

EFFECTS OF GROWTH RATE AND PARENTAL PREDATION RISK
ON FLEDGING OF RHINOCEROS AUKLETS
(CERORHINCA MONOCERATA)

by

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Effects of Growth Rate and Parental
Predation Risk on Fledging of
Rhinoceros Auklets (Cerorhinca
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Abstract

Variation in growth and age and mass at fledging of nestling rhinoceros auklets (Cerorhinca monocerata) was studied on Pine Island, British Columbia, in 1989 and 1990. Mass at fledging was positively related to growth rate, whereas age at fledging was inversely related to growth rate in both years. The results of a supplementary feeding study in 1989 showed that food-supplemented chicks grew faster and fledged at a younger age and heavier mass than did unsupplemented chicks, replicating the patterns observed in unmanipulated nestlings. A significant seasonal decline in mass at 10 days of age was found in both years of the study. Mass at fledging also declined with hatch date, but there was no significant effect of hatch date on chick growth, suggesting that the observed patterns can not be attributed to a seasonal decline in food availability. These results are examined with respect to the predictions of a model which has been derived using a life history approach to the fledging decision in alcids.

In 1990, the effects of predation risk on parental provisioning were examined. Chicks in high and low risk areas of the colony hatched on approximately the same date, received similar amounts of food to 46 days of age, grew at the same rate, reached similar peak masses and fledged at similar masses. However, chicks in high predation areas fledged at a younger age than did chicks in low predation areas. These data are consistent with the hypothesis that parents in high risk areas terminated provisioning several days before those in lower risk areas. The inverse relationship

between mass at fledging and age at fledging was significant in both high and low risk areas. The regression line for the high risk habitats lies below that for the low risk habitats, as predicted by a model which examines optimal time of fledging from the perspective of the parents.

Acknowledgements

I would like to take this opportunity to thank my committee members for their part in producing this thesis. Ron Ydenberg, my senior supervisor, spent many hours discussing both the theoretical framework of this research and the interpretation of the results with me. Alton Harestad and Kees Vermeer provided guidance during the planning of the project and patiently worked through previous drafts of this manuscript.

One person alone could not have chased four hundred uncooperative rhinoceros auklet chicks around their convoluted burrows. I was assisted in my field work by Yolanda Morbey in 1990 and Laura Nagel in 1989. I thank Yolanda for her ever-enthusiastic help and I apologise that the summer was not as cold, wet or stormy as I had warned her it would be. Laura had to endure rougher conditions and constant adaptations to the surprises offered by my first field season, and I thank her also.

Life on Pine Island would not have been the same without the incredible hospitality and warm friendship offered by the lightkeepers who allowed us to invade their island home. In particular, I thank Doug and Gwen Fraser for answering my unending questions about life on the coast; I salute Doug for trying at least one bite of anything I cooked and stand in awe of Gwen's creation of the most decadent desserts in the world. I also greatly enjoyed the time I spent with the Nicholsons. I thank Richard and Carole for all our discussions of politics, religion, sex and everything else not discussed in polite company. Carlin

and Ryland made sure I was never lonely and completed the preliminary field work on the behavioural ecology of midnight turkeys upon which I may base my Ph.D. As for Isaac, well, Isaac was busy growing his hair.

The lightkeepers, along with personnel at the Canadian Coast Guard in Victoria, also provided invaluable logistical support, without which my work would have been more difficult and less successful. They ensured that my supplies and mail (not necessarily listed in order of importance) arrived at my tentstep and for this I thank them. The occasional work crews that stayed on the island provided comraderie, a lot of laughs and beer (also not necessarily in order of importance).

I must also take this opportunity to acknowledge the influence of Lorna on my work. She explained to me my real motives for studying seabirds on isolated islands; may all her romances be harlequins.

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CHAPTER I

GENERAL INTRODUCTION

Behavioural ecology involves the study of behavioural strategies in relation to environmental factors. This approach has recently been applied to fledging behaviour in the Alcidae, an avian family of interest because of the extensive inter- and intra-specific variation in nestling developmental patterns. Specifically, the mass and age at fledging have been examined with respect to fitness trade-offs faced by the nestlings and their parents.

In a series of dynamic programming models, the optimal time of fledging has been considered from the perspective of both the nestling and the parent (Ydenberg 1989, Clark and Ydenberg 1990a). Both models assume that the chick faces a trade-off between a relatively safe nest habitat with low growth and a more dangerous ocean habitat with potentially higher growth. From the chick's perspective, optimal time of fledging is calculated as the best time to make the transition between the two habitats, assuming that natural selection will favour the fledging decision that maximizes survival to breeding (Ydenberg 1989). The optimum is expected to be sensitive to variation in growth rate.

The optimum time of fledging must also be considered from the parental perspective, because it seems likely that parents control fledging to some degree through food deliveries (Bertram 1988). Assuming a cost of reproduction (reviewed by Reznick 1985, Nur

1987), parents face a trade-off between current and future reproduction and natural selection should favour behaviour that maximizes lifetime reproductive success (Williams 1966). In long-lived species that experience high survival costs as a result of breeding activities, selection should favour behaviours that reduce the cost of a single breeding effort (Williams 1966, Stearns 1980). For many species of alcid, provisioning the nestlings at the colony exposes the adults to a risk of predation (eg. Harris 1980, Kaiser 1989, Nelson 1989). However, as a review of predation risk as a cost of reproduction points out (Magnhagen 1991), few studies have shown that individuals adopt different strategies according to predation risk. The second fledging model incorporates predation risk and makes predictions about changes in parental behaviour in the face of such risk (Clark and Ydenberg 1990a).

The optimum fledging time predicted from the perspective of the parent differs from that predicted from the chick's perspective (Clark and Ydenberg 1990a). This parent-offspring conflict is expected because the fitness interests of the nestlings and parents differ; parents are selected to invest less than the offspring are selected to demand (Trivers 1974). The degree of difference should be sensitive to predation risk as the costs to the parents change.

In this thesis, I examine variation in fledging behaviour of nestling rhinoceros auklets (Cerorhinca monocerata) in light of the predictions of the two models discussed above. In Chapter II, I use intra- and inter-annual comparisons of the natural variation found at one colony as well as the results of an experimental

manipulation of growth rates to test the predictions of the first model. In Chapter III, I examine the effects of predation risk on parental provisioning strategies and on chick fledging.

CHAPTER II

VARIATION IN CHICK AGE AND MASS AT FLEDGING

Introduction

Among species in the family Alcidae, there is high intra-specific variability in juvenile life histories (reviewed in Gaston 1985, Harris and Birkhead 1985, Ydenberg 1989). Developmental parameters such as nestling growth rate, peak mass, age at fledging and mass at fledging may vary over a breeding season, within and between colonies as well as between years. Rhinoceros auklets (*Cerorhinca monocerata*), for example, fledge between 43 and 65 days of age at 50 - 85 % of adult body mass (Vermeer and Cullen 1979, this study). The observed variation in juvenile development is often characterized as a proximate response to factors such as variations in food availability and quality, nest site quality or ambient temperature (eg. Nettleship 1972, Vermeer and Cullen 1979, Gaston 1985). Few researchers, however, have discussed how selective pressures might influence the evolution of behaviour in response to this environmental variation.

Life history theory provides an evolutionary view of the patterns in the time of fledging found in alcids. Ydenberg (1989) considered the question of when to fledge as the best time for the chick to make the transition between two habitats with contrasting fitness characteristics: the nest and the ocean. Assuming that the burrow represents a safe environment in which growth is slow, whereas the ocean offers a potentially higher growth rate at a

higher risk of mortality, the optimal time of fledging can be calculated using dynamic programming (Ydenberg 1989).

The predicted optimal time of fledging is sensitive to the chick growth rate in the nest. When growth in the nest varies, the model predicts a negative relationship between mass and age at fledging, with faster growing chicks fledging heavier and at a younger age than slower growing chicks (see Ydenberg 1989, Fig. 5). The model also predicts a seasonal decline in mass at fledging; variation in growth rate is expected to contribute to this decline.

Rhinoceros auklets exhibit one of the widest ranges of growth rate, age at fledging and mass at fledging of alcids; these parameters vary both within and between years (Leschner 1976, Vermeer and Cullen 1979, Wilson 1977, Bertram 1988). My study was designed to examine the variation in the time of fledging in rhinoceros auklets at one colony, using three comparisons: 1) natural intra-annual growth rate variation in 1989 and 1990, 2) experimentally induced variation in growth rate in 1989 and 3) natural inter-annual variation between 1989 and 1990. The predictions tested were that faster growing nestlings would fledge earlier and at a higher mass than more slowly growing young, thus producing an overall negative relationship between the age and mass at fledging. The model also predicts a seasonal decline in fledging mass and the data were examined for this effect.

Materials and Methods

In mid-June, 1989, approximately 120 rhinoceros auklet burrows

on Pine Island, B.C. ($50^{\circ} 58' N$; $127^{\circ} 41' W$) were excavated for use in a supplementary feeding study. Excavation involved digging holes through the roof of burrow tunnels until the entire burrow was accessible; between visits, access holes were covered with cedar shingles, soil and moss. All chicks found were weighed to the nearest 2.5 g on a 500 g Pesola scale and wing lengths were measured to the nearest millimetre, from the wrist to the tip of the flattened wing, using Vernier calipers. Once the primaries began to emerge, wing lengths were measured from the wrist to the feather tip using a flexible plastic ruler. Burrows containing incubating adults were immediately covered because adults are extremely sensitive to disturbance in the burrows during this phase (Leschner 1976, Wilson 1977). These burrows were rechecked after ten days.

Nine newly-hatched chicks (i.e., with wet downy plumage) were found and were measured every day for two weeks. The regression of age on wing length described by the data from these known-age nestlings was used to assign ages to all other chicks in this study. Wing length is considered a reliable estimator of chick age because it is relatively independent of the nutritional status of the chick (Vermeer and Cullen 1979). However, the variation in wing length for a given age increases after the first two weeks (Leschner 1976, Wilson 1977), and so only burrows that contained chicks under two weeks of age upon initial excavation were used in the supplementary feeding study. The known-age chicks were not included in any further studies.

When the chicks in the study burrows reached 13 days of age and were capable of swallowing experimentally preferred fish, they were assigned alternately to one of two experimental groups:

Supplemented - Chicks between 13 days of age and fledging were fed 30 g of freshly thawed surf smelt (Hypomesus pretiosus) every second day as a supplement to the food delivered to them by their parents. Thirty grams was chosen because it approximates the mean mass of fish brought per trip by provisioning adults to their chicks on Pine Island in July 1985 and 1986 (Bertram and Kaiser 1988). Chicks were weighed and measured before being fed (N = 55).

Unsupplemented - Chicks were handled as above but not given any supplementary fish (N = 55).

Growth rates were calculated for each chick as the slope of the regression line relating chick age and mass between the beginning of the experiment (13 days) and 37 days of age. This interval corresponds closely to the linear portion of the chick growth curve, which extends from about 10 to 38 days. Fledge dates were taken as the first day a chick was not found in its burrow. Mass at fledging is the mass on the last day the chick was weighed.

In 1989, an additional 65 burrows in undisturbed areas of the colony were used for inter-annual comparisons of chick growth and fledging. The burrows were excavated as outlined above, but the nestlings were not disturbed between 10 and 42 days of age. After

42 days, the chicks were weighed and measured every second day until fledging. In 1990, a similar protocol was followed to monitor a group of 70 undisturbed burrows. In both years, daily growth rates for these undisturbed birds were calculated for each chick as: $(\text{mass at 42 days of age} - \text{mass at 10 days of age})/32$. Age and mass at fledging were determined as in the supplementary feeding experiment.

Comparisons of hatch date, mass at various ages, growth, peak mass, mass at fledging, age at fledging and date at fledging were made using a one-way ANOVA procedure. ANCOVA tests were used to compare the regression statistics describing chick growth parameters. All statistical analyses were performed using the SYSTAT software package (Wilkinson 1989).

In both studies outlined above, some study burrows became inaccessible during the breeding season: burrows became connected to neighbouring tunnels or the habitat was judged too fragile to support repeated disturbances. All data from these burrows were excluded from analyses. Similarly excluded were data from four chicks that had not fledged by the time I left the island and two chicks that left their burrows before being fully feathered. All six of these chicks had very low growth rates. Thus, the final sample sizes (42 supplemented and 45 unsupplemented chicks in the supplementary feeding study; 56 and 53 undisturbed burrows in 1989 and 1990, respectively) were smaller than the initial numbers.

Results

The inverse relationship between mass at fledging and age at fledging for undisturbed chicks was significant in both 1989 and 1990 (Fig. 2.1); the slope of the regression was steeper in the latter year. Confirming that the early fledgers were indeed the fastest growers, a significant negative relationship between age at fledging and growth rate was also found in both years (Fig. 2.2). As expected, mass at fledging and growth rate were significantly positively related in 1989 and 1990 (Fig. 2.3).

The experimental supplementary feeding of rhinoceros auklet chicks significantly increased the growth rate of supplemented chicks above that of unsupplemented chicks (Table 2.1), but within the range found for undisturbed chicks (Fig. 2.4). The mean growth rate for the undisturbed chicks was higher than that for the supplemented birds ($F = 16.78$, $df = 1,99$, $P = < 0.001$), indicating that the extensive handling of chicks involved in the experimental procedure had a negative influence on chick growth. Fledging mass was significantly greater in the supplemented birds than in the unsupplemented birds. In contrast, age and date at fledging were significantly lower in the supplemented nestlings. No differences were found between treatments in hatch date and mass at 13 days; these two parameters were measured before the manipulations began.

A significant inverse relationship between mass and age at fledging occurred in both the supplemented and unsupplemented groups (Fig. 2.5). The slopes of the two regression lines are the same, but the former line is higher over the range measured.

