Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*

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We examine the provisioning constraints of a pursuit-diving seabird in a cold ocean regime by comparing the behaviour of common murres *Uria aalge* rearing chicks at two colonies in the Northwest Atlantic during 1998-2000. Funk Island is the largest (340,000–400,000 breeding pairs) and most offshore (60 km) colony of common murres in eastern Canada. Seventy-five percent of the Northwest Atlantic population of common murres breeds on this island. Great Island is one island within the Witless Bay Ecological Reserve, which is the second largest breeding aggregation (100 000 breeding pairs) and is located near-shore (2 km). The primary forage fish species in Newfoundland waters is capelin *Mallotus villosus*, which spawns on or near coastal beaches during summer. Therefore, the two study colonies differ in their distance to food resources and colony size. It is within this natural context that we compare: (1) prey types and frequency of delivery (amount of prey), (2) parental time budgets, and (3) the mass and condition (mass/wing length) of fledglings at both colonies. Similarly sized female capelin (100–150 mm) were delivered to chicks at both colonies. Foraging time per day per parent, a proxy of foraging effort, was similar at both colonies (Great Island: 5.1 h; Funk Island: 5.5 h), as was the percentage of time spent with mates (Great Island: 12.3%; Funk Island: 10.9%). Foraging trips, however, were longer at Funk Island (4.1 h) than at Great Island (2.9 h). This resulted in lower feeding rates of chicks (0.17 feeds per h) and poorer condition of fledglings (2.9 g/mm) at Funk Island compared to those at Great Island (0.22 feeds per h; 3.9 g/mm). We hypothesize that provisioning efforts are constrained at Funk Island by (1) distant food resources and increased competitor density, resulting in longer foraging trip durations and (2) the time spent paired with mates at the colony, which may reflect a minimum time required to maintain breeding sites due to higher breeding densities at Funk Island compared to Great Island. Demographic consequences of this poor fledgling condition at Funk Island are unknown, but fledglings may sufficiently accelerate growth at sea due to their closer proximity to an important nursery area. If fledgling survival is compromised, however, the lower potential for growth at Funk Island will impact the entire Northwest Atlantic population of common murres.

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Birds that deliver food to offspring at a breeding site are central-place foragers (Orians and Pearson 1979). Provisioning effort, chick growth and chick survival is limited by the parents' ability to transport food between feeding and breeding sites. The primary factor limiting a parent's ability to provision chicks is the time and energy expended during a round trip from the breeding site (Orians and Pearson 1979). Many factors alter travel times either directly or indirectly. Direct factors include the abundance, availability, types and distribution of prey relative to the breeding site (Pyke 1984). These factors can be influenced by density-dependent competitive interactions among conspecifics on foraging grounds (e.g. Birt et al. 1987) and other environmental conditions (e.g. tidal cycle, Slater 1980; sea state, Birkhead 1976). Density-dependent factors are

primarily important when there are large numbers of breeders in an area, evidenced by negative relationships between colony size and (1) reproductive performance (Wittenberger and Hunt 1985, Hunt et al. 1986, Brown et al. 1990), (2) per capita growth rates (Lewis et al. 2001), and (3) prey depletion (Birt et al. 1987). The behavioural mechanisms causing these trends have been studied only recently (e.g. Kitaysky et al. 2000). They are the focus of this study.

Life history theory purports that parents of long-lived species should maximize potential lifetime fitness by balancing present and future costs and benefits of reproduction (Stearns 1992). Parents likely provision young at levels below their maximum physiological capabilities to mitigate the costs of reproduction on adult survival and future fecundity (Cairns 1987, Golet et al. 1998, Golet and Irons 1999). Physiological capabilities depend on the age and physiological state of the parent (e.g. body mass or condition; Chaurand & Weimerskirch 1994, Weimerskirch et al. 1997, Weimerskirch 1998), which may be influenced by proximate biological factors (e.g. food availability, predation risk; Burger and Piatt 1990, Harfenist 1995, Harfenist and Ydenberg 1995, Ydenberg et al. 1995). Parents may be able to buffer higher reproductive costs (e.g. increased provisioning effort) by decreasing the time spent resting (time-buffering hypothesis; Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994). The ability of parents to increase provisioning rates, however, is limited by their maximum physiological capabilities, above which adult survival becomes compromised (Stearns 1992).

The common murre *Uria aalge* is a long-lived, colonial seabird that lays a single-egg clutch. This species breeds in large colonies both on cliff-ledges and on flat terrain, and breeds at higher densities than most other avian species (Birkhead 1977, 1978). Colonies on flat terrain generally have the highest densities of breeders (> 10 birds/m^2) relative to cliff-ledges (Birkhead 1977, Birkhead and Nettleship 1980). Breeding common murres compete vigorously to occupy and maintain breeding sites (Birkhead 1985) and if a breeding site is lost, there is a high probability that individuals will not breed during the next year (Harris et al. 1996). Chicks are reared at the colony for three weeks and they depart at approximately 25% of adult body mass (Harris and Birkhead 1985). Upon colony departure, chicks are unable to fly and are accompanied by the male parent at sea for 1–2 months (Swennen 1977), where they often attend important nursery areas (Camphuysen 2002, Davoren et al. 2003a).

