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BROOD SIZE, FOOD PROVISIONING AND CHICK GROWTH IN THE PIGEON GUILLEMOT *CEPPHUS COLUMBA*[1]

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Abstract. We studied the effects of brood size and chick age on food provisioning rates to Pigeon Guillemot *Cepphus columba* nests, and differences in growth parameters between chicks in broods of one and broods of two. Provisioning rates increased with chick age in the first part of the nestling period, and then declined. This decline was steeper in 1985, when overall provisioning rates were higher. Per-chick provisioning rates were lower to broods of two, resulting in one of the chicks having a lower growth rate, and possibly a lower fledging mass, than its sibling. Growth parameters of the faster growing chick in broods of two did not differ significantly from those of solo chicks. The decline in provisioning rate late in the nestling period is probably not due to reduced food availability. It may be due to reduced energetic demands of the chicks or to a deliberate strategy on the parents' behalf to induce fledging. At present we lack the information to distinguish between these two hypotheses.

Key words: Pigeon Guillemots; Alcidae; food provisioning; brood size; chick growth.

INTRODUCTION

Most members of the auk family (Alcidae) lay a clutch of one egg. The generally accepted explanation for this is that parents cannot successfully rear larger broods because of limitations on their ability to provide food for chicks (Lack 1968, Birkhead and Harris 1985). This explanation is supported by twinning experiments, which have normally shown that birds with artificial broods of two have been unable to rear both chicks successfully (Birkhead and Harris 1985 and references therein). *Cepphus* guillemots typically lay a clutch of two eggs, and their ability to rear two chicks is probably due to their feeding on inshore benthic fishes rather than the offshore pelagic prey exploited by most other alcids (Bradstreet and Brown 1985). Because their foraging trips are shorter, they can deliver food to their nests at a higher rate, and consequently rear more chicks.

Although the modal clutch size of *Cepphus* guillemots is two, a significant proportion (5–28 percent) of breeders in most populations studied lay only one egg (Birkhead and Harris 1985). These are often young, inexperienced birds (Asbirk 1979). Birds breeding later in the season also tend to have smaller clutches (Preston 1968, Petersen 1981, Emms and Morgan 1989, Ewins 1989), though this is partly explained by young birds tending to breed later (Asbirk 1979). Birds laying clutches of two normally have a proportionately higher reproductive output than those laying clutches of one, mainly because eggs from one egg clutches have a lower hatching success (Petersen 1981, Emms and Morgan 1989, Ewins 1989), but sometimes because fledging success per chick also is lower (Cairns 1981). Food delivery rates to broods of two are normally higher than to broods of one, but per-chick rates are often no different (Cairns 1981) or lower in broods of two (Koelink 1972, Asbirk 1979, Petersen 1981).

Food provisioning rates are also influenced by chick age. Previous studies have found a variety of patterns, and it is important to distinguish between those measuring *delivery* rates (*number* of fish per unit time) and those estimating *provisioning* rates (*biomass* or *energy* per unit time). Drent (1965), Bianki (1967), and Koelink (1972) found that delivery rates increased with chick age, and Petersen (1981) found that rates increased until chicks were 25–30 days old and then declined markedly. Asbirk (1979) and Cairns (1987) found no effect of chick age on delivery rates, though mean fish size increased with chick age, so that older chicks were provisioned at a higher rate. Cairns's (1987) calculations also suggested a slight decline in provisioning rates for

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chicks older than 25 days. Of these studies, only Cairns's (1987) data were analyzed statistically, and none controlled for other factors that can affect delivery rates, such as time of day (e.g. Drent 1965, Slater and Slater 1972, Petersen 1981, Cairns 1981, 1987), or tidal state (Belopol'skii 1957, Preston 1968).

The aims of our study were (1) to investigate how brood size and chick age influence food provisioning rates in the Pigeon Guillemot *Cepphus columba* when confounding variables are controlled for statistically; (2) to assess why provisioning rates may decrease in the latter part of the nestling period; and (3) to determine the consequences of lower per-chick provisioning rates for the growth of individual chicks within broods of two.