Figure 2.1. Relationship between mass and age at fledging in undisturbed burrows in 1989 ($y = -5.1 x + 663.4$; $r^2 = .699$; $F = 125.23$, $df = 1, 54$, $P < 0.001$) and 1990 ($y = -7.0 x + 729.4$; $r^2 = .600$; $F = 76.42$, $df = 1, 51$, $P < 0.001$). ANCOVA: homogeneity of slopes - $F = 4.44$, $df = 1$, $P = 0.037$

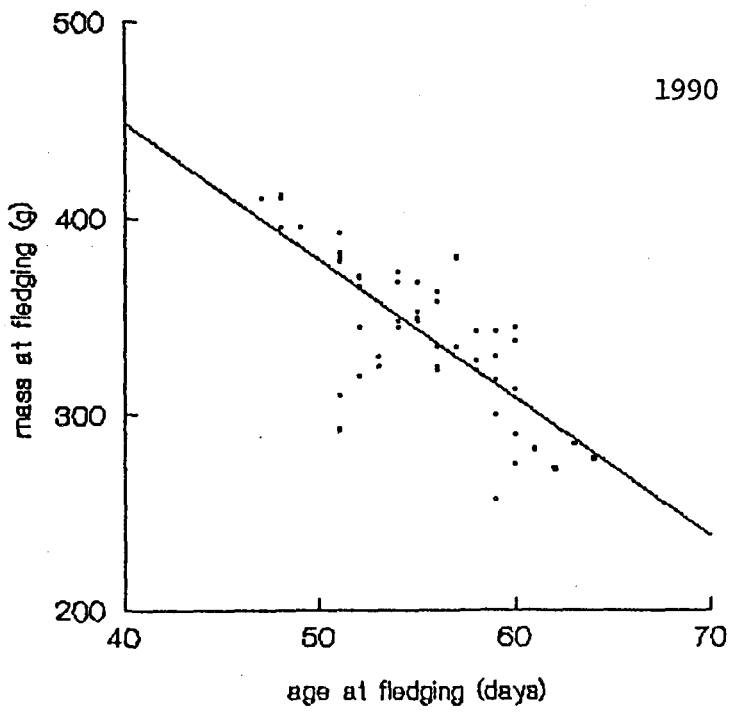
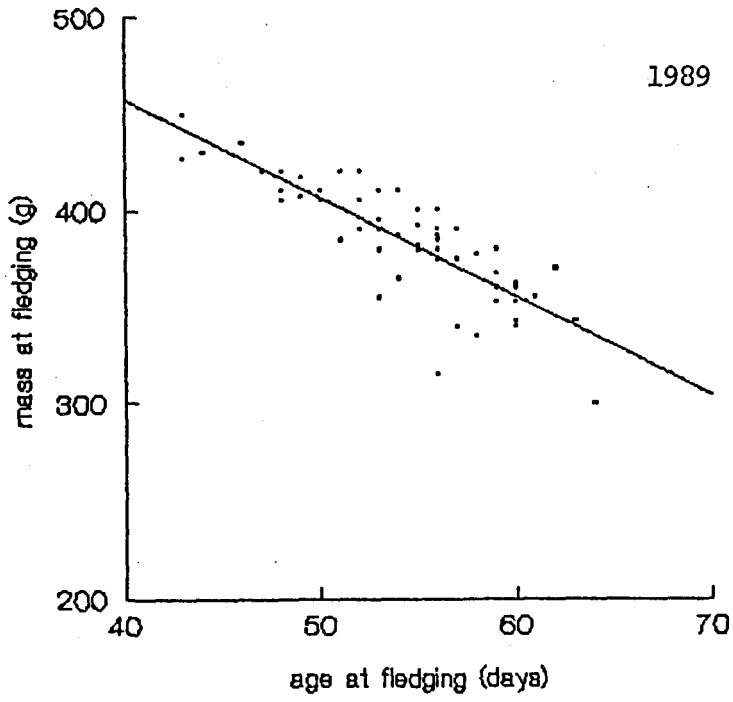


Figure 2.2. Relationship between age at fledging and growth rate in undisturbed burrows in 1989 ($y = -3.0 x + 77.9$; $r^2 = .462$; $F = 46.43$, $df = 1, 54$, $P < 0.001$) and 1990 ($y = -2.1 x + 68.6$; $r^2 = .367$; $F = 29.62$, $df = 1, 51$, $P < 0.001$). ANCOVA: homogeneity of slopes - $F = 2.08$, $df = 1$, $P = 0.152$; homogeneity of y-intercepts - $F = 74.16$, $df = 1$, $P < 0.001$

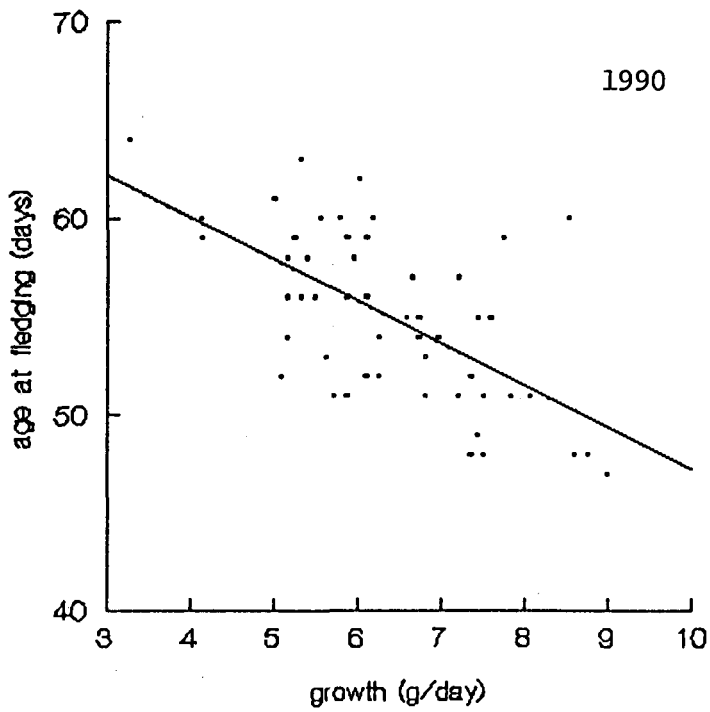
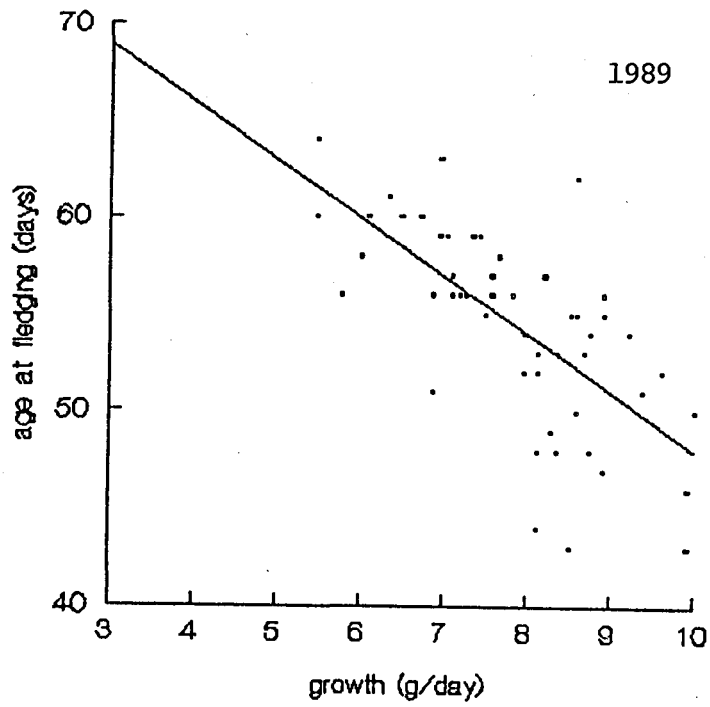


Figure 2.3. Relationship between mass at fledging and growth rate in undisturbed burrows in 1989 ($y = 21.8 x + 212.5$; $r^2 = .651$; $F = 100.70$, $df = 1, 54$, $P < 0.001$) and 1990 ($y = 22.8 x + 198.1$; $r^2 = .508$; $F = 52.72$, $df = 1, 51$, $P < 0.001$). ANCOVA: homogeneity of slopes - $F = 0.07$, $df = 1$, $P = 0.792$; homogeneity of y-intercepts - $F = 137.27$, $df = 1$, $P < 0.001$

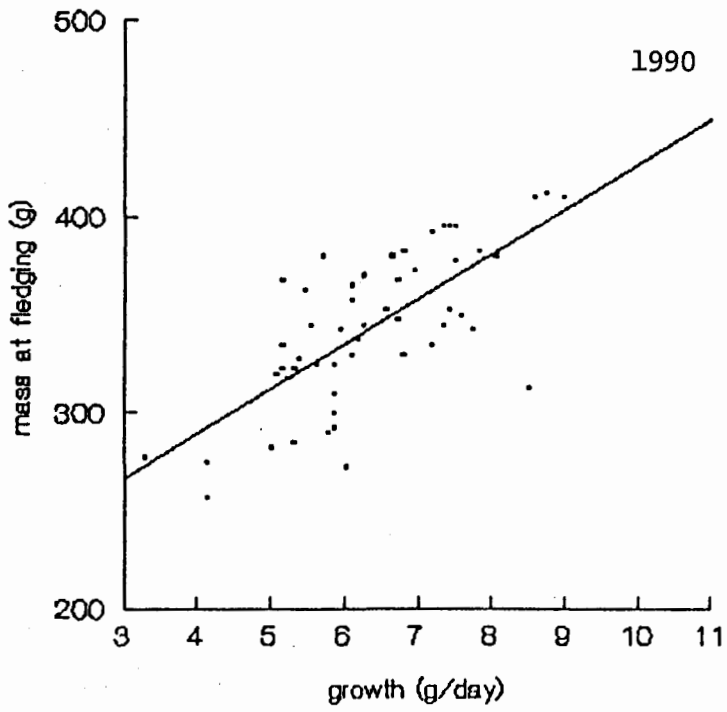
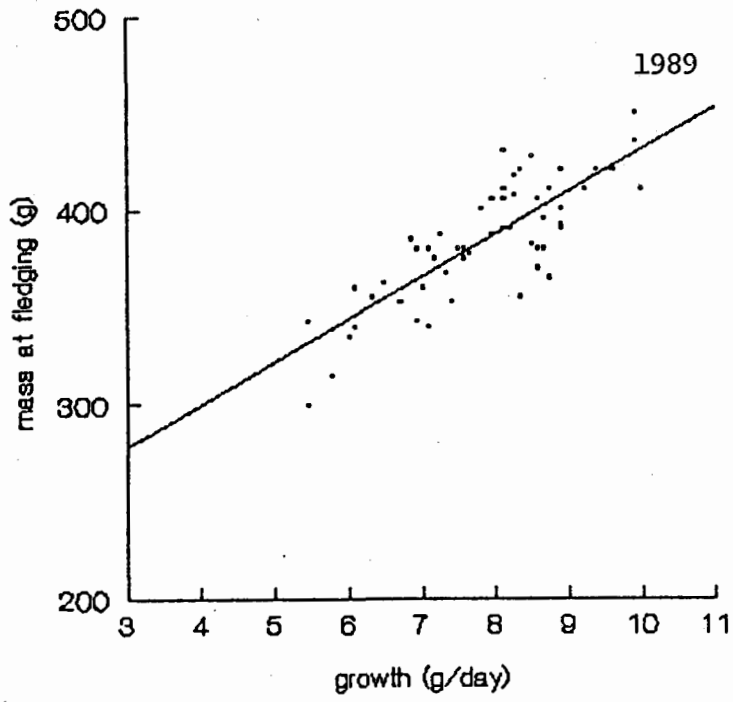


Table 2.1. Growth parameters of rhinoceros auklet chicks in supplementary feeding study, Pine Island, 1989.

	SUPPLEMENTED (N = 42)		UNSUPPLEMENTED (N = 45)		F
	<u>Mean</u>	<u>S.D.</u>	<u>Mean</u>	<u>S.D.</u>	
Hatch date ^a	17.0	5.14	16.8	4.88	0.02
Mass at 13 days (g)	170.5	16.96	164.6	15.79	2.84
Growth (g/day)	7.4	.75	6.3	.85	38.85 ^b
Peak mass (g)	415.8	19.65	381.3	31.41	37.10 ^b
Mass at fledging (g)	411.1	22.67	372.3	28.54	48.98 ^b
Age at fledging (d)	50.0	3.91	55.4	4.65	34.95 ^b
Fledge date ^a	66.9	6.36	72.2	7.10	13.47 ^b

^a day 1 = June 1

^b P < 0.001

Figure 2.4. Frequency distributions of growth rate for supplemented, unsupplemented and undisturbed rhinoceros auklet chicks in 1989.