After each foraging trip, murres deliver to their chicks a single fish, which in Newfoundland is almost exclusively capelin (*Mallotus villosus*; Davoren and Montevecchi unpubl. data). Capelin is a small pelagic fish that spawns on or near coastal beaches during the summer in Newfoundland (Templeman 1948). Large concentrations of capelin form inshore near beaches prior to spawning (e.g. Nakashima and Wheeler 2002) and provide dense aggregations of prey for breeding seabirds, large piscivorous fishes and marine mammals. In a related study, large aggregations of capelin schools were predictably found within the foraging ranges of murres from two major colonies in Newfoundland: Funk Island (∼ 45 km from the colony) and Great Island (< 5 km from the colony; Davoren et al. 2003b).

To gain a better perspective on provisioning constraints of a pursuit-diving seabird in a cold ocean regime, we compare the provisioning behaviour of common murres breeding at these two colonies: (1) Funk Island, the site of the largest and most offshore colony in eastern Canada and (2) Witless Bay Ecological Reserve, the second largest colony located in the near shore. Specifically, we compare: (1) prey types and frequency of delivery (amount of prey), (2) parental time budgets, and (3) the mass and condition (mass/wing length) of fledglings. Given the differences in distances to foraging areas from each colony, we predict that parents at Funk Island will make longer foraging trips. Based on life history theory, we further predict that food delivery rates to chicks will be similar at both colonies but the time spent with mates at the colony will be lower at Funk Island (Cairns 1987, Burger and Piatt 1990), or alternatively, food delivery rates to chicks will be lower at Funk Island relative to Wiltess Bay, along with fledgling condition.

Methods

Study area

This study was conducted on Great Island (47°11′N, 52°49′W), Witless Bay and on Funk Island (49°45′N, 53°11′W) off the east coast of Newfoundland (Fig. 1). Funk Island lies approximately 60 km offshore, whereas Great Island is approximately 2 km from the coast, and the colonies are 280 km apart (Fig. 1). The population of common murres on Funk Island is 340 000–400 000 breeding pairs (b.p., Birkhead and Nettleship 1980), whereas the population in Witless Bay is 100 000 pairs (Canadian Wildlife Service unpubl. data). The population of murres in Witless Bay occurs on three islands: Great Island (3000 b.p.), Gull Island (1000 b.p.) and Green Island (96 000 b.p.). A diversity of seabird species breed in Witless Bay and on Funk Island, most of which have high proportions of capelin in their diets (Rodway and Montevecchi 1996, Montevecchi and Myers 1997, Regehr and Montevecchi 1997, Davoren and Montevecchi unpubl. data; Table 1). The proportion of these species vary between Funk Island and Wiltess Bay; however, the total biomass of capelin-feeding seabirds at Funk Island is 2.5 higher than in Witless Bay, primarily owing to the larger number of common murres.
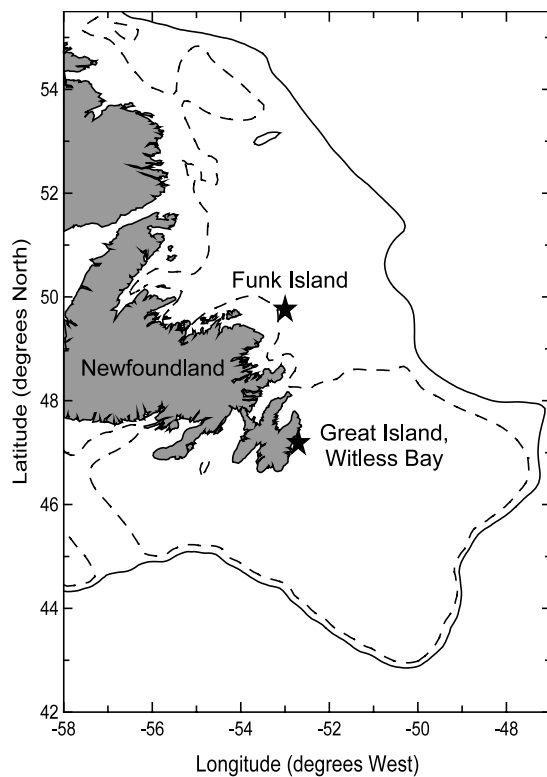
Fig. 1. Map of the Northwest Atlantic showing the Witless Bay (Great Island) and Funk Island Seabird Ecological Reserves off the east coast of Newfoundland, and showing the 200 m (dashed line) and 500 m (solid line) depth contours.