METHODS

The study was carried out in 1984 and 1985 on the 200 pairs of Pigeon Guillemots breeding on Mitlenatch Island (40°57′N, 125°00′W), a 35.5 ha rocky island in the Strait of Georgia, British Columbia, Canada. We systematically searched for nests early in the season and visited occupied nests every 1–5 days throughout the breeding period. We weighed chicks every 3–5 days in 1984 and daily in 1985 using 0–100 g and 0–500 g Pesola scales. In 1985, when nests were checked daily, chicks from two-egg clutches typically hatched on the same day ($n = 8$) or on successive days ($n = 16$). In one case the inter-hatch interval was two days. When chicks hatched on different days, the first chick normally had gained mass by the time the second chick hatched and was easily distinguishable from its younger sibling. When chicks hatched on the same day, a size hierarchy normally developed within a few days. For convenience, we will refer to the heavier chick in a brood of two as the α chick and the lighter chick as the β chick.

We observed food delivery rates to nests in several nest groups. Observations were made from a blind, or from locations distant (100–200 m) or concealed from the nest group using binoculars and 20–40 power telescopes. During each 2 hr observation period we recorded the number of food deliveries to each nest, the type of fish delivered, and its size, estimated as a multiple of the guillemot's bill length to the nearest quarter bill length. While this method may inaccurately estimate *absolute* size, it should not result in systematic biases within our own data set. Fish were classified as blennies (Blennioidea), sculpins (Cottidae), lingcod *Ophiodon elongatus,* flatfish (Bothidae, Pleuronectidae), sandlance *Ammodytes hexapterus,* rockfish *Sebastes* spp., shiner perch *Cymatogaster aggregata,* herring (Clupeidae), and unidentified. We chose starting times so that the tidal height halfway through the period was either 0.75 m, 2.30 m, or 3.85 m. These heights corresponded to low-, mid-, and high-tide periods within the daily tidal cycle.

Mass-length regressions for locally caught blennies, sculpins, flatfish, and shiner perch were used to calculate provisioning rates to individual nests in grams wet mass per hour. Lingcod masses were calculated from the mass-length regression for sculpins, since these fish were similar in shape and the masses of three lingcod found in guillemot nests closely fitted the predicted regression for sculpins. Data were excluded from these calculations if parents delivered fish for which we did not have mass-length regressions, or if any fish were unidentified.

We fitted logistic equations to the growth curves of individual chicks and used the asymptotic mass parameter A as a measure of fledging mass (Ricklefs 1967). Masses were log-transformed before analysis. Because nestling guillemots typically reached their maximum mass near fledging, A was a reasonable estimate of fledging mass. The mass on the last day in the nest would have been a poor measure because masses varied considerably (up to 30–40 g) from day to day during the final part of the nestling period. We calculated growth rates in g/day by fitting linear regressions to the linear phase of growth, when chicks were 5–20 days old. This is preferable to using the growth curve constant K of the logistic equation, as recommended by Ricklefs (1967), because K measures the speed of approach to the asymptote and can give misleading results if comparisons are made between chicks reaching different asymptotes (Hussell 1972, Gaston 1985).

Statistical analyses were done using the BMDP statistical package (Dixon 1985). Proportional data were arcsin square root transformed where appropriate.

RESULTS

FISH TYPES AND SIZES

The majority of the fish delivered in both years were either blennies or sculpins. Small numbers of lingcod, flatfish, sandlance, rockfish, shiner

TABLE 1. Frequencies and percentages of fish types delivered to nests.

Fish type	1984		1985	
	Number	Percentage	Number	Percentage
Blennies (Blennioidea)	306	43.7	119	30.8
Sculpins (Cottidae)	171	24.4	105	27.2
Lingcod *Ophiodon elongatus*	48	6.9	53	13.7
Flatfish (Bothidae, Pleuronectidae)	55	7.9	10	2.6
Sandlance *Ammodytes hexapterus*	5	0.7	0	0.0
Rockfish *Sebastes* spp.	22	3.1	24	6.2
Shiner Perch *Cymatogaster aggregata*	1	0.1	17	4.4
Herring (Clupeidae)	13	1.9	0	0.0
Unidentified	80	11.4	58	15.0