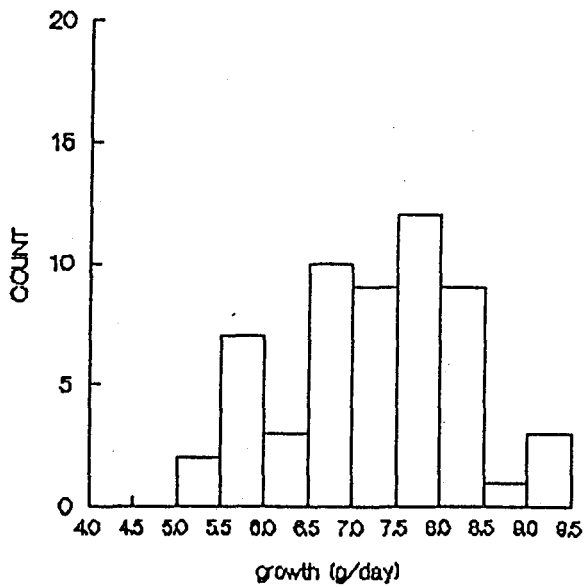
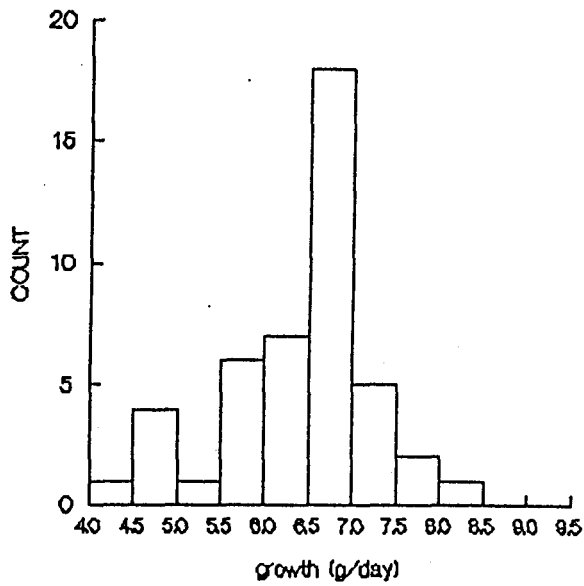
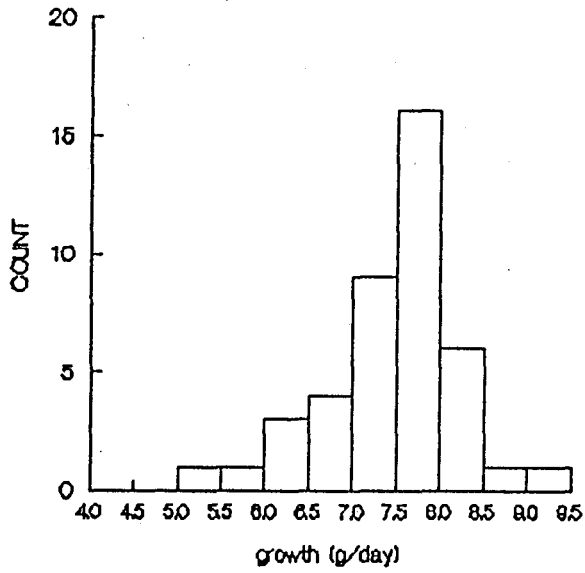
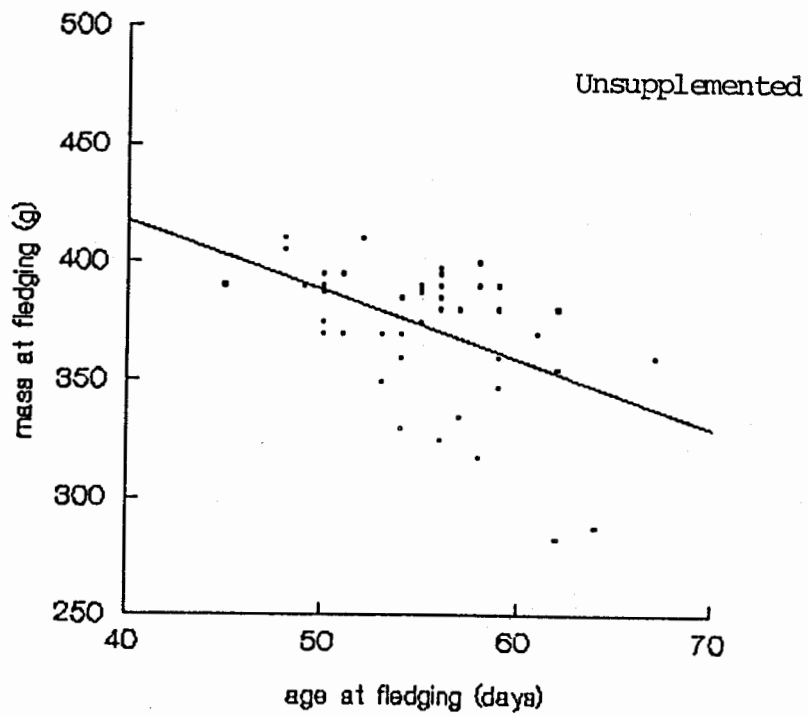
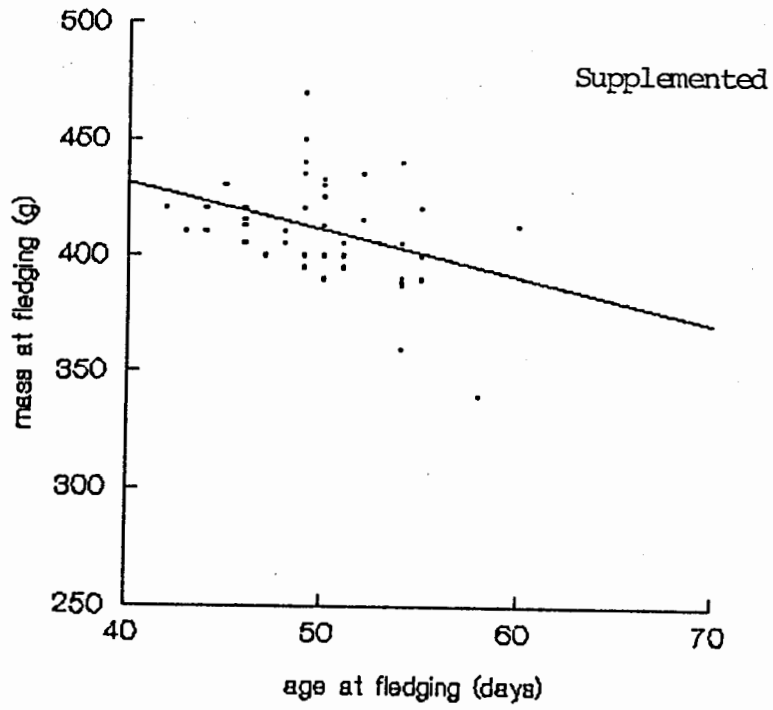


Figure 2.5. Relationship between mass and age at fledging for supplemented ($y = -2.0 x + 511.6$; $r^2 = .120$; $F = 5.48$, $df = 1,40$, $P = 0.024$) and unsupplemented ($y = -2.9 x + 534.9$; $r^2 = .229$; $F = 12.76$, $df = 1,43$, $P = 0.001$) rhinoceros auklet chicks in the supplementary feeding study. ANCOVA: homogeneity of slopes - $F = 0.58$, $df = 1$, $P = 0.449$; homogeneity of y-intercepts - $F = 18.82$, $df = 1$, $P < 0.001$



Growth parameters of undisturbed chicks in 1989 and 1990 are given in Table 2.2. Mass at 10 and 42 days, growth, and mass at fledging were significantly higher in 1989 than in 1990. Hatch and fledge dates and age at fledging, however, were the same in both years.

Mass at fledging declined with hatch date in both years of the study; however, the decline was significant only in 1990 (Fig. 2.6). The slopes of the relationships were similar between years, but the intercept was significantly higher in 1989. A significant seasonal decline in mass at 10 days was found for the undisturbed chicks in both years (Fig. 2.7). As above, the slopes of the regressions were the same between years, but the intercept was significantly higher in 1989. Thus, after standardizing for hatch date, chicks in 1989 were heavier both at ten days of age and at fledging than were chicks in 1990. Hatch date was not significantly related to growth rate in either year (Fig. 2.8).

Discussion

The model of alcid fledging behaviour from the chick's perspective produced three main predictions (Ydenberg 1989). Firstly, mass at fledging and age at fledging should be inversely related. Secondly, mass and age at fledging should vary with growth rate: faster growing chicks should fledge earlier and at a heavier mass than slower growing chicks. Thirdly, fledging mass should decline over the season.

The natural intra-annual variation in growth rates in both

Table 2.2. Growth parameters of rhinoceros auklet chicks from undisturbed burrows on Pine Island in 1989 and 1990.

	1989 (N = 56)		1990 (N = 53)		F
	<u>Mean</u>	<u>S.D.</u>	<u>Mean</u>	<u>S.D.</u>	
Hatch date ^a	15.7	4.27	16.4	5.19	0.54
Mass at 10 days (g)	128.8	12.94	117.8	18.81	12.69 ^b
Mass at 42 days (g)	380.3	33.09	321.7	43.11	63.71 ^b
Growth (g/day)	7.9	1.12	6.4	1.21	44.41 ^b
Mass at fledging (g)	383.9	30.35	343.5	38.68	37.00 ^b
Age at fledging (d)	54.4	4.94	55.0	4.27	0.44
Fledge date ^a	70.1	6.62	71.4	7.01	0.92

^a day 1 = June 1

^b $P \leq 0.001$

Figure 2.6. Relationship between mass at fledging and hatch date in undisturbed burrows in 1989 ($y = -1.5 x + 410.1$; $r^2 = .057$; $F = 3.27$, $df = 1, 54$, $P = 0.076$) and 1990 ($y = -2.4 x + 382.1$; $r^2 = .101$; $F = 5.76$, $df = 1, 51$, $P = 0.02$). ANCOVA: homogeneity of slopes - $F = 0.81$, $df = 1$, $P = .369$; homogeneity of y-intercepts - $F = 7.24$, $df = 1$, $P = 0.008$

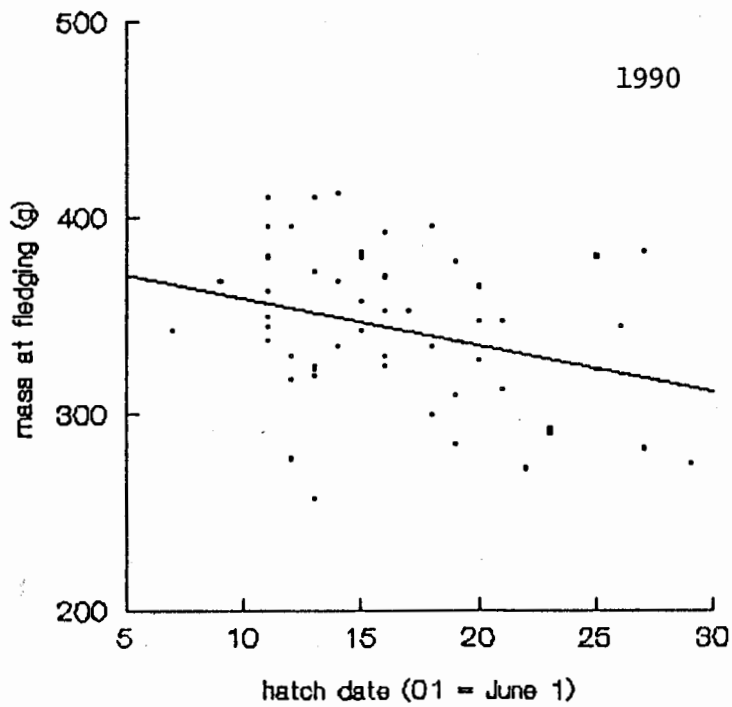
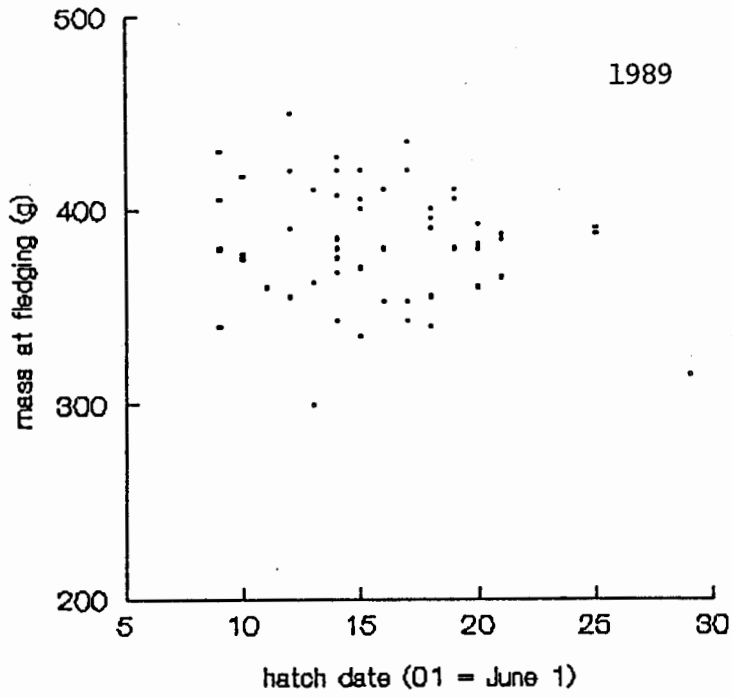


Figure 2.7. Relationship between mass at ten days of age and hatch date in undisturbed burrows in 1989 ($y = -1.1x + 145.9$; $r^2 = .129$; $F = 7.98$, $df = 1, 54$, $P = 0.007$) and 1990 ($y = -1.1x + 136.5$; $r^2 = .099$; $F = 5.59$, $df = 1, 51$, $P = 0.022$). ANCOVA: homogeneity of slopes - $F = 0.006$, $df = 1$, $P = 0.94$; homogeneity of y-intercepts - $F = 12.20$, $df = 1$, $P = 0.001$