Colony observations

At both colonies, 20–25 focal breeding sites were observed during chick-rearing (July–August) in 1998 and 1999. Breeding sites were observed during the first and second week of chick-rearing at both colonies to control for the influence of chick age on provisioning rates. Observations on Great Island were conducted from a

blind approximately 20 m above a cliff-side subcolony of common murres. Yellow dye (picric acid) was used to mark breeders for individual recognition. On Funk Island, breeding pairs in a flat-ground subcolony were observed using a spotting scope from a distance of ~ 75 m. Individuals were not marked but ~ 75% of the pairs observed included bridled and non-bridled mates, making within-pair individual recognition more reliable. Although the same subcolony areas were observed in both years, focal breeding sites varied between years due to differential timing of breeding and breeding failures. We concluded that the majority of individuals observed were different in each year because murres exhibit high breeding site fidelity (91%; Harris et al. 1996).

Trained observers monitored focal breeding sites on 4 h shifts (05.30–09.30, 09.30–13.30, 13.30–17.30, 17.30–21.30 h) throughout the 16 h of daylight (05.30–21.30). Full dawn to dusk observations, however, were not always possible due to reduced visibility (e.g. fog, heavy rain) and, thus, the number of 4 h shifts conducted per day ranged from 1 to 4. Arrivals and departures of focal parents were recorded to the nearest minute. Instantaneous visual scans (Martin and Bateson 1986) of breeding sites were conducted every 15 min to confirm that arrivals and departures of focal parents were not missed. If the exact time of arrival or departure was missed, it was approximated to the time of the scan. The times that chicks were fed and the species delivered to each chick were recorded. Whole fish observed outside of the adult's bill during chick feeds were allocated to one of three broad size categories: small (< 100 mm), medium (100–150 mm) and large (> 150 mm). Adult bill length (46 mm; Harris and Wanless 1985) was used as a size reference (Uttley et al. 1994). Fish that were only observed in the bill of the adult were not assigned to a size category because murres can hold fish at different depths in their throat. Fish delivered to chicks were also collected on Funk

Table 1. The number of individuals breeding and non-breeding (number of breeders × 0.3, Montevecchi 2001) of each seabird species that feeds on capelin *Mallotus villosus* in the Witless Bay and Funk Island Seabird Ecological Reserves.

Capelin-feeding bird species	Individual mass (kg)[1]	Witless Bay		Funk Island	
		No. individuals[2,3]	Biomass (kg)	No. individuals[2]	Biomass (kg)
Common murre	0.99	203 840	201 802	1 030 799	1 020 491
Thick-billed murre	0.93	1560	1451	650	605
Atlantic puffin	0.46	347 360	159 786	5200	2392
Northern gannet	3.20	0	0	15 795	50 544
Razorbill	0.69	858	592	520	359
Black-legged kittiwake	0.44	99 918	43 964	2106	927
Herring gull	1.12	15 184	17 006	1300	1456
Great black-backed gull	1.68	585	983	260	437
Total		669 305	425 583	1 056 630	1 077 209

[1] Diamond et al. (1993)
[2] Cairns et al. (1989)
[3] Updated by Canadian Wildlife Service unpubl. data.

Island in 1998–1999 using a net attached to a long pole to capture returning adults (Davoren and Montevecchi unpubl. data). The species, sex and total length (snout to tip of tail) of each fish were recorded.

Data analysis of colony observations

Actual and approximate arrival and departure times of each focal parent were used to calculate the time spent away from the colony (foraging trip duration) and the percentage of time mates spent paired at the colony (duration paired). Foraging trip duration was calculated based on the assumption that the duration between disappearance and reappearance of an adult from the breeding site constituted a "foraging trip". Mean foraging trip duration ± 1 SE was calculated for each focal parent over all 4 h observation shifts. Mean foraging trip duration per focal parent was compared among colonies and years using a two-way ANOVA. Interaction terms that were non-significant ($\alpha = 0.05$) are not reported and all means are reported as ± 1 SE.

The mean number of fish delivered by both parents per chick per h was calculated for each 4 h shift and over dawn to dusk observations (05.30–21.30, 4 shifts). The mean duration mates spent paired at breeding sites per pair (mean duration paired) also was calculated for each 4 h shift and over dawn to dusk observations. Chick-feeding rates and durations paired vary throughout the day (Burger and Piatt 1990, Davoren 2001) and dawn to dusk observations were not always possible. Therefore, a 4 h shift was selected at each colony to compare chick feeding rates and durations paired between colonies and years to increase our sample size. There were no inter-annual differences in mean chick feeding rates or mean mate paired duration at each colony (Davoren 2001) and, thus, data were pooled for