perch, and herring were also delivered (Table 1). The proportions of fish types delivered varied significantly among nests in both years (1984: $\chi^2 = 62.9, P = 0.0001, df = 18, n = 10$ nests; 1985: $\chi^2 = 90.8, P = 0.0001, df = 14, n = 8$ nests. Fish types were categorized as blennies, sculpins, and "others" and nests were included in the analysis only if expected frequencies for all fish categories were greater than five). The proportions of fish types delivered also varied significantly between brood sizes. In 1984, broods of two received more blennies and fewer sculpins than expected ($\chi^2 = 10.0, df = 2, P < 0.01, n = 363$ fish). In 1985, broods of two received more sculpins and fewer 'others' than expected ($\chi^2 = 14.6, df = 2, P < 0.001, n = 276$ fish). To what extent these differences were due to an effect of brood size *per se*, rather than to the variation among nests described above is unclear.

Both blenny and sculpin sizes differed significantly among chick age categories. For blennies, there was a marked increase in fish size in the third week of the nestling period (Fig. 1A). For sculpins the pattern was less obvious, but size

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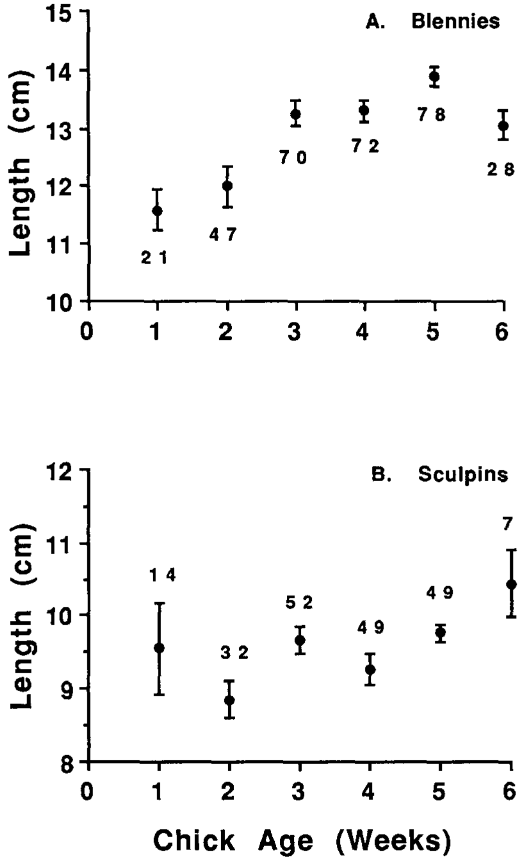
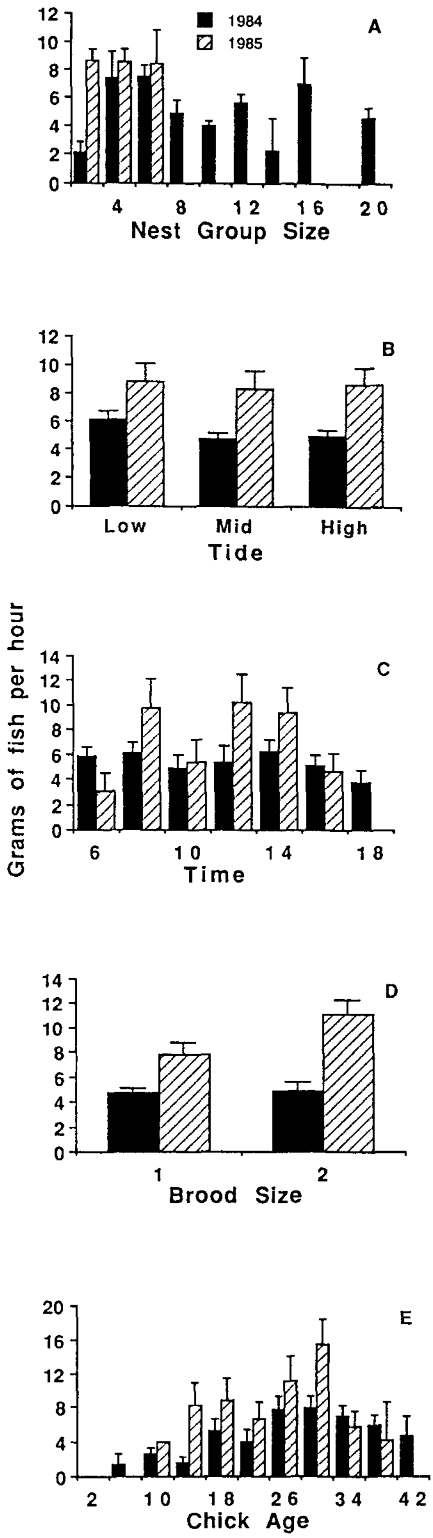