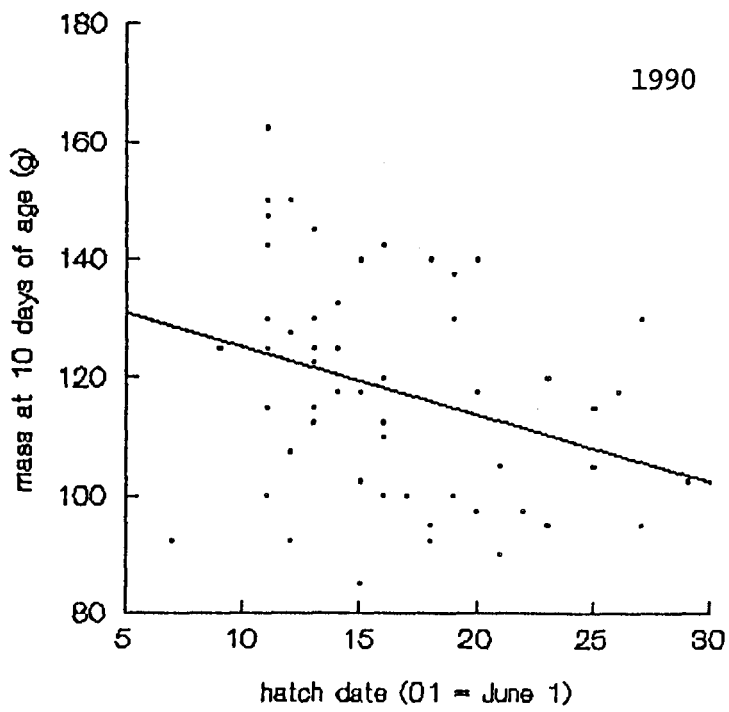
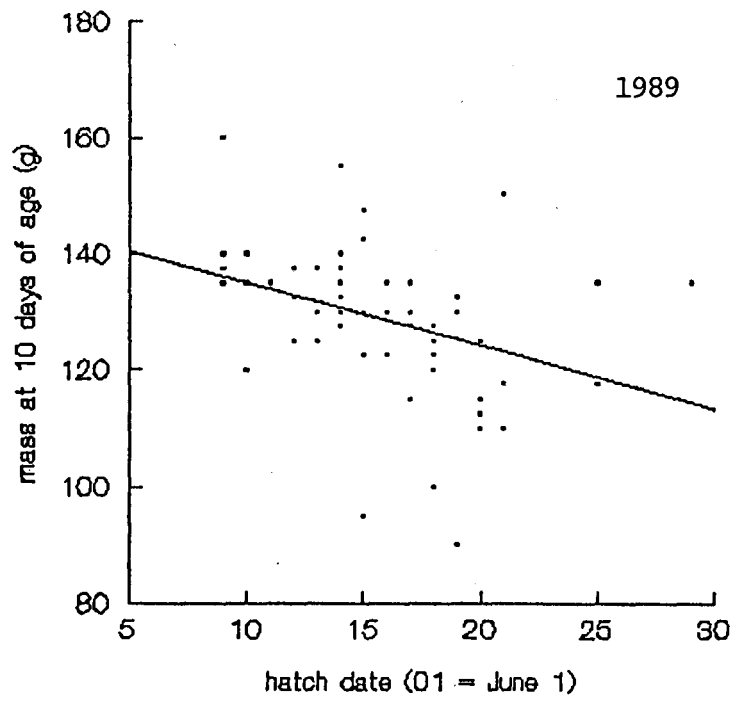
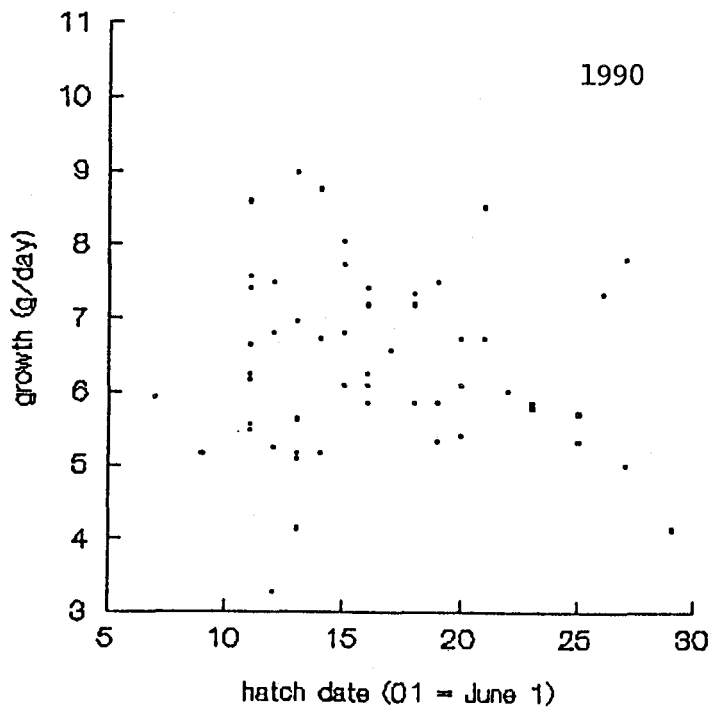
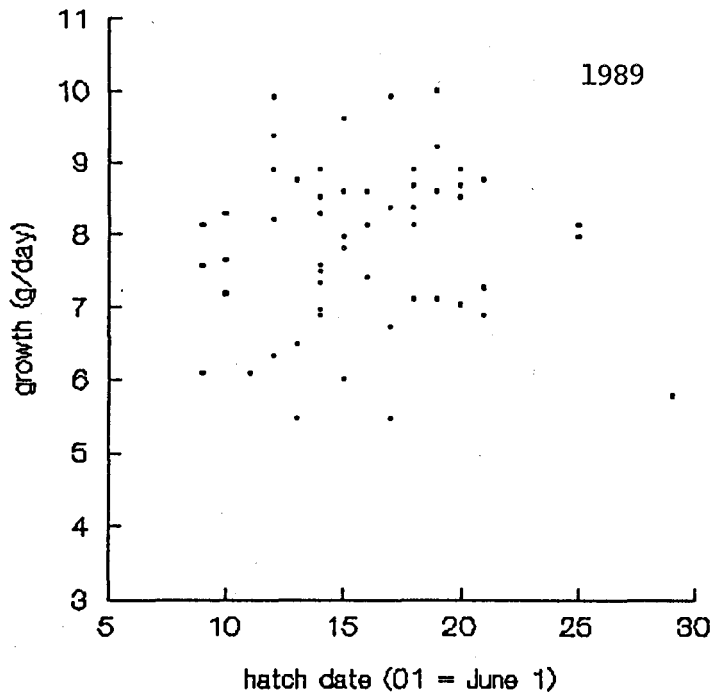


Figure 2.8. Relationship between growth rate and hatch date in undisturbed burrows in 1989 ($F = 0.13$, $df = 1,54$, $P = 0.72$) and 1990 ($F = 0.26$, $df = 1,51$, $P = 0.61$).

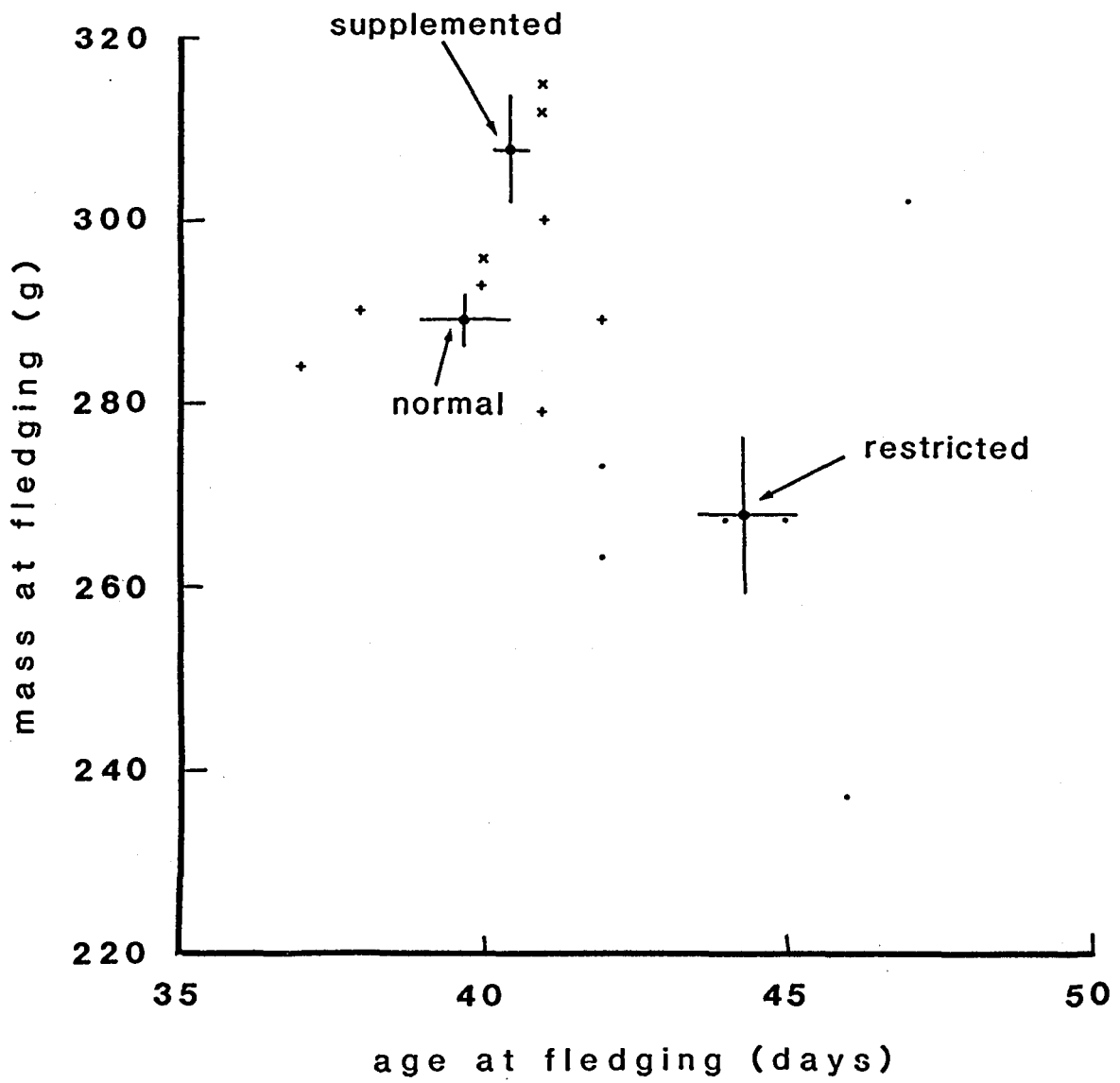


1989 and 1990 produced the predicted patterns. Fledging mass was positively related to growth rate and fledging age was negatively related to growth rate. These patterns produce the inverse relationship between mass and age at fledging predicted by the model and found in both years of the study. Thus, in the intra-annual comparisons, rhinoceros auklet chicks that grew faster fledged at a heavier mass and younger age than those that grew more slowly.

The supplementary feeding study was designed to test experimentally the effects of growth on the chick fledging decision. The supplemented chicks grew faster and, as predicted by the model, had a higher mean fledge mass and a lower mean fledge age than did the unsupplemented controls.

Data from the literature on alcids suggests that the trends described above are not confined to rhinoceros auklets. Harris (1984, p. 212) has summarized studies of nestling Atlantic puffins (Fratercula arctica), a close relative of the rhinoceros auklet, that involved growth rate manipulations. These studies include supplementary feeding studies, twinning studies and a single-parent study. A plot of the fledging mass and age from data provided in Harris' (1984) summary (Fig. 2.9) shows that, as predicted by the model, those chicks that received supplementary food and grew faster fledged at a higher mass than did those that received less food and grew more slowly. Chicks on a restricted food diet fledged at an older age than did those on a normal diet, as expected, but no difference in fledging age was found between

Figure 2.9. Relationship between fledging mass and fledging age in six feeding manipulation studies on nestling Atlantic puffins (data from Harris 1984, p. 212). 'Supplementary' includes chicks fed either supplementary or unlimited food; 'normal' includes chicks maintained on a normal diet; 'restricted' includes twinned chicks, chicks fed by a single adult and chicks fed 80 g food/day. Bars indicate means \pm S.E. of the study means of each diet level reported by Harris (1984).



normally-fed chicks and those receiving extra food. It should be noted that the methodology used in these studies was not standardized and that the 'supplementary' and 'restricted' classifications include a range of treatments. For example, 'restricted' includes twinned chicks, chicks fed by only one adult and chicks fed 80 g/day of food.

The inter-annual comparison of chick growth parameters of rhinoceros auklets on Pine Island did not exhibit the same patterns as did the intra-annual and experimental comparisons. Although mass at ten days, growth and mass at fledging were all significantly higher in 1989 than in 1990, age at fledging was the same in the two years. The inter-annual comparison is the weakest of my three tests because other environmental variables such as predation rate and the post-fledging growth rate are not controlled between years. As I discuss in greater detail in Chapter III, higher predation levels should select for earlier fledging. If predation by bald eagles (Haliaeetus leucocephalus) was lower in 1989, the opposing selective pressures of faster growth rate and lower predation may have counteracted each other, resulting in no observed difference in fledging age. Although I did not measure predation in 1989, fisheries data suggest that in 1989 salmon availability was greater than in 1990 (D. Shutte, DFO, pers. comm.) Bald eagles, with excellent fishing prospects, may have spent less time foraging on rhinoceros auklets in 1989 than they did in 1990.