both years at each colony. The mean feeding rate per h per chick (n = number of chicks) and the mean duration paired per pair (n = number of pairs) for each 4 h shift was compared with dawn to dusk observations using an one-way ANOVA and a post hoc Tukey's multiple comparisons test (Table 2). The chick feeding rate per h at Great Island did not differ significantly among observation periods ($F_{4,202} = 1.563$, $P = 0.186$), whereas duration paired did differ significantly ($F_{4,183} = 2.775$, $P = 0.029$). Alternately, the chick feeding rate per h at Funk Island differed significantly among observation periods ($F_{4,257} = 3.379$, $P = 0.010$), whereas the duration paired did not ($F_{4,161} = 0.432$, $P = 0.785$). The smallest differences were observed between the dawn to dusk period and the 09.30–13.30 shift and at both colonies (Table 2). Therefore, the mean duration paired per pair and mean feeding rate per h per chick in the 09.30–13.30 shift were compared between colonies and years using a two-way ANOVA. The percent composition of chick diets, by number of fish delivered to chicks, was calculated at each colony. The frequency of fish in each visually estimated size category was compared between colonies using a χ^2 test.

For the purpose of discussion, we estimated the time spent foraging per day per parent at each colony as a proxy of foraging effort. The time available to forage per day per parent was calculated by subtracting the mean mate paired duration from 16 h of daylight. The time observed to forage per day per parent was calculated by multiplying the observed chick feeding rates by 16 h of daylight to determine the number of foraging trips per day and then multiplying this by the mean foraging trip duration. Data used in calculations were mean values calculated over all 4 h shifts in both years of this study at each colony. We assumed that the time parents spent away from breeding sites was devoted

Table 2. Mean $\pm$ SE duration paired (%) and chick feeding rates per hour at Great Island and Funk Island in 1998 and 1999 combined. n = the number of pairs observed for % duration paired and the number of chicks observed for chick feeding rates. Single factor ANOVA and mean differences of pairwise comparisons derived from Tukey multiple comparisons tests are used to compare means during 4 h observation periods with those of the entire 16 h day.

Colony/observation period	Comparison with full day							
	% Duration paired				Chick feeding rate			
	n	Mean $\pm$ SE	Mean differences	P	n	Mean $\pm$ SE	Mean differences	P
Great Island (inshore)								
05.30–9.30	47	14.6 $\pm$ 1.2	0.050	0.581	53	0.22 $\pm$ 0.02	0.003	1.000
09.30–13.30	44	11.6 $\pm$ 1.2	0.004	1.000	52	0.22 $\pm$ 0.01	0.002	1.000
13.30–17.30	45	14.4 $\pm$ 1.6	0.033	0.870	50	0.18 $\pm$ 0.02	0.040	0.549
17.30–21.30	26	18.9 $\pm$ 2.0	0.106	0.049	28	0.24 $\pm$ 0.03	0.009	0.998
05.30–21.30	26	14.1 $\pm$ 2.2	–	–	25	0.22 $\pm$ 0.02	–	–
Funk Island (offshore)								
05.30–9.30	33	12.4 $\pm$ 2.7	0.014	0.996	53	0.22 $\pm$ 0.02	0.054	0.276
09.30–13.30	28	11.5 $\pm$ 1.7	0.005	1.000	52	0.16 $\pm$ 0.02	0.007	0.999
13.30–17.30	33	12.4 $\pm$ 2.3	0.010	0.999	52	0.19 $\pm$ 0.02	0.023	0.921
17.30–21.30	27	15.0 $\pm$ 2.3	0.036	0.890	52	0.12 $\pm$ 0.02	0.042	0.545
05.30–21.30	45	12.7 $\pm$ 1.1	–	–	53	0.16 $\pm$ 0.01	–	–

exclusively to foraging activities and that chicks were never left unattended by parents at the colony. Available and observed foraging effort at each colony was qualitatively compared.

Fledgling measurements

The masses and wing chord lengths of chicks were recorded prior to colony departure on Great Island (July 19–23) and Funk Island (August 6–12) in 2000. Capelin spawning is progressively later with increasing latitude (Nakashima 1992) and results in later breeding of murres at more northerly colonies. Therefore, measurement periods of fledglings were later at Funk Island. The age of the chicks measured at both colonies were unknown. At Funk Island, breeding sites are located at the center of the island and chicks must travel across the island to reach departure ledges. Chicks at Funk Island were captured and measured during transit to departure ledges and, thus were known fledglings. At Great Island, breeding sites are located on cliff-ledges and chicks depart the colony by leaping from ledges and fluttering to the water below and, thus, chicks could not be captured easily immediately prior to colony departure. Therefore, we measured a size range of older chicks once the mass exodus of chicks at Great Island began (∼ July 19, 2000). Chicks were measured near dusk at both colonies to control for variability in mass owing to the time interval since last feeding. Flattened wing chord was measured to the nearest 1 mm using a wing rule. Fledgling mass was measured to the nearest 1 g using a 500 g Pesola spring balance. Owing to differences in sampling regimes at each colony, a condition index (body mass divided by wing length) was calculated for each fledgling to standardize across birds of different sizes. Condition indices of fledglings were compared between colonies using a t-test. Wing length and body mass also were compared between colonies using a two-way ANOVA, to determine whether any differences in condition were due to varying body mass or wing length.