FIGURE 1. The effect of chick age on the sizes of (A) blennies and (B) sculpins delivered to nests. Blenny sizes differed significantly among chick age categories (ANOVA: $F = 10.34$, df = 5, 310, $P < 0.0001$, Brown-Forsythe test not assuming equal variances among groups [Brown and Forsythe 1974]). Means for the two youngest age categories were significantly different from all others (1–2: $P < 0.01$, 1–3: $P < 0.01$, 1–4: $P < 0.001$, 1–5: $P < 0.05$, 2–3: $P < 0.05$, 2–4: $P < 0.05$, 2–5: $P < 0.001$; all other tests n.s.; all P-values are for separate variance t-tests (see Snedecor and Cochran 1967) and Bonferroni probabilities for multiple comparisons (see Neter et al. 1985). Sculpin sizes also differed significantly among chick age categories (ANOVA: $F = 2.99$, df = 5, 198, $P = 0.048$, Brown-Forsythe test). Only the means between age categories 2 and 5 were significantly different ($P < 0.05$). Sample sizes are given above data points.



appeared to increase from the second week of the nestling period onwards (Fig. 1B).

FOOD PROVISIONING RATES

In 1984 chick age, time of day, and tidal state all had significant effects on provisioning rates. Square terms for chick age and time of day were also significant, indicating that the effects of these variables were curvilinear (Table 2). Provisioning rates increased during the first half of the nestling period, and then decreased. Rates were higher in the morning and evening hours, and were lower at high tides (Table 2, Fig. 2). In 1985 only chick age and its square had significant effects. Again, provisioning rates increased in the first half of the nestling period and then decreased (Table 2, Fig. 2). In neither year did nest group size or brood size have significant effects on provisioning rates, though Figure 2d suggests that rates were higher to broods of two in 1985, and the failure to find a significant difference in this year may have been a problem of statistical power. Overall, mean provisioning rate was lower in 1984 (4.76 ± 0.33 SE) than in 1985 (9.36 ± 0.79 SE). Since the energy densities of the main fish types are similar (Dunn 1975, Cairns 1987), these patterns are unlikely to be affected by any systematic changes in the proportions of fish types delivered.

Date was not included in these analyses because it was highly correlated with chick age. To determine whether the decrease in provisioning rates in the second half of the nestling period was due to a decrease in food availability late in the season, rather than to an effect of chick age per se, we analyzed the data for the first and second halves of the nestling period separately. Because of the reduced sample sizes and the large amount of error variance in the data set, the overall regressions were significant only in the first half of 1984 and the second half of 1985. In 1984, time and its square and chick age and its square both

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FIGURE 2. The effect of (A) nest group size, (B) tidal state, (C) time of day, (D) brood size, and (E) chick age on food provisioning rates (g/hr) to nests. Overall means and standard errors are plotted. 1984: $n = 251$; 1985: $n = 176$. Since the effects of the other variables are not controlled for in any of the figures, these histograms provide no statistical information and are presented simply as a visual aid. See Table 2 for statistical analysis.

TABLE 2. Multiple regression of factors affecting food provisioning rates (g/hr) to nests. Square terms for time of day and chick age were used to look for curvilinear effects of these variables. In broods of two chick age was arbitrarily defined as the age of the older chick. 1984: $n = 251$, $R^2 = 0.099$, F-ratio for regression ANOVA = 3.815, $P < 0.0001$; 1985: $n = 176$, $R^2 = 0.112$, $F = 3.041$, $P = 0.0049$.

