FLEDGING VARIABILITY AND THE APPLICATION OF FLEDGING MODELS TO THE BEHAVIOUR OF CASSIN'S AUKLETS *(Ptychoramphus aleuticus)* AT TRIANGLE ISLAND, BRITISH COLUMBIA

by

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at Triangle Island, British Columbia

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Abstract

A seasonal decline in fledging mass is commonly reported in the Alcidae. The traditional explanation for this phenomenon is a seasonal decline in nestling growth rates, due either to declining food availability or delayed breeding of lower quality parents. An alternative explanation considers the differential growth and mortality rates faced by chicks in the nest and at sea under time-limitation. The appeal of this model is its prediction of a seasonal decline in fledging mass in the absence of a seasonal decline in growth rates. The model also predicts that fast-growing chicks should fledge heavier and younger than slow-growing chicks. My primary objective was to determine whether the fledging mass and age of Cassin's Auklets (*Ptychoramphus aleuticus*) conformed to both predictions of this fledging model. I observed the natural variation in growth and fledging behaviour and in addition manipulated the hatching date of a subset of chicks at Triangle Island, British Columbia during the 1994 breeding season. The data met the second prediction of the fledging model, but fledging mass did not decline over the season as predicted. When I used Cassin's Auklet parameter values in the fledging model, the predicted fledging mass did not decline over the season, and thus matched the observed variation in fledging behaviour. I conducted sensitivity analyses by varying the parameter values and modifying the growth and mortality functions to understand the conditions necessary to predict a seasonal decline in fledging mass. Since fledging behaviour did not vary over the season in Cassin's Auklets, I constructed a fledging model without time-limitation. This simplified model also predicted that fast-growing chicks should fledge heavier and younger than slow-growing chicks.

Acknowledgements

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Chapter I

General introduction

In the avian family Alcidae, nestlings undergo a dramatic ontogenetic niche shift from the nest to the ocean (Ydenberg 1989). For some species, nest departure is simultaneous with the first flight (fledging), but for others, fledging occurs later. For simplification, I will use the term 'fledging' to refer to nest departure, 'fledging behaviour' to refer to the nestling's mass and age at fledging, and 'fledging strategy' to refer to a set of rules, presumably transmitted genetically, that govern fledging. Fledging behaviour varies greatly between and within species and with varying ecological conditions. Interspecific fledging strategies are presumably genetically based. At the intraspecific and intracolonial level, the nestling's environment and condition also influence fledging behaviour. If individuals use a flexible fledging strategy to maximize their inclusive fitness (the phenotypic gambit), fledging behaviour can be studied in a life history framework (Lessells 1991). After a short introduction to life history theory, I will describe the patterns of fledging behaviour in Alcidae and outline the objectives of my research.

Life history theory (LHT) gives an explanation for how variation in life history traits could have evolved (Lessells 1991). The two important tradeoffs underlying LHT are between current and future reproduction and between life history traits. The former, also called the cost of reproduction, is expressed either in decreased survival or fecundity. The major assumption of LHT is that both these tradeoffs are genetically correlated. Individuals balance these tradeoffs against environmental sources of mortality to maximize inclusive fitness, and through natural selection, express optimal life histories. A phenotypic approach to modelling life history tradeoffs has advantages and disadvantages over a genetic approach (Grafen 1991; Lessells 1991; Van Noordwijk 1987; Yodzis 1989). The main advantage of the phenotypic approach is that predictions can be made about how ecological parameters affect optimal life histories. The predictions can then be compared to field or lab observations and tested by experimentation. Yodzis (1989) list some disadvantages of the phenotypic approach. If the genetics of the trait of interest are unknown, it is impossible to assume an optimal phenotype will result from natural selection. Achieving an optimal phenotype may be impossible because no genotype corresponds to this phenotype or because complicated genetics preclude the optima from being reached.

Difficulty in finding genetic correlations between life history traits and between current and future reproduction has prompted much defense of the validity of LHT (Lessells 1991; Nur 1988; Reznick 1988). Three methods (phenotypic correlations, experimental manipulations, and selection experiments) have been used to establish life history tradeoffs. Phenotypic correlations generally fail because the condition of parents, breeding experience, and the relative effects of condition on fitness of parents and offspring can cause a positive correlation between life history traits (Nur 1988). Experimental manipulations of one life history trait may also indirectly affect life history traits or the response to the manipulation may be strategic (Lessells 1991). Selection experiments can establish the genetic correlations between life history traits, but unfortunately, the results are inconclusive. Despite these methodological difficulties, some argue a cost of reproduction and tradeoffs between life history traits are well founded in logic (Lessells 1991; Nur 1988; Reznick 1985).

Life history theory can be used to examine the selective forces shaping the evolution of the diverse modes of development in Alcidae. Modes of development within the Alcidae range from precociality to semi-precociality (Sealy 1973; Ydenberg 1989). Precocial species, represented by *Synthliboramphus* murrelets, fledge at 1-4 days at 10-15% of mean adult mass. While in the burrow, the two downy nestlings are not fed. Both parents accompany the chicks during fledging and feed the them once at sea. The intermediate fledging strategy is represented by the three murre species (*Alca* and *Uria* spp.). Nestlings fledge at 15-25 days at 15-30% of mean adult mass. One parent, usually the male, accompanies the fledgling at sea. Semi-precocial fledging occurs in the rest of the alcids: the puffins (*Cerorhinca* and *Fratercula* spp.), auklets (*Aethia* and *Ptychoramphus* spp.), *Cepphus* guillemots, *Brachyramphus* murrelets, and the Dovekie (*Alle alle*). The one nestling (or sometimes two in guillemots) remains in the nest for 25-60 days and fledges at 40-100% of mean adult mass. In most of these species, nestlings fledge on their own and are independent of parents once at sea.

Interspecific variation in these development patterns has usually been explained by interspecific differences in ecological factors such as feeding ecology, predation risk, body size, and habitat preferences (Cody 1973; Gaston 1985; Sealy 1973). For example, Rhinoceros Auklet (*Cerorhinca monocerata*) are piscivorous puffins with high wing loading. They nest on islands that are usually safe for burrow-bound nestlings, but dangerous for incoming and outgoing adults. Similar to all alcids, their annual mortality is low and their life span is long. Each parent comes to the colony once per night to feed their nestling. Possible evolutionary explanations for the slow growth rate of nestlings include: 1) low feeding frequency because of nocturnal behaviour at the colony or distance to food (Cody 1973); 2) small food loads because of high wing loading (Gaston 1985); 3) necessity of precocial development of thermoregulation to allow nestlings to remain alone in the burrow during the day (Gaston 1985; Ricklefs 1983); or any combination of these. Variation in fledging behaviour could arise from natural selection or could be constrained by the growth rate of the chick. A modelling approach can clarify these verbal arguments and allow for interesting predictions to be made about the effects of specific ecological factors on the optimal life history trait.

Intraspecific variation in life history traits could also arise from phenotypic adjustment. Nestlings could adjust their fledging behaviour in response to their own condition or to environmentally imposed conditions. In this case, genetic correlations between life history traits may not exist between life history traits. Intraspecific correlations between life history traits can not be evidence for life history tactics; however, they can be used as evidence of evolutionary tactics in which physiological and developmental traits interact with life history traits (Stearns 1980). Ydenberg (1989) developed a dynamic fledging model describe and make predictions about intraspecific fledging behaviour in Common Murres (*Uria aalge*). The nestling's fledging decision considered the relative growth benefits and mortality costs in the nest and ocean under time-limitation. The model predicts two phenomena commonly reported in the literature. Within intermediate and semi-precocial species, fledging mass often declines with fledging date (e.g., in some colonies and years, Birkhead and Nettleship 1982; Harris 1982; Vermeer 1987). This pattern has usually been attributed directly to a seasonal decline in growth rates due to delayed breeding of poorer quality parents and/or seasonal deterioration of food availability (Hatchwell 1991a; Lack 1966). The implicit assumption of this explanation is a positive correlation between growth rate and fledging mass, which is a second widely reported phenomenon (e.g., Harris 1978; Hatchwell 1991b). Ydenberg's (1989) model predicts that fast-growers should fledge heavier and younger than slow-growers, and in the absence of a seasonal decline in growth rates, a negative correlation between fledging mass and fledging date. Ydenberg's (1989) model can also deal with naturally selected life history traits. When the model's parameters are varied, this can represent differences in selective pressures between isolated populations or distinct species. The same prediction holds: nestlings in a fast-growing population or species should fledge heavier and younger than nestlings in a slow-growing population or species.

I studied the intraspecific variation in growth and fledging behaviour in Cassin's Auklets (*Ptychoramphus aleuticus*), on Triangle Island, British Columbia. The abundance of burrows and the accessibility of nestlings made this colony an ideal study site. My primary objective was to determine whether fledging behaviour of Cassin's Auklets conformed to both predictions of Ydenberg's (1989) fledging model. I measured a large number of nestlings and quantified the relationships between growth and fledging behaviour (Chapter 2). Egg size, the effect of egg size on growth, tick abundance, and the effect of tick abundance on growth are also discussed here. I conducted an experiment to test whether late hatched nestlings fledged lighter and younger than early hatched nestlings, as predicted by the fledging model. However, this experiment was more suitable for elucidating why growth rates declined over the season (Chapter 3). I conducted sensitivity analyses on the fledging model by varying the parameter values and modifying the growth and mortality functions to understand the conditions necessary to predict a seasonal decline in fledging mass (Chapter 4). Since fledging behaviour did not vary over the season in Cassin's Auklets, I also constructed a fledging model without time-limitation.

Chapter II

Intraspecific variability in nestling growth and fledging behaviour

Introduction

Most information on Cassin's Auklets (*Ptychoramphus aleuticus*) comes from long-term studies on the Farallon Islands, California (Ainley et al. 1990). In British Columbia, intensive studies of the growth and feeding ecology of Cassin's Auklets have been conducted on Triangle Island (Vermeer 1984, 1985, 1987) and on some Queen Charlotte Island colonies (Vermeer and Lemon 1986). Manuwal and Thoresen (1993) and Campbell (1991) have recently reviewed the geographical distribution, feeding behaviour, breeding biology, phenology, and other aspects of Cassin's Auklet natural history.

Cassin's Auklets have a monogamous mating system and are not noticeably sexually dimorphic. Pairs share incubation and chick-rearing duties, but evidence suggests that females spend more energy provisioning nestlings and males spend more time defending territories and attracting mates (Ainley et al. 1990). Breeding usually begins at 3 years (Speich and Manuwal 1974) and adults live for 10-20 years (Ainley et al. 1990).

During the breeding season, adults feed at sea diurnally and visit the colony nocturnally. At the colony, adults arrive after dusk and leave en masse before dawn. Strict nocturnal behaviour and synchronous arrivals and departures may function to reduce predation risk from gulls (Western Gulls, *Larus occidentalis* on the Farallones and Glaucous-winged Gulls, *L. glaucescens* on Triangle Island), Bald Eagles (*Haliaeetus leucocephalus*), or Peregrine Falcons (*Falco peregrinus*). Parents feed offshore on zooplankton (Cody 1973; Speich and Manuwal 1974) and transport food back to their nestlings in a specialized throat pouch. Food loads are regurgitated directly to the nestling (Speich and Manuwal 1974).

Cassin's Auklets most likely feed in the productive upwelling waters over the continental slope. Offshore from the Farallones, dense concentrations have been observed at the continental slope, which is part of the 'upwelling domain' in the eastern North Pacific (Ainley et al. 1990; Favorite et al. 1976). In British Columbia, in order of importance, nestlings are fed calanoid copepods (mostly *Neocalanus cristatus*), euphausiids (*Thysanoessa spinifera*, *T. longipes*, and *Euphausia pacifica*), and larval and juvenile fishes (*Ammodytes hexapterus*, *Hemilepidotus* sp., *Sebastes* sp., and *Hexagrammos* sp.), although the composition of food loads varies within and between seasons (Vermeer 1981, 1984, 1985).

The onset and range of egg-laying depend on latitude and regional food availability. At lower latitudes, such as the Farallones, the breeding season is long enough for auklets to lay replacement and second clutches, although these clutches have lower reproductive success (Ainley et al. 1990). In British Columbia, replacement and second clutches have not been documented. In British Columbia, egg-laying begins by late March or early April and fledging is over by August (Manuwal 1979). Vermeer (1981) suggested this schedule would allow chick-rearing to coincide with the zooplankton bloom in the eastern North Pacific. On a smaller scale, timing of breeding is also influenced by breeding experience. On the Farallones, breeding experience and mate retention positively influence reproductive performance, as estimated by fledging mass, and experienced birds tend to breed earlier (Emslie et al. 1992).

One egg is laid and incubated for ~38 days (Astheimer 1991). Parents switch incubation duties at night every 24 hours and brood newly hatched nestlings for 5-6 days (Manuwal 1974; Speich and Manuwal 1974). After this interval, nestlings remain alone in burrow in the day and are fed twice per night, once by each parent. Depending on nestling age, year, and colony, total food delivered to a nestling per night varies from 38-50 g wet mass (Speich and Manuwal 1974; Vermeer 1981, 1984, 1985). Nestling growth approximates a logistic growth function, except prior to fledging when nestlings typically lose mass (Sealy 1973; Vermeer and Cullen 1979).

Nestlings fledge with completed juvenal plumage at 39-57 days and 65-100% of mean adult body mass (Ainley et al. 1990; Manuwal 1974; Vermeer 1981, 1987). It is not known whether nestlings fledge at a particular percentage of their final adult mass. The variation in fledging mass and age exists between colonies, years, and individuals. At each scale, the variation probably has both a genetic and environmental component. Intercolony variation is likely influenced by ecological factors such as prey composition and availability, weather conditions, predation risk, and habitat quality. Interannual variation is likely influenced by prey composition and availability and weather conditions. In general, predation risk and habitat quality are likely consistent between years at the same colony. However, at colonies with significant predation, the population size of predators could cause interannual variation in predation risk. These ecological factors cannot explain all of the variation at the intraspecific level. The age and experience of parents, or parental quality, also influence fledging behaviour at this level. In experimental studies on alcids, fledging behaviour depended on the growth rate of the nestling (Harfenist 1991; Harris 1978). Specifically, faster growers fledged heavier and younger. Seasonal variation in fledging behaviour could be caused by seasonal variation in growth rates or could occur independently of seasonal variation in growth rates. In this chapter, I will document the natural variation observed in the timing of breeding, egg size, growth rates, and fledging behaviour of Cassin's Auklets, on Triangle Island, British Columbia. I will focus on the relationship between growth and fledging behaviour.

Methods

Study site

Studies were conducted on Triangle Island, one of the Scott Islands, located 45 km northwest of Cape Scott, Vancouver Island, British Columbia (50° 52' N 129° 05' W, area = 44 ha, elevation = 194 m) (Fig. 2.1). Middens in South and Northeast Bay suggest that Triangle Island was once important for First Nations people. Although the middens are composed primarily of mussel shells, seabirds and their eggs were probably eaten as well. Early this century, year-long residents staffed a light station; since then, there has been little human disturbance except for the occasional natural history expedition or seabird study. In March 1994, a long-term study of seabirds on Triangle was intitiated by the Canadian Wildlife Service/Simon Fraser University/NSERC Wildlife Chair, primarily to monitor the productivity and population dynamics of the nesting seabirds. A cabin was erected to house six people over the entire breeding season to conduct these studies.

Carl et al. (1951) give an inventory of all the plants and animals on Triangle Island. The predominant vegetative cover is salmonberry (*Rubus spectabalis*) and two grass species (*Calamagrostis nutkaensis* on the top of the island and *Deschampsia caespitosa* on the slopes). Rodway et al. (1990) describe the seabird abundance and distribution. Large numbers of Cassin's Auklets, Rhinoceros Auklets (*Cerorhinca monocerata*), Tufted Puffins (*Fratercula cirrhata*) (547 000, 25 000, and 26 000 breeding pairs, respectively) and a small number of storm-petrels (*Oceanodroma furcata, O. leucorhoa*) burrow extensively in grassy areas. Other nesting seabirds include Common Murres (*Uria aalge*) (4077 breeding pairs) and Pigeon Guillemots (*Cepphus columba*) (331 individuals). Cassin's Auklets prefer burrowing on grassy slopes, away from densely burrowing Rhinoceros Auklets and Tufted Puffins (Rodway et al. 1990; Vermeer et al. 1979). Glaucous-winged Gulls prey on Cassin's Auklet nestlings, and circumstantial evidence

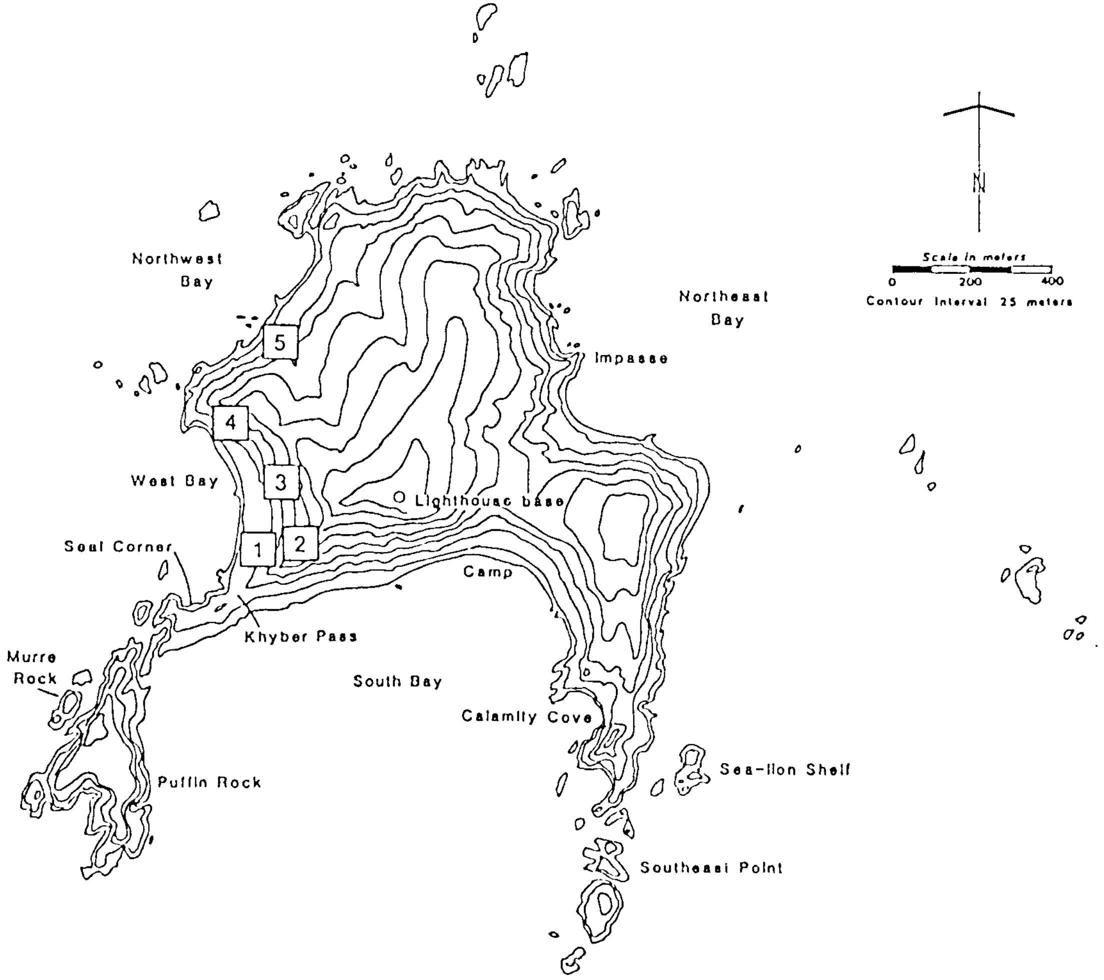

Figure 2.1. Map of Triangle Island showing site locations. 1 = Fringe Beach, 2 = West Beach, 3 = Lily Slope, 4 = Far West, 5 = Fern Grove. Based on Figure SC010-1 in Rodway et al. (1990).

suggests that Bald Eagles and Peregrine Falcons are important predators on adults (Rodway et al. 1990; pers. obs.)

Thomson (1981) discusses the oceanography of British Columbia waters. At the northern end of Vancouver Island, the continental shelf is 20 km wide, and Triangle Island lies at the eastern edge of the continental slope. Major oceanographic influences west of Vancouver Island include fresh water runoff, tidal activity, and especially, coastal winds. The greatest tidal activity occurs near Brooks Peninsula and offshore islands. This intense tidal activity may be linked to the abundance of sea life in the Scott Islands (Thomson 1981). Together, these factors influence the degree of upwelling that occurs at the continental slope, and therefore, the food availability for Cassin's Auklets.

Sampling protocol

To observe natural variation in growth and fledging behaviour, I excavated 250 burrows during incubation. I excavated an additional 85 burrows for an experiment to test the effect of parental quality on growth rates of nestlings (Chapter 3). Burrows along established trails in five sites were selected for excavation on the basis of signs of occupancy, such as worn entrances or faecal matter. Fringe Beach (in West Bay) and Fern Grove (in Northwest Bay) were located on level ground; West Slope, Lily Slope, and Far West (in West Bay) were located on the lower steep slopes. These sites within the colony were selected because they support high densities of Cassin's Auklet burrows, they are distinct from the Rhinoceros Auklet and Tufted Puffin colony, and they are easily accessible from the shore (Rodway et al. 1990). In each West Bay site, 40-60 burrows were excavated. Only 20 burrows were excavated in Fern Grove. Excavation required digging vertical holes to allow access to all areas of the burrow. Access holes were patched with square cut shingles and covered with soil and vegetation to reduce erosion.

When an egg was found, egg length and egg width were measured to nearest 0.1 mm with Vernier calipers. Starting on 10 May, I checked the burrow every three days until the egg hatched. I estimated hatchling age by categorizing hatchlings with different wing chord lengths into even-sized hatching date classes. For wing chord lengths of 16.0 - 17.8 mm, hatchlings were considered 0 days old; 17.9 - 18.9 mm, 1 day old; 19.0 - 19.9 mm, 2 days old; and 20.0 - 22.2 mm, 3 days old. Six wet, downy nestlings considered newly hatched upon discovery had a mean wing chord length of 17.6 ± .6 mm (6). Although some variation in size at first measurement is due to hatching size, in general, more variation is due to age.