Results

On Great Island, 57 breeding sites were monitored (1998: 26; 1999: 31) for a total of 244 h (1998: 108 h; 1999: 136 h). Mean foraging trip duration was calculated for 48 focal individuals in 1998 and 52 in 1999. Mean chick feeding rate was calculated for 23 chicks in 1998 and 29 in 1999. Mean duration paired was calculated for 19 pairs in 1998 and 25 in 1999. On Funk Island, 54 breeding sites were monitored (1998: 22; 1999: 32) for a total of 172 h (1998: 76 h; 1999: 96 h). Mean foraging trip duration was calculated for 28 focal individuals in 1998 and 55 in 1999. Mean chick feeding

rate was calculated for 22 chicks in 1998 and 30 in 1999. Mean duration paired was calculated for 17 pairs in 1998 and 25 in 1999. In 2000, 35 chicks were measured on Great Island and 43 were measured on Funk Island.

Amount of prey delivered

We observed 915 fish deliveries to chicks, of which 73% were identified to species. Almost all were capelin at both colonies in both years (Table 3). Seventy-one percent of the fish that were identified (n = 477) were allocated to a size class. The majority of identified fish fell into the medium (100–150 mm) size category at both Great Island (1998: 87%, n = 172; 1999: 76%, n = 66) and Funk Island (1998: 85%, n = 27; 1999: 80%, n = 211) and, thus, there were no significant differences in fish length between colonies or years ($\chi^2_6 = 8.937$, P > 0.05). Visual observations of prey types and sizes were confirmed at Funk Island by capturing adults returning to the colony with fish. There were high percentages of female capelin (1998: 86%, 1999: 98%) and fish lengths were similar to those observed (1998: 139.4 ± 1.4 mm, n = 101; 1999: 144.7 ± 1.6 mm, n = 62). Mean feeding rates per chick per h, however, were significantly higher at Great Island compared to Funk Island ($F_{1,104} = 8.76$, P = 0.004; Table 4). There were no significant differences in mean feeding rates per chick per h between years ($F_{1,104} = 3.53$, P = 0.063; Table 4).

Parental time budgets

There was no significant difference in mean durations paired per pair between colonies ($F_{1,86} = 0.004$, P = 0.953) or years ($F_{1,86} = 0.99$, P = 0.322; Table 4). Mean foraging trip durations per parent were significantly longer at Funk Island (1998: 244.9 ± 42.5 min; 1999: 214.6 ± 21.8 min) compared to Great Island (1998: 163.3 ± 1.5 min; 1999: 147.6 ± 12.1 min; $F_{1,183} = 11.10$, P = 0.001) and there were no inter-annual differences ($F_{1,183} = 1.19$, P = 0.276; Fig. 2).

Table 3. Percentage by number of known fish species delivered to common murre chicks that were visually identified at Great Island and Funk Island in 1998 and 1999. The number of prey items, or sample size, is given in parentheses.

Prey species	1998		1999	
	Great	Funk	Great	Funk
Capelin	94 (225)	100 (34)	99 (94)	85 (257)
Male	3 (6)	0 (0)	0 (0)	0 (0)
Female/immature	91 (219)	100 (34)	99 (94)	85 (257)
Sandlance	6 (15)	0 (0)	1 (1)	15 (46)

Table 4. Comparisons of the time spent paired with mates (% duration paired), chick-feeding rates and fledging mass (g), condition (g/mm wing length) and success (%) of common murres from this study and other inter-colony or inter-annual comparisons. All data are reported as mean $\pm$ SE or range and only values for dawn to dusk watches are used unless otherwise indicated.