	1984				1985			
Variable	Slope	SE	t	P (2-tail)	Slope	SE	t	P (2-tail)
Intercept	1.135				−13.795			
Nest group size	0.020	0.078	0.259	0.796	0.354	0.738	0.480	0.632
Tidal state	−1.553	0.556	−2.795	0.006	2.040	1.256	1.625	0.106
Time of day	−0.424	0.183	−2.315	0.022	0.767	0.530	1.446	0.150
Time of day^2	0.016	0.006	2.476	0.014	−0.026	0.017	−1.465	0.145
Brood size	0.359	0.756	0.475	0.635	3.038	1.790	1.698	0.091
Chick age	0.664	0.186	3.578	0.0005	1.061	0.487	2.179	0.031
Chick age^2	−0.012	0.004	−3.023	0.003	−0.025	0.010	−2.675	0.008

still had significant effects on provisioning rates; tidal state no longer did (Table 3). This suggests that chick age itself, rather than date, may be the significant variable. In 1985, although the overall regression was significant ($R^2 = 0.17$, $F = 2.746$, df = 7, 92, $P = 0.012$), none of the coefficients for individual variables were.

CHICK GROWTH RATES

Growth parameters did not differ significantly between years, so data were pooled for further analysis. Growth rates differed significantly among the three chick types (solo chicks and α and β chicks in broods of two). This was due to solo chicks and α chicks both growing faster than β chicks. (Figs. 3 and 4A). Asymptotic masses also differed among chick types, although no pairwise differences were significant (Fig. 4B). Growth rates and asymptotic masses were positively correlated ($r = 0.32$, df = 46, $P = 0.025$).

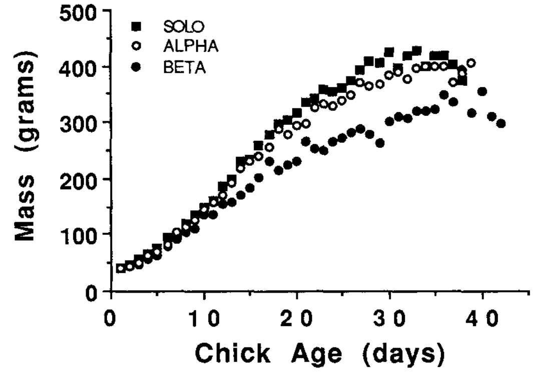

FIGURE 3. Growth curves for solo chicks and α and β chicks in broods of two. Mean weights for all chicks in each category at each age are plotted. For clarity, standard errors are not provided. Sample sizes range from 10–12 for the youngest chicks to 2–3 for the oldest.

DISCUSSION

FISH TYPES

In both years the majority of identified fish delivered were either blennies or sculpins, as was found by Drent (1965) and Koelink (1972). The observed variation among nests in the proportions of different fish types, also documented in other studies (e.g., Drent 1965, Koelink 1972, Kuletz 1983), suggests either that individual birds specialize on different prey types, or that they have preferred foraging areas that differ in the relative abundances of prey types. Kuletz (1983) found evidence for both possibilities.

FOOD PROVISIONING RATES

The most consistent factor affecting provisioning rates was chick age. In both years, rates increased

TABLE 3. Multiple regression of factors affecting food provisioning rates (g/hr) to nests in the first half of the 1984 breeding season. $n = 130$, $R^2 = 0.186$, F-ratio for regression ANOVA = 3.969, $P = 0.0006$.