Half the nestlings were measured frequently (at hatching, 5 days, then every fifth day until fully feathered, and then every second day until they fledged) and half the nestlings were measured less often (at hatching, 5 days, 25 days, then every fifth day until fully feathered, and then every second day until they fledged). The former 'treatment' will be referred to as natural variation growth (NV-G) group; the latter, as the natural variation control (NV-C) group. Differences in growth rate or fledging behaviour between these two groups would indicate that handling nestlings had an adverse effect. Of the 250 burrows, 70 lost an egg or nestling due to predation or abandonment, 11 couldn't be followed to fledging due to erosion of the burrow or because it was too late in the season ('stopped'), and a further 12 received slightly different treatments ('other') (Table 2.1).

At each burrow visit, nestling mass was measured to the nearest 0.5 g (up to 50 g) or 1 g (> 50 g) using a spring scale (Pesola or Avinet). Flattened wing chord length was measured to the nearest 0.1 mm (< 25 mm) or 1 mm (> 25 mm) using Vernier calipers. The number of ticks on the plantar surface of the right and left web were recorded. All nestlings were banded with a USFWS stainless steel band (3a) at 25 days of age.

Statistical analysis

All burrows initially excavated for the experiment are exluded from the analyses of natural variation because of the potential confounding effects. For the analyses of

Table 2.1. The treatment and fate of non-experimental burrows found with eggs.

Treatment	# burrows
NV-G: followed to fledging	76
NV-C: followed to fledging	81
Egg predated or abandoned	48
Nestling died	22
Late or eroded burrow not followed to fledging	11
Other: hatching date experimentally delayed by 3 days	2
Other: temperature probe installation to monitor incubation	10
Total	250

breeding success, the 'stopped' and 'other' groups are excluded. The 'stopped' and 'other' groups are included in the analysis of egg size variation. For the growth and fledging behaviour analyses, only nestlings from the NV groups that fledged successfully were included. This excluded five nestlings with a condition termed 'shut-eye.' These nestlings experienced weight loss and a general weakening accompanied by permanently shut eyes. Samples of stricken nestlings were sent to a wildlife veterinarian, but the cause of the symptoms could not be ascertained.[1]

In the analyses, egg volume index (length * width^2) represents egg size (Cairns 1987). The variables 'fledging age,' 'fledging mass,' and 'fledging wing' are the last recorded age, mass, and wing chord length prior to fledging. 'Peak age' is the age at which nestlings were at their 'peak mass,' 'mass recession' is peak mass minus fledging mass, and 'recession duration' is fledging age minus peak age. Growth rate was estimated for the linear phase of growth, between the ages of 5 and 25. Although I attempted to measure all nestlings at the same age, this was not always possible due to weather, and due to my method of estimating the age of nestlings when first measured. For example, a nestling on day 5 might be 4 - 7 days old. Likewise a nestling on day 25 might be 24 - 27 days old.

Two methods were used to estimate growth rate over the region of maximum growth between ages 5 and 25. Method 1 used the following calculation: (mass at day 25)-(mass at day 5)/(age at day 25)-(age at day 5). Growth to day 25 was significantly greater than growth to day 30 (paired t-test; $t_{130} = 10.435$, $p = .0001$). Method 2 was the slope of the regression equation relating mass and age between ages 5 and 25, and therefore could only be estimated for NV-G. The correlation between the two growth

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[1] Seven 'shut-eye' chicks were sent to Trent Bollinger, Canadian Cooperative Wildlife Health Centre, Dept. of Veterinary Pathology, Western College of Veterinary Medicine, Univ. of Saskatchewan, Saskatoon, Saskatchewan. These chicks were found on the colony, out of burrows, during the day.

rate estimates was high ($r = .791$, $p = .0001$, $n = 70$), but Method 2 gave higher estimates (paired t-test, $t_{70} = -3.321$ $p = .0014$). Because of this bias, only growth rates estimated by the Method 1 were used. This variable will be called 'growth rate.' Similarily, wing length growth rate ('wing growth rate') was calculated as: (wing length at day 25)-(wing length at day 5)/(age at day 25)-(age at day 5).

Egg size, hatching date, growth rate, and the fledging behaviour variables are all continuous rather than discrete, thus regression models or analysis of variance (ANOVA) models are appropriate. Since autocorrelations (correlations between independent variables) can cause spurious results in regression anlayses, I tried to exclude redundant variables. In most analyses, only 'growth rate' was used as a measure of growth since it was significantly correlated to mass at day 25 and to wing growth rate ($r = .936$, $p = .0001$, $n = 140$ and $r = .621$, $p = .0001$, $n = 141$, respectively). In specific cases, I was interested in the relationship between wing growth rate and fledging wing. Fledging wing was considered a measure of structural size at fledging.

All analyses were done using SAS statistical software. Means are given as $\bar{x} \pm \sigma$ (n), α-level is .05, t-tests are two-tailed, and F-statistics are based on partial (type III) sum of squares.

Results

Timing of breeding

Hatching dates ranged over 33 days, from 6 May-7 June with a mean hatching date of 18 May; fledging dates ranged over 41 days from 13 June-23 July with a mean fledging date of 1 July (Fig. 2.2).

Breeding success

Hatching success (# of eggs hatched/# eggs laid) was .79 (179/227) and fledging success (# nestlings fledged/# nestlings hatched) was .88 (157/179), giving an overall

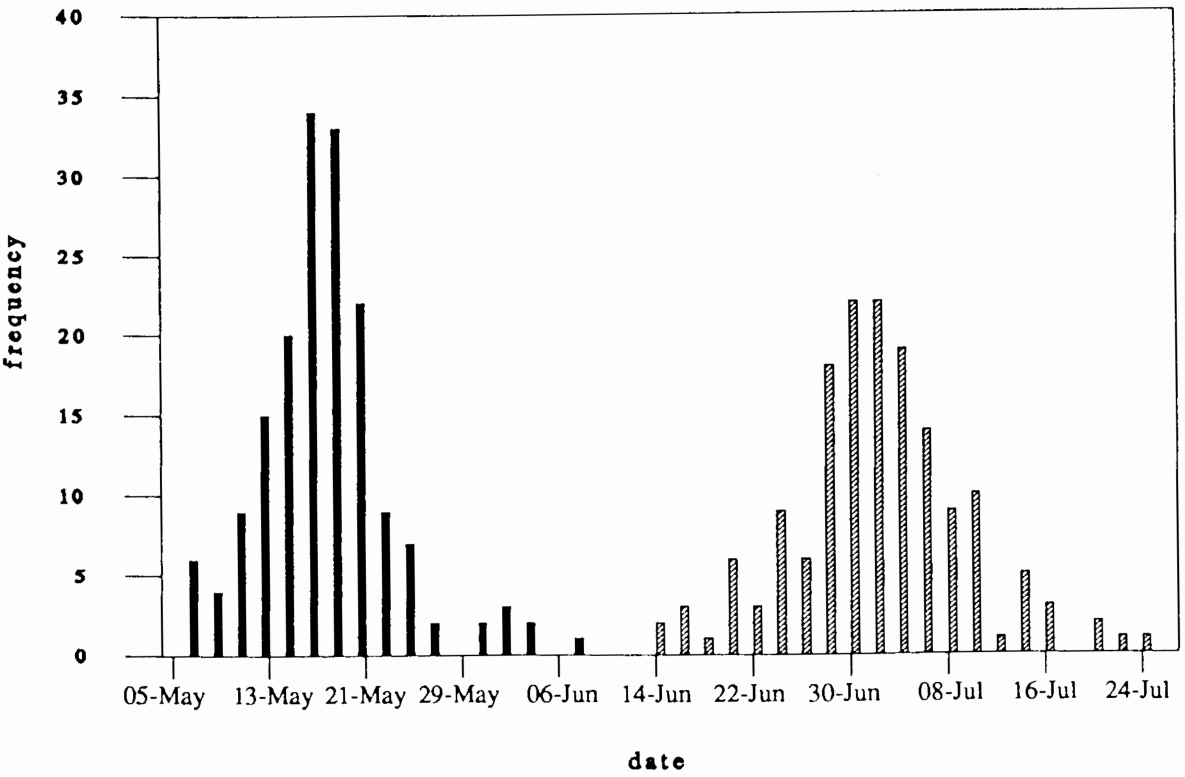

Figure 2.2. Frequency distribution of hatching dates (solid bars, n = 179) and fledging dates (hatched bars, n = 157) for NV-G and NV-C nestlings. Each bar represents a two day period.

reproductive success (# nestlings fledged/# eggs laid) of .69. Hatching success is likely an overestimate because egg searching did not begin until after birds began incubating.

Egg predators were most likely mice but voles were common in the colony as well. Abandoned eggs eventually disappeared or were predated.

Egg or nestling loss (due to predation or abandonment) occurred most frequently during the period 20 May-June 3 (Fig. 2.3). The proportion of total egg and nestling loss also peaked during this period. Sixteen of the initial 227 eggs were predated or abandoned before hatching checks began on 10 May. This loss occurred over an unknown number of days. However, if it occurred over ten days, which is probably an underestimate, daily egg mortality (.007) would still be less than in mid-May.[2] Most nestling mortality occurred in nestlings < 10 days old (Fig. 2.4).

There was not a strong seasonal trend in fledging success (Fig. 2.5). However, most of the nestlings that eventually died hatched before peak hatching.

Egg mortality was highest in Fringe Beach, but not significantly ($\chi^2_4 = 5.873$, $.10 < p < .25$) (Fig. 2.6). Nestling mortality was similar across sites ($\chi^2_4 = 4.278$, $.25 < p < .50$) (Fig. 2.6).

Egg size variation

For all burrows (excluding the experimental group), egg length was 47.4 ± 1.8 mm (221) and ranged from 41.5 - 52.4 mm; egg width was 34.1 ± 1.1 mm (221) and ranged from 31.1 to 38.3 mm. Mean egg volume index (length * width^2, Cairns 1987) was 55.2 ± 4.7 cm^3 (221). Egg volume differed between sites ($F_{4,216} = 2.70$ $p = .03$) (Fig. 2.7). Based on least square means comparison, eggs in West Slope were bigger than in Fringe Beach and Far West ($t = 2.985$, $p = .003$ and $t = 2.337$, $p = .02$, respectively). Eggs that

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[2] To calculate daily egg mortality from egg mortality over 10 days, the function $1 - M = e^{-\mu t}$ was used (Ydenberg 1989). If M is mortality over t days (16/227), μ is daily mortality, and $t = 10$ days, $\mu = .007$.

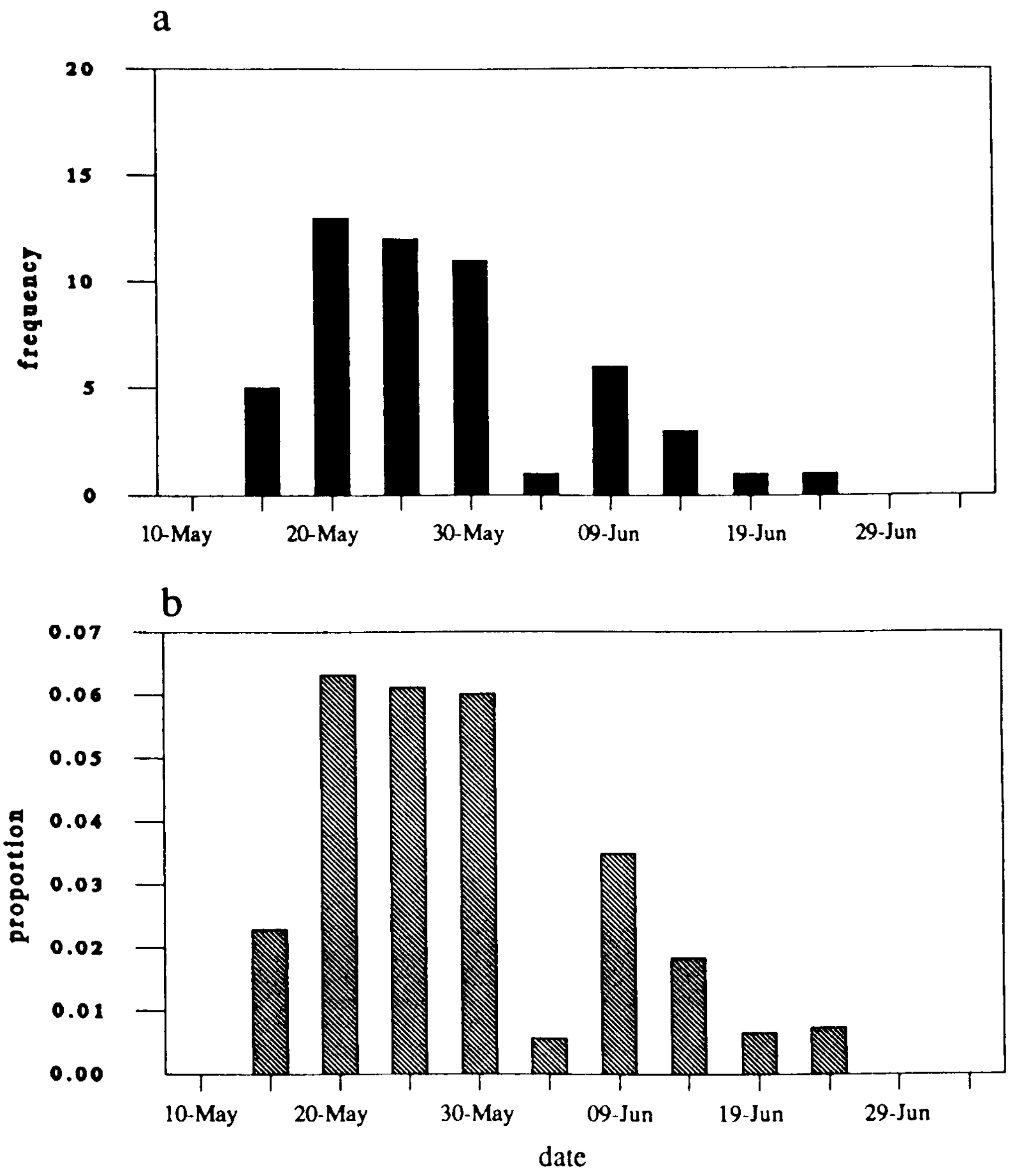

Figure 2.3. Frequency (a) and proportion (b) of mortality events over the season. Mortality includes egg loss due to predation or abandonment or nestling death. Proportion of mortality is the frequency of mortality divided by the total number of eggs and nestlings present during each five day period. Only NV-G and NV-C nestlings are included (n = 53).

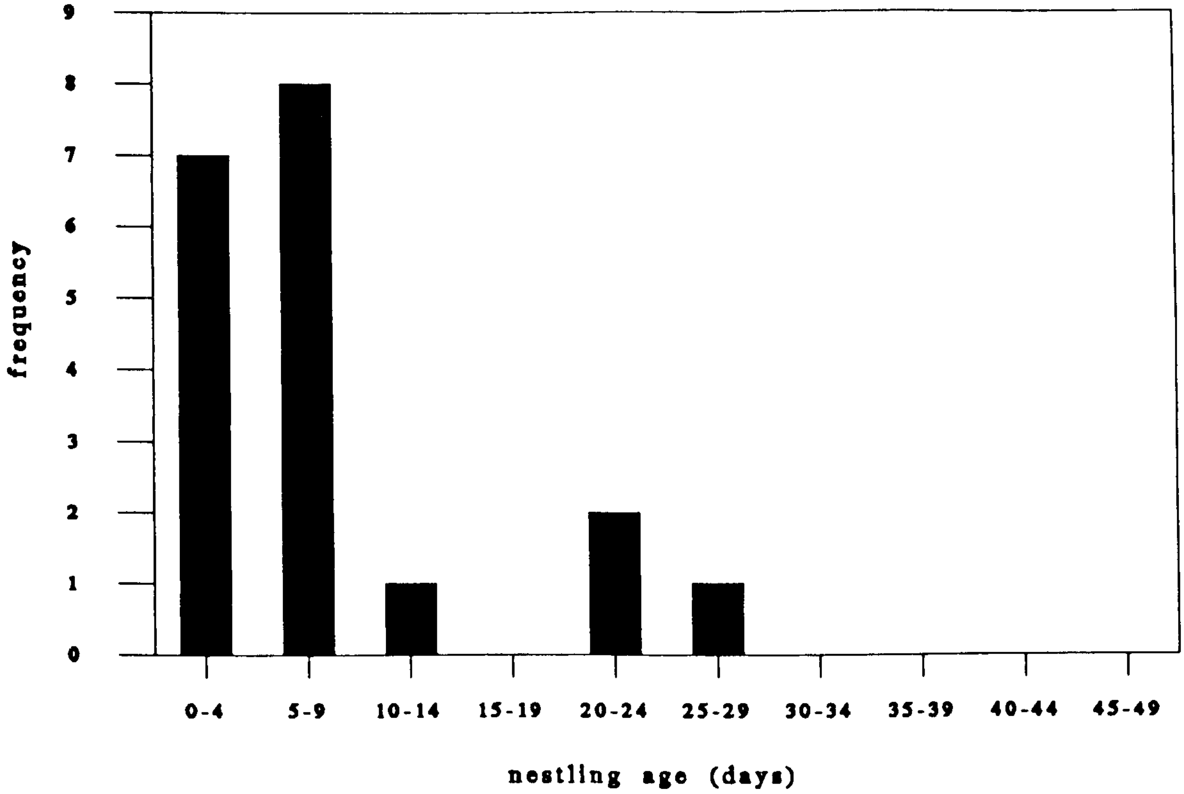

Figure 2.4. The frequency of nestling mortality with age. Each bar represents a five day period. This includes mortality in all NV burrows (n = 19). Although 22 nestlings died, the age at which nestlings died was only known for 19 nestlings.

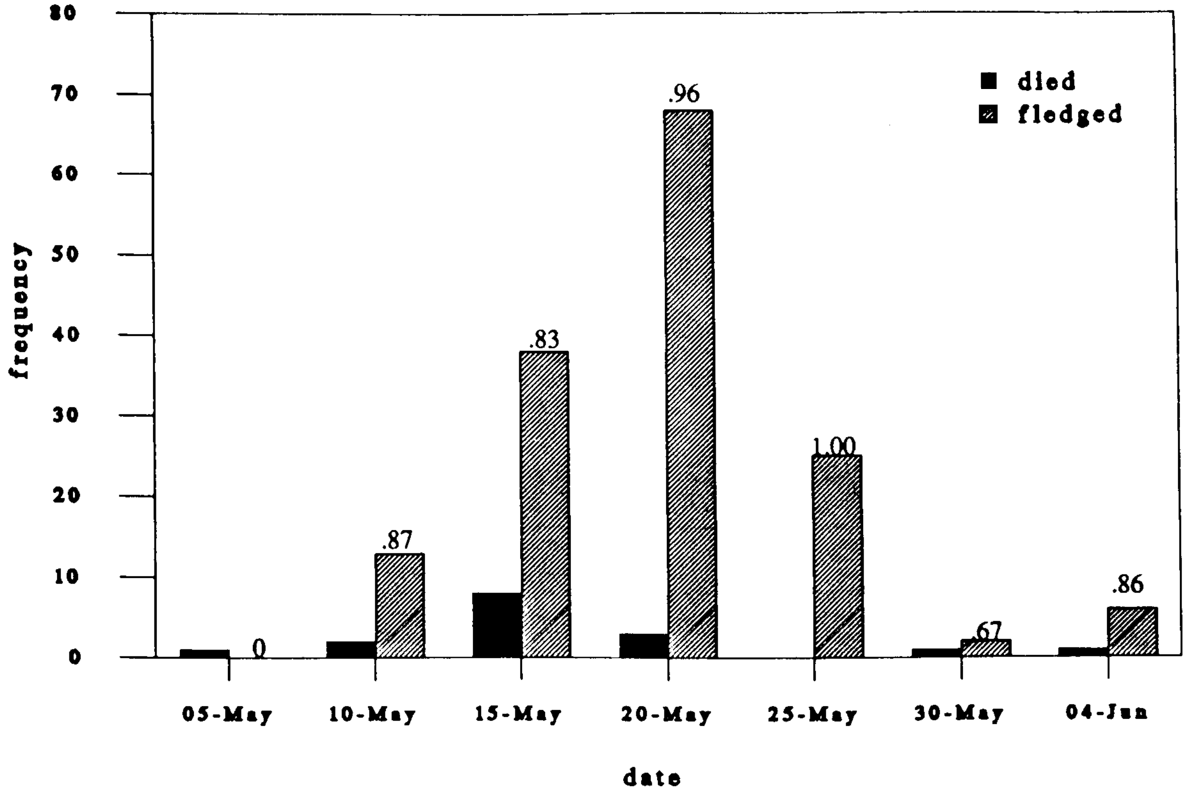

Figure 2.5. The frequency of nestlings that died (n = 16) or fledged (n = 157) with increasing hatching date. Each bar is labelled with the fledging success (# nestlings fledged/# nestlings hatched) for that five day period.

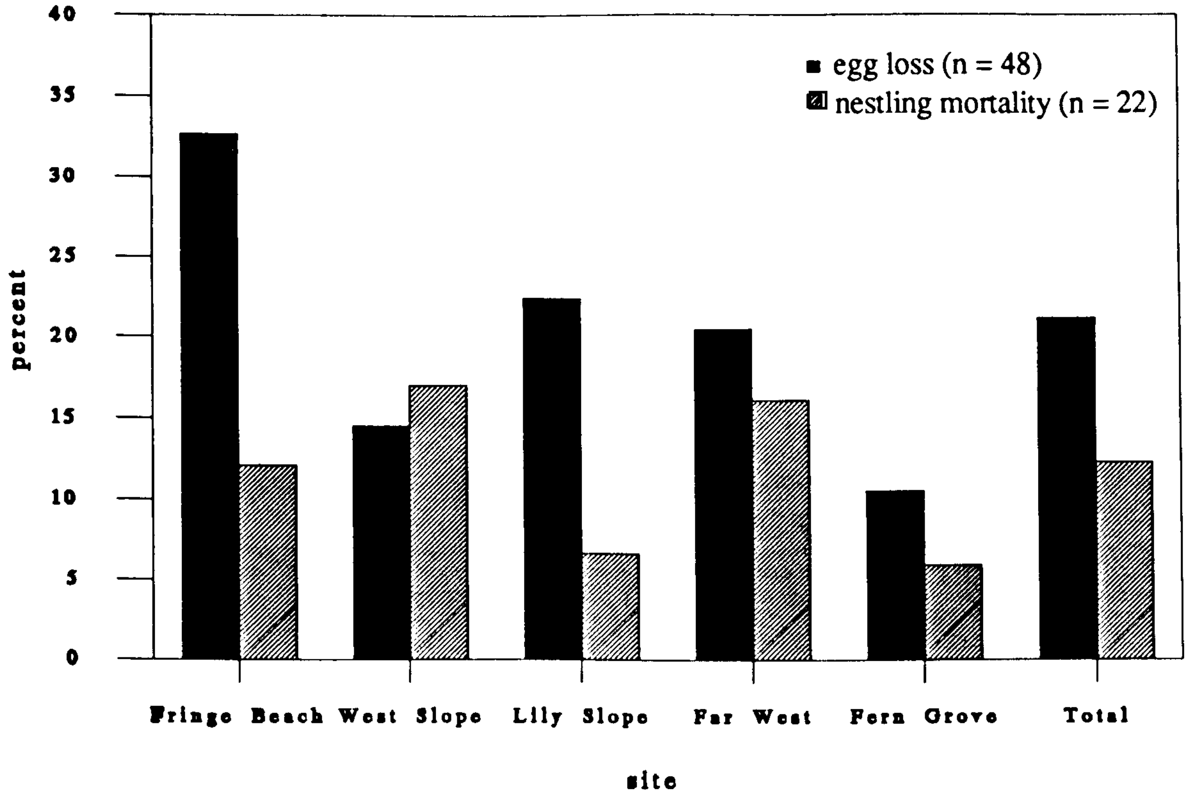

Figure 2.6. Percent egg loss (due to predation or abandonment) and nestling mortality in the five study sites and in total.