Colony/year	% Duration paired in daylight	Chick feeding rate (fish/h)	Fledging mass[1] and condition	Fledging success	Author(s)
Great I, Newfoundland (1998–2000)	11.9 $\pm$ 1.4 (1998) 11.4 $\pm$ 1.9 (1999)	0.22 $\pm$ 0.02 (1998) 0.22 $\pm$ 0.02 (1999)	245.4 $\pm$ 4.1 g (2000) 3.9 $\pm$ 0.1 g/mm	80% (1998) 88% (1999)	This study
Funk I, Newfoundland (1998–2000)	14.6 $\pm$ 4.0 (1998) 10.6 $\pm$ 2.0 (1999)	0.10 $\pm$ 0.04 (1998) 0.17 $\pm$ 0.04 (1999)	191.6 $\pm$ 4.0 g (2000) 2.9 $\pm$ 0.1 g/mm	68% (1998) 66% (1999)	
Gull I, Newfoundland (poor food yr: 1984) (good food yr: 1983, 85)	19.4 $\pm$ 9.7 (1984) 33.5 $\pm$ 10.8 (1983)[3] 28.4 $\pm$ 13.0 (1985)[3]	0.29 $\pm$ 0.02 (1984)[3] 0.24 $\pm$ 0.02 (1983)[3] 0.26 $\pm$ 0.03 (1985)[3]		100% 82% 92%	Burger and Piatt 1990
Skomer I, Wales (1985–87) (1973–75)	– –	0.20 $\pm$ 0.01 0.17 $\pm$ 0.01	211.6 $\pm$ 2.1 g 214.9 g		Hatchwell 1991 Birkhead 1977
Sumburgh Hd, Shetland (good food yr: 1991) (poor food yr: 1990)	40 (range: 6–78) 2.4 (range: 0–18)	0.31 $\pm$ 0.01 0.15 $\pm$ 0.01	[2] [2]		Uttley et al. 1994
Chisik I, Alaska Gull I, Alaska	3–5 8–32	0.29 $\pm$ 0.03 0.37 $\pm$ 0.05	3.7 $\pm$ 0.2 g/mm 4.2 $\pm$ 0.2 g/mm		Zador and Piatt 1999
Gannet I, Labrador (1981–83)	–	0.18–0.28[3, 4]	238 $\pm$ 2.2 g	95–97%[4]	Birkhead and Nettleship 1982, 1985, 1987
(1996–97)	–	0.21–0.28[3,4]	233 $\pm$ 9.4 g	96–97%[4]	Bryant et al. 1999
Stora Karlso, Baltic Sea (Control) (Experimentally delayed)	–	0.11 $\pm$ 0.02 0.14 $\pm$ 0.03	255–260 g 220 g		Hedgren and Linnman 1979

[1] Other fledging masses are: 202 g (Johnson 1944), 250 g (Pearson 1968), 215 g (Birkhead 1977), 253 g (Belopolski 1957), 274 g (Cody 1973) and 208 g (Johnson and West 1975).
[2] Significant differences in chick measurements between years at the same colony or between colonies.
[3] Calculated from 4 h observation periods.
[4] Values estimated from figures.

The observed and available foraging time per day per parent, or foraging effort, was similar at both colonies. The observed foraging time per day per parent, however, was 1.3–1.4 times less than the amount of time available to forage (Table 5). This discrepancy was consistent at both colonies, resulting in approximately 10–11% of each parent's day unaccounted for (Table 5). This implies that there was a bias in our measurement of foraging trip durations, mate paired duration or fish delivery rates to chicks. Chicks are generally fed immediately upon arrival of the parent (GKD pers. obs.) and, thus, chick-feeds would have been missed if the arrival of a parent was not directly observed. Therefore, the rates of food delivery that we observed are probably lower than actual rates, but the bias was similar at both colonies making inter-colony comparisons appropriate.

Fledgling condition

Fledging murres had a significantly higher condition index at Great Island compared to Funk Island ($t_{76} = 2.31$, $P < 0.0001$; Table 4). These differences were due primarily to significantly higher body masses at Great Island compared to Funk Island ($F_{1,76} = 86.98$, $P < 0.0001$; Table 4), whereas wing lengths were similar at Great (63.1 ± 1.3 mm) and Funk islands (66.3 ± 1.1 mm; $F_{1,76} = 3.84$, $P = 0.058$). The slopes of mass versus wing length for fledglings at Great Island (slope = 3.9 g mm^{-1}) was significantly higher than that for fledglings at Funk Island (slope = 2.9 g mm^{-1}; $t_{(2)74} = 68.74$, $P < 0.0001$; Fig. 3), suggesting that fledglings also grew faster at Great Island compared to Funk Island.