Variable	Slope	SE	t	P (2-tail)
Intercept	0.517			
Nest group size	−0.157	0.108	−1.449	0.150
Tidal state	−1.304	0.800	−1.631	0.105
Time of day	−0.617	0.221	−2.791	0.006
Time of day^2	0.024	0.009	2.820	0.006
Brood size	0.745	0.916	0.813	0.418
Chick age	0.930	0.326	2.853	0.005
Chick age^2	−0.020	0.008	−2.233	0.027

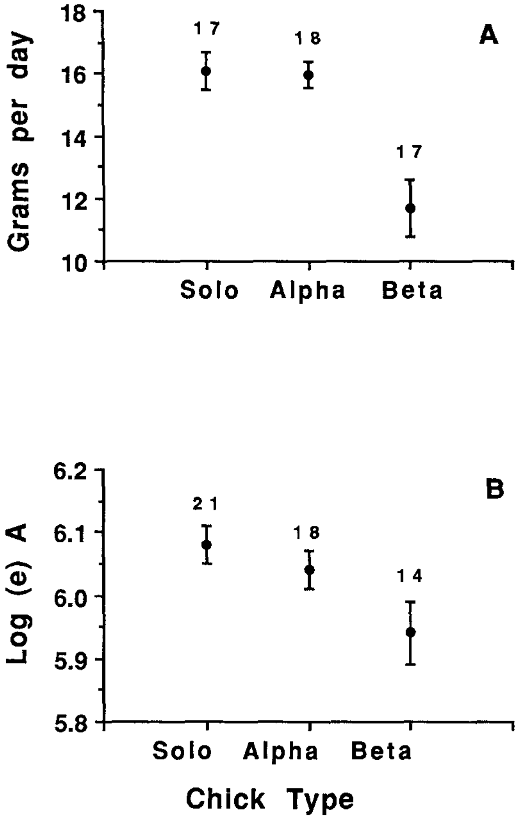

FIGURE 4. The effect of chick type on (A) growth rate in g/day and (B) fledging mass, calculated as the asymptotic mass parameter A of the logistic growth curve (see Methods). Growth rates differed significantly among chick types (ANOVA: $F = 14.1$, df $= 2, 49$, $P < 0.0001$, Brown-Forsythe test), due to β chicks growing more slowly than the other types (solo-α: n.s., solo-β: $P < 0.01$, α-β: $P < 0.001$, all P-values are for separate variance t-tests and Bonferroni probabilities). Similarly, asymptotic mass differed among chick types (ANOVA: $F = 4.25$, df $= 2, 50$, $P = 0.037$, Brown-Forsythe test), although no individual t-tests were significant. Sample sizes are given above data points.

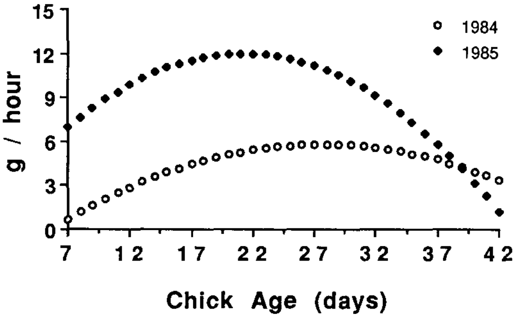

FIGURE 5. Predicted mean food provisioning rates as a function of chick age, based on fitted partial regression coefficients from Table 2. For all independent variables other than chick age, overall mean values for each year were used in the regression equation.

during the first half of the nestling period and then declined. What causes this decline? One possibility is that prey availability decreases late in the season. Two lines of evidence suggest that this explanation is probably incorrect. First, provisioning rates to chicks fledging in the first half of the 1984 breeding season still decreased in the latter part of the nestling period (Table 3), suggesting that chick age has an effect at least partly independent of date. Second, Moulton (1977), working approximately 350 km southeast of Mitlenatch, found that the biomass of fish in the rocky nearshore habitats where guillemots forage peaked between July and September and did not decline until October, well after guillemot chicks have fledged.