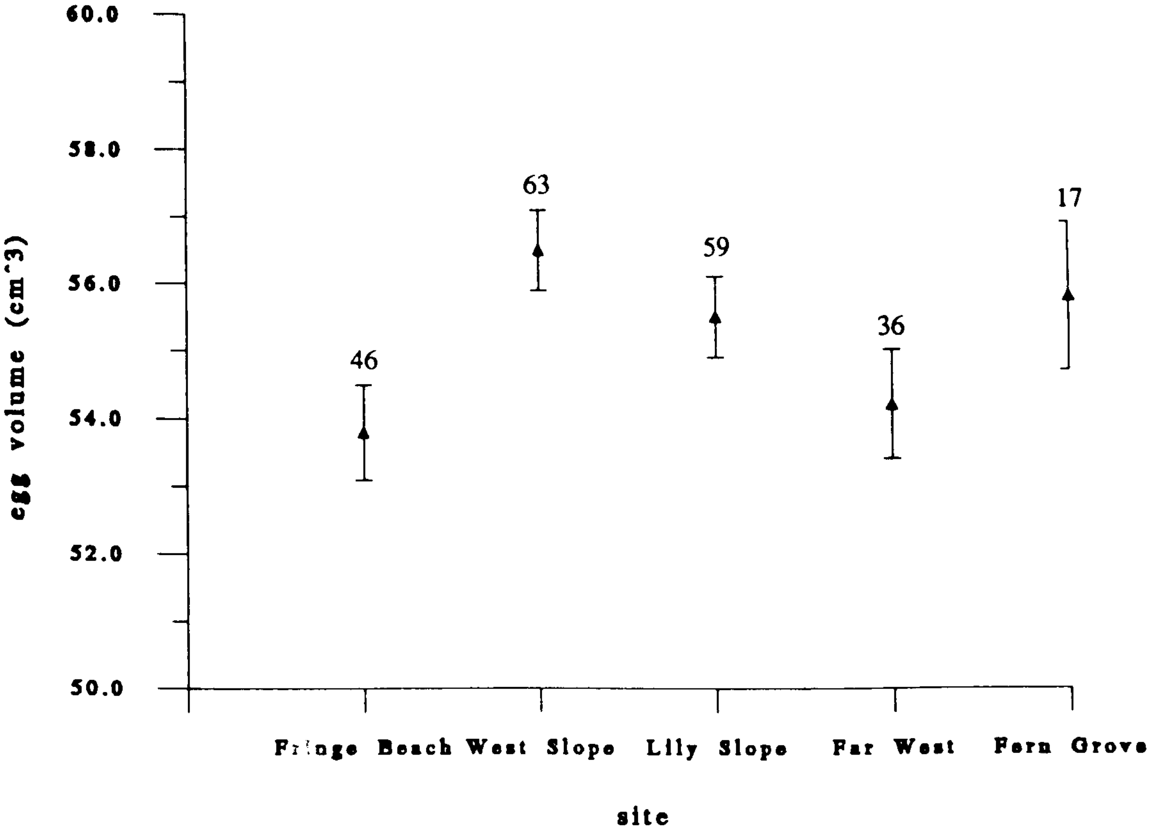

Figure 2.7. Comparison of mean egg volume (egg length * egg width^2) between sites. Errors bars represent the standard deviation and sample sizes are given above the error bars. Eggs in West Slope were significantly bigger than in Fringe Beach and Far West.

eventually were predated or abandoned did not differ in volume from the rest ($F_{1,208} = .90$, $p = .3$). Egg volume did not vary over the season ($y = 55.2 + 1.85x$, $t_{162} = .027$, $p > .5$). Egg volume affected mass and wing length at the nestling's first measurement, when nestlings were 0 - 3 days old ($y = 7.16 + .0003x$, $t_{160} = 4.429$, $p = .0001$, $r^2 = .109$ and $y = 15.06 + .00007x$, $t_{160} = 3.783$, $p = .0002$, $r^2 = .082$) but did not affect mass and wing length at 5 days ($y = 36.8 + .0008x$, $t_{148} = .797$, $p = .4$, $r^2 = .004$ and $y = 22.7 - .0000006x$, $t_{148} = -.042$, $p > .5$, $r^2 = 0$). Nestlings from greater volume eggs had significantly higher growth rates ($y = 2.77 + .00003x$, $t_{139} = 2.341$, $p = .02$, $r^2 = .037$) but not wing growth rates ($y = 2.12 + .00001x$, $t_{140} = 1.601$, $p = .1$, $r^2 = .018$). However, the slopes are so small that over a 20 cm^3 range in egg volume, growth rate would only differ by .0006 gd^{-1} and wing growth rate would differ by .0002 mmd^{-1}.

Growth and fledging behaviour

The least variable aspects of growth and fledging behaviour were fledging age, fledging mass, fledging wing, peak age, and peak mass (Table 2.2). Typically, nestlings gained mass slowly until age 5 d, underwent fast linear growth until age 25 d, and then grew slowly until reaching peak mass (Fig. 2.8). Prior to fledging most nestlings lost mass. Until peak mass was reached, the growth function approximated a logistic curve. Using proc nlin in SAS, the best fitting logistic curve used $K = 166$ g, $N(0) = 23.1$ g, and $r = .13$ in the following function: $N(t) = K/(1 + (K - N(0))/N(0))e^{-rt}$, where $N(t)$ is mass on day t, K is nestling asymptotic mass, $N(0)$ is hatching mass, and r is the growth rate constant. Following a linear increase in wing length between ages 10 d and 40 d, wing length appeared to stabilize at ~120-125 mm (Fig. 2.9).

There was an overall difference in hatching date, fledging age, fledging mass, fledging wing, peak age, peak mass, and growth rate between NV-G and NV-C, indicating a handling effect (MANOVA, Wilks' Lambda $F_{7,131} = 3.983$, $p = .0006$). This was probably attributable to differences in fledging age (ANOVA, $F_{1,145} = 4.52$, $p = .04$, $r^2 =$

Table 2.2. Mean, standard deviation, and coefficient of variation ($\sigma/\bar{x} * 100\%$) of growth and fledging variables for NV nestlings that fledged.

Variable	$\bar{x} \pm \sigma(n)$	Coefficient of variation
mass at age 5	41.7 ± 5.5 g (143)	13.2
mass at age 25	133 ± 16 g (142)	12.0
peak mass	171 ± 12 g (152)	7.0
fledging mass	162 ± 12 g (151)	7.4
wing at age 5	22.8 ± 1.7 mm (144)	7.5
wing at age 25	80 ± 9 mm (142)	11.2
fledging wing	125 ± 4 mm (151)	3.3
growth rate	4.49 ± .69 gd^{-1} (140)	15.4
wing growth rate	2.82 ± .41 mmd^{-1} (141)	14.6
peak age	42 ± 4 d (147)	8.8
fledging age	46 ± 3 d (147)	7.1
total mass recession	10 ± 8 g (151)	81.5
recession length	3 ± 2 d (147)	72.2

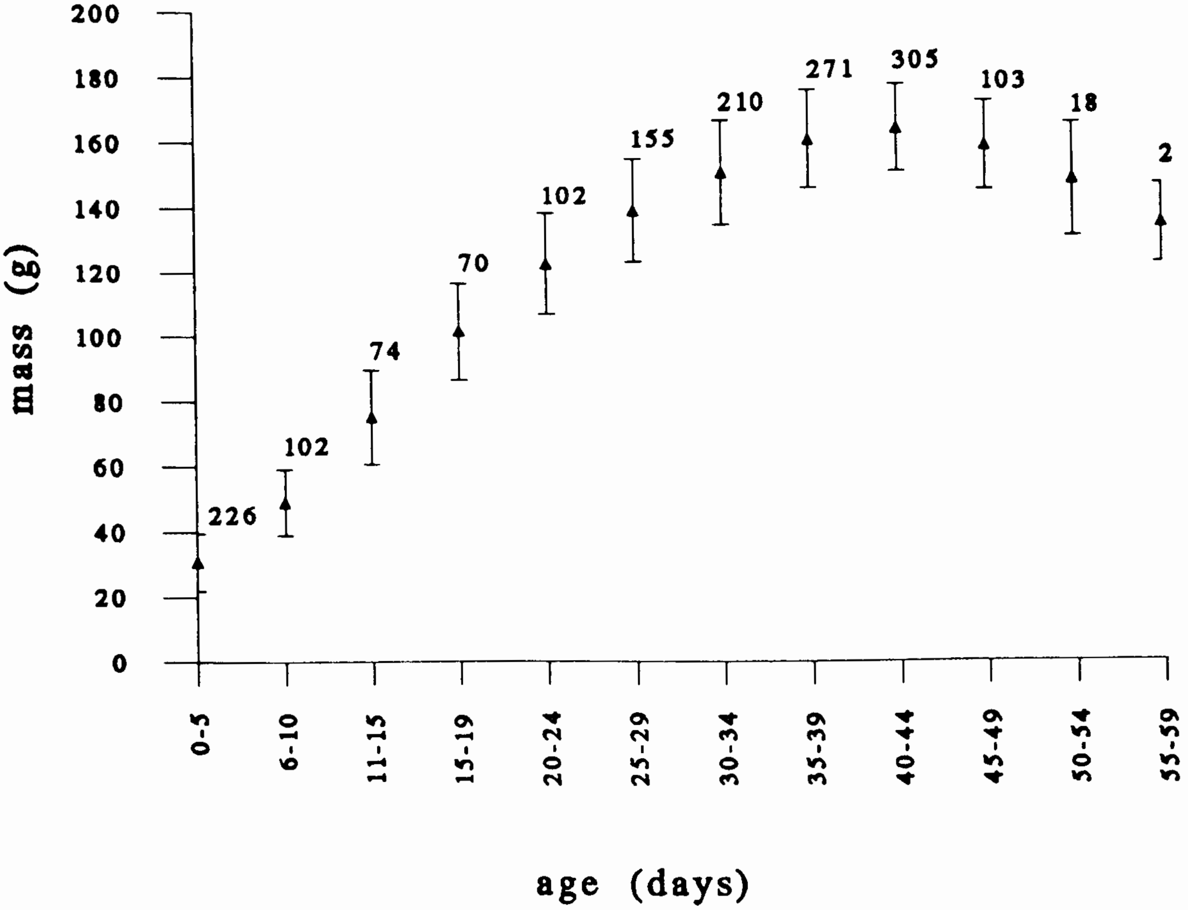

Figure 2.8. Growth curve for all NV-G and NV-C nestlings. For each five day age category, mean mass, error bars representing standard deviation, and sample size are given. For ages > 30 d, multiple measures on the same individual may be included.

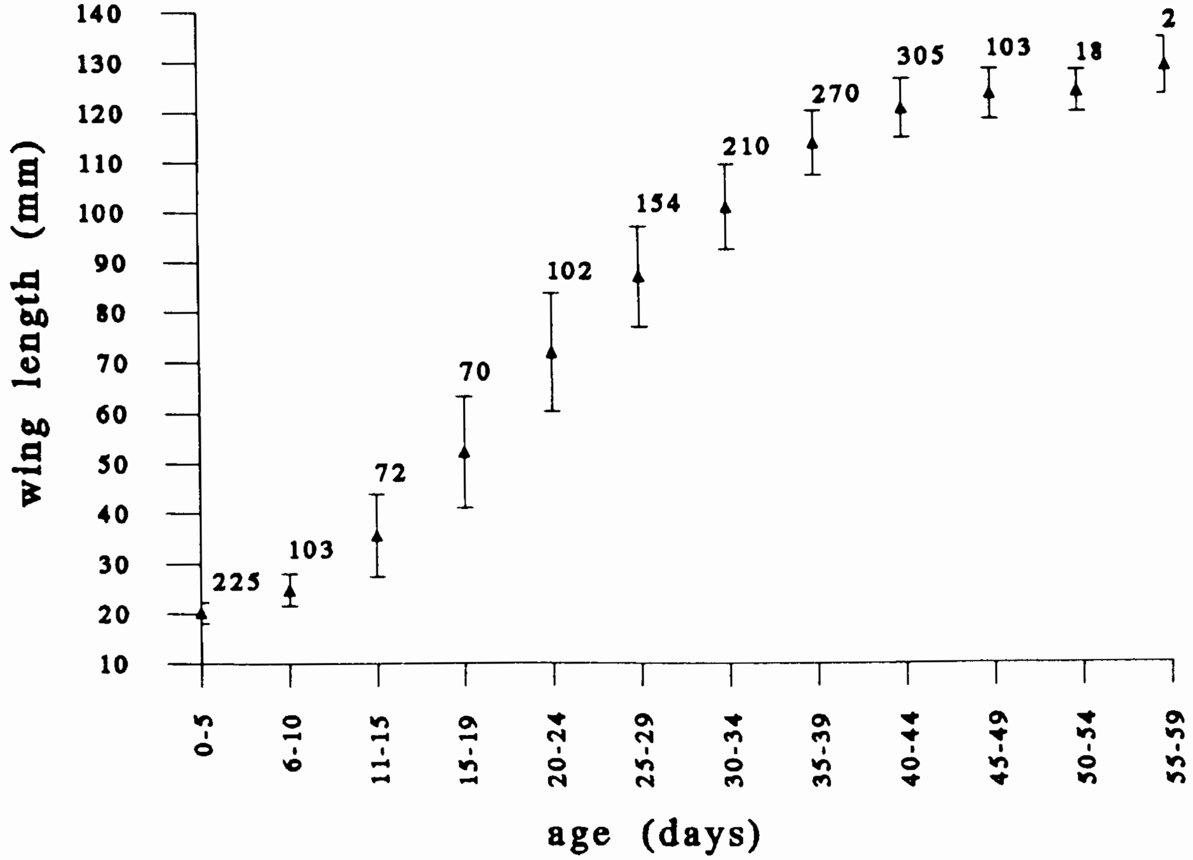

Figure 2.9. Wing growth curve for all NV-G and NV-C nestlings. For each five day age category, mean wing length, error bars representing standard deviation, and sample size are given. For ages > 30 d, multiple measures on the same individual may be included.

.030), peak age (ANOVA, $F_{1,145} = 5.02$, $p = .03$, $r^2 = .033$) and growth rate (ANOVA, $F_{1,138} = 6.83$, $p = .01$, $r^2 = .047$). Nestlings that were measured less frequently (NV-C) grew faster (4.63 ± .69 gd^{-1} (70) vs. 4.34 ± .66 gd^{-1} (70)), peaked mass at a younger age (42 ± 4 d (76) vs. 43 ± 3 d (71)), and fledged younger (45 ± 3 d (76) vs. 46 ± 3 d (71)). Therefore, NV-G and NV-C are treated separately in subsequent analyses.

There was no overall site effect on hatching date, fledging age, fledging mass, fledging wing, peak age, peak mass, and growth rate for NV-G or NV-C (MANOVA, Wilks' Lambda $F_{28,210.5} = 1.219$, $p = .2$ and $F_{28,214.1} = .823$, $p > .5$, respectively).

Relationship between growth and fledging behaviour

Growth rates were divided into two groups of approximately the same size to test the overall effect of growth rate on fledging age, fledging mass, fledging wing, peak age, and peak mass. NV-G was divided at the mean growth rate of 4.34 gd^{-1}; NV-C was divided at 4.63 gd^{-1}. For both NV-G and NV-C, growth rate had a significant effect on these parameters (MANOVA, Wilks' Lambda $F_{5,64} = 9.354$, $p = .0001$ and $F_{5,70} = 6.732$, $p = .0001$, respectively). The effect of growth rate on these parameters was also analysed with linear regression models. For both NV-G and NV-C, fledging mass increased with growth rate ($t_{67} = 4.556$, $p = .0001$ and $t_{68} = 4.123$, $p = .0001$, respectively) (Fig. 2.10), fledging age decreased with growth rate ($t_{67} = -4.877$, $p = .0001$ and $t_{68} = -5.744$, $p = .0001$, respectively) (Fig. 2.11), peak age decreased with growth rate ($t_{67} = -3.860$, $p = .0003$ and $t_{68} = -3.723$, $p = .0004$), and peak mass increased with growth rate ($t_{67} = 7.289$, $p = .0001$ and $t_{68} = 4.466$, $p = .0001$, respectively) (Fig. 2.12). The effect of growth rate on fledging wing was not significant for NV-C ($t_{68} = .589$, $p > .5$) but was for NV-G ($t_{67} = 6.156$, $p = .02$), but the two slopes were not significantly different from each other ($t_{135} = 1.167$, $p > .2$ (Zar 1984). The common slope for NV-G and NV-C was not significant ($t_{137} = 1.589$, $p = .1$) (Fig. 2.13). Wing growth rate did not differ between NV-G and NV-C

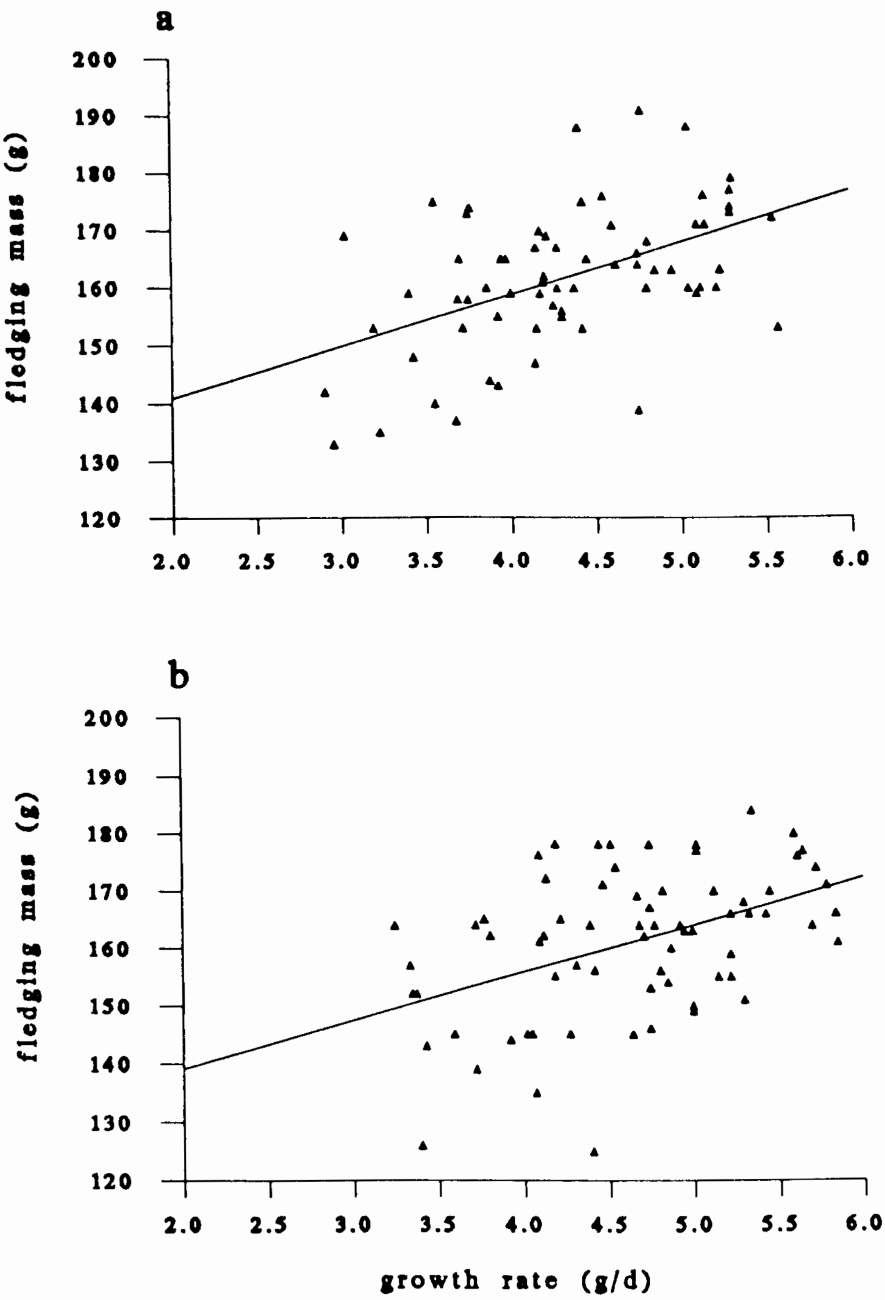

Figure 2.10. Fledging mass vs. growth rate for NV-G (a) and NV-C (b). For NV-G, the regression equation is $y = 123.7 + 8.9x$, $r^2 = .237$ ($t_{67} = 4.556$, $p = .0001$); for NV-C, $y = 122.8 + 8.2x$, $r^2 = .200$ ($t_{68} = 4.123$, $p = .0001$).