Discussion

Prey items delivered to chicks were similar and parents appeared to maintain similar foraging times per day, or foraging effort, at both colonies. Parents at the larger, offshore colony (Funk Island) made longer foraging trips and did not compensate for these longer trips by decreasing the time spent paired with mates at the colony relative to the smaller, inshore colony (Great Island). This resulted in lower provisioning rates at Funk Island, which led to slower chick growth and ultimately to poorer condition of fledglings at Funk Island compared to Great Island.
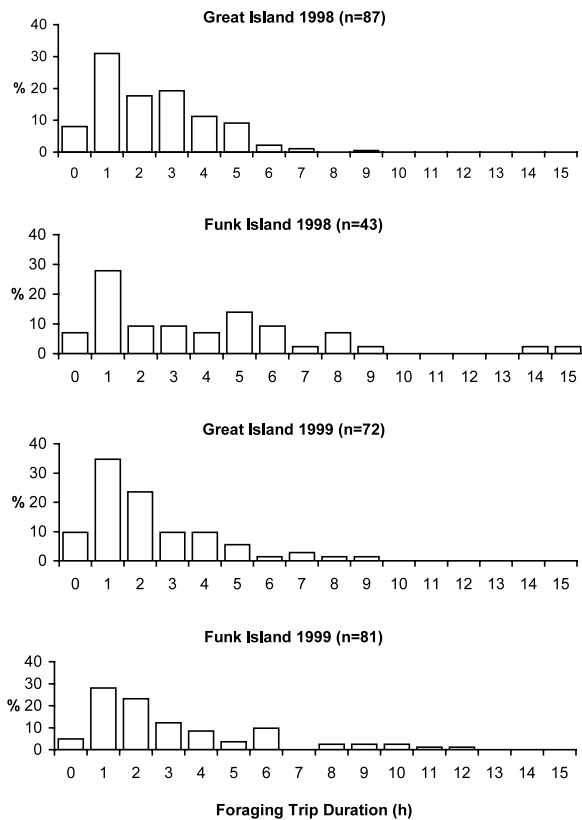
Fig. 2. The percent frequency of foraging trip durations preceding deliveries of fish to chicks by common murres at Great Island and Funk Island during 1998 and 1999. The number of foraging trips observed at each colony in each year is represented by n.
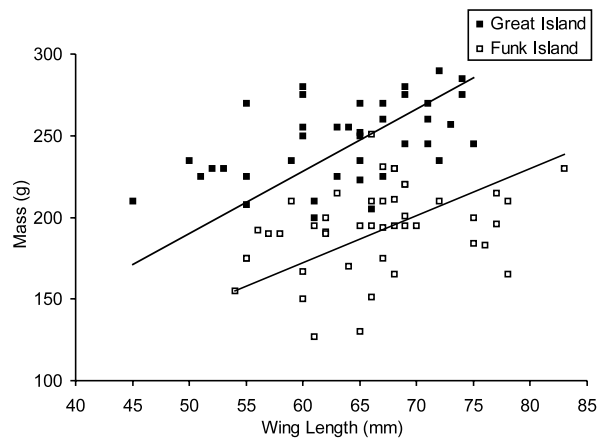

Fig. 3. Relationship between body masses and wing lengths of common murre fledglings at Great and Funk islands in 2000. Funk Island fledglings: slope = 2.9 g mm^{-1}, $r^2 = 0.079$, n = 43; Great Island fledglings: slope = 3.9 g mm^{-1}, $r^2 = 0.326$, n = 35.

Foraging trip durations

Longer foraging trip durations at Funk Island relative to Great Island could reflect both longer distances to foraging areas and more time spent feeding within foraging areas. The duration of a foraging trip could depend on the distance between major aggregations of prey and breeding colonies (Kitaysky et al. 2000, Davoren 2001). Capelin spawn primarily on or near beaches during summer in Newfoundland (Templeman 1948) and, thus, they are distributed primarily near suitable beaches (Nakashima and Wheeler 2002). This near-shore distribution of capelin resulted in foraging areas being closer to the smaller, inshore colony (< 5 km) compared to the larger, offshore colony (~ 45 km; see Davoren et al. 2003b). In addition, the higher biomass of capelin-feeding birds around Funk Island compared to Great Island (Table 1) could reduce an individual's foraging efficiency, thereby increasing the time spent foraging, in at least two ways. Competitors may interfere with the foraging activities of others (Hoffman et al. 1981, Shealer and Burger 1993), resulting in reduced intake rates of prey (e.g. Stillman et al. 1996; Cresswell 1997, 1998) or individuals could avoid areas with high competitor density (e.g. Davoren and Burger 1999, Maniscalco et al. 2001). Competitors could also directly reduce prey abundance within foraging ranges by depleting prey fields near colonies (e.g. Birt et al. 1987), causing individuals to fly to more distant foraging areas (Lewis et al. 2001). Overall, a combination of longer distances to capelin aggregations and higher avian densities of capelin-feeders within foraging areas may have contributed to increased foraging trip durations from Funk Island compared to Great Island.

Table 5. The available and observed amount of time spent foraging per day per parent, as a proxy of foraging effort, based on the mean foraging trip duration, duration paired and chick feeding rates per h calculated at each colony over all 4 h shifts in both 1998 and 1999.

Parameter	Great Island	Funk Island
(A) Mean foraging trip duration	2.9 h	4.1 h
(B) Mean duration paired	12.3% (2.0 h)	10.9% (1.7 h)
(C) Hours of daylight	16 h	16 h
(D) Mean chick feeding rate per h	0.22	0.17
(E) Available foraging time per day per adult (C–B/2)	7.0 h	7.1 h
(F) Observed foraging time per day per adult ([C × D × A]/2)	5.1 h	5.5 h
(G) Ratio–Available: Actual (E: F)	1.4	1.3
(H) % of 16 h day not accounted for ([E–F]/16] × 100)	11.9%	10.0%

Provisioning behaviour

Even though parents made longer foraging trips, they did not reduce the time spent paired with mates at Funk Island relative to Great Island. This paired time at breeding sites is usually referred to as off-duty, resting or 'buffer' time, due to the parents' ability to adjust this when more time and energy is required for self-feeding or chick-provisioning ('time-buffering hypothesis'; Burger and Piatt 1990). The percentage of time murres spent paired with mates at both colonies was well within ranges reported in the literature for this species (Table 4). So why didn't parents at Funk Island reduce this paired time to increase food delivery rates to chicks?