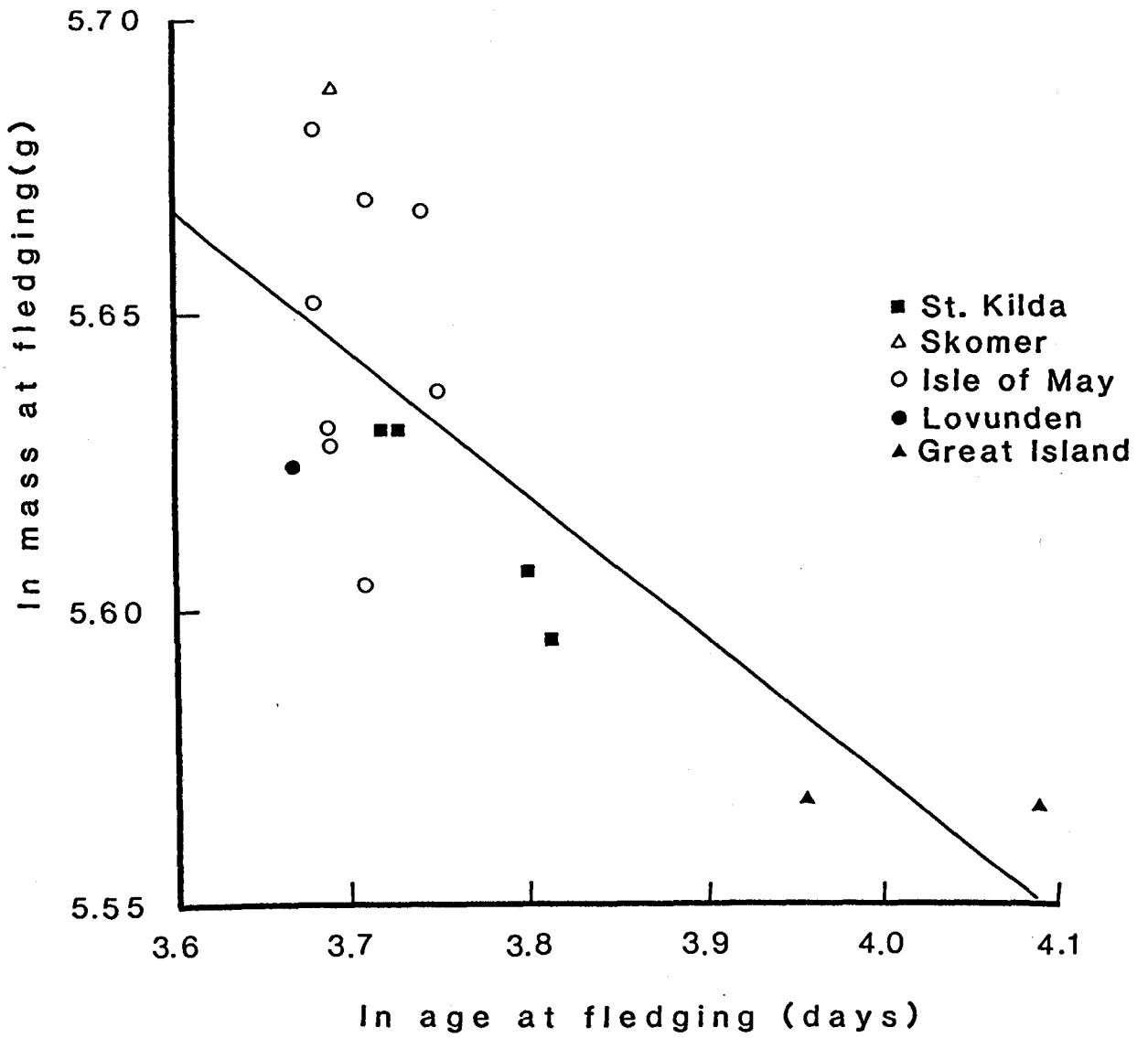
In contrast to the results of my inter-annual comparisons, in an inter-annual study of rhinoceros auklets on Triangle Island,

B.C., Vermeer and Cullen (1979) found the patterns predicted by the model. Chicks grew faster in 1978 than they did in 1976; they also fledged at a higher mass and after a shorter nestling period in 1978 than they did in 1976. Watanuki (1987) reported similar variation in mass and age at fledging in an inter-annual study of rhinoceros auklets in Japan: in the year of higher chick growth, chicks fledged earlier and at a higher mass.

Further evidence of the generality of this negative relationship between mass and age at fledging may be found in nestling growth data from five colonies of Atlantic puffins (summarized in Harris 1984, p. 211) (Fig. 2.10). The regression of mass at fledging on age at fledging is significant. Unfortunately, the growth rates for these colonies are not given.

The third prediction of the model is that the optimal mass at fledging should decrease as the season progresses (Ydenberg 1989). A seasonal decline in fledging mass was found for undisturbed chicks in both 1989 and 1990; the relationship was significant in 1990 and a strong trend in 1989. Seasonal declines have also been reported for many species of alcid including the Atlantic puffin (Nettleship 1972, Harris 1982), the common murre (Uria aalge) (Hedgren 1979) and the thick-billed murre (Uria lomvia) (Gaston and Nettleship 1981, Birkhead and Nettleship 1982). According to a life history approach to fledging behaviour, this decline is expected because the potential for growth is higher at sea, so chicks that hatch late in the season should accept the risk of higher mortality in that habitat earlier in order to maximize their

Figure 2.10. Relationship between fledging mass and fledging age in nestling Atlantic puffins from five colonies in Europe and Canada (data from Harris 1984, p. 211). The regression line for the ln-ln transformed data is $y = - 0.2x + 6.5$ ($r^2 = .567$; $F = 18.32$, $df = 1,14$, $P = 0.001$).



size at the beginning of winter (Ydenberg 1989). The slope of the relationship should be sensitive to differences in chick growth rate, producing a shallower slope in years of good growth (Ydenberg 1989). The slope of the regression from 1989, a better growth year, is less than that from 1990, but the difference is not significant.

Seasonal declines in fledging mass may also be expected if the availability and/or quality of food declines over the season (eg. Hedgren and Linnman 1979, Birkhead and Nettleship 1982). However, if food resources deteriorate during the season, growth rates should be inversely related to hatch date; no seasonal trend in growth rate was found for undisturbed birds in either year of this study. Wilson (1977) suggested that decreasing food resources were a cause of slower growth and lower fledging mass in late-hatched rhinoceros auklet chicks in Washington. Wilson (1977) made his comparisons, however, using the ten earliest- and ten latest-hatched chicks in his sample. In 1990, I found a sample of six very late-hatched chicks (hatched after June 30) which I did not include in my group of undisturbed chicks for that year. The mean growth rate for these chicks was 4.6 g/day, which is substantially lower than the mean of 6.4 g/day determined for the undisturbed chicks; the mean fledge mass of 281.2 g was correspondingly low. This suggests that, although food availability does not decline throughout the season on Pine Island, a deterioration in food resources at the very end of the season may occur. Wilson's (1977) findings may have been the result of a similar pattern.

A negative seasonal trend in egg mass may also contribute to the decline in fledging mass (Gaston 1985). Birkhead and Harris (1985) suggested that such a reduction in egg size may be the outcome of the trade-off faced by late-laying females between lay date and egg size. They concluded that the best strategy would be to minimize the delay in laying and produce a smaller egg. Although egg mass was not measured in this study, due to the high probability of causing adult desertion, chick mass at 10 days was measured; chick mass shortly after hatching has been shown to be related to egg size in thick-billed murres (Birkhead and Nettleship 1982) and razorbills (Alca torda) (Lloyd 1979). A significant seasonal decline in mass at 10 days was found in 1989 and 1990. However, because those chicks that were the lightest at 10 days of age are not those that fledged at the lightest mass, the seasonal decline in egg mass is not sufficient to explain the trend in fledging mass.

Another factor which might contribute to the seasonal decline in fledging mass, particularly in high arctic species, is a decline in temperature toward the end of the breeding season that may affect the energy demands of the chicks (Gaston 1985). As the temperature on Pine Island increased from June through August (Pine Island weather station, unpublished data), it is unlikely that temperature affects fledging state of rhinoceros auklets.

In using data from rhinoceros auklets to test the predictions of a model based on reproductive parameters of common murres, I have assumed that the trade-off between low growth rate with low

mortality in the nest and potentially higher growth rate with higher mortality at sea is a general one. The data needed to determine the applicability of the assumptions to rhinoceros auklets are lacking. Because chick mortality was very low in the colony (in 1989, only three of 178 chicks died in the burrow, giving a daily mortality rate of 3.1×10^{-4}), the assumption of lower mortality rates in the burrow than at sea is reasonable (see Appendix 1). In addition, because chick growth rate approaches zero at the end of the nestling period, it seems reasonable that chicks have a higher potential growth rate at sea. Thus, although the shape of the fledging boundary for rhinoceros auklets will differ from that computed for the common murre, the qualitative predictions of the model are still valid.

The model discussed above considers fledging from the chick's perspective, with the assumption that the chick controls the time of fledging. Fish are often found in rhinoceros auklet burrows after the chicks have fledged (pers. obs.), indicating that, in some cases, the chicks leave even though at least one parent is still delivering food. This suggests that chicks leave when they are ready, and are not abandoned by their parents. Citing similar evidence, Harris (1976) concluded that nestling Atlantic puffins desert their parents and not visa versa. However, Bertram (1988) found that rhinoceros auklet parents seem to provision according to their own schedule and not according to the needs of the chick in the latter half of the nestling period. Thus, parents may also control fledging through food deliveries. Chapter III will

consider why and how the optimal time of fledging from the parents' perspective differs from that from the offspring's perspective.

CHAPTER III

PREDATION RISK AND PARENTAL PROVISIONING: EFFECTS ON NESTLING GROWTH AND FLEDGING

Introduction

In Chapter II, I examined the optimal time to fledge from the perspective of the nestling; I did not consider the role of the parents in determining the fledging behaviour of the chick. According to life history theory, breeding adults face a trade-off between current and future reproduction; individuals should adjust their behaviour during reproduction to maximize their expected lifetime reproductive success (Williams 1966). Parental investment, defined as any behaviour by the parent that increases its offspring's chance of surviving and reproducing at the expense of the parent's ability to invest in future offspring (Trivers 1972), should, therefore, reflect this trade-off.

For seabirds, provisioning of the young at the colony is a form of parental investment. The susceptibility of adults to predation during feeding visits has been described for several species (eg. Adelie penguins, Pygoscelis adeliae, Ainley and DeMaster 1980; Atlantic puffins, Fratercula arctica, Harris 1980; Leach's storm petrels, Oceanodroma leucorhoa, Watanuki 1986; Cassin's auklets, Ptychoramphus aleuticus, Nelson 1989). Because most seabirds are long-lived and experience low mortality between breeding seasons (Evans and Nettleship 1985, Hudson 1985), selection should favour those individuals with behaviours that

reduce mortality during the breeding season (Williams 1966). Adult seabirds have been known to change their behaviour in response to the risk of predation. Harris (1980) found that Atlantic puffins decrease the time spent at the colony and the mass at fledging of their young in response to predation by great black-backed gulls (Larus marinus). Similarly, Leach's storm petrels in Japan reduce their activity and increase the synchrony of their arrivals at the colony on moonlit nights when the predation rate by slaty-backed gulls (Larus schistisagus) is high (Watanuki 1986).

Using data from studies on the Atlantic puffin, Clark and Ydenberg (1990a) showed that the optimal age at fledging from the parent's perspective is lower than that from the chick's perspective and the difference increases when the parent incurs a higher risk when feeding the chick. Chicks are assumed to fledge as soon as feeding ceases in this analysis, and the model, therefore, also predicts that chicks in habitats of high adult mortality will fledge at a younger age than will those in safer habitats.

Rhinoceros auklets (Cerorhinca monocerata), a close relative of Atlantic puffins, are burrow-nesting alcids whose nocturnal provisioning habits are assumed to be a tactic to avoid predation (Cody 1973, Vermeer et al. 1979). On breeding colonies along the coast of British Columbia and Alaska, strong circumstantial evidence indicates that adults may be subject to predation by bald eagles (Haliaeetus leucocephalus) (Degange and Nelson 1982, Kaiser 1989, pers. obs.). If the risk of predation is a significant cost

of reproduction, the provisioning patterns of birds breeding in high predation areas of a colony and those breeding in low predation areas should differ. This study was designed to examine parental provisioning tactics in relation to the level of predation risk in rhinoceros auklets, and the effects of different tactics on chick growth and fledging. The two main predictions are that 1) adults in high risk areas of the colony will terminate provisioning earlier than will those in low risk areas and 2) the inverse relationship between age and mass at fledging (discussed in Chapter II) will be significantly lowered in the high predation risk habitats.

Materials and Methods

Four study plots were established on Pine Island, B.C., (50° 58'; 127° 41') in 1990: two were in areas that had experienced bald eagle predation on rhinoceros auklets in 1989 (the 'high predation' plots) and two were in areas where no evidence of predation had been found (the 'low predation' plots). No differences in structural characteristics of the habitat were found between these plots. Predation frequency was measured in 1990 by counting the number of piles of auklet feathers in each plot every second day; the location of each pile was noted so that only fresh kills were counted on subsequent days. In addition, the number of occupied burrows in each plot was counted so that an estimate of predation risk could be made. Occupancy was determined by the occurrence of feathers, droppings or broken pieces of green vegetation at the

burrow entrance.

In mid-June, 25 to 30 active burrows were excavated in each plot (see Chapter II for details of excavation methods). Chicks were weighed, measured and aged according to the methods outlined in Chapter II. All chicks were weighed and measured every four days between ages 9-10 and 41-42 days. They were then weighed and measured every second day until fledging. Date and mass at fledging were determined as described in Chapter II.

Growth rates were calculated for each chick from the slope of the regression line relating chick age and mass between 10 and 38 days of age. Hatch date, mass at 10, 38 and 44 days of age, peak mass, growth, mass at fledging, date of fledging and age at fledging were compared between high and low predation areas using a mixed-model nested ANOVA (Sokal and Rohlf 1981, p. 272).

The amount of food delivered to the chicks was estimated using a hooding procedure (Hatch 1984, Bertram et al. in press). In the late afternoon, after a chick had been weighed and measured, a hood of loose weave cotton was placed over the chick's head and tied into place. The chick was then tethered to a spot near the nest chamber using a string tied around its leg and to a stake. Tethering was necessary to prevent hooded chicks wandering from their burrows (Bertram et al. in press). Early on the following morning, the hoods and tethers were removed and the burrow was thoroughly searched for fish left by the parents. Fish were wiped clean and weighed to the nearest gram on a 300 g Ohaus electronic balance before being fed to the chick. Thus, these "burrow load"

(Hatch 1984) measurements include all the food delivered to a chick in a night and may be the result of one or both adults feeding.

Hooding began when the chicks were 13-14 days old. Although I had planned to determine burrow loads for all chicks in excavated burrows every four days until fledging, in some burrows this proved impossible. In several burrows, the procedure was not suitable because the tunnels were located over rock, thus precluding tethering, or two burrows became joined part way through the breeding season. On two days of heavy rain I chose not to hood the downy chicks because of the difficulty in keeping them dry during handling. In addition, some chicks struggled quite extensively against either the tether or hood: the nest chamber was disrupted and there was much loose dirt in the chamber and adjoining tunnel. This usually happened with chicks that were close to fledging age and the procedure was not continued for these chicks. Measurements from those chicks for which burrow load data are not available were included in growth calculations.