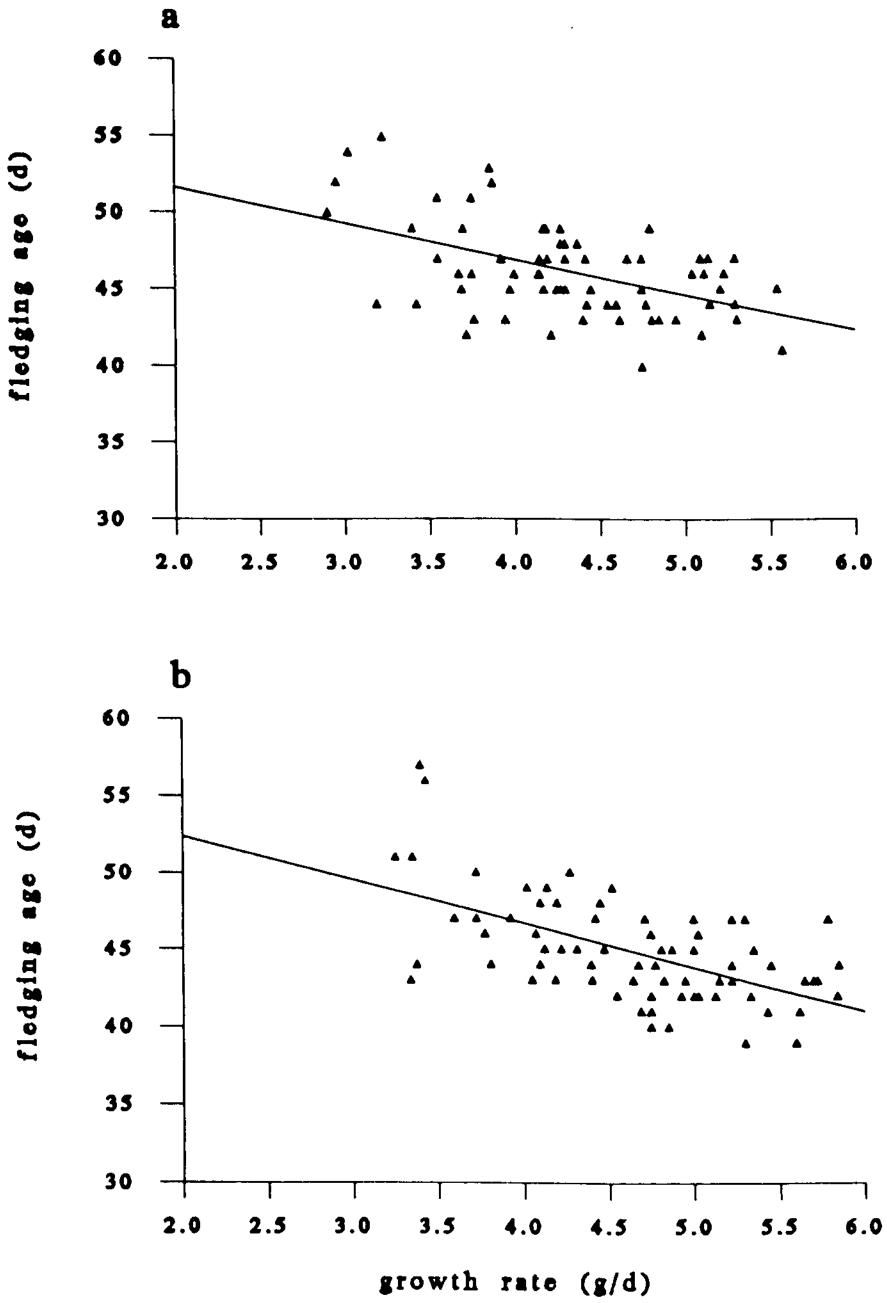

Figure 2.11. Fledging age vs. growth rate for NV-G (a) and NV-C (b). For NV-G, the regression equation is $y = 56.4 - 2.4x$, $r^2 = .262$ ($t_{67} = -4.877$, $p = .0001$); for NV-C, $y = 58.1 - 2.8x$, $r^2 = .327$ ($t_{68} = -5.744$, $p = .0001$).

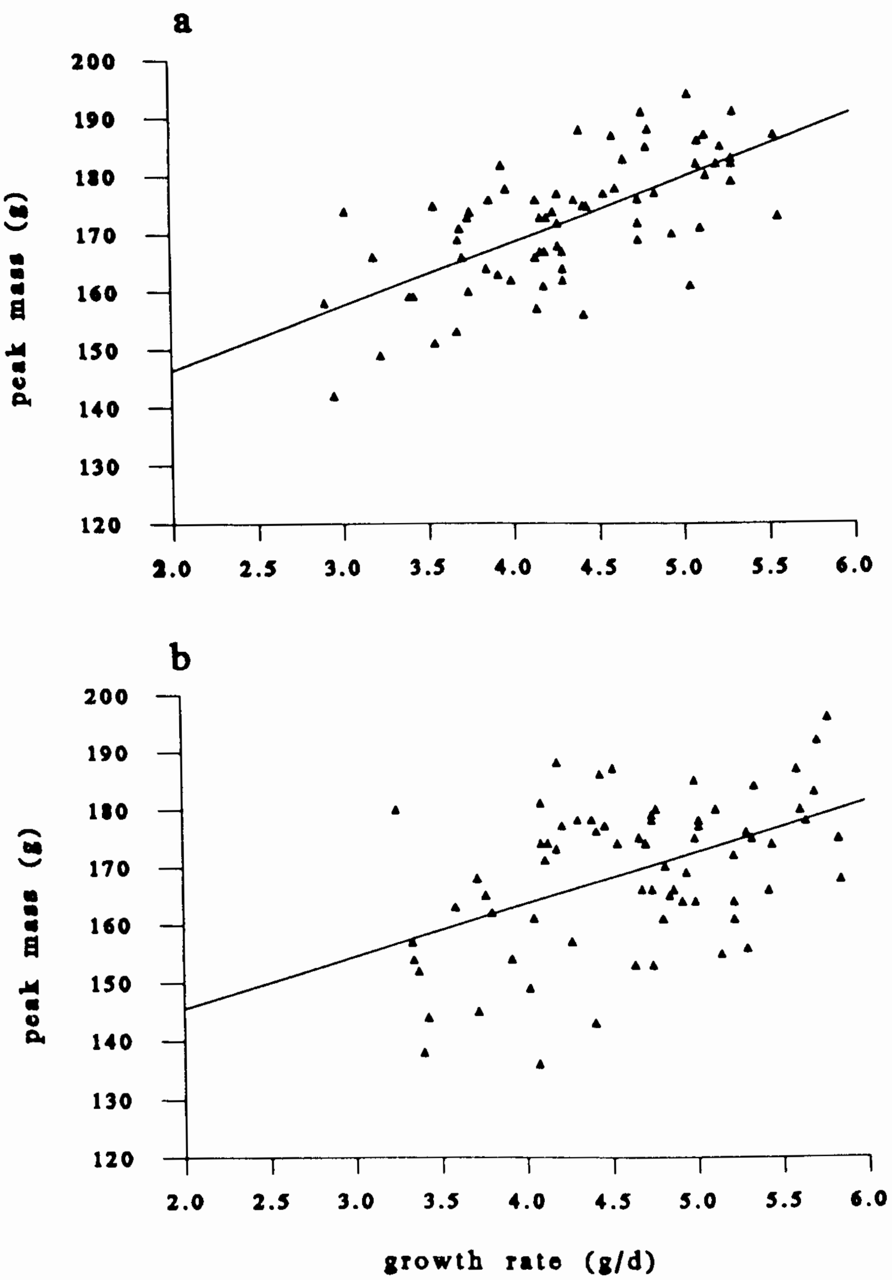

Figure 2.12. Peak mass vs. growth rate for NV-G (a) and NV-C (b). For NV-G, the regression equation is $y = 124.3 + 11.0x$, $r^2 = .442$ ($t_{67} = 7.289$, $p = .0001$); for NV-C, $y = 127.8 + 8.9x$, $r^2 = =.227$ ($t_{68} = 4.466$, $p = .0001$).

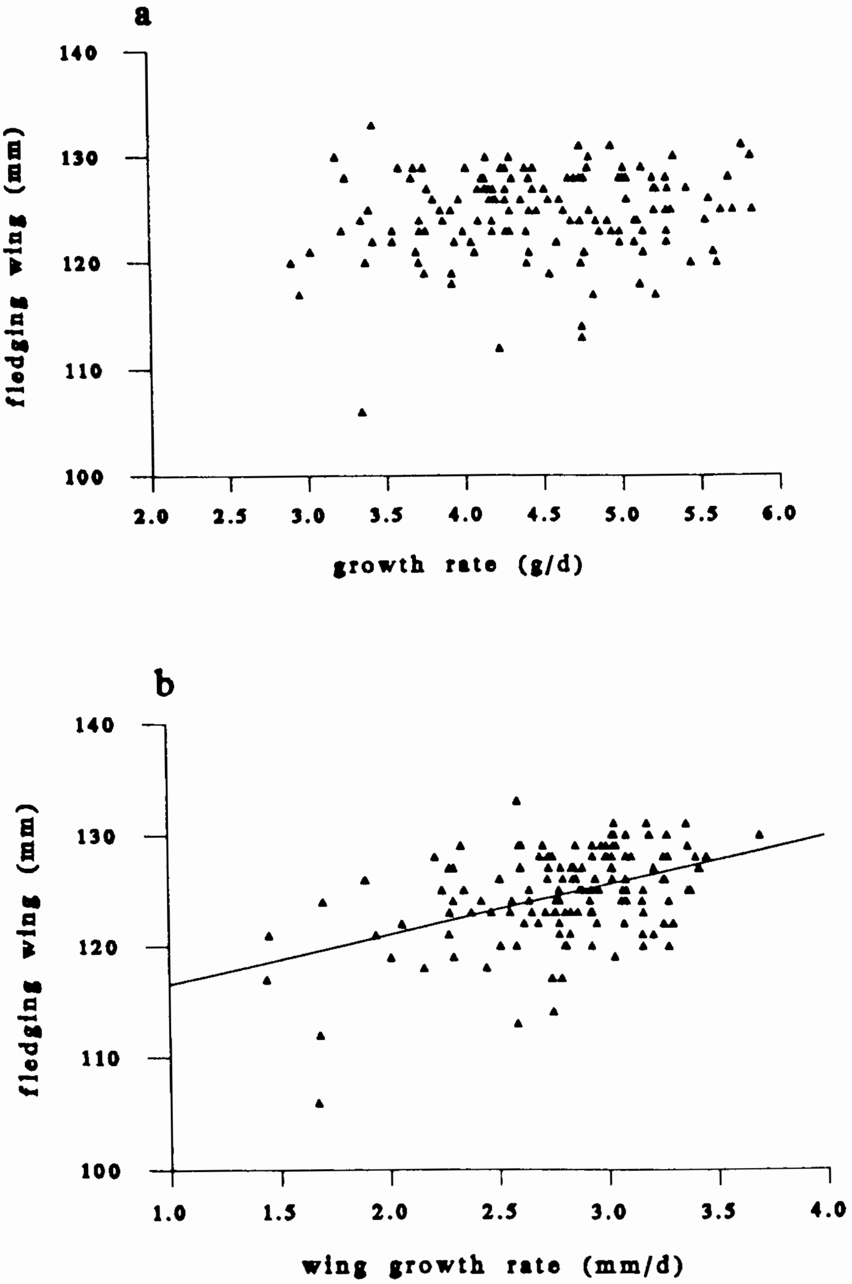

Figure 2.13. Fledging wing vs. growth rate for pooled NV-G and NV-C (a) and fledging wing vs. wing growth rate (b). The slope in (a) is not significant ($y = 121.1 + .8x$, $r^2 = .018$, $t_{137} = 1.589$, $p = .1$). The slope in (b) is ($y = 112.1 + 4.5x$, $r^2 = .199$, $t_{138} = 5.852$, $p = .0001$.

(ANOVA, $F_{1,139} = 1.52$, $p = .2$). With increasing wing growth rate, nestlings fledged with longer wings ($t_{138} = 5.852$, $p = .0001$, $r^2 = .199$) (Fig. 2.13).

Seasonal variation in growth and fledging behaviour

Since the effect of hatching date on growth rate did not differ between NV-G and NV-C, they were pooled (ANCOVA, group * hatching date interaction effect, $F_{1,136} = .58$, $p = .4$). Growth rate declined with hatching date in NV-G and NV-C (Regression, $t_{138} = -4.554$, $p = .0001$, $r^2 = .121$) (Fig. 2.14). A quadratic function fit the data better, presumably because of the increase in growth rates measured at the end of the season (Fig. 2.14, see Chapter 3 for a thorough discussion of this non-linear seasonal trend in growth rates).

The relationship between wing growth rate and hatching date also did not differ between NV-G and NV-C (ANCOVA, group * hatching date interaction effect, $F_{1,137} = .06$, $p > .5$). In NV-G and NV-C, wing growth rate declined with hatching date (Regression, $t_{139} = -7.122$, $p = .0001$) (Fig. 2.15).

Seasonal changes in other parameters were also examined, keeping in mind that the variation could be partitioned into both seasonal (or hatching date) effects and growth rate effects. To separate these effects, simple regression models with only hatching date as the independent variable were first made for each dependent variable, and then the effect of adding growth rate as a covariate was determined (Table 2.3). If the significant effects were true seasonal effects and not caused by the seasonal decline in growth rates, the addition of growth rate would reduce the significance of the hatching date effect. To simplify the problem, NV-G and NV-C were pooled. This was justified since the interaction effect between group and hatching date was nonsignificant in ANOVA models for fledging age ($F_{1,143} = .19$, $p > .5$), fledging mass ($F_{1,142} = .00$, $p > .5$), fledging wing ($F_{1,142} = .10$, $p > .5$), peak age ($F_{1,143} = .82$, $p = .4$), and peak mass ($F_{1,143} = .03$, $p > .5$).

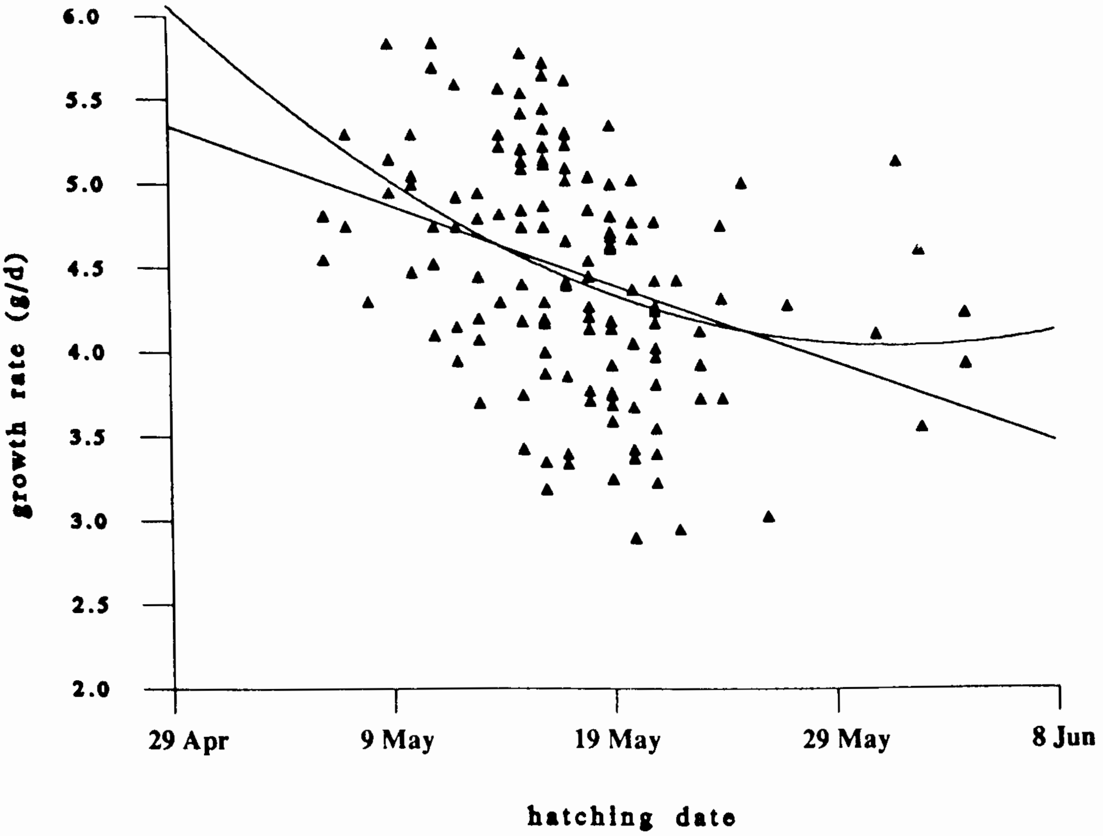

Figure 2.14. Growth rate vs. hatching date for NV-G and NV-C pooled. The linear regression equation is $y = 8.15 - .05x$, $r^2 = .131$ ($t_{138} = -4.554$, $p = .0001$). The best fit quadratic function is $y = 20.2 - .35x + .002x^2$.

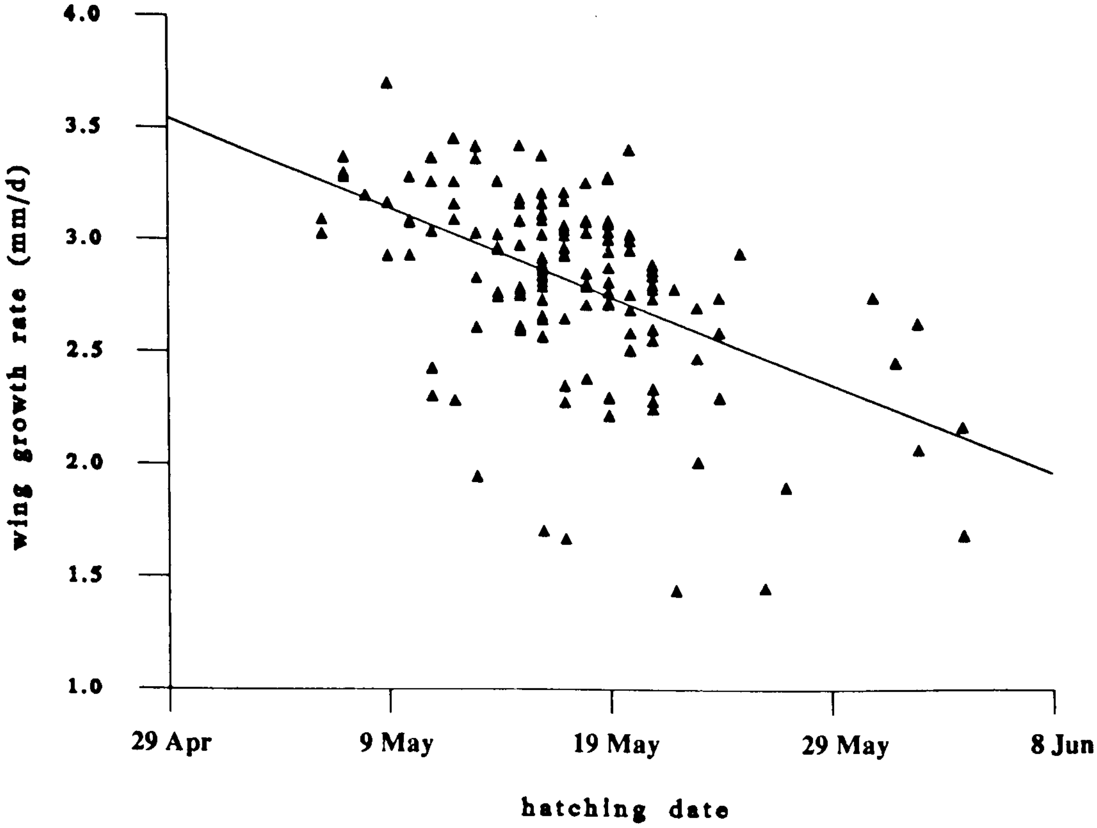

Figure 2.15. Wing growth rate vs. hatching date for NV-G and NV-C pooled. The slope of the regression equation is significant ($y = 5.92 - .04x$, $r^2 = .267$, $t_{139} = -7.122$, $p = .0001$).

Table 2.3. Statistics for two regression models to separate hatching date from growth rate effects on each independent variable (y). Model 1 is the effect of hatching date (x_1) on y and Model 2 is the effect of hatching date and growth rate (x_2) on y. The t-statistics and p-values are given for the hypothesis that the slope associated with x_1 is not significantly different from zero, based on the partial sum of sqares (Type III SS).

Independent variable (y)	Model 1: $y = x_1$	Model 2: $y = x_1 + x_2$
fledging age	$t_{145} = 2.165$, $p = .03$	$t_{137} = -.288$, $p > .5$
fledging mass	$t_{146} = -1.281$, $p = .2$	$t_{136} = 1.146$, $p = .3$
fledging wing	$t_{144} = -2.929$, $p = .004$	$t_{136} = -2.111$, $p = .04$
peak age	$t_{145} = 1.565$, $p = .1$	$t_{137} = -.181$, $p > .5$
peak mass	$t_{145} = -.632$, $p > .5$	$t_{137} = 2.360$, $p = .02$

Neither fledging mass, peak age, nor peak mass varied significantly with hatching date ($y = 180.4 - .24x$, $y = 35.3 + .09x$, and $y = 179.8 - .12x$) (Table 2.3). Given that growth rates declined significantly over the season and higher growth rates caused greater fledging mass, younger peak age, and greater peak mass, seasonal variation in these parameters was expected. When including growth rate as a covariate in the analyses of fledging mass and peak age variation, as expected, there was no hatching date effect. However, when growth rates were included as a covariate in the analysis of peak mass variation, peak mass increased with hatching date.

Fledging wing decreased and fledging age increased with hatching date (Table 2.3). The seasonal increase in fledging age was due to the seasonal decline in growth rate. The seasonal decline in fledging wing at first appears to be a true seasonal effect, since controlling for growth rate did not affect the significance of the hatching date effect. However, the effect of growth rate on fledging wing was not significant ($t_{136} = .737$, $p = .5$). When the seasonal decline in fledging wing was statistically controlled for by using wing growth rate instead, which does affect fledging wing (($t_{137} = 5.042$, $p = .0001$), the hatching date effect is eliminated ($t_{137} = .107$, $p > .5$).

Fledging mass declined with fledging date (Regression, $y = 215.7 - .44x$, $t_{144} = -2.978$, $p = .003$, $r^2 = .058$). In a regression model including fledging age as as covariate, the fledging date effect was eliminated and the fledging age effect was significant ($t_{145} = -2.823$, $p = .005$).