One explanation is that the time spent paired with mates at the colony has important functions other than resting, such as breeding site and pair bond maintenance. Murres at Funk Island breed on flat-ground at much higher densities than the cliff-nesters at Great Island (Montevecchi and Tuck 1987). Aggressive and defensive interactions among individuals at breeding sites are more frequent in high-density areas (Birkhead 1977) and these interactions generally peak during chick-rearing when high numbers of non-breeding, prospecting birds attend breeding ledges (Birkhead 1985). Maintaining a breeding site is critical because if it is lost, there is a high probability that individuals will not breed in the following year (Harris et al. 1996). The non-brooding parent generally defends the breeding site (Birkhead 1978), while the brooding parent avoids such aggressive interactions (Birkhead 1985). Therefore, the time spent paired with mates at Funk Island may reflect a minimum amount of time required to maintain breeding sites when breeding at high densities.

Another explanation is that there is a fixed proportion of time that parents allocate to foraging each day regardless of foraging conditions. This proportion may be species-specific and may not vary among environments (Obst et al. 1995), owing to functional relationships between provisioning effort, adult body condition and adult survival (Cairns 1987). Previous studies have shown that murres reduce 'buffer time' when increased energy must be expended to maintain self-feeding or chick-provisioning (Burger and Piatt 1990, Bryant et al. 1999, Finney et al. 1999). When a ceiling of energy expenditure is reached during provisioning, however, parents do not further reduce buffer time (Uttley et al. 1994). Parents in this study maintained a similar amount of foraging time per day, or foraging effort, during chick-rearing at both colonies. It is possible that parents at Funk Island had reached their energetic ceiling, causing them to favour their own survival over that of their offspring in any given year, as predicted by life history theory (Trivers 1974, Charnov 1982).

Fledgling condition

It is also possible that parents did not compromise their own survival or that of their chicks, but that parents and fledglings at Funk Island simply moved to the food source, rather than parents delivering food, due to the higher provisioning constraints (e.g. longer foraging trips). This could explain why parents did not further decrease the time spent paired at Funk Island and would suggest that parents were not working above their physiological capabilities. Body mass reflects energy reserves, or fasting endurance (Hatch 1983), although no significant relationship has been found between fledging mass of murres and the probability of being resighted at the colony in future years (Hedgren 1981, Harris et al. 1992). Conversely, attaining an adequate body mass before independence from parents at sea (Bayer et al. 1991) and the onset of winter (Harris et al. 1992) appears to be critical. Growth rates are higher at sea than at the colony (Birkhead 1977, Varoujean et al. 1979) and, thus, moving to the sea might be the most efficient way to accelerate growth rates when provisioning rates are limited. Such a strategy would be effective at Funk Island because an important nursery area for fledgling-adult pairs during the post-fledging period was found close to Funk Island (~ 250 km) but far from Great Island (~ 600 km; Davoren et al. 2003a). Chicks, however, must attain an adequate wing length for safe transition from nesting ledges to the sea (Gilchrist and Gaston 1997). Chicks can allocate more energy to wing growth when provisioning rates are low (Wilhelm and Storey unpubl. data) and chicks with higher wing growth leave the colony earlier (Hipfner and Gaston 1999). Therefore, conditions at Funk Island may result in chicks allocating more energy to wing growth than body mass gain, and at the first opportunity, fledging is initiated to allow compensatory growth to begin at sea.

Population dynamics considerations

Overall, if fledglings from Funk Island are able to attain adequate body masses at sea during the post-fledging period, one would not expect lower survival and recruitment into the breeding population. Population trends available for these common murre colonies suggest that the Witless Bay colony is increasing, whereas the Funk Island colony is stable (Canadian Wildlife Service unpubl. data). This is consistent with the hypotheses that the Funk Island colony is either at carrying capacity or that fledgling survival is not high enough to allow population growth. If the latter is true, lower potential for colony growth at Funk Island could impact the entire Northwest Atlantic population of murres because 75% of the population breeds on this island (Cairns et al. 1989). Conservation and manage-

ment of populations require detailed knowledge of the mechanisms underlying changes in demographic parameters (Forbes and Kaiser 1994). The integration of provisioning behaviour, colony departure decisions (e.g. Ydenberg et al. 1995), and prey distribution with colony size will help refine population models and increase our understanding of population dynamics at a range of breeding aggregations.

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