Burrow loads were examined in relation to chick age. The provisioning patterns of high and low predation areas were compared using an ANCOVA procedure. ANCOVA tests were also used for comparisons between predation levels of trends found in chick growth parameters. All statistical analyses were performed using the SYSTAT statistical package (Wilkinson 1989).

As described in Chapter II, a group of 53 undisturbed chicks was also followed in 1990. The burrows were situated in areas of the colony for which predation risk was not assessed.

RESULTS

No signs of bald eagle predation on rhinoceros auklets were found in either of the low predation study plots between June 22 and August 29; 25 and 22 feather piles were found in the two high predation plots during this period (Table 3.1). Predation was fairly constant from the beginning of monitoring (7 days after the mean hatch date) until early August, but ceased almost completely after the first four days in August (Fig. 3.1). This corresponds to the pattern of eagle sightings on the island during the day: more than ten eagles were commonly observed daily in June and July, whereas only a few eagles were seen after the first week in August.

Predation risk per 1,000 provisioning visits (Table 3.1) was calculated for each area by dividing the number of predation events by the estimated total number of adult provisioning trips made into the area. The latter figure was estimated using the number of occupied burrows and predation events given in Table 3.1, and assuming that: 1) each parent visited every second night for the first 30 days and then twice every three nights until the chick fledged (based on the regression of burrow load on chick age, given in Fig. 3.2, and assuming a 30 g load per trip); and 2) depredated parents were lost after the first 20 days (based on the relatively constant predation rate during July).

Chick growth parameters are summarized in Table 3.2. There were no significant differences in any of the measures for the two plots nested within each predation level, and the data have been grouped for ease of presentation; however, all statistics were

Table 3.1. Plot characteristics and predation risk of high and low predation plots, Pine Island, 1990.

<u>Plot</u>	<u>Risk</u>	<u>Occupied Burrows</u>	<u>Density^a</u>	<u>Predation Events</u>	<u>No. of Provisioning Trips^b</u>	<u>Predation Risk^c</u>
1	low	535	0.53	0	34,775	0.00000
2	low	414	0.54	0	26,890	0.00000
3	high	760	0.60	25	43,505	0.00057
4	high	611	0.52	22	35,020	0.00063

^a occupied burrows/m²

^b estimation procedure described in text

^c number of predation events/number of parental provisioning trips

Figure 3.1. Cumulative tally of predation events recorded in high predation plots between June 23 and August 26, 1990, Pine Island. Mean hatching date = 16.5; mean fledging date = 67.4.

PREDATION EVENTS - 1990

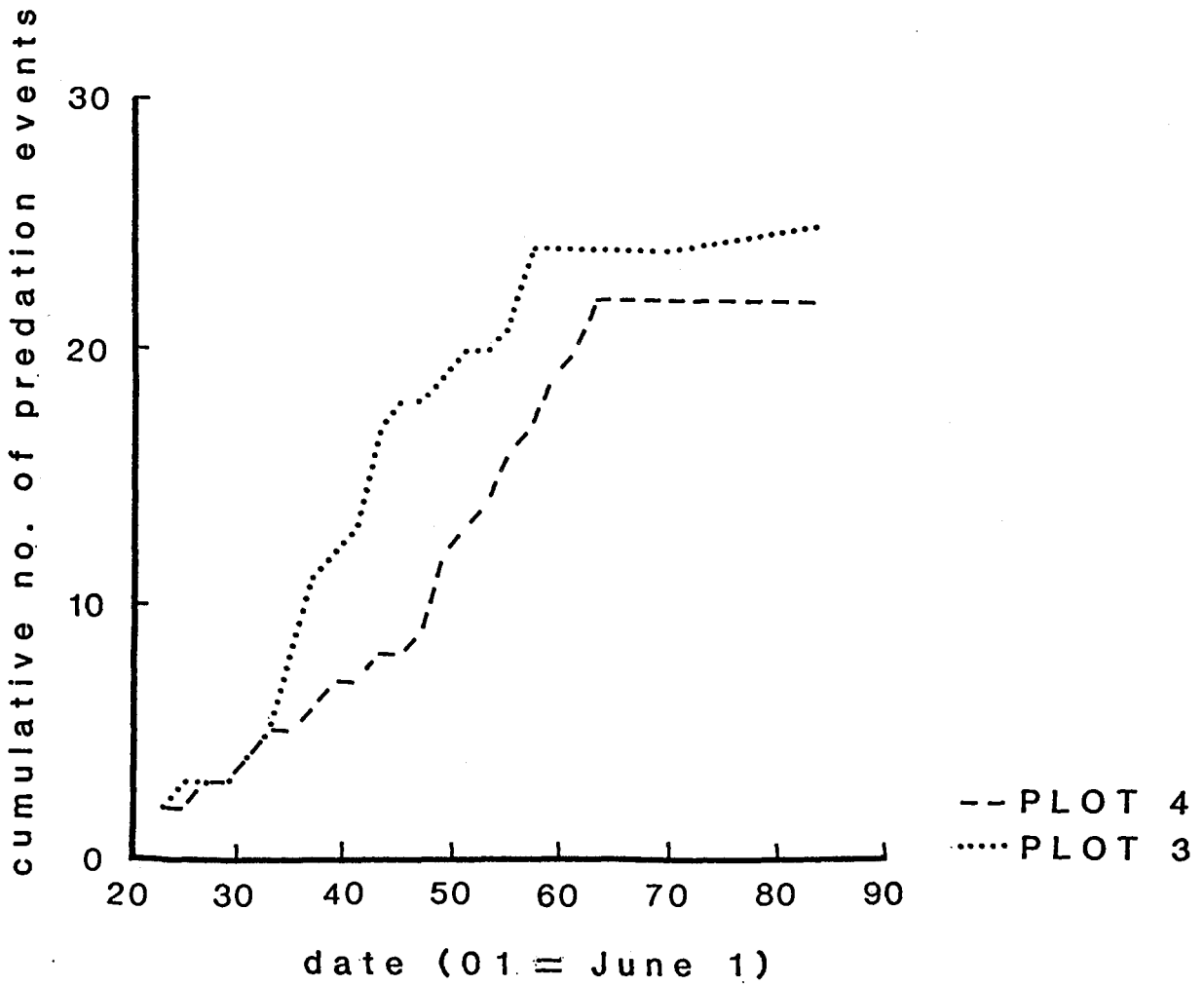


Figure 3.2. Relationship between chick age and burrow load in high predation ($y = 1.1 x + 3.1$; $r^2 = .472$; $F = 356.87$, $df = 1,399$, $P < 0.001$) and low predation ($y = 1.0 x + 3.4$; $r^2 = .400$; $F = 256.33$, $df = 1,384$, $P < 0.001$) plots. ANCOVA: homogeneity of slopes - $F = 0.197$, $df = 1$, $P = 0.66$; homogeneity of y-intercepts - $F = 1.02$, $df = 1$, $P = 0.31$

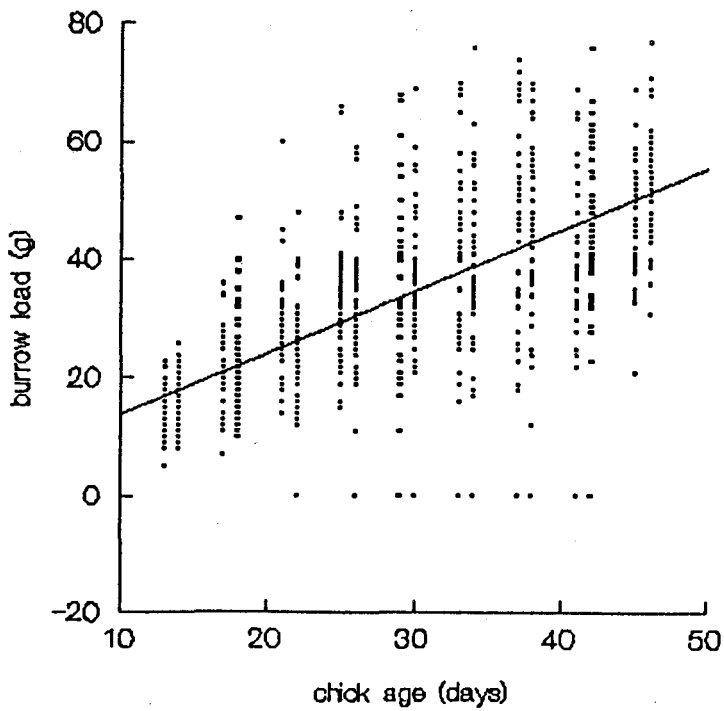
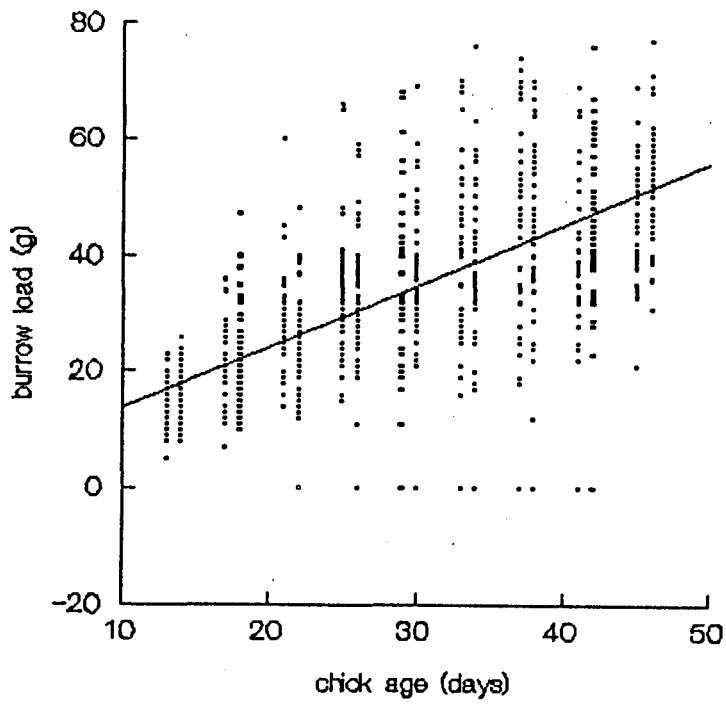


Table 3.2. Growth parameters of rhinoceros auklet chicks from high and low predation areas of Pine Island, 1990.

	HIGH PREDATION (N = 46)		LOW PREDATION (N = 45)		F
	Mean	S.D.	Mean	S.D.	
Hatch date ^a	16.5	4.54	15.4	4.60	1.51
Mass at 10 days (g)	120.5	18.02	120.1	21.05	0.03
Mass at 38 days (g)	302.3	32.03	300.2	40.36	0.03
Growth (g/day)	6.6	1.23	6.5	1.17	0.05
Peak mass (g)	350.7	24.84	349.9	43.18	0.16
Mass at fledging (g)	346.3	27.12	341.0	46.48	0.36
Age at fledging (d)	50.9	2.23	56.2	4.33	51.41 ^b
Fledge date ^a	67.4	4.85	71.6	7.52	9.35 ^c

^a day 1 = June 1

^b P < 0.001

^c P = 0.003

performed on the full nested-plot design. The only variables that differed significantly between the high and low predation areas of the colony were age at fledging and date of fledging: chicks in high predation areas fledged about five days younger and four days earlier than did chicks in low predation areas.

Relationships between mass and age at fledging in the high and low predation plots are shown in Fig. 3.3. The regression lines do not differ significantly in slope; the intercept for the former area is higher. These lines lie above and below, respectively, the regression line for 1990 undisturbed birds. The inverse relationship between age at fledging and growth is significant in both the high ($y = -0.6x + 54.9$; $F = 5.63$, $df = 1,44$, $P = 0.02$) and low ($y = -2.2x + 70.6$; $F = 24.90$, $df = 1,43$, $P < 0.001$) predation risk habitats. Mass at fledging is positively related to growth in both high ($y = 9.7x + 282.5$; $F = 10.63$, $df = 1,44$, $P = 0.002$) and low ($y = 30.1x + 146.9$; $F = 58.19$, $df = 1,43$, $P < 0.001$) risk plots.

There was no difference between the provisioning regressions from the high and low predation areas (Fig. 3.2). Data from chicks older than 46 days were not used to fit the lines because most chicks resisted the hooding procedure at or just after this age.

A significant seasonal decline in mass at fledging was found in the low predation areas only (Fig. 3.4). The slope of the regression is steeper for the low predation plots than the high predation plots. Peak mass also declined through the season in both high ($y = -1.7x + 379.0$; $F = 4.82$, $df = 1,44$, $P = 0.03$) and

Figure 3.3. Relationship between age and mass at fledging in high predation ($y = -5.3 x + 617.5$; $r^2 = .193$; $F = 10.50$, $df = 1,44$, $P = 0.002$) and low predation ($y = -8.7 x + 828.5$; $r^2 = .655$; $F = 81.54$, $df = 1,43$, $P < 0.001$) plots. ANCOVA: homogeneity of slopes - $F = 2.90$, $df = 1$, $P = 0.09$; homogeneity of y-intercepts - $F = 6.50$, $df = 1$, $P < 0.001$

For undisturbed birds: $y = -7.0 x + 729.4$; $F = 76.4$, $df = 1,51$, $P < 0.001$

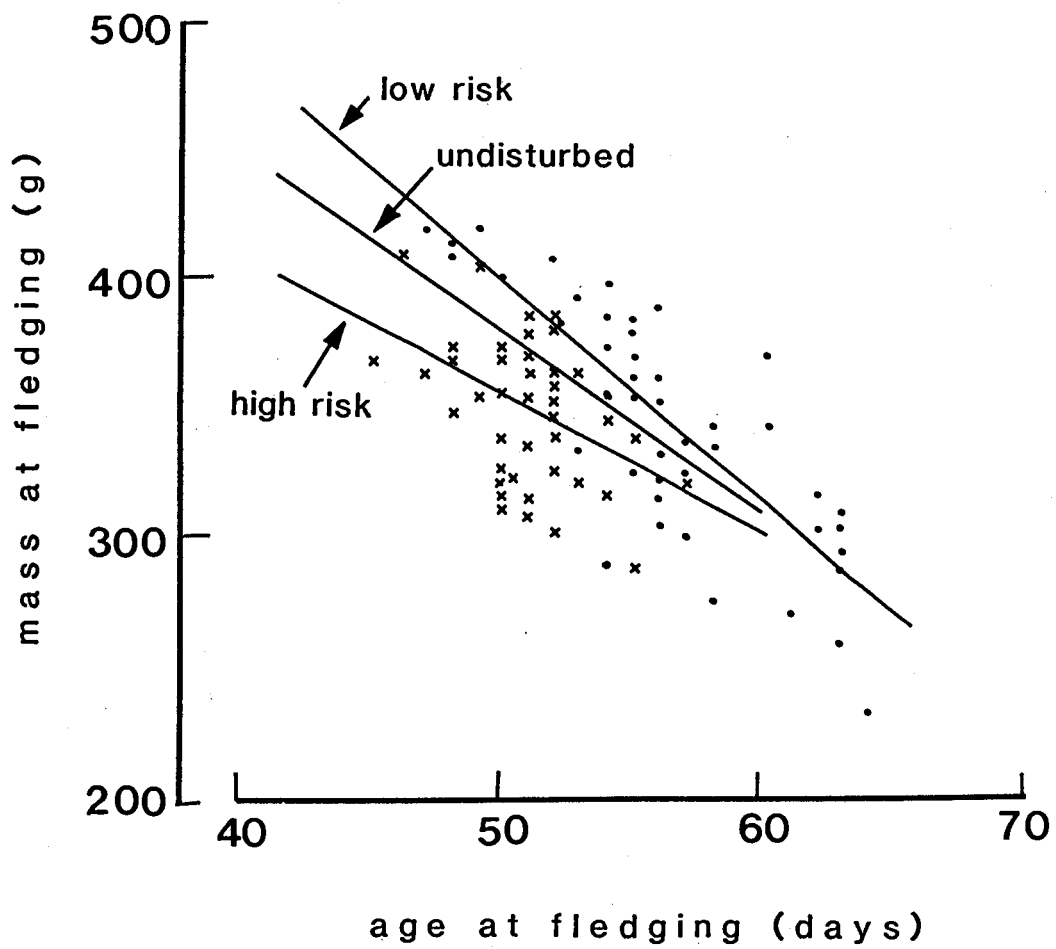
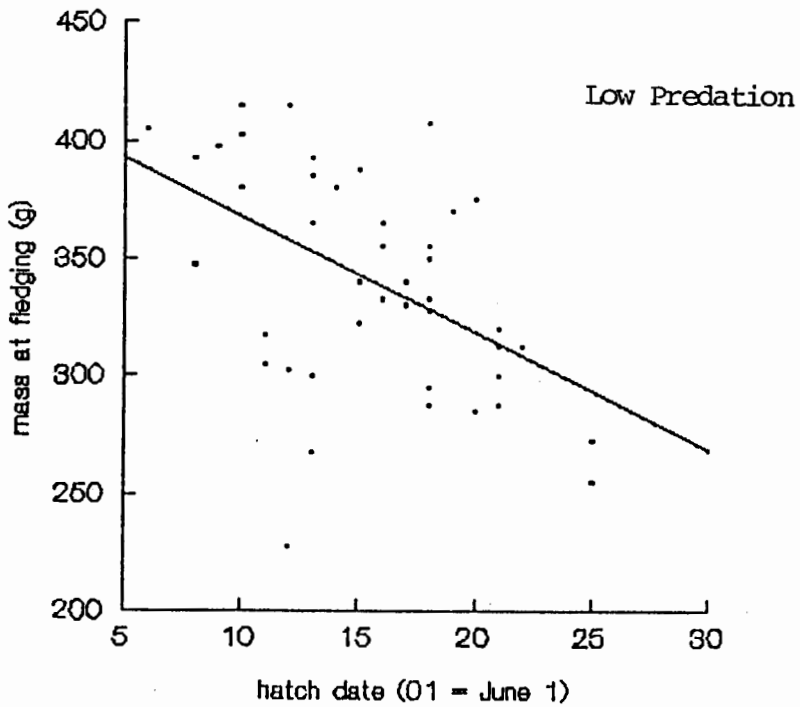
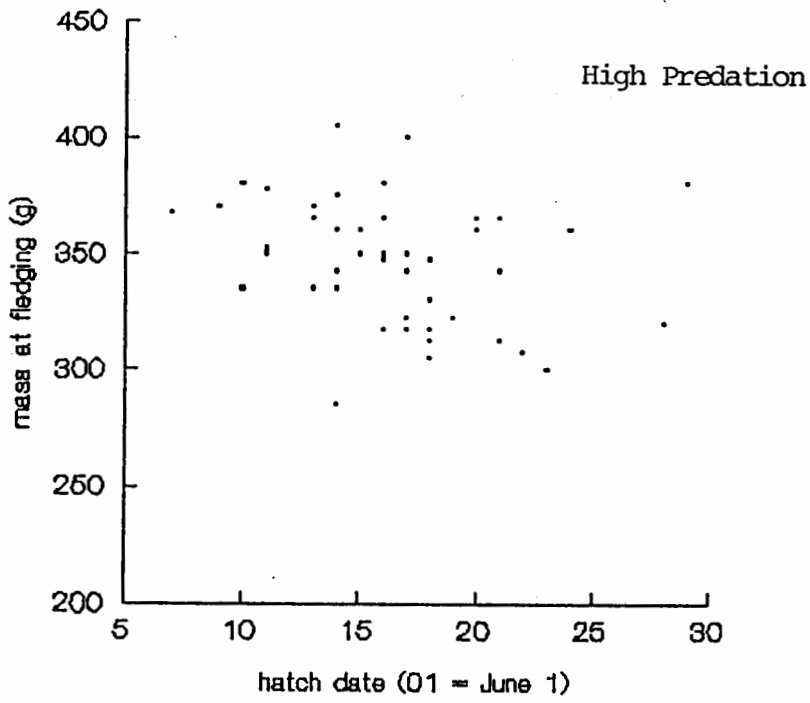


Figure 3.4. Relationship between hatch date and mass at fledging in high predation ($F = 3.66$, $df = 1,44$, $P = 0.06$) and low predation ($y = -5.0x + 417.9$; $r^2 = .243$; $F = 13.80$, $df = 1,43$, $P = 0.001$) plots. ANCOVA: homogeneity of slopes - $F = 4.37$, $df = 1$, $P = 0.04$



low ($y = - 5.3 x + 432.0$; $F = 20.32$, $df = 1,43$, $P < 0.001$) predation risk plots. Mass at ten days was inversely related to hatch date at both levels of predation and the decline was significant and similar in both (Fig. 3.5). A significant relationship between hatch date and growth was found in the low predation areas, but not in the high predation plots (Fig. 3.6).

Discussion

My results suggest that parental behaviour is similar in high and low predation areas throughout most of the nestling period. Nestlings in both habitats grew at the same rates, reached similar peak masses and received the same amounts of food until my measurements ceased at 46 days of age. In the high predation areas, however, the chicks fledged at a younger age but not a lower mass. Thus, it seems that adults in all areas provisioned at the same rates until the chicks were capable of fledging; shortly after this time the nestlings from the high predation plots left the colony while those from the low predation plots continued to be fed at a rate which provides enough energy for the chicks to maintain, but not increase, their mass. Unfortunately, due to methodological problems (see Materials and Methods section), the feeding patterns of adults with chicks older than 46 days are unknown.

For alcids, there appears to be no consistent relationship between mass at fledging and post-fledging survival (eg. Lloyd 1976, Hedgren 1981, Harris and Rothery 1985). Thus, once the chick is capable of fledging, there is no apparent advantage for the

Figure 3.5. Relationship between hatch date and mass at ten days of age in high predation ($y = -1.7 x + 148.3$; $r^2 = .472$; $F = 9.70$, $df = 1,44$, $P = 0.003$) and low predation ($y = -1.7 x + 146.8$; $r^2 = .400$; $F = 7.19$, $df = 1,43$, $P = 0.01$) plots. ANCOVA: homogeneity of slopes - $F = 0.003$, $df = 1$, $P = 0.95$; homogeneity of y-intercepts - $F = 0.36$, $df = 1$, $P = 0.55$

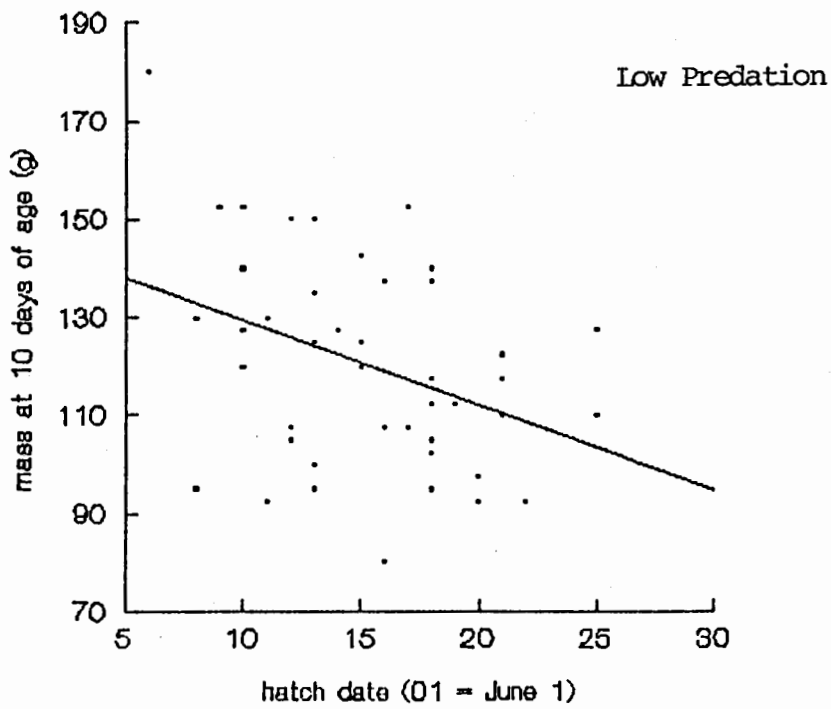
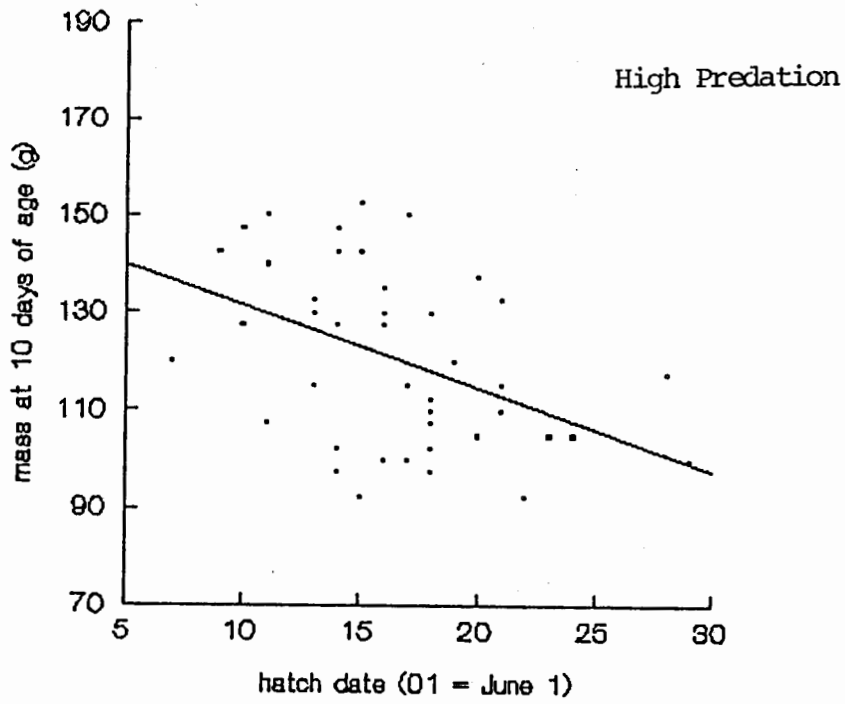
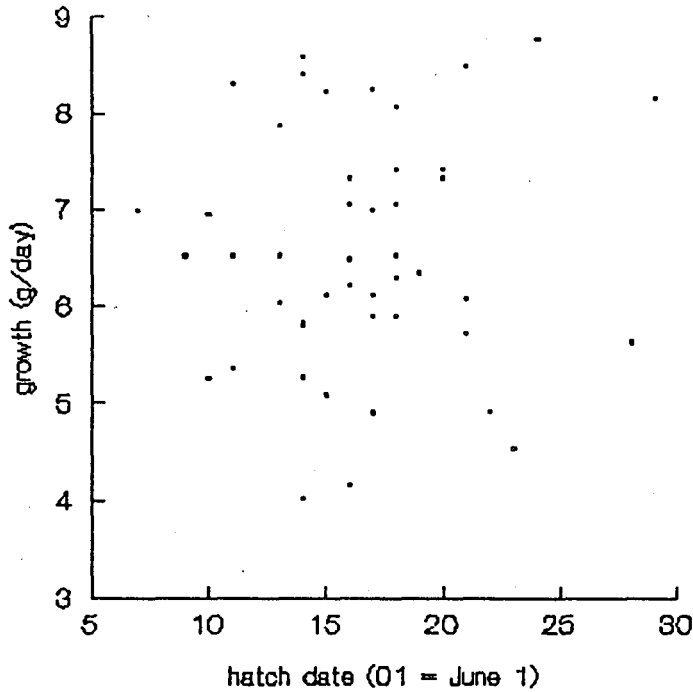
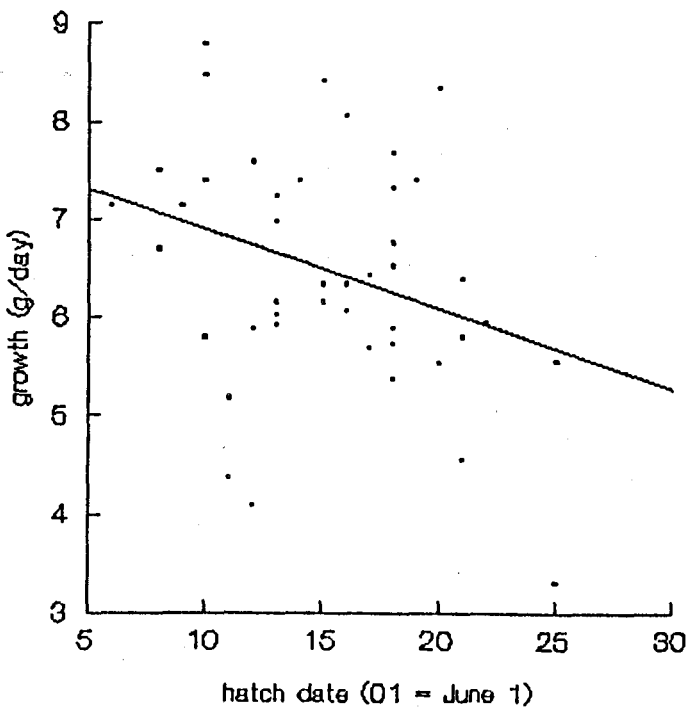


Figure 3.6. Relationship between hatch date and growth rate in high predation ($F = 0.16$, $df = 1,44$, $P = 0.687$) and low predation ($y = -0.1 x + 7.7$; $r^2 = .103$; $F = 4.92$, $df = 1,43$, $P = 0.03$) plots.



High
Predation



Low
Predation

parents to continue to feed the chick at a rate sufficient to increase its mass. This view is supported by the results of this study: parents in the low predation risk areas of the colony did not provide enough food for the fully feathered chicks to increase in mass. The main advantage to a prolonged nest period may be the safety of the burrow in comparison to the ocean for chicks (Ydenberg 1989). Another possible advantage is extended time for continued development. Although no heavier, chicks in low predation habitats fledged with significantly longer wings (158.9 mm) than did chicks from high predation areas (154.6 mm) ($N = 91$, $F = 22.11$, $P < 0.001$); other aspects of development may also proceed during this time.

No significant differences were found in hatch date or mass at ten days. These two parameters should be unaffected by predation at the colony as it appears that eagles do not begin to take auklets regularly until a few days into the latter's chick-rearing period. Few auklet remains were found on Pine Island in mid-June at the beginning of this study although feathers are usually evident for up to a month after first appearing (pers. obs.).

A negative regression of mass at fledging on age at fledging is apparent in both habitats. This relationship arises from the interaction of two other patterns consistently found in the studies discussed in Chapter II: a positive relationship between mass at fledging and growth rate and an inverse relationship between age at fledging and growth rate. The lines for the low and high predation plots lie on either side of the line for the undisturbed chicks

(chosen without regard for the associated predation risk). This suggests that my predation study plots do represent the two extremes on Pine Island. The regression line for the low predation plots lies above that for the high predation areas, indicating that a chick growing at a given rate will fledge earlier and at a lighter mass if it inhabits a high predation risk area than if it lives in a low risk area. The relative position of these two regression lines is predicted by a model which examines the optimal time of fledging from the parents' perspective (Clark and Ydenberg 1990a). This pattern is produced because the cost of reproduction is greater in the high risk areas and, thus, parents in these areas maximize reproductive success by ceasing their provisioning trips earlier, thus forcing the chick to fledge earlier.

It is interesting to note the pattern of predation events on Pine Island. All but one incident occurred before August 3, which is three days before the mean fledge date in the two high predation areas. Thus, the risk of predation apparently declines substantially during the time when most chicks are fledging. If adults can track the seasonal changes in eagle numbers, and if there is an advantage to maintaining the chick in the burrow for additional time, we might expect that those chicks that had not fledged by early August should be treated similarly to those in low predation areas. Because this is not found, it is possible that adults can not respond to seasonal changes in predation risk and, therefore, continue to provision according to a previously set pattern. It is also possible that the continued risk, even if

smaller, still represents a cost to the adult that outweighs any benefit provided by maintaining the chick in the burrow for a few extra days.

Because provisioning was measured in terms of burrow loads, it is possible that the adults from high predation areas made less frequent provisioning trips, but carried a heavier load on each trip. However, previous studies on rhinoceros auklets and Atlantic puffins have found that inter-annual differences in growth rates resulted from changes in feeding frequency, but not in the amount of food brought in per feeding trip (Harris and Hislop 1978, Bertram and Kaiser 1988). Similarly, the risk of kleptoparasitism by gulls did not affect the size of meals delivered by Atlantic puffins, but the feeding frequency was lower where the risk was higher (Nettleship 1972). Schaffner (1990) suggested that, although increasing the size of the food load per trip while decreasing the trip frequency would be advantageous to white-tailed tropicbirds (Phaethon lepturus) attempting to avoid attacks during arrivals at the colony, the chicks' swallowing capacity sets a constraint on the meal size. Rhinoceros auklet food loads are probably not similarly constrained because the chicks are capable of picking up fish left on the floor of the nest chamber (pers. obs.). It is also possible that parents from different habitats were bringing fish which differed in caloric content (Bertram and Kaiser 1988). Although the types of fish brought were not quantified in this study, with the exception of five individuals, all the identifiable fish recovered in the burrow searches were

Pacific sandlance (Ammodytes hexapterus) during most of July, and Pacific herring (Clupea harengus) at the end of July and beginning of August. Thus, it seems unlikely that there was a significant difference in the quality of fish delivered to different regions of the island.

The results of this study differ from those of other studies that have examined the effects of risk on provisioning rates and chick growth. Harris (1980) compared various reproductive parameters of Atlantic puffins in Scotland that were subjected to high and low rates of great black-backed gull predation. Chicks from high predation areas reached a lower peak mass later and fledged at an older age and lighter mass than did chicks from lower predation areas. Although no differences were found in mean number of feedings or mean mass of loads between the two types of habitat, Harris (1980) suggested that he had too few observations to be confident that no difference in feeding rates occurred. Thus, it seems that the puffins facing a higher risk of predation visit less frequently or bring in less food, causing their chicks to grow more slowly.

Similarly, in Newfoundland, Atlantic puffins in areas subjected to high rates of kleptoparasitism by herring gulls (Larus argentatus) fed their chicks less frequently throughout the season than did birds in areas with lower rates of robbing, and the chicks in the former group grew slower and fledged at a lower mass (Nettleship 1972). The arrival of fish-carrying puffins at the colony tends to be clumped in time; puffins seem to wait offshore

with fish in order to be able to arrive on the colony in groups and 'swamp' the gulls (Harris and Hislop 1978, Rice 1987). This swamping tactic is an effective anti-robbing technique (Rice 1987), but results in fewer feeding trips and lower nestling growth rates. The synchronization of arrivals and departures to and from the colony by rhinoceros auklets may serve as an anti-predator technique (Leschner 1976, Wilson 1977, Watanuki 1990).

A nearly identical seasonal decline in mass at ten days was found in both high and low predation areas. It is unlikely that this decline was caused by a seasonal reduction in food availability, because chick growth showed no consistent relationship with hatch date. As discussed in Chapter II, the seasonal reduction in egg size found in some alcids may be a result of the trade-off a late-laying female faces between lay date and egg size (Birkhead and Harris 1985).

Seasonal declines in peak and fledging mass have also been reported in many studies of breeding alcids (eg. Hedgren and Linnman 1979, Lloyd 1979, Birkhead and Nettleship 1982, Wilson and Manuwal 1986), although the trends are often not consistent between colonies or between years (Gaston 1985). In the present study, a seasonal decline in peak mass is evident in both types of area; the steeper negative slope in the low predation plots results from the inverse relationship of hatch date with growth in these areas. Similarly, a significant inverse relationship between mass at fledging and hatch date was found in the low predation area and a strong trend was found in the high predation plots. Although such

seasonal declines may be due to a seasonal decline in available food in some cases (Birkhead and Nettleship 1982), the lack of relationship between growth and hatch date for the Pine Island auklets suggests that other factors are important. The decline is predicted because later hatching chicks should leave the colony at an earlier age (and correspondingly lighter mass) in order to take advantage of the potentially higher growth rate at sea and reach a high mass before the onset of winter (Ydenberg 1989).

The results outlined above are consistent with those expected if the observed provisioning pattern is the outcome of parent-offspring conflict (Trivers 1974) and it is advantageous for the chick to remain in the burrow. As chicks approach fledging and are increasingly able to survive at sea, the costs to the parent of further investment (in terms of decreased parental survival) should eventually exceed the benefits (in terms of increased chick survival). At this point, adults should cease feeding even if chick fitness is not maximized.

As risk of predation may detrimentally affect reproduction in rhinoceros auklets, and varies in intensity around the colony, why do the auklets breed at all in dangerous places? Although most of the periphery of Pine Island is saturated with burrows, auklets have not colonized the interior of the island. The pattern of colony expansion on Pine Island seems to indicate that there is an advantage to nesting on the periphery: the most active area of new excavations was on the edge of the island next to a heavily depredated section of the colony. The decrease in predation risk

that might accompany a shift to the interior may be outweighed by a concomitant increase in risk of injury to birds flying into the colony at night (Vermeer and Lemon 1986).

CHAPTER IV

GENERAL CONCLUSIONS

In Chapter II, I used intra- and inter-annual comparisons of undisturbed nestlings, as well as the results of a supplementary feeding experiment, to test the predictions of a model that calculates the optimal fledging decision, from the perspective of the chick, based on relative mortality and growth rates in the burrow and at sea (Ydenberg 1989). In intra-annual comparisons in 1989 and 1990, mass at fledging was positively related to growth rate, whereas age at fledging was inversely related to growth rate. These patterns produced a significant inverse regression of mass at fledging on age at fledging in both years: rhinoceros auklet chicks that grew faster fledged at a heavier mass and younger age than did those chicks that grew more slowly. These trends are predicted by the model. The supplementary feeding study experimentally increased the growth rates of a sample of chicks. Again, chicks that grew faster fledged earlier and at a higher mass than did chicks that grew slower.

The inter-annual comparison of chick developmental parameters does not support the predictions of the model as completely. I suggest that variables that could not be controlled, such as oceanic feeding conditions or predation risk, may have been confounding factors in the inter-annual comparisons and, thus, this is the weakest test of the model.

I also showed that certain patterns of chick development were

consistent for undisturbed chicks in both years of the study. I found a seasonal decline in mass at ten days of age and in mass at fledging. The lack of a similar decline in chick growth rate over the season suggests that a deterioration of food resources did not occur. An alternative explanation for the seasonal decline in fledging mass is provided by the fledging model.

In Chapter III, I attempted to determine the effect of risk of predation to the provisioning adult on the behaviour of the parent and the chick. I found that nestlings in high and low predation risk habitats hatched at the same time, received the same amount of food until the age of 46 days and reached similar peak masses. Chicks in high predation risk areas of the colony, however, fledged at a younger age but similar mass as did chicks from low risk areas.

My results suggest that adults' provisioning behaviour is similar in all areas of the colony until the chicks are capable of fledging. Chicks in high risk areas leave their burrows soon after this point, but chicks in low risk habitats stay in their burrows for about five more days and continue to be fed at a rate that maintains their mass. As the chicks approach fledging, the costs to the parents of continued feeding trips should eventually outweigh the benefits of keeping the chick in the burrow; the point at which this happens is expected to be earlier in areas of high predation risk because the costs to the parents are higher in these areas. My results are consistent with this interpretation. The advantage for the chick to remain in the burrow may be the relative

safety of burrows when compared to that at sea or the opportunity for continued development.

I also found a significant inverse relationship between mass at fledging and age at fledging in both the high and low predation risk plots. The regression line for the high risk habitats falls below that for the low risk habitats; thus, a chick growing at a given rate will fledge earlier and at a lighter mass if it inhabits a high risk area than if it inhabits a low risk area. This pattern is predicted by a model that considers the optimal time of fledging from the perspective of the parents (Clark and Ydenberg 1990a).

The general correspondence of my results to the predictions generated by a life history approach to optimal time of fledging in rhinoceros auklets supports the validity of this approach. It suggests that relative mortality and growth rates in burrows and at sea and predation risk to provisioning parents are important variables in the determination of time of fledging.

One important factor that is still unknown is the nature of the parent-chick interactions around the time of fledging. The models considered here predict how the optimal fledging age should change with variation in other parameters from the perspective of either the chick or the adult. Due to methodological difficulties, I was unable to determine the sequence of events at fledging and it is still unclear to what extent the chick or parent control the time of fledging. A more appropriate approach may be to model the fledging decision as the outcome of an evolutionary conflict between parents and offspring using a dynamic ESS model, as was

done by Clark and Ydenberg (1990b) for doves (Alle alle).
Future research should examine this process.

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APPENDIX 1

One of the assumptions of the optimal fledging models considered in this thesis (Ydenberg 1989, Clark and Ydenberg 1990a) is that the mortality rate for chicks is greater at sea than that in the burrows. In 1989, three of 178 chicks died in the burrow, giving a daily mortality rate of 3.1×10^{-4} . The daily mortality of chicks at sea can be estimated as follows: Given a 7 % annual mortality for adults (the mean value for Atlantic puffins, from Hudson 1985), of 356 parents (2×178), 24.9 will die each year. Assuming a constant breeding population size, this means that 24.9 breeding spaces will open each year. Thus, of the 175 chicks alive at the end of the nestling period, 150.1 ($175 - 24.9$) will die prior to breeding. If the young reach maturity in their fourth year, this mortality will occur over 1406 [$(4 \times 365) + 1 - 55$] days. The corresponding daily mortality rate (m) is determined from the equation $175e^{-m(1406)} = 24.9$. Solving this equation yields $m = 1.4 \times 10^{-3}$.

Thus, given the assumptions outlined above, the daily mortality rate for chicks is approximately 4.5 times higher at sea than in the burrow. The assumptions are likely to be conservative, as the mortality rate in the sea is probably highest immediately following fledging.