Mass recession

The amount and duration of mass recession were positively correlated ($r = .391$, $p = .0001$, $n = 146$).

To determine what factors affected the amount of mass recession, I initially included hatching date, peak age, peak mass, growth rate, and wing growth rate as independent variables in a multiple regression analysis. Using a backwards iterated selection procedure based on p-level > .1, peak age (x_1), peak mass (x_2), and wing growth rate (x_3) were retained in the model ($y = 10.2 - .51x_1 + .19x_2 - 4.33x_3$, $F_{3,135} = 6.92$, $p = .0002$, $r^2 = .133$). The amount of mass lost prior to fledging decreased with peak age, increased with peak mass, and decreased with wing growth rate. Mass growth rate was excluded during the selection procedure because it was highly correlated with wing growth rate. When wing growth rate was excluded from the initial model, peak age, peak mass, and growth rate were retained in the selected model, but the significance of growth rate was less than wing growth rate was in the first model ($F_{1,135} = 2.90$, $p = .09$ vs. $F_{1,137} = 23.86$, $p = .0001$).

To determine what factors affected the duration of mass recession, the same type of analysis was used but the initial independent variables were hatching date, peak age, peak mass, and growth rate. The duration of mass recession decreased with peak age (x_1) and growth rate (x_2) ($y = 26.4 - .41x_1 - 1.32x_2$, $F_{2,137} = 37.92$, $p = .0001$, $r^2 = .356$.

Neither the amount or duration of mass recession varied over the season (Regression, $t_{144} = 1.064$, $p = .3$ and $t_{145} = .495$, $p > .5$, respectively).

Effect of ticks on nestlings

The analysis of tick abundance and their effect on growth rate included only NV-G nestlings that fledged. The ticks were *Ixodes uriae* nymphs (identified by P. Belton, Simon Fraser University). Tick infestations levels ranged from 1-45 ticks with most nestlings having 1-5 ticks (Fig. 2.16). Ticks were most abundant in West Slope, Lily Slope, and Far West, the sites with dirt or rocky soil (Table 2.4). The average age at which ticks were most abundant was 15.6 days. When tick abundance was categorized into three groups, 0, 1-10, and >10 ticks, tick abundance had an overall effect on fledging age, fledging mass, fledging wing, peak age, peak mass, growth rate, and wing growth rate (MANOVA, Wilks' Lamba $F_{7,60} = 3.09$, $p = .008$). Using univariate analyses, tick

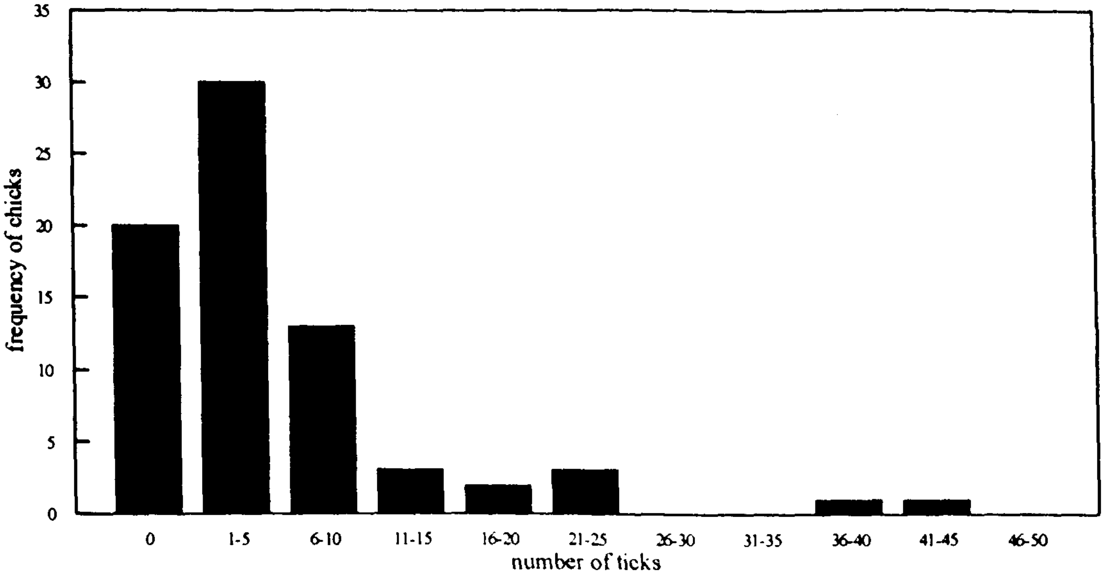

Figure 2.16. Frequency of nestlings with different levels of tick infestation. Number of ticks is categorized into multiples of five. Only NV-G nestlings that fledged are included.

Table 2.4. Frequency and percentage of nestlings with ticks on their webs, categorized by site, for NV-G nestlings that fledged.

Site	Total # of nestlings	# of nestlings with ticks	% of nestlings with ticks	site habitat
Fringe Beach	15	7	46.7	mostly flat, sandy
West Slope	19	17	89.5	sloped, dirt and rock
Lily Slope	20	19	95.0	sloped, dirt and rock
Far West	11	9	81.8	sloped, dirt and rock
Fern Grove	8	1	12.5	flat, lady ferns, dirt
Total	73	53	72.6	

abundance had a significant effect on fledging age, fledging wing, peak age, and wing growth rate ($F_{2,68} = 3.21$, $p = .05$; $F_{2,69} = 3.55$, $p = .03$; $F_{2,68} = 3.97$, $p = .02$; and $F_{2,68} = 5.88$, $p = .004$, respectively) (Table 2.5). Tick abundance did not influence fledging mass, peak mass, growth rate, or amount or duration of mass recession.

In a general linear model controlling for site effects, hatching date did not affect the maximum number of ticks on nestlings ($F_{1,64} = 2.40$, $p = .2$). One nestling had a maximum of 45 ticks and hatched at the end of the season. This data point was considered an outlier; when excluded, r^2 increased from .118 to .140

Discussion

Evidence from the literature reveals that the breeding phenology of Cassin's Auklets was similar in 1994 to previous years when studies had been conducted on Triangle Island (Vermeer 1981). On the Farallones, breeding tends to start slightly earlier and extends for longer, but the peak of hatching occurs at a similar time to Triangle Island. On the Farallones, egg-laying ranged from 11 March - 21 July and peak egg-laying occurred during 1-14 April (Ainley et al. 1990). If eggs were incubated for an average of 39 days, peak hatching would have occurred during 10-23 May, similar to what I found. The extensive range of hatching dates on the Farallones is due to the laying of second and replacement clutches (Ainley et al. 1990). The shorter breeding season at higher latitudes probably prevents the laying of second clutches. However, this slight peak in hatching on 2 June could be indicative of replacement clutches, possibly from adults that failed earlier.

Reproductive success on Triangle Island in 1994 (.69) was similar to that found in 1978 and 1979 (.67) (Vermeer 1981). Similarily, on Frederick Island in the Queen Charlotte Islands, reproductive success in 1980 and 1981 was .65 (Vermeer and Lemon 1986). In contrast, average reproductive success for first clutches (.829) on the Farallones was much higher than on Triangle Island (Ainley et al. 1990). Over 14 years at the

Table 2.5. Comparison of wing growth rate, fledging wing, peak age, and fledging age for different levels of tick infestation. The effect of tick abundance on each of these parameters was significant ($F_{2,68}$ = 5.88, p = .0044; $F_{2,69}$ = 3.55, p = .0341; $F_{2,69}$ = 3.21, p = .0464; and $F_{2,68}$ = 3.97, p = .0235, respectively). For each, $\bar{x} \pm \sigma(n)$ are given.

Parameter	Level of tick infestation		
	0	1-10	>10
wing growth rate	2.87 ± .40(18)	2.83 ± .34(43)	2.38 ± .58(10)
fledging wing	126.3 ± 3.4(19)	125.2 ± 3.4(43)	122.9 ± 2.6(10)
peak age	42.3 ± 2.5(18)	42.6 ± 3.4(43)	45.7 ± 4.2(10)
fledging age	45.7 ± 2.1(18)	45.8 ± 3.0(43)	48.3 ± 4.0(10)

Farallones, reproductive success ranged from .716 - .929, over which even the minimum is higher than that observed at Triangle Island (Ainley et al. 1990).

Hatching success did not differ between Triangle Island and the Farallones. Compared to the hatching success of .79 on Triangle Island, at the Farallones, average hatching success for first clutches from 1970 - 82 was .789 and ranged from 72 - 92 (Ainley et al. 1990). On Frederick Island in 1980 and 1981, hatching success was slightly lower (.730 and .681) than on Triangle Island. The intercolony differences in reproductive success therefore arises from differences in fledging success rather than hatching success. The cause of the intercolony variation in fledging success is not known, but could be due to differences in food availability, predation risk, or habitat quality.

The traditional explanation for variation in success is age and breeding experience of parents (Perrins 1970). Breeding experience affected hatching success in Gannets (*Sula bassanus*) (Nelson 1966) and in Cassin's Auklets (Emslie et al. 1992) and inexperienced Razorbills (*Alca torda*) may have been more inclined to lose their nestlings (Lloyd 1979). In this study, the behaviour of the rodents also infuences hatching success. Experience had no effect on fledging success in Cassin's Auklets, which suggests the importance of stochastic events causing nestling mortality (Emslie et al. 1992).

Egg loss (due to predation or abandonment) and nestling mortality peaked immediately after the peak of hatching. This pattern seems logical for nestling mortality, which occurred most frequently in young nestlings. How the high frequency of egg loss at the end of the incubation stage arises is interesting. Most abandoned eggs were eventually predated. Abandoned eggs could have been kicked out of the burrow by a Cassin's Auklet and subsequently eaten by rodents or birds, or rodents could have eaten them within the burrow. If the egg was predated on the first night it is abandoned, it would be impossible to distinguish whether abandonment was temporary or permanent. It is not known whether rodents only depredate eggs that have been abandoned, although it is doubtful a mouse or vole could fight off an adult from its egg. If egg abandonment occurred more frequently late during incubation, this could lure rodents to specialize on eggs at this time. An increase in abandonment could result from deteriorating mate bonding in inexperienced breeders. Alternatively, temporary egg neglect could have occurred regularly throughout incubation, but rodents specialized on eggs later when most burrows would have eggs. The concurrence of the frequency and proportion of egg loss at least suggests that rodents specialized on eggs and did not always take a proportional amount of eggs.

Parasite infestations of nestlings generally have an adverse effect on avian populations (Loye and Carroll 1995). Parasites may cause reduced fledging weight, nest or colony site avoidance, or nestling mortality. In seabirds, Peruvian guano birds deserted colonies infested with ticks (Duffy 1983). The level of tick abundance did have an effect on wing growth rate, fledging wing, peak age, and fledging age in Cassin's Auklets. It appears that with more ticks, structural growth is slowed and nestlings stay longer in the nest possibly in an attempt to regain wing length. However, their fledging wing is still shorter than in non-infested nestlings. Mass gain was not affected by the level of tick infestation and ticks did not cause nestling mortality.

By placing the study sites in high density areas of the colony, I intended to exclude suboptimal sites. In Fringe Beach, the hatching success was lower than in the other sites, but not significantly. The differences in habitat quality and predation risk between Fringe Beach and the other sites and could influence hatching success. Fringe Beach is a flat, sandy site slightly higher than beach level. Using a sandy substrate for burrowing is disadvantageous since erosion can cause burrows to collapse, especially in very wet or very dry conditions. Level areas of the colony have two potential disadvantages. The act of fledging could be difficult since nestlings are thought to fly to sea. Also, since Cassin's Auklets cannot walk well on land, they may be more susceptible to predation from avian predators. Inexperienced breeders could be forced to use a suboptimal site, such as Fringe

Beach. If so, low hatching success could be a result of high temporary or permanent egg abandonment rates by inexperienced breeders. Eggs of inexperienced breeders may have an increased probability of being infertile and inexperienced breeders may have higher 'divorce' rates during incubation. However, low hatching success could also be caused by higher predation rates of temporarily abandoned eggs or of eggs that are more susceptible to predation. Higher predation rates could occur if more predators are present in Fringe Beach.

If egg volume is used as an index of parental quality, this may determine whether poorer quality parents bred in Fringe Beach. The assumption is that with experience, adults would make larger eggs. Eggs were smaller in Fringe Beach, but the possibility that the laying of smaller eggs is a strategy to reduce predation by rodents cannot be discounted. This is unlikely however, since eggs that were predated did not differ in volume from successful eggs. Variation in egg size could be entirely under genetic control. If this were the case, eggs could be smaller in Fringe Beach because of greater between-site than within-site relatedness between individuals. Breeding in Fringe Beach could in fact be advantageous because ticks, which decrease the growth rate of nestlings' wings, are almost completely absent. The tradeoffs in habitat quality are difficult to disentangle and conclusion cannot be made without focussed studies.

Difficulties also arise when determining whether there is seasonal variation in parental quality, because the effects are confounded with variation in food availability. Fledging success did not decline linearly over the season as might be expected if poorer quality birds bred later. Rather, nestling mortality was lowest for nestlings that hatched during the peak of hatching. A hypothesis for this observation is that early and late in the season, the environmental conditions were suboptimal for nestling growth and survival. Early in the season, food shortages or cool temperatures may have adversely affected newly hatched nestlings. The fastest growth occurred in the earliest hatched nestlings, suggesting that food shortages may not have been important. If cool temperatures were important, nestlings that survived this cool period until they could thermoregulate may have had higher growth rates due to higher food availability early in the season or the earlier breeding of higher quality parents. At the end of the season, both food shortages and the delayed breeding of poorer quality adults could cause high nestling mortality.

If there was no environmental influence on egg size but high quality parents provisioned nestlings better than poor quality parents, then egg size should not be correlated to growth rate or hatching size. However, egg volume was positively correlated with growth rate and hatching size, even though the relationships were slight. If high quality parents laid larger eggs, three hypotheses could explain a positive correlation between egg size and growth rate. First, high quality parents may provision nestlings at a higher rate; second, growth rate could be strongly influenced by egg size; and third; a positive genetic correlation could exist between egg size and growth rate. If nestling growth rate was constrained by nutrients available in the egg, one might expect egg volume to affect structural growth. Since egg volume did not affect wing growth rate, the second hypothesis is not supported.

Egg volume did not affect mass and wing at five days possibly because the first few meals nestlings received compensated for the initial differences in hatching size. In older nestlings when there was greater variability in nestling size, differences in growth rate between nestlings hatched from different sized eggs may have been more pronounced. Experimental studies to test the effect of changing egg size on subsequent nestling size and growth rate would be the only way to test these hypotheses, and unfortunately, manipulating egg size would be next to impossible.

The main intention of this chapter was to quantify the relationships between growth and fledging behaviour, and to determine how growth and fledging behaviour varied over the season. Within each treatment group, there were strong relationships between growth and fledging behaviour. Fast-growing nestlings fledged heavier and younger than slow-growing nestlings. Fast-growing nestlings also reached a higher peak mass at a younger age than slow-growing nestlings. Growth rate was not related to fledging wing, but wing growth rate was.

Unfortunately, increased handling affected growth and fledging behaviour. Nestlings that were measured less frequently grew faster and fledged younger. This effect of handling on nestling growth shows how fledging age depends on the growth rate. One might have expected fledging mass to be higher in the less frequently handled group as well. However, the handling did not appear to have a great enough effect on growth rate to cause the correlated effect on fledging mass given that for the analysis of fledging age variation, the r^2-value was so low.

Other studies have shown these intraspecific relationships between growth rate and fledging mass and age. Faster growing nestlings fledged heavier in Atlantic Puffins (*Fratercula arctica*) (Harris 1978), Rhinoceros Auklets (Harfenist 1991), Pigeon Guillemots (Emms and Verbeek 1991) but not in Common Murres (Hatchwell 1991b) or in another study of Atlantic Puffins (Hudson 1979). I cannot discount the probability that other studies failed to report the absence of a positive relationship.

At the intercolony level, the relationship between fledging age and mass holds. Over thirteen years on the Farallones, fledging age was 42.2 ± 3.2 (413) and fledging mass was 151.6 ± 14.6 g (576) (Ainley et al. 1990). Since adult mass on the Farallones is ~165 g, fledging mass was ~92% of mean adult mass (Ainley et al. 1990). On Triangle, fledging mass was 162 ± 12 g (151), fledging age was 46 ± 3 d (147), and adults are approximately 190 g; therefore, nestlings fledged at ~85% of mean adult mass. Nestlings on the Farallones fledged younger and at relatively heavier masses. However, this may not be statistically different since fledging mass and adult mass can be quite variable.

A number of factors influence the growth trajectory of a nestling which may subsequently affect fledging behaviour. Allometric changes in metabolism with size are important for shaping a typical growth trajectory and results in a logistic curve (Werner 1988). Parental provisioning behaviour may further modify the growth trajectory (Sealy 1973). For example, if the colony is dangerous, parents may reduce provisioning rates late during the nestling period to reduce their own risk of mortality, thus causing mass recession. Nutrient limitation may further modify the shape of the growth trajectory. For example, Taylor and Konarzewski (1992) suggested that calcium limitation forced parents to overfeed Dovekie (*Alle alle*) nestlings such that they could get enough calcium. Owing to the mechanics of flight, the nestlings would then lose this mass to reduce wing loading once they fledged.

The growth trajectory of Cassin's Auklets follows a logistic curve but prior to fledging, nestlings lose mass. The mechanism for mass recession is not known, but could be caused by a reduction in provisioning or increased exercise (Sealy 1973). Staying in the burrow while losing weight could serve two purposes. It might be a bet-hedging strategy against unpredictable rates of food delivery. Nestlings would trade off a possibility of another feeding against mass loss. If the burrow is safer than the ocean, staying in the nest for a few days would be favourable. Nestlings reaching a higher peak mass at a young age lost more weight prior to fledging. This pattern of mass recession observed between fast- and slow-growing nestlings is difficult to understand without understanding why mass or how mass is lost in the first place. Large nestlings may lose mass at a faster rate than small nestlings for a physiological reason. Alternatively, larger nestlings may be behaving differently. Large nestlings may undergo a longer period of mass recession because they had extra weight to buffer them while taking advantage of the safety of the nest. For nestlings with a similar peak mass and peak age, those with a faster wing growth rate lost less weight. This suggests the importance of remaining in the nest if structural growth is not complete.

Given the constraints of the growth trajectory, however their growth trajectory was imposed, nestlings must make a decision as to when they should fledge. They could be using a simple rule, such as fledge at a certain mass, wing length, wing loading, or proportion of final adult size. If one assumes that fledging behaviour is optimal in relation to the growth trajectory, a behavioural ecological approach can be used, which can be powerful in formulating predictions. A fledging model for Common Murres using this approach was developed by Ydenberg (1989). The model considers the differential growth and mortality rates faced by nestlings in the nest and at sea under time limitation. Basically, the nest offers safety from predators whereas the ocean is dangerous. Nestlings cannot complete their growth to adult size in the nest, but must complete their growth at sea. When nestling growth rate is increased in the model by increasing the intrinsic growth rate constant or nestling asymptote, the optimal fledging mass increases. This occurs because for fast growth, mass-specific growth rates decline at a younger age than for slow growth. For fast-growers, it is beneficial to fledge at a younger age to take advantage of faster growth at sea.

Although my observations conform to the predictions of Ydenberg's model, this does not discount the possibility that nestling use a different fledging strategy. Perhaps nestlings balance the maximum fledging wing length possible given their growth trajectory with fledging mass to optimize wing loading. For slow-growing nestlings, the mass and age for optimal wing loading may occur in older, but smaller nestlings. Alternatively, nestlings could fledge once their wing lengths grew to 120-125 mm. In the figure depicting wing growth, wing length appeared to stabilize after 39 days. However, since nestlings began to fledge at 39 d, this apparent levelling off of wing length is caused by slow-growers reached wing lengths of 120-125 mm at older ages. Corroborating this, wing length was more variable at 25 days than at fledging. Models of fledging behaviour could be made based on these tradeoffs in the same way as Ydenberg's model based fledging behaviour on a different set of tradeoffs.

Growth rates tended to decrease over most of the season, but at the end of the season, growth rates increased. Because of this non-linearity, a quadratic function fit the data better than a linear regression model. The late-hatching cohort could potentially be from failed breeders that laid replacement eggs. Some of the data support this hypothesis, although the evidence is only circumstantial. The breeding phenology showed a slight increase in hatching dates centered around 2 June. If incubation length is 39 days and if it takes 12 days to form a new egg (Ainley et al. 1990), these eggs would have been laid before 10 April. Therefore, a first breeding attempt could have occurred, since the first lay date of the population was 29 March. The second line of evidence is the increase in growth rates observed at the end of the season. If the seasonal decline in growth rates was due to the delayed breeding of inexperienced parents, one would expect similar growth rates between the earliest hatched cohort and the re-layed cohort. However, one would also expect a similar increase in wing growth rates at the end of the season, which was not observed. Given the data collected, it is not possible to distinguish whether the seasonal decline of growth rates was due to a seasonal decline in parental quality or food availability, or both. Also, the pattern of breeding success and egg size variation cannot help to discriminate between these two causes.

Since there was a strong relationship between growth rate and fledging behaviour, one would expect fledging mass to decrease and fledging age to increase with hatching date. However, as indicated by low r^2-values, hatching date only explained a small proportion of the variation in fledging behaviour. Doing series of univariate regression models increases the chance of finding significance, so the seasonal effect on each fledging parameter is not conclusive. There was at least some logic in the observed variation in fledging age. Fledging age decreased with hatching date but this was due to the seasonal decline in growth rates. Also, the seasonal decline in fledging wing was caused by the seasonal decline in wing growth rate. In contrast, peak age did not increase and fledging mass did not decrease over the season despite the strong relationships between these variables and growth rate, based on low p-values. Likewise, peak mass did not decrease with hatching date. However, the r^2-values for these relationships are low, and the amount of variation in growth rate explained by hatching date was only .13. Possibly, given the combination of low r^2-values, the expected seasonal variation in fledging behaviour becomes clouded.

Possibly, fledging behaviour compensates for seasonal variation in growth rates such that the seasonal effects on fledging behaviour are negligible. The analysis of peak mass does suggest the possibility of compensation, since peak mass increased with hatching date when growth rates were controlled for. To further support some kind of compensatory behaviour, mass and wing are more variable at 25 days than at fledging. The least variable aspects of growth and fledging behaviour were fledging age, fledging mass, fledging wing, peak age, and peak mass.

