuals relative to their mates', pairs showed variable parenting strategies. In some pairs, males brooded and/or provisioned more than their mate. Only one pair showed consistent role partitioning (Chapter 3). Role partitioning is expected to be an effective strategy to increase reproductive success in species with biparental care (reviewed in Nol 1985). This, however, may not apply to species with high wing loading and expensive flying demands, such as murres (Pennycuick 1987). In such species, the energy expenditure discrepancy between brooding and provisioning are presumably large and could cause parental contribution to be disproportionately skewed to one sex. Nonetheless, some females are the primary provisioner within a pair, as shown by the overall higher provisioning rates of females. Although wing length does not differ between the sexes, females can be structurally smaller (Threlfall and Mahoney 1980). Therefore, females may be able to fly at a lower energetic cost. This, however, remains to be tested.

7.3 COMMON MURRE PHYSIOLOGY AND VARIABLE FORAGING CONDITIONS

7.3.1 Chicks

Although parents can compensate to some degree for fluctuating food conditions, chicks reared when food availability is low have lower body mass compared to chicks reared when food availability is high (Harris 1978; Barrett et al. 1987; Øyan and Anker-Nilssen 1996; Chapter 4). However, most studies report no relationship between wing growth and nutrition (reviewed in Gaston 1985). The finding in Chapter 4 that chicks reared when food was less abundant grew longer wings is surprising and requires further investigation. Because catching murres is disturbing and the focus of this thesis was centered on behaviour and dawn to dusk attendance, chick-catching effort was kept to a minimum. Consequently, reported sample sizes are small and data do not cover the entire range of chick ages. Rearing chicks in captivity and exposing them to different food conditions may be a more appropriate way to test if wings do grow faster in food-deprived chicks. This finding has interesting evolutionary insights on the unique developmental strategy employed by the Common Murre, an "intermediate" species. Based on a theoretical model attempting to explain the different timings of nest departure employed by auks (Ydenberg 1989; Ydenberg et al. 1995), Hipfner and Gaston (1999) found that wing length, and not body mass, was important in predicting age of departure of two other intermediate species: the Thick-billed Murre (*Uria lomvia*) and Razorbill (*Alca torda*). Longer wings may allow for a safer transition between nest site and sea (Hipfner and Gaston 1999). Rapid wing growth can benefit chicks as well as parents by allowing earlier departure, thereby bringing the chick to the food source (Birkhead 1977). Early departure may be further selected for when food conditions are poor.

The interaction between sex steroids and growth may provide an alternate explanation for the observed wing length difference in chicks. When capelin arrive inshore to spawn, males are presumably high in testosterone and females high in estrogen. Common Murres prey on male, female and immature capelin, but show a preference for gravid females (Davoren 2001; pers. obs.), suggesting that chicks are potentially ingesting high levels of exogenous estrogen when capelin are abundant. Although estrogen and other sex steroids are necessary to stimulate bone growth, high levels may have an opposite effect and hinder skeletal growth (Hurwitz and Pines 1993; Norris 1997). Quantifying hormone intake in chicks and examining the relationship between sex steroids and growth may provide further insight on factors affecting growth.

7.3.2 Adults

Throughout the chick rearing period, male and female Common Murres did not differ in any of the physiological responses investigated: both sexes showed decreasing body condition and similar corticosterone and haematocrit levels (Chapter 5). This may be expected if males and females are working equally hard, or at their own maximum capacity, to provision the chick. Both sexes showed high motivation to forage and demonstrated similar foraging effort (Chapter 3). However, there are challenges associated with obtaining blood measurements in the field, which may affect the reliability and/or validity of using corticosterone and haematocrit levels to assess chick-rearing demands of Common Murres.

Blood samples taken within 2-3 minutes after capturing the bird are considered to reflect baseline levels of corticosterone (Wingfield et al. 1997). Obtaining blood samples from murres within that time is feasible, as shown in Chapter 6. Most murres on our study site, however, showed some level of disturbance when another murre was being caught, due to their close proximity to one another. It is possible that the corticosterone levels of murres are rising in response to the catching process, whether they are caught with the noose pole or not. Therefore, only individuals that are caught at the beginning of the catching session, which usually lasts 4-5 hours, may have true baseline levels. Exploring attendance patterns and behaviours exhibited by Common Murres throughout the catching session in relation to their baseline levels is necessary to ensure that true baseline corticosterone levels are being measured.

One of the assumptions made in Chapter 5 is that murres may have higher haematocrits as a result of engaging in more foraging activity. There is evidence, however, that haematocrits may not be a valid measure of increased foraging demands in avian species (Stephenson et al. 1989; Wanless et al. 1997). A better index to measure increased diving activity is blood volume (Stephenson et al. 1989). Haematocrit levels may nonetheless reflect the health of an individual (Howard and Hamilton 1997), which in turn may provide some evidence of increased chick rearing demands. Other useful haematological measures that appear to be easily collected in the field include mean corpuscular volume and heterophile:lymphocyte ratio. Although not linked to diving activities, they may provide additional information on the health of individuals (Ots and Hõrak 1996; Bearhop et al. 1999).

7.4 IMPLICATIONS OF FINDINGS

Monitoring the behaviour and physiology of the same individuals across multiple years reduces and may even eliminate much of the variability associated with individual differences. Such a design provides a more sensitive test than a completely between-subjects design, improving the likelihood that differences observed among individuals are due to external factors, such as environmental change, rather than to idiosyncratic factors. Incorporating behavioural findings at the group and pair level can reveal a more complete understanding on the topic of interest, particularly when examining interactions between individuals. For example, at the group level, female Common Murres showed higher foraging effort and spent more time brooding the chick than males, leading one to conclude that the sexes show differential care during chick rearing. However, at the pair level, mates tended to brood and/or provision equally, suggesting that different pairs of murres coordinate their chick-rearing efforts in different ways. Observing consistent differences between pairs across years allows one to investigate a variety of variables that may be associated with different chick rearing strategies. In the case of this study, these factors may include individual age or experience, the length of the pair bond, the degree of genetic relatedness of mated pairs, and whether extra-pair copulation has occurred.

The development of a radioimmunoassay for blood spots of an avian species has important implications for avian field endocrinology. Using blood spots as an alternative to serum provides a simple tool to research endocrine functions in places and on species that have not been investigated due to their remote settings. Monitoring endocrine levels of groups or sub-populations provides information on their health, potential vulnerability to sudden environmental changes (Wingfield et al. 1997), and reproductive status. Because spots require little amounts of blood, this procedure can also potentially be used to assess the physiological condition of chicks (Kitaysky et al. 1999; Sockman and Schwabl 2001).

Clearly, there is much more to learn about the behavioural and physiological plasticity of individuals. The ability of individuals to adapt to short and long-term environmental change is no doubt a functional trait, particularly in long-lived seabirds, that has critical impacts at the population level. Subtle behavioural differences of individuals may provide early detection of possible anthropogenic impacts on colonies.

By the time these effects have impacted population parameters, such as adult survival or reduced reproductive success, it may be too late to reverse the process.

7.5 LITERATURE CITED

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