A second possibility is that the energy requirements of chicks decrease as growth slows down when they approach adult size. In some seabirds the decrease in energy requirements due to slower growth is compensated for by an increase in requirements for maintenance, so that total requirements actually increase throughout the nestling period, or decrease only very slightly towards the end (Ricklefs 1979, 1987; Montevecchi et al. 1984; Klaassen et al. 1989). However, for fast-growing species the decline after the peak may be more marked (Roby 1991). *Cepphus* guillemots are relatively fast growing compared to other alcids (Gaston 1985), so there could be a relatively sharp decline in requirements near fledging. To try to assess whether the decline in provisioning rates can be explained by a decline in energy requirements, we calculated predicted mean provisioning rates as a function of chick age based on the regression coefficients of Table 2 (Fig. 5). In 1984 the decline in provisioning rate late in the nestling period was small, and can probably be explained by reduced metabolic demands. In 1985 the decline was much larger, from 12 g/hr on day 21 to 6.5 g/hr on day 35, the mean fledging age. It would be surprising if such a large decrease, reflecting a reduction in provisioning rate of about 45 percent, resulted *solely* from a decrease in metabolic demands. However, since overall provisioning rates were much higher in 1985, chicks probably matured faster, and so required less food later in the nestling period.

A third possibility is that parents deliberately reduced delivery rates to induce fledging at an optimal time for themselves (Ydenberg 1989). Since foraging trips are energetically expensive (Drent and Daan 1980, Roby and Ricklefs 1986) and may incur an increased risk of predation (Harris 1980, Watanuki 1986), reduced delivery rates probably are beneficial to parents. If chick survivorship is only weakly dependent on fledging mass above some minimum threshold mass, a decline in provisioning rate late in the nestling period may only slightly reduce the fitness of current offspring, but considerably reduce the reproductive costs to the parents. To test this hypothesis we need to know how survival rates of both chicks and adults are affected by provisioning rates. Such data are not yet available for *Cepphus.*

CHICK GROWTH RATES

Provisioning rates did not increase significantly with brood size in either year. Consequently, provisioning rates per chick were lower to broods of two, resulting in the β chick having a lower growth rate (Figs. 3, 4A). Neither Drent (1965) nor Koelink (1972) mention an effect of brood size on provisioning rates, but several studies of Black Guillemots *C. grylle* showed that delivery rates increased with brood size (Asbirk 1979, Cairns 1981, Petersen 1981).

In this study, the cost of lower per-chick provisioning rates to broods of two clearly fell mainly on one of the chicks (Figs. 3 and 4). Growth rates of solo and α chicks did not differ from one another, but both grew significantly faster than β chicks. A similar pattern was found for asymptotic masses, though the effect was less marked. Figure 3 shows that β chicks did not compensate for their lower growth rates by remaining in the nest longer and eventually fledging at the same mass as their older sibs. Rather, they fledged at lighter masses *and* took longer to do so: β chicks normally fledged 4–8 days after their sibs.

Artificially increasing the brood size to three has normally resulted in chicks fledging at lower masses (Koelink 1972, Petersen 1981), but Asbirk (1979) found that fledging masses were actually higher in five cases where pairs raised three young. Despite Asbirk (1979), it appears that pairs with broods of two, or artificial broods of three, do not normally supply food at optimal rates for both their chicks. This could be due to parents being unable to provide extra food because of foraging limitations, or to a trade-off between present and future reproduction (Williams 1966, Charnov and Krebs 1974). Although we have no direct evidence for the latter hypothesis, two pieces of evidence suggest that it is worth considering. First, provisioning rates declined rapidly in the latter part of the nestling period in 1985. If parents had provided food to broods of two at the maximum observed rate throughout the nestling period this should have allowed the β chick to reach a higher fledging mass, even if it grew more slowly. We argued earlier that the observed changes in provisioning rate with chick age were probably not a consequence of changes in food availability. Second, Asbirk (1979) found that birds laying two eggs and rearing one or two young to fledging had a lower survival rate than those laying two eggs but rearing no young. The change in survival rate from 92 percent to 83 percent reduced the expectation of further life from 11.5 years to 4.8 years. Sample sizes were small, so the difference in rates was not significant, but note that even small decreases in survival rate greatly reduce the expected number of future breeding opportunities.

The longer nestling periods and lower fledging masses of β chicks could reduce their probability of overwinter survival. However, while some studies of seabirds have shown that early fledging and higher fledging masses increase survivorship (Perrins et al. 1973, Jarvis 1974), studies of several alcid species have failed to find such an effect (Lloyd 1976; Hedgren 1979, 1981; Harris and Rothery 1985). As far as we are aware, no data are available for *Cepphus* guillemots chicks.

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