The observed seasonal fledging mass decline was due to the interaction between fledging mass and fledging age. The earliest fledging nestlings fledged the youngest and heaviest and the latest fledging nestlings fledged the oldest and lightest. This finding demonstrates the importance of controlling for nestling age when looking for a seasonal fledging mass decline.

The seasonal variation in growth and fledging behaviour at the Farallones appears to be much different than on Triangle Island. The growth rate constant did not decline over the season in the Farallones (Ainley et al. 1990), but fledging age did. Later in the season, nestlings fledged sooner. Also, fledging mass declined with fledging date. Interestingly, Ydenberg's (1989) model predicts that fledging mass and fledging age should decline over the season, in the absence of seasonal declines in growth rates. The applicability of Ydenberg's fledging model to the fledging behaviour of Cassin's Auklets is discussed in greater detail in Chapter 4.

Chapter III

Why do nestling growth rates decline over the season?

Introduction

At some alcid colonies and in some years, nestling growth rates decline with hatching date (Bertram et al. 1991; Birkhead and Nettleship 1982; Gaston and Nettleship 1981; Gaston et al. 1983; Harfenist 1991; Hedgren and Linnman 1979; Lloyd 1979; Manuwal 1979; Sealy 1981; Vermeer 1981, 1987; Vermeer and Cullen 1982; Wilson and Manuwal 1986; see Table 3 in Ydenberg et al. 1995). The lack of a consistent seasonal pattern in growth rates could mean that growth rate is principally influenced by environmental factors, and in productive years, growth rates do not decline over the season. Some studies do show that low growth rates are associated with poor feeding conditions (Barrett et al. 1987; Wehle 1983). However, not finding a seasonal decline in growth rates could be due to low sample size, especially if the decline is slight. None of the studies reported a seasonal increase in growth rates, and none of the studies conducted power analyses to determine the sample size required to find a significant seasonal decline in growth rates.

In the following list, I discuss several hypotheses for why growth rates decline over the season. Figure 3.1 schematically shows how these hypotheses are related and how they operate at different levels. The explanations fall into two categories, the first being 'constraint' arguments and the second being 'adaptive' arguments. Constraint arguments fall under the seasonal deterioration hypothesis, in which growth rates reflect a general decrease in food availability over the season. Adaptive arguments suggest that growth rates vary in response to conditions according to some evolutionary strategy.

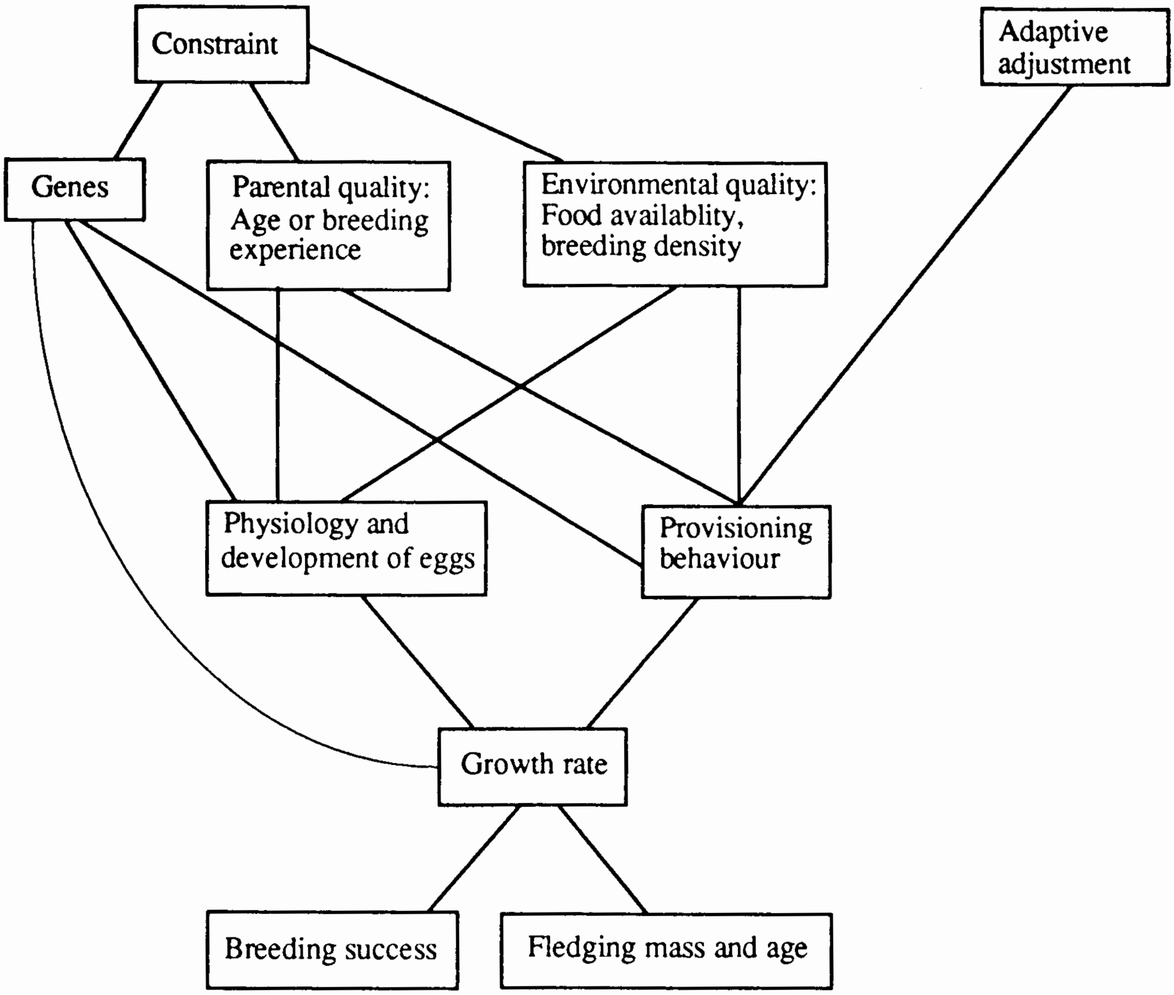

Figure 3.1. Factors causing variation in growth rate in Alcidae. The figure reads from top to bottom and the lines connecting boxes represent causal relationships. Adaptive adjustment could occur if synchronization of fledging or time constraints were important. Growth rate is what ultimately influences breeding success and fitness.

Hypotheses for seasonal growth rate decline

1) *Young inexperienced birds breed later.* Hatchwell (1991a) supports this hypothesis with the following observational and experimental evidence on Common Murres (*Uria aalge*): a) naturally late breeders provisioned nestlings at a lower rate, b) experimentally delayed clutches had greater reproductive success than naturally late clutches, and c) age-specific size was the same between experimentally delayed clutches and early control clutches. According to Harris (1980), higher-quality birds may breed early because later, there is time to relay a replacement egg if necessary. In Razorbills (*Alca torda*), replacement clutches were more successful than eggs laid at same time (Lloyd 1979).

2) *Decline in food quality or availability* (Lack 1966).

3) *Decline in adult size.* Adult size influences growth rate because there is an inverse relationship between size and extra weight adults are able to carry (Gaston 1985).

4) *Declining hatching mass.* The size hatching may constrain nestlings to a particular growth trajectory (Gaston 1985; Birkhead and Nettleship 1982).

5) *Declining egg size.* Egg size may constrain nestlings to a particular growth trajectory (Hedgren and Linnman 1979). Egg volume declines with laying date in Thick-billed Murres (*Uria lomvia*) (Birkhead and Nettleship 1982), Atlantic Puffins (*Fratercula arctica*) (Harris 1980), Razorbills (Lloyd 1979), Gannets (*Sula bassanus*) (Nelson 1966), and Black Guillemots (*Cepphus grylle*) (Cairns 1987). Egg size could be constrained by food availability or parental quality (Perrins 1970). The laying of smaller eggs by young birds is supported by a studies on Razorbills (Lloyd 1979) and Gannets (Nelson 1966). Older Gannets also laid eggs earlier because of their age and social status (Nelson 1966). However, there is no evidence that larger eggs cause faster growth in nestlings. Gannet nestlings from heavier eggs did not survive better (Nelson 1966) and Razorbill nestlings from heavier eggs did not grow faster (Lloyd 1979).

6) *Adaptive adjustment.* Parents may adjust provisioning rates and the timing of breeding in an adaptive way to maximize their reproductive success. Synchronizing breeding may be important if the risk of predation is higher for late breeders or for late fledging nestlings (Birkhead and Nettleship 1982). The earlier laying of smaller eggs could be an adaptive strategy to minimize the cost of delayed laying (Birkhead and Nettleship 1982). In Common Murres, eggs hatched before median laying date and nestlings fledging later than median fledging date experienced a greater mortality rate (Hatchwell 1991a). Adjustment of fledging age would also result in synchronization (Hatchwell 1991a). Synchrony may be important to forage successfully. Colonies may act as information centers, such that foragers ‘inform’ others of where to find food (Hedgren and Linnman 1979). Gaston (1985) proposed that parents may reduce their effort late in the season because late nestlings may have lower value to parents in terms of fitness. The reason late nestlings may have lower fitness may be because the amount of time they have to grow to adult size is limited at the end of the season (Ydenberg 1989; Ydenberg et al. 1995). Predation risk may also influence the provisioning behaviour of adults (Wilson 1993).

7) *Breeding density.* Breeding density can affect growth rates in Common Murres, and if breeding density increases over the season, this could cause a seasonal decline in growth rates (Hatchwell 1991a).

A long-standing argument in the seabird literature is whether growth rates are driven primarily by food availability or by parental quality. The relative importance of these two factors is difficult to ascertain due to the methodological difficulties of measuring food availability and parental quality. As Fig. 3.1 shows, parental quality and food availability both can affect physiology, development, and provisioning behaviour. Therefore, using surrogates of parental quality such as egg size or provisioning behaviour is inaccurate since they are also affected by food availability. Mate retention and breeding experience positively influenced fledging mass of Cassin's Auklets (*Ptychoramphus aleuticus*) (Emslie et al. 1992). If age or years of breeding experience cannot be measured, the only way to discriminate between these alternative hypotheses is experimental manipulation.

Manipulating hatching date is the best test to discriminate between parental quality and food availability as factors affecting the growth rates of nestlings. To manipulate hatching date, one could force the laying of a replacement egg (used for Common Murres, Hatchwell 1991a; Hedgren and Linnman 1979) or temporarily remove the egg and replace with a dummy egg (Wiggins et al. 1994). Both methods increase the investment by parents which could affect the quality of the nestling, although the former method increases the investment more. Forcing the laying of replacement eggs resulted in the laying of smaller volume eggs (Hedgren and Linnman 1979). Also, when forcing the laying of replacement eggs, it would be difficult to know whether the egg had the same parents. In cliff-nesting Common Murres, leg-banding is commonly done, and the identity of the egg-layers can be observed. Large-scale banding of Cassin's Auklets began on Triangle Island during the 1994 field season by catching them nocturnally in nets. In the future, the identity of parents could be determined by taking adults out of burrows during incubation, but this method is intrusive and could cause high rates of abandonment.

I decided to force egg neglect on Cassin's Auklets to determine if fledging behaviour was dependent on hatching date independently of growth rate. I used this methodology instead of forcing the laying of replacement eggs because of the problems with the latter method and because the laying of replacement eggs has not been recorded for Cassin's Auklets at Triangle Island. Egg switching experiments to alter the hatching date as perceived by the parents would not manipulate the real hatching date of the egg, but would elucidate the effect of date and nestling age on nestling growth rates. However, my initial intention was to test a hypothesis put by Ydenberg et al. (1995) which required the manipulation of hatching dates. Since growth rates declined over the season, the experiment was useful for elucidating the cause of the seasonal decline of growth rates. If nestling growth rates decline over the season because poorer quality parents breed later, growth rates should not differ between manipulated (delayed) nestlings and unmanipulated nestlings with similar laying dates. Alternatively, if nestling growth rates decline over the season because food availability declines, growth rates of manipulated nestlings should be lower than for unmanipulated nestlings with similar laying dates.

Methods

Sampling protocol

I monitored the growth and fledging behaviour of Cassin's Auklet nestlings at Triangle Island, British Columbia in two main groups of burrows. The first group was large and experienced no manipulation. The second group had their hatching dates manipulated.

For the experiment, an initial 82 burrows were excavated prior to or very early during incubation. These burrows were selected randomly within Fringe Beach, West Slope, and Lily Slope, along trails maintained over the season. Fringe Beach is a level site with sandy soil; West Slope and Lily Slope are steep sites with dirt and rock soil. Vertical holes were dug to allow access to all areas of the burrow. Access holes were patched with square cut shingles and covered with soil and vegetation to reduce erosion. Burrows were checked regularly until the egg was laid. To reduce the number of times I checked an individual burrow, I monitored use of burrows by daily twig checks. Three to four twigs were laid vertically, in parallel, against the entrance. Each day, twig knock-downs were recorded and twigs were re-aligned. When twigs were knocked down, I assumed an adult visited the burrow the previous night. In burrows with consistent knock-downs, I checked every three days for an egg.

Every second egg found had its hatching date manipulated (this group will be referred to as the experimentally delayed (E-D) group. I removed the egg, measured its length and width to the nearest 0.1 mm with Vernier calipers, and weighed it to the nearest 0.5 g with a spring scale (Pesola or Avinet). The egg was replaced with a hard-boiled chicken egg (length = 52.0 ± 1.0 mm (19), width = 39.5 ± .8 mm (19)).

I forced five days of egg neglect at the start of incubation. Short periods of egg neglect are common in Cassin's Auklets (Astheimer 1991). In 1981 and 1982, 26% and 29% of eggs were neglected at least one day, usually during the first days of incubation; the lowest rates of egg neglect occurred between 12 and 25 days of incubation during rapid embryonic growth (Astheimer 1991). Although five days of egg neglect may have killed the embryo, I was attempting to delay the hatching date enough to detect differences in nestling growth and fledging behaviour. In a previous study, incubating Cassin's Auklets accepted pre-warmed dummy eggs in every case (Astheimer 1991). Although the embryos survived placement in unused burrows, upon return to their natal burrow they had lower metabolic rates and longer incubation periods. Egg neglect had no effect on hatching or fledging success if it occurred early (Astheimer 1991). Also, in Ancient Murrelets (*Synthliboramphus antiquus*), which neglect eggs throughout incubation, neglect did not affect hatching success (Gaston and Powell 1989).

I stored the removed eggs in a plastic egg carton buried under sand to keep them cool, thus preventing embryo development. After five days, the egg was re-weighed and returned to its original burrow. Every alternate egg found received the same disturbances five days apart, but was not removed from incubation (this group will be referred to as the experimental control (E-C) group. If the adults abandoned their eggs following the disturbance, having a control group would demonstrate whether it was due to the disturbance itself, or due to giving them a chicken egg to incubate. Excessive burrow examination during incubation has been known to cause desertion (Manuwal 1974;

Vermeer 1981). Egg switches were discontinued once egg laying was beyond the peak and the boiled chicken eggs began to smell rotten. Of the initial 82 burrows, 27 received the E-D manipulation and 25 received the control treatment.

We estimated the hatching date for each egg based on its lay date and an average incubation period of 38 days (for E-C) (Manuwal and Thoresen 1993) and 43 days (for E-D). Burrows were checked on this day, and then every three days until the egg hatched. Nestlings were measured at hatching, 5 d, 25 d, every fifth day until they were fully feathered, and then every second day until they fledged. At each visit, mass was measured to the nearest 0.5 g (up to 50 g) or 1 g (> 50 g) using a spring scale (Pesola or Avinet). Flattened wing chord length was measured to the nearest 0.1 mm (< 25 mm) or 1 mm (> 25 mm) using Vernier calipers. All nestlings were banded with a USFWS stainless steel band (3a) at 25 days of age.

The initial 82 burrows were followed for the entire season to determine the fate of each and to determine the duration of egg-laying. Twig-checks for burrows with eggs were continued to determine if abandonment would occur later during incubation. If twigs did not get knocked-down for three days in a row, we checked the contents of the burrow to determine cause of abandonment (the egg could be cold or depredated).

An additional 250 burrows were excavated during incubation to monitor natural variation in growth and fledging parameters (see Chapter 2 for protocol). These burrows were located in Fringe Beach, West Slope, Lily Slope, and in two additional sites, Far West and Fern Grove. Half of the nestlings were measured at the same ages as nestlings in the experimental burrows and will be referred to as the NV-C group; the other half were also measured at 10 d, 15d, and 20 d and will be referred to as the NV-G group.

Statistical analyses

The variables 'fledging age,' 'fledging mass,' and 'fledging wing' are the last recorded age, mass, and wing chord length prior to fledging. Growth rate is an estimate for the linear phase of growth, between the ages of 5 and 25 days. Although I attempted to measure all nestlings at the same age, this was not possible due to weather, and due to my method of estimating the age of nestlings when first measured (see Methods, Ch. 2). Therefore, a nestling on day 5 might be 4 - 7 days old. Likewise a nestling on day 25 might be 24 - 27 days old. Growth rate was calculated as (mass at 25 days - mass at 5 days)/(age at 25 days - age at 5 days). Wing growth rate was calculated as (wing length at 25 days - wing length at 5 days)/(age at 25 days - age at 5 days).

In the analyses of breeding success, differences between the E-D and E-C groups and between the E groups combined and the NV groups combined were analyzed using χ^2-analysis of 2 x 2 contingency tables. 'Shuteyes' were included. In the analyses of growth rates and fledging behaviour, shuteyes were excluded since they had unusually low growth rates. The data from the E-D and E-C groups were treated as paired samples rather than discrete samples. Each pair had similar laying dates, and therefore, the experimentally delayed egg hatched five days later than the control. Both non-parametric and parametric tests were used to analyze differences between pairs, but in most cases, only results from non-parametric tests are presented.

Parametric paired t-tests were done in Excel, non-parametric paired t-tests and χ^2 tests and were done by hand after Zar (1984), and the rest of the analyses were done using SAS statistical software. Means are given as $\bar{x} \pm \sigma$ (n), α-level is .05, t-tests are two-tailed unless otherwise noted, and F-statistics are based on partial (type III) sum of squares.

Results

Seasonal variation in nestling growth rates in the NV groups

The relationship between growth rate and hatching date was fitted with a quadratic function ($y = 20.2 - .4x + .002x^2$) (Fig. 3.2, see also Chapter 2). The quadratic function fit

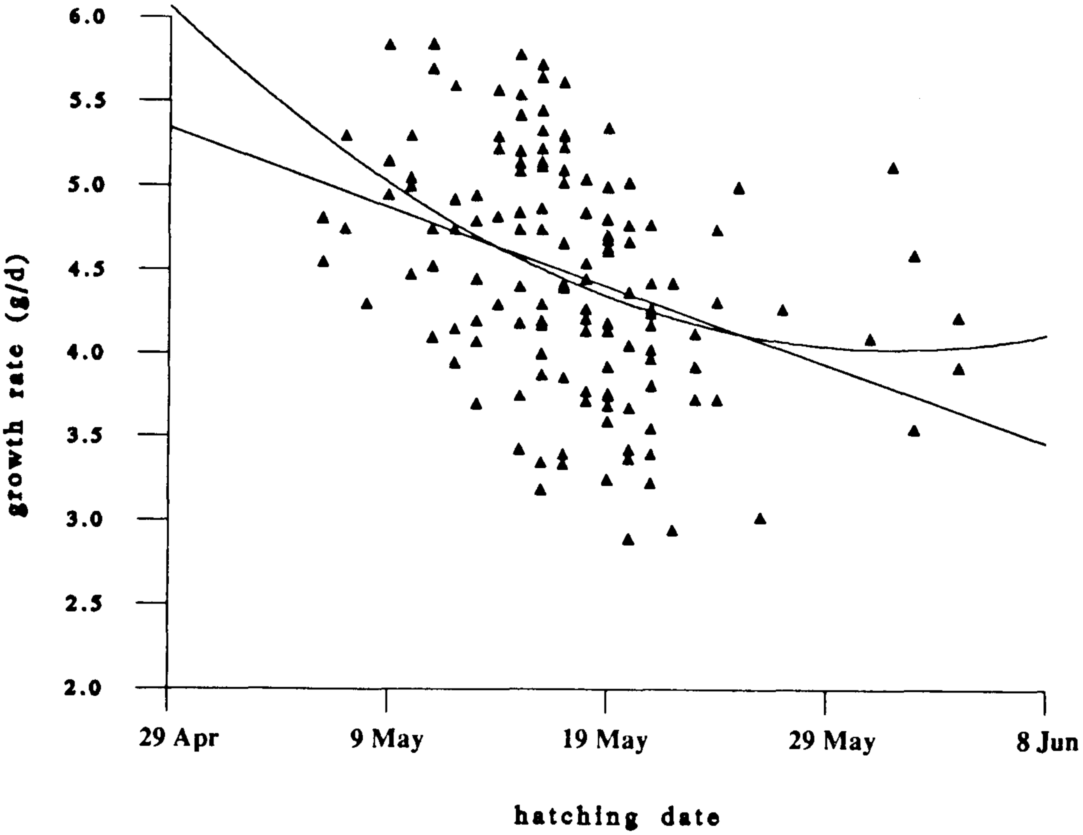

Figure 3.2. Growth rate vs. hatching date for both NV groups. The linear regression equation is $y = 8.15 - .05x$, $r^2 = .131$ ($t_{138} = -4.554$, $p = .0001$). The best fit quadratic function is $y = 20.2 - .35x + .002x^2$. Because of the increase in growth rates at the end of the season, the quadratic function fits the data better than the linear function.

the data fit better than a linear function based on a higher adjusted-r^2 (.137 vs. .124), a lower PRESS statistic (58.196 vs. 58.911), a lower Mallow's C_p (3.000 vs. 4.007), a better 1:1 relationship between observed and predicted growth rate, and a more symmetrical residual plot (Fig. 3.3, Fig. 3.4) (Myers 1990). A linear function underestimated growth rates early and late in the season and overestimated growth rates during mid-season.

The general seasonal decline in growth rates could be caused by a seasonal decline in food availability or a seasonal decline in parental quality (Fig. 3.5). In both cases, growth rate should decline with hatching date and age-specific growth should decline with calendar date. In the former case, the relationship between age-specific growth and date should not differ for different hatching dates; in the latter case, depending on the strength of the decline in food availability and sample size, an interaction should be detected. Age-specific growth should decline with nestling age if food availability is more important.

I first determined how growth rates varied with date when controlling for nestling age. I fit a polynomial function to the growth of all the nestlings that fledged in the NV groups. Growth data for ages > 32 were excluded, since this was the youngest peak age observed. All nestlings gained weight from 0 to 32 days of age. The best fitting polynomial relating mass (y) to age (x) was $y = 20.6 + 3.38x + .078x^2 - .00006x^4$ ($F_{3,799}$ = 4425.3, p = .0001, r^2 = .943). This model was selected from all combinations of polynomials using the terms x - x^6 because it had the lowest Mallow's C_p (3.53). The residuals of this polynomial function were used to represent age-specific growth. The residuals declined with hatching date ($y = 42.3 - .542x$, $t_{801} = -7.21$, p = .0001, r^2 = .061) and with calendar date ($y = 9.62 - .102x$, $t_{801} = -3.05$, p = .002, r^2 = . 012). The relationship between the residuals and date depended on the hatching date (ANCOVA, interaction effect: $F_{25,751} = 3.03$, p = .0001); for different hatching dates, growth rates did not vary consistently within nestling periods. However, residuals did not decline with nestling age ($t_{801} = 0.00$, p = 1).

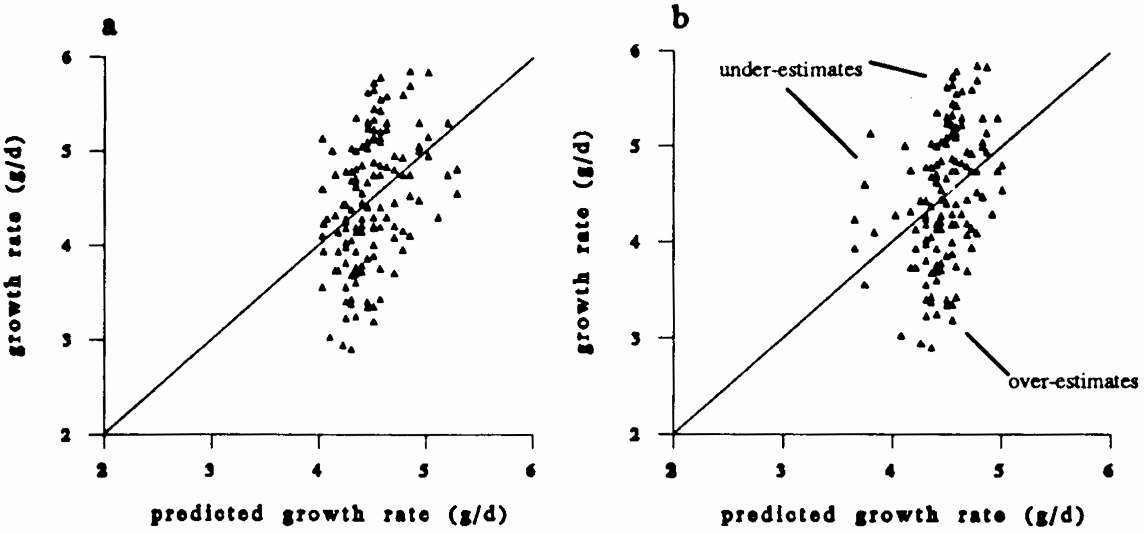

Figure 3.3. Observed growth rate vs. predicted growth rate based on a quadratic function (a) and linear function (b) relating growth rate to hatching date for both NV groups. Plot (a) is more symmetric around the 1:1 line indicating a better fit. The linear function tends to under-estimate growth rates early and late in the season and over-estimates growth during mid-season.

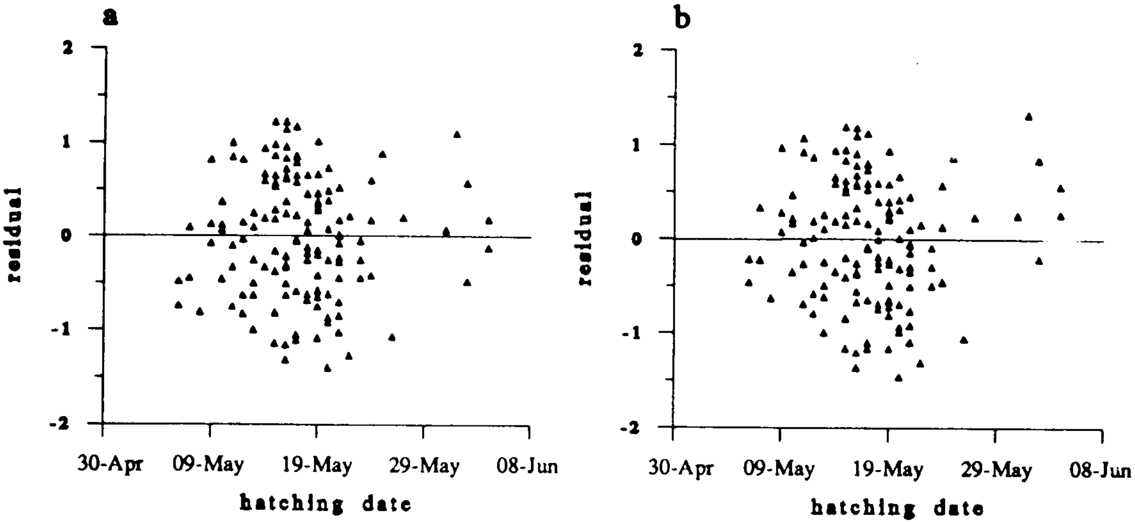

Figure 3.4. Residuals of a quadratic (a) and linear (b) function relating growth rate to hatching date plotted against hatching date for both NV groups. The more symmetrical plot in (a) indicates that the quadratic function fits the data better.

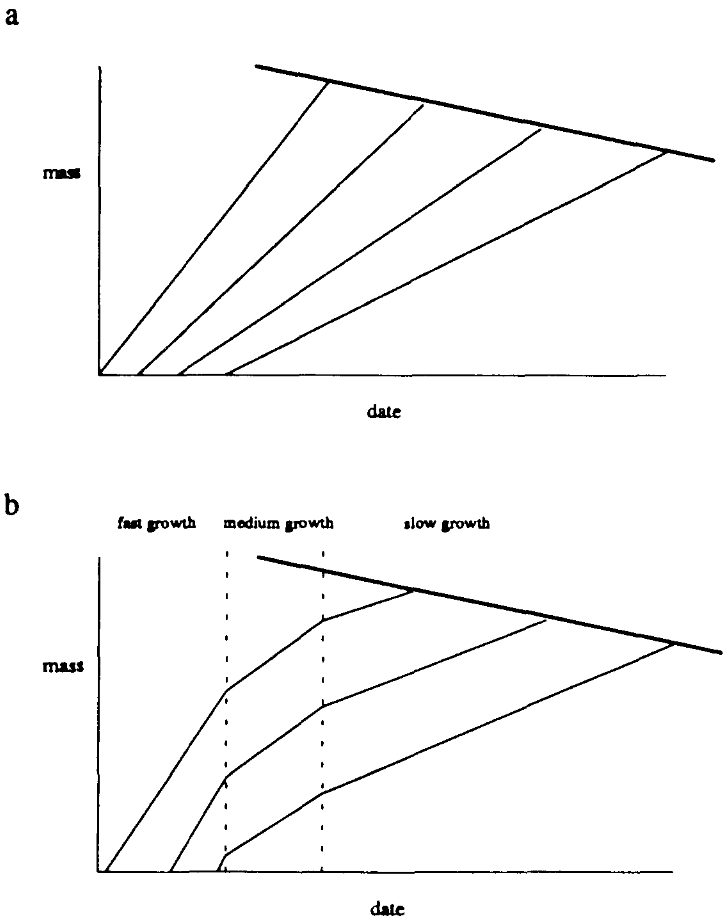

Figure 3.5. Expected seasonal variation in naturally occurring mass when parental quality declines over the season (a) or food availability declines over the season (b). The thick solid line represents a negative relationship between fledging mass and fledging date. The thinner lines represent cohorts of nestlings hatching on a particular date. In (a), nestlings grow at a constant rate. Later hatched chicks grow slower because of delayed breeding of poorer quality parents. In (b) the vertical dotted lines separate dates with fast, medium, and slow growth. The growth rate at a particular mass varies directly with food availability. Growth rates decline over the season because food availability declines. In both (a) and (b), a negative correlation would be found between growth rate over the linear phase and hatching date.

For the same polynomial equation, the residuals and the ratio of the observed:predicted mass were plotted against date to determine the temporal variation in growth (Fig. 3.6). In young nestlings, the variation in mass was much smaller than in older nestlings, therefore, using a ratio controlled for this heterogeneous variance. Peaks of fast growth occurred near 11 May and 8 June; peaks of slow growth occurred near 15 May and 25 June. Fluctuations in food availability could occur at any temporal scale. Without knowing the feeding conditions or provisioning behaviour at these times, this pattern could represent random noise.

For all models describing the residual (y) as a linear combination of date (x - x^6) the model with the lowest Mallow's C_p was selected. The best fitting polynomial, $y = 249 - .00626x^3 + .000148x^4 - .00000123x^5 + 3.52*10^{-9}*x^6$ (adjusted $r^2 = .048$), has a one minimum at 1 July, over the relevant range of x. Likewise, for all models describing the ratio (y) as a linear combination of date (x - x^6), the best fitting polynomial is $y = 37.0 - 1.54x + .0246x^2 - .000172x^3 + .000000444x^4$ (adjusted $r^2 = .023$). This equation also has a minimum at 1 July, indicating the influence of the low growth rates near 25 June on the polynomial equation. Date had a significant effect on the residual (ANOVA, $F_{51,751} = 2.52$, $p = .0001$, $r^2 = .146$). Therefore, there is statistical evidence that on some days, growth was higher than expected.

Comparison between the NV and E groups

The NV groups had the earliest mean hatching date (17 May) followed by E-C (21 May), and E-D (25 May), although the ranges overlapped (Fig. 3.7). Observed hatching dates ranged from 6 May - 14 June.

Hatching date was significantly later in E-D than in E-C (paired t-test, $t_{10(.025)} = 1.812$, $p = .0001$). E-D eggs were incubated for an average of 5.3 days longer than E-C eggs. Eggs that were removed from burrows lost .2 ± .3 g (14) over five days of removal.

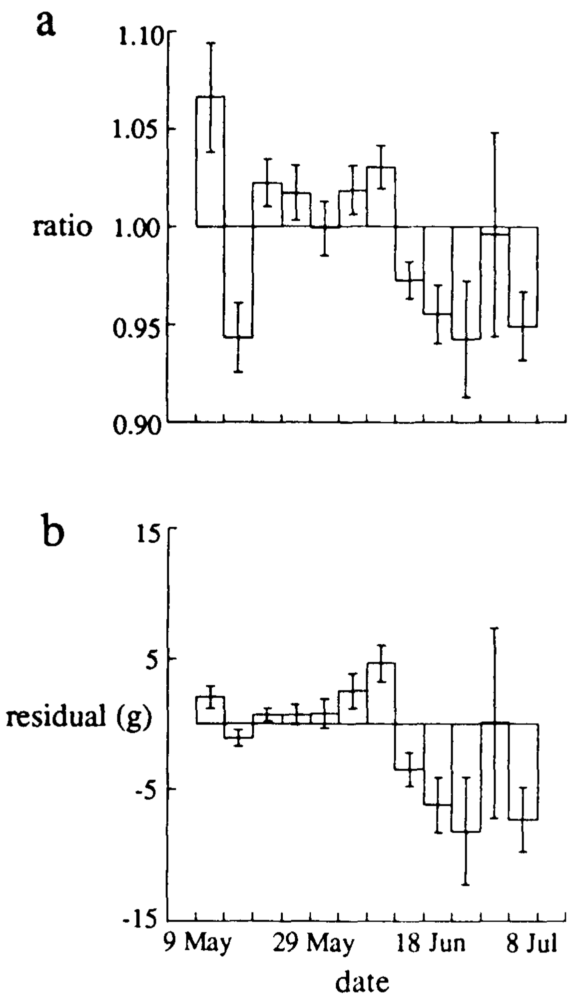

Figure 3.6. Bar graphs showing the seasonal variation in the nestling growth rates for both NV groups. In (a), the ratio is between observed mass and predicted mass based on the polynomial equation describing mass (*y*) vs. age (*x*), $y = 20.6 + 3.38x + .078x^2 - .00006x^4$. The mean ratio and standard error bars are given for each five day period. In (b), residuals were calculated from the same polynomial equation. The mean residual value and standard error bars are given for each five days period. Peaks of fast growth occur near 11 May and 8 June; peaks of slow growth occur near 15 May and 25 June.

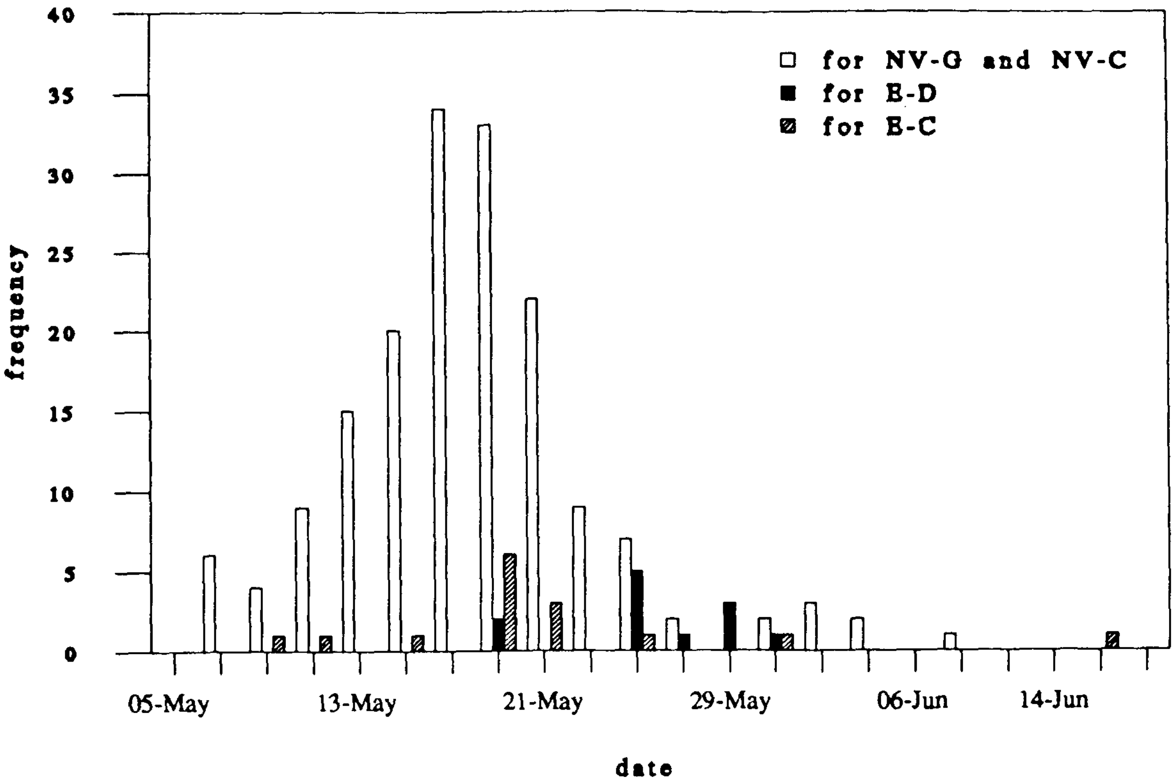

Figure 3.7. Distribution of hatching dates in the NV-G and NV-C, E-D, and E-C groups. For each two day period, the number of eggs hatched is presented. The peak of hatching occurred slightly later in the E-C group than in the NV groups. The peak of hatching in the E-D group occurred 6 days later than in the E-C group.

Hatching success (# eggs hatched/# eggs laid) did not differ between E-D (.56) and E-C (.64) ($\chi^2_1 = .114$, $p > .5$) but hatching success of both experimental groups combined differed from that in the NV groups (.75) ($\chi^2_1 = 4.444$, $p = .04$). Fledging success (# fledged/# eggs hatched) was similar in E-D (.73) and E-C (1.00) ($\chi^2_1 = 2.813$, $p = .1$) and fledging success of both experimental groups combined was similar to that in the NV groups (.88) ($\chi^2_1 = .040$, $p > .5$). Breeding success (# nestlings fledged/# eggs laid) was similar in E-D (.41) and E-C (.64) ($\chi^2_1 = 1.959$, $p = .2$) and breeding success of both experimental groups combined was similar to that in the NV groups (.66) ($\chi^2_1 = 3.049$, $p = .08$).

Egg volume did not differ between the NV and E groups ($F_{1,207} = .78$, $p = .4$). Neither first measured mass nor wing length differed between E-D and E-C (Wilcoxon paired-sample test, $T > T_{.05(1),10}$ and $T > T_{.04(1),9}$).

Comparison of nestling growth rates and fledging behaviour between the E-D and E-C groups

A comparison of the growth rates and fledging behaviour between E-D and E-C nestlings is given in Table 3.1. Using parametric analysis, growth rates were similar between E-D and E-C (paired t-test, $t_{(1),9} = .82$, $p = .2$). If a seasonal decline in food availability was responsible for the seasonal decline in growth rates, delaying hatching date by five days should cause a corresponding decline in growth rates by .15 gd^{-1}, based on the regression equation relating growth rate to hatching date given in Chapter 2. A sample size of over 500 is required to find a true difference of .15 gd^{-1} between E-D and E-C with $\alpha(1) = .025$ and $\beta(1) = .25$ (Zar 1984). According to the quadratic function relating growth rate to hatching date for NV and late burrows, day 86 (25 May), the average hatching date for E-D, the predicted growth rate is 4.09 gd^{-1}; at day 81 (21 May), the average hatching date for E-C, the predicted growth rate is 4.08 gd^{-1} (see Chapter 2). The

Table 3.1. Differences in observed behaviour between the E-D and E-C groups, based on paired samples

Parameter	$\bar{x}$ for E-D	$\bar{x}$ for E-C	Parametric paired t-test, based on differences (E-D) - (E-C)	Non-parametric paired t-test, based on differences (E-D) - (E-C).
hatching date	25 May	20 May	$t_{(1),11} = 5.64$, $p = .0001$	------
hatching mass	23.5 g	24.6 g	$t_{(1),11} = -.71$ $p = .2$	$T > T_{(1),10}$, $p > .05$
hatching wing length	18.2 mm	18.9 mm	$t_{(1),11} = -1.5$ $p = .08$	$T > T_{(1),9}$, $p > .05$
fledging age	45 d	45 d	$t_{(1),11} = -.16$, $p = .4$	$T > T_{(1),9}$, $p > .05$
fledging mass	152 g	154 g	$t_{(1),10} = -.24$, $p = .4$	$T > T_{(1),11}$, $p > .05$
fledging wing	121 mm	124 mm	$t_{(1),10} = -1.57$, $p = .07$	$T > T_{(1),10}$, $p > .05$
growth rate	4.20 gd^{-1}	3.91 gd^{-1}	$t_{(1),9} = .82$, $p = .2$	$T+ < T_{(1)10}$, $p < .05$
wing growth rate	2.62 mmd^{-1}	2.76 mmd^{-1}	$t_{(1),9} = -.78$, $p = .2$	$T > T_{(1),10}$, $p > .05$

slight difference in growth rates at this part of the season further reduces the power of the analysis to detect a true difference.

Using non-parametric analysis, E-D nestlings grew significantly faster than E-C nestlings (Wilcoxon paired-sample test, $T_+ = T_{.05(1),10}$). In contrast, wing growth rate did not differ between E-D and E-C nestlings ($T > T_{.05(1),10}$). Fledging mass, fledging age, and fledging wing also did not differ between E-D and E-C nestlings ($T > T_{.05(1),11}$, $T > T_{.05(1),9}$ and $T > T_{.05(1),10}$, respectively).

Discussion

In general, growth rates declined over the most of the season, but near the end of the season, growth rates increased. To determine whether the seasonal pattern of growth rates was due to variability in food availability or parental quality, I analyzed the age and date effects on mass in nestlings that were not manipulated. In addition, I compared growth and fledging behaviour in nestlings with and without their hatching dates experimentally delayed.

The analysis of the natural variation in mass quickly revealed a methodological problem. The calendar date not only had a linear effect on daily growth, there was also a large day to day effect. In general, mass at a given age decreased over the season, as expected since growth rates over the linear phase declined over the season. A day to day effect meant that on some days, mass was higher than expected for all nestlings whereas on other days, mass was lower than expected. However, without knowing the temporal scale of fluctuations in food availability, this day to day effect could be real or random. Since all the growth data was included, multiple measures on the same nestlings could explain some of the day to day effects. If a nestling grew particularly fast one day, perhaps the next day it grew slower. One could model the phase of the moon, weather conditions, or provisioning behaviour and correlate these patterns with the peaks in mass to help elucidate what causes the temporal pattern growth rate. At least, the peak of low growth centered near 25 June is probably a real phenonemon, since it strongly affected the best fit function relating the residual to date.

The relationship between age-specific growth and calendar date was affected by hatching date. Nestling growth does not vary consistently for nestling with similar hatching dates, which was expected if the seasonal decline in growth rates was due to the delayed breeding of poorer quality parents. This was most likely a result of the large day to day variation in growth rates. The sensitivity of nestling growth makes it difficult to distinguish the cause of the seasonal decline in growth rates. The hypothesis that declining food availability drove the seasonal decline in growth rates was also not supported since age-specific growth rates did not decline with nestling age.

If poorer quality parents bred later, experimentally delaying hatching date should not affect the growth rate of nestlings in the delayed group compared to the experimental control group. Nestlings in the delayed group should also grow faster than non-experimental nestlings with similar hatching dates. Conversely, if there is no relationship between parental quality and timing of breeding, then nestlings in the delayed group should have similar growth rates to non-experimental nestlings with similar hatching dates, and slower growth rates than the experimental controls.

The experimental data cannot discriminate between the alternative hypotheses, mostly because of methodological problems. One problem with the experiment was the low sample size. This arose partly because of abandonment or predation of eggs early during incubation. Some of the abandonment that occurred in the experimental burrows might have been due to the disturbance I caused rather than to natural abandonment. Excessive burrow examination during incubation has been known to cause desertion (Manuwal 1974; Vermeer 1981). Hatching success was lower in the experimental groups than in the natural variation groups. Excavation of burrows prior to egg-laying may also have dissuaded adults from using burrows, thus reducing the initial number of eggs used in the experiment. To support this hypothesis, hatching dates in the experimental burrows were later than in the natural variation burrows, which were not excavated until after egg-laying.

The major problem with the experiment was that hatching dates were only delayed by five days, and since the seasonal decline in growth rates was slight, this manipulation is unlikely to detect an effect on growth rates with sample sizes less than 500. Furthermore, the seasonal pattern in growth rates was better fit by a quadratic function. According to this function, within the range of hatching dates observed in the experimental control and delayed groups, growth rates should not have declined. Imposing the neglect at the beginning of incubation was necessary for consistency, but this meant the experimental control and delayed groups hatched over a broad time scale. Ideally, the experimental manipulation would have taken place on the same date on newly laid eggs. If for example this date was 10 April, then two groups, the first with a laying date of 10 April and the second with a laying date of 15 April, would be the controls for the experiment.

Even with five days of imposed neglect, this may have had adverse consequences for nestlings. Forcing egg neglect may slow the development rate of the egg which could subsequently decrease the growth rate of the nestling. In Ancient Murrelets, Crested Auklets (*Aethia cristatella*), and Least Auklets (*Aethia pusilla*), egg neglect resulted in longer incubation (Sealy 1984). However, given the similarity in breeding success, hatching size, and wing growth rate between the E-D and E-C groups, imposed neglect at the beginning of incubation probably did not adversely affect the development of nestlings.

If adults provision nestlings based on the time invested, forcing adults to incubate for longer may affect adult provisioning behaviour. For example, parents may be in poorer condition and at greater predation risk from visiting the colony for more days than they expected. Therefore, the optimal provisioning strategy would change. Parents could terminate provisioning early or provision less frequently to reduce the number of times they had to visit the colony, thereby reducing their own predation risk. To compensate for a reduced number of visits, parents may also increase food load size to ensure that nestlings still fledged heavy. A faster-growing nestling would also fledge earlier, which would further benefit the parents in terms of fewer visits to the colony. If parents do not sense the imposed neglect or the effect of the imposed neglect on their own condition, their own condition may still be adversely affected. If the five-day delay did reduce the provisioning ability of parents, delayed nestlings would be expected to grow slower than controls.

The only difference found between the experimentally delayed and control groups besides hatching date, was growth rate. In contrast to what was expected, growth rates in the delayed nestlings were faster than in the control nestlings. An explanation for this is that parents compensated for the imposed neglect by increasing provisioning rates. This is only circumstantial evidence, since provisioning rates were not measured. If this experiment was repeated on Cassin's Auklets, a number of methodological problems could be circumvented. The neglect should be imposed on nestlings all on the same day. To do this, a large number of burrows should be excavated before eggs are laid, and then occupancy could be monitored with temperature probes. This procedure may help increase the occupancy of burrows by reducing the number of times a burrow is disturbed prior to egg-laying. At the peak of egg-laying, the delayed group and two control groups can be set up. One control group should be set up on the same day as the delayed group and the other should be set up five days later. The tradeoff is that not all eggs will be at the same stage during incubation, but this can be factored into statistical analyses later. Once eggs hatch, provisioning behaviour should be measured in addition to mass, wing length, and age. This is a difficult procedure especially in Cassin's Auklets because regurgitated zooplankton loads are not easily quantifiable. One possible means to get this information would be to use scales placed underneath the incubation chamber in the burrows. If this works, nestling mass, provisioning rates, and food load size could all be measured without disturbance. Given these modifications to the methodology, and a strong linear decrease in growth rates with hatching dates, the effect of hatching date on the growth and fledging behaviour could be resolved.

Chapter IV

Modelling fledging behaviour

Introduction

Life history transitions during ontogeny are associated with changes in ecological and environmental conditions (Werner 1988). The ability of the organism to cope with these changes is dependent on the organisms' state (e.g. mass, size, or developmental stage) and therefore, the timing of life history transitions is state-dependent. State-dependent models make predictions about the optimal state at which to switch habitats or life history stages. Some recent optimality models have also considered how the time at which the state is reached could affect the strategy (Rowe and Ludwig 1991; Ydenberg 1989). These time-constrained models are important when resources (food, mates, nesting sites) are only available at certain times.

Ydenberg (1989) and Ydenberg et al. (1995) used a time-constrained life history model to predict optimal fledging times in the Common Murre (*Uria aalge*) and Rhinoceros Auklet (*Cerorhinca monocerata*). The optimal fledging strategy considered the relative costs (mortality) and benefits (growth) faced by the nestling in the nest and at sea. These costs and benefits depended not only on the nestling's state (mass), but also on the amount of time left in the season. The use of a time-constrained model was justified because breeding at high latitudes is seasonal and nestlings must complete their growth in a short amount of time (Ydenberg 1989). The model made a specific prediction about how optimal fledging mass should vary over time. The prediction is a single negatively sloped 'fledging boundary' relating optimal fledging mass to fledging date. Nestlings 'move' in mass-date space according the specified growth rate function given in the model and fledge once they 'cross' the fledging boundary. Since the fledging boundary has a negative slope, nestlings hatched later in the season will fledge at a lower mass and younger age even in the absence of a seasonal decline in growth rate. The interpretation is that under time-limitation, nestlings hatched later in the season risk the dangers of the ocean at an earlier age to take advantage of higher growth there.

The appeal of this model is its quantitative approach and its alternative explanation for a commonly reported phenomenon in the seabird literature. Alcid biologists measuring nestling growth and fledging behaviour commonly report a decline in fledging mass with fledging date, termed the 'seasonal fledging mass decline' at least in some years and at some colonies (Birkhead and Nettleship 1982; Gaston et al. 1983; Harfenist 1991; Harris 1982; Harris 1984; Hedgren 1979; Vermeer 1987; Vermeer and Cullen 1982; Wilson and Manuwal 1986). This is usually attributed to a seasonal decline in growth rate, caused either by a seasonal decline in food availability or parental quality (Perrins 1970). For find support for this hypothesis, growth rates should decline with hatching date and a positive correlation should be found between growth rate and fledging mass. In the studies showing a seasonal fledging mass decline, Birkhead and Nettleship (1982), Hedgren (1979), Gaston et al. (1983), and Wilson and Manuwal (1986) reported a seasonal decline in growth rates. Harfenist (1991) did not find a negative correlation between growth rate and hatching date. In Vermeer (1987) and Vermeer and Cullen (1982), early and late hatched nestlings grew at similar rates for the first two weeks but after this period, late hatched nestling grew slower. Of these eight cases, only Birkhead and Nettleship (1982) and Harfenist (1991) report a positive correlation between growth rate and fledging mass, but other studies corroborate this relationship (Emms and Verbeek 1991; Harris 1978; Hatchwell 1991a; Perrins et al. 1973; this study, Ch. 2). Ydenberg's (1989) model predicts a seasonal fledging mass decline in the absence of a seasonal decline in growth rates, suggesting the importance of mass-dependent growth and mortality rates on the fledging strategy. Cody (1973) and Sealy (1973) also recognized the importance of habitat-specific growth and mortality rates on the evolution of the life histories in the Alcidae.

Why should slower growers fledge at a lighter mass, as proposed by Perrins (1970)? If nestlings all fledged at the same age, fast-growers would fledge heavier than slow-growers. However, slow-growers often fledge at an older age (Barrett et al. 1987; Emms and Verbeek 1991; Harris 1978; Hatchwell 1991b). If nestling growth rates are varied in Ydenberg's (1989) model, the model predicts that fast-growing nestlings should fledge heavier and younger than slow-growing nestlings. Fast-growing nestlings fledge heavier because their growth rates decline as they reach asymptotic size at a younger age than do slow-growing nestlings.

As mentioned previously, the seasonal fledging mass decline refers to the negative relationship observed between fledging mass and fledging date. It is important to discuss the three different ways this negative correlation could arise (Fig. 4.1). In scenario (a), growth rates do not decline over the season, but a negative correlation between fledging mass and fledging date arises because the earliest nestlings grew fast and the latest nestlings grew slow. In scenario (b), fast-growers fledge younger and growth rates decline over the season. In scenario (c), fast-growers fledge younger, growth rates do not decline over the season, and later in the season, nestlings fledge at a lighter mass and younger age due to time-constraints, as in Ydenberg (1989) and Ydenberg et al. (1995). To find support for this prediction, the effects of fledging age on fledging date (a) and the effects of growth rate on fledging date (b) must be controlled for first. Ideally, growth rates should not decline over the season. If they do, it may be difficult to support the predictions of the model. Experimental manipulations can test whether the seasonal effect is real.

To date, one study has attributed the seasonal fledging mass decline to the tradeoff between mass dependent growth and mortality in the nest and at sea under time-limitation

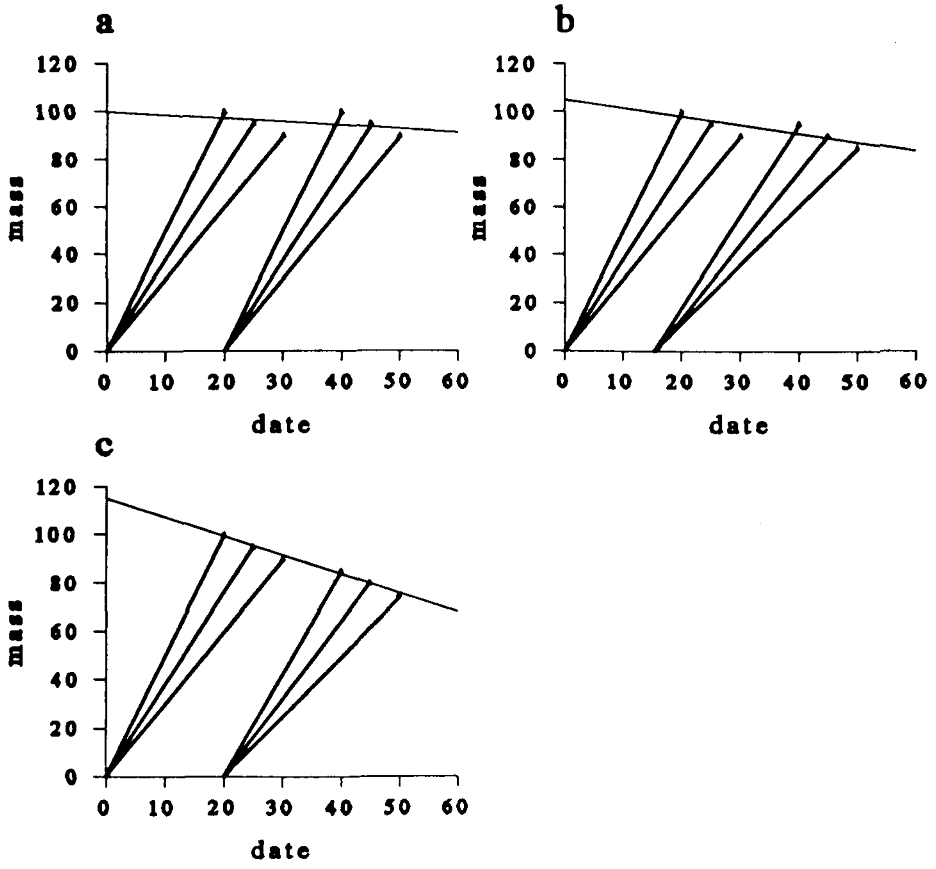

Figure 4.1. Three different mechanisms to produce a negative correlation between fledging mass and fledging date. In each figure, each line represents a nestling with a particular hatching date, growth rate, fledging mass, and fledging age. For simplification, growth rates are constant over the nestling period. The best fit line between fledging mass and fledging date is shown for each case. In (a), growth rates do not decline over the season, but there is still variation in growth rates. A negative correlation between fledging mass and fledging date arises because the earliest nestlings grow fast and the latest nestlings grow slow. In (b), growth rates decline over the season. The negative correlation is stronger than in (a) because of the declining growth rates. In (c), growth rates do not decline over the season. Later in the season, nestlings fledge at a lighter mass and younger age due to time-constraints.

(Harfenist 1991; Ydenberg et al. 1995). However, this prediction of the model has yet to be experimentally tested. My initial intention was to test the prediction that later hatched nestlings should fledge lighter and younger by manipulating the hatching date of Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia. To be an appropriate experiment, I needed to observe a negative correlation between fledging mass and hatching date. Otherwise, I could not expect fledging behaviour to change for nestlings with experimentally delayed hatching dates. Unfortunately, fledging mass did not decline significantly with hatching date (see Ch. 2). Growth rates did decline with hatching date, so fortunately, the experiment was suitable for examining another question, namely the cause of the seasonal decline in growth rate (see Ch. 3).

To understand why a seasonal fledging mass decline was not observed in my study, I studied and modified Ydenberg et al.'s (1995) fledging model based on Rhinoceros Auklets. The time-dependence in their model required the use of dynamic programming to solve the problem (Mangel and Clark 1988). Dynamic programming problems are computer intensive and it is often difficult to understand the important tradeoffs, and some of the model's assumptions may be oversimplifications of biological reality. In the following list, the shortcomings or appropriateness of each of the model's assumptions is discussed:

1. *Nestling and juvenile daily mortality rates are size independent.*

I found that Cassin's Auklet nestling mortality was mass or age specific (Fig. 4.2). Most nestling mortality occurred in young nestlings; very little occurred in old nestlings, albeit mortality near fledging cannot be distinguished from actual fledging. Unfortunately, in the two most comprehensive reviews of Cassin's Auklets, mass or age specific mortality is not mentioned (Ainley et al. 1990; Manuwal and Thoresen 1993). Juvenile mortality rate is probably dependent on experience and size, because presumably it takes time to

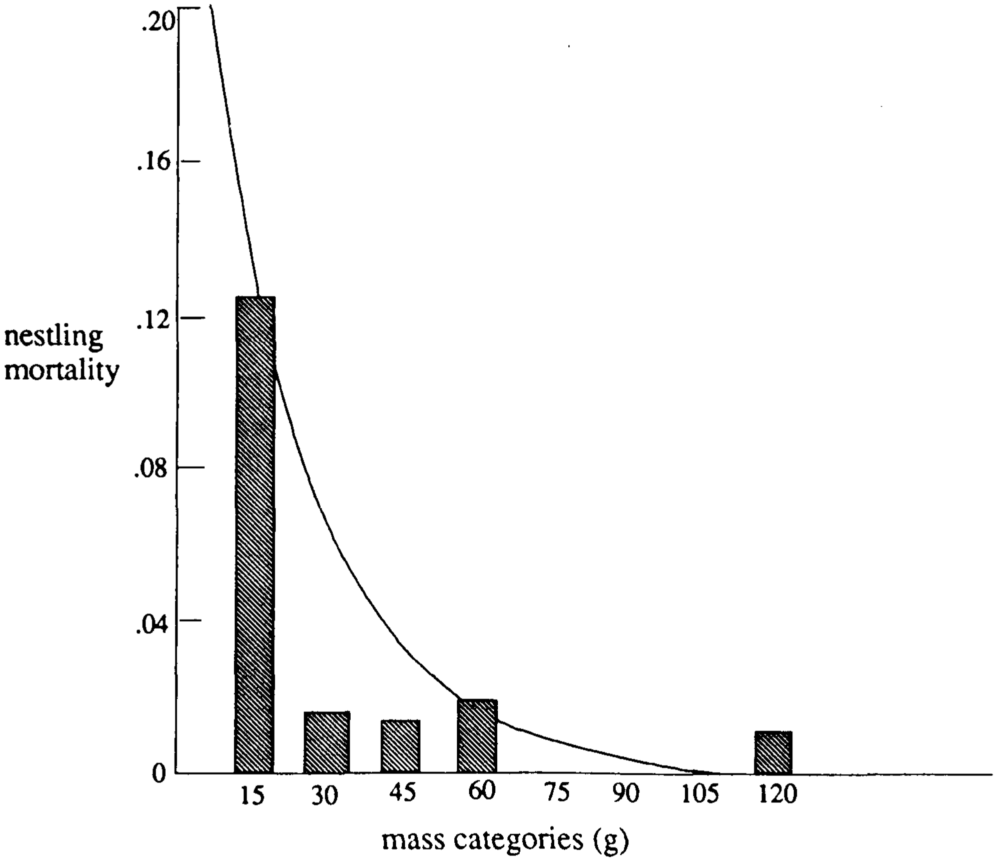

Figure 4.2. Observed Cassin's Auklet nestling mortality (# nestlings that died/# nestlings in total) per 15 g mass category. The fitted function is $y = .13e^{-.05(x-15)}$ (n = 22).

learn to forage effectively and evade predation once at sea. Also, large juveniles may have an advantage over small juveniles because their extra mass would buffer them against starvation during this learning period (Harris 1984). However, extra weight at fledging could cause lower wing loading, which could increase mortality rates during the fledging act.

2. *Daily mortality rate is greater at sea than in the nest.*

Although nestling mortality rates are easy to measure, measuring juvenile mortality rates requires intensive mark-recapture programs. Gaston (1992) estimated annual survival rate of Cassin's Auklets to be .881 (.726-.954 is the 95% confidence interval). Converted to a daily mortality rate, mortality rate at sea (.001) is less than mortality rate in the nest (.003).[1] However, these estimates must be treated with caution. The estimate of adult mortality is biased since emigration cannot be accounted for. Also, two confounding factors affect the relative mortality between the nest and ocean. First, mortality could occur either by predation or by starvation. Mortality due to starvation does not occur independently of changes in the growth rate function. This can be understood by considering how the fledging model treats mortality. For each mass and age, the model calculates whether fledging will result in higher fitness rather than staying in the nest. If the nestling stays, its growth rate is determined by the growth function. The mortality that occurs is stochastic and not mass dependent. Therefore, the assumption of higher juvenile mortality should apply to nestlings growing at a similar rate. If predation and starvation

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[1] If annual adult survival rate is .881, annual adult mortality rate is .119. Assuming a stable population size, 11.9% of each year's cohort will not survive to 3 years, the age at first breeding (Manuwal and Thoresen 1993). Over 3 years, .5N - .119N juveniles (N = population size, .5N = initial number of juveniles) will die. Given that μ_a is the proportion of juveniles that die over 3 years, and t is the number of days over which this mortality occurs, daily mortality rate (μ) can be calculated using the following function: $1 - \mu_a = e^{-\mu t}$, where t = 1049 days (365*3-46 days) and μ_a = .762 ((.5N - .119N)/.5N). Daily juvenile mortality rate is therefore .001. Given that 22/179 nestlings died over 46 days (the mean fledging age), using the same equation, daily nestling mortality rate is .003.

mortalities are not separated, the mass dependency of mortality is important when comparing nestling and juvenile mortality.

3. *The growth function in the nest is a logistic curve.*

   Alcid nestlings typically lose mass prior to fledging, which is not a component of the logistic growth function (Sealy 1973).

4. *The growth function in the nest is deterministic, not stochastic.*

   Growth and mortality are more likely stochastic processes. However, making growth stochastic had no effect on the outcome of the model (Ydenberg et al. 1995).

5. *Growth rate at sea is constant until adult mass is reached.*

   In contrast, the growth function at sea probably approximates a logistic curve, in which growth slows down as adult mass (asymptotic mass) is reached.

6. *Growth rate at sea is greater than growth rate in the nest.*

   According to Ainley et al. (1990), Cassin's Auklets grow slower after fledging than before. However, the growth function of nestlings approximates a logistic curve. As nestlings reach asymptotic mass, their growth rate declines to zero. For nestlings fledging greater than a certain mass, growth rate would be faster in the ocean than in the nest.

7. *Fitness (survival to breeding) is dependent on the mass attained at the end of the season and the optimal time to fledge is that which maximizes fitness.*

   The relationship between mass at the end of the season and fitness is difficult to establish because of the methodological problems involved in finding and capturing juveniles at sea and monitoring their subsequent fitness. Even if this were possible, using phenotypic correlations to support this relationship is problematic (Nur 1988; Reznick 1985). Studies on alcids which attempt to find a positive correlation between fledging mass and subsequent survival fail to find it (Harris 1982; Hedgren 1981).

The choice of parameter values may also affect the outcome of the model. This becomes especially important if real parameter values are unknown or vary within a range. Sensitivity analyses can determine whether the predictions explicitly depend on the assumptions being met and on the parameter values used. I first modified the model by using parameters estimated for Cassin's Auklets. I then performed sensitivity analyses on both the Rhinoceros Auklet and Cassin's Auklet versions of the model for two purposes. The first purpose was to elucidate why the predictions of the two versions differed. The second purpose was to determine how the model responded to modifications that addressed some of the shortcomings listed above. In particular, the parameter values used in the growth and mortality functions and the shape of the growth function were modified. Finally, I developed a simpler, non-dynamic fledging model for Cassin's Auklets and compared it to the dynamic fledging model.

Methods and Results

Dynamic fledging model

Rhinoceros Auklet version

Using Quick Basic programming language, the dynamic fledging model was written and executed as in Ydenberg et al. (1995) using Rhinoceros Auklet parameters and the following equations:

$$F(x,t) = \max E(\Phi(X(T)|X(t) = x)$$

$$F(x,T) = \Phi(x)$$

$$F(x,t) = \max\left\{(1-\mu_n)F(x+g_n(x),t+1), (1-\mu_o)^{T-t}\Phi(x+(T-t)g_o)\right\} \text{ for } t < T$$

$F(x,t)$ = fitness function for each (mass, time) pair
$\Phi(x)$ = fitness as a function of x
T = time horizon, last day of the season
μ_n = daily nestling mortality rate
μ_o = daily juvenile mortality rate
$g_n(x)$ = nestling growth rate as a function of x
g_o = daily juvenile growth rate

For every (x,t) pair, the program computed the optimal decision of whether to stay in the nest or fledge. The complete solution (or the decision matrix) was exactly as presented in Ydenberg et al. (1995) (Fig. 4.3). Early in the season, nestlings fledge heavier. Since the growth rate function is deterministic, nestlings of a given mass are a particular age. Therefore, early in the season, nestlings also fledge younger.

The fledging boundary does not extend across the entire range of t. Prior to ~25 days before the time horizon, nestlings remain in the nest until the fledging boundary is reached. The range across which the fledging boundary extends will be referred to as the 'duration of the seasonal effect.' The implication of this is that if the time horizon occurs later in season, for example, on 31 August, no nestlings should fledge before 6 August. The upper slope of the solid ('fledge') region comes from the growth rate in the ocean and the limit put on final mass. For nestlings above this slope, they lose mass according to the nestling growth function and fledge when ocean growth results in them just reaching adult mass. If they fledge earlier, they risk the dangers of the ocean but do not get heavier than adult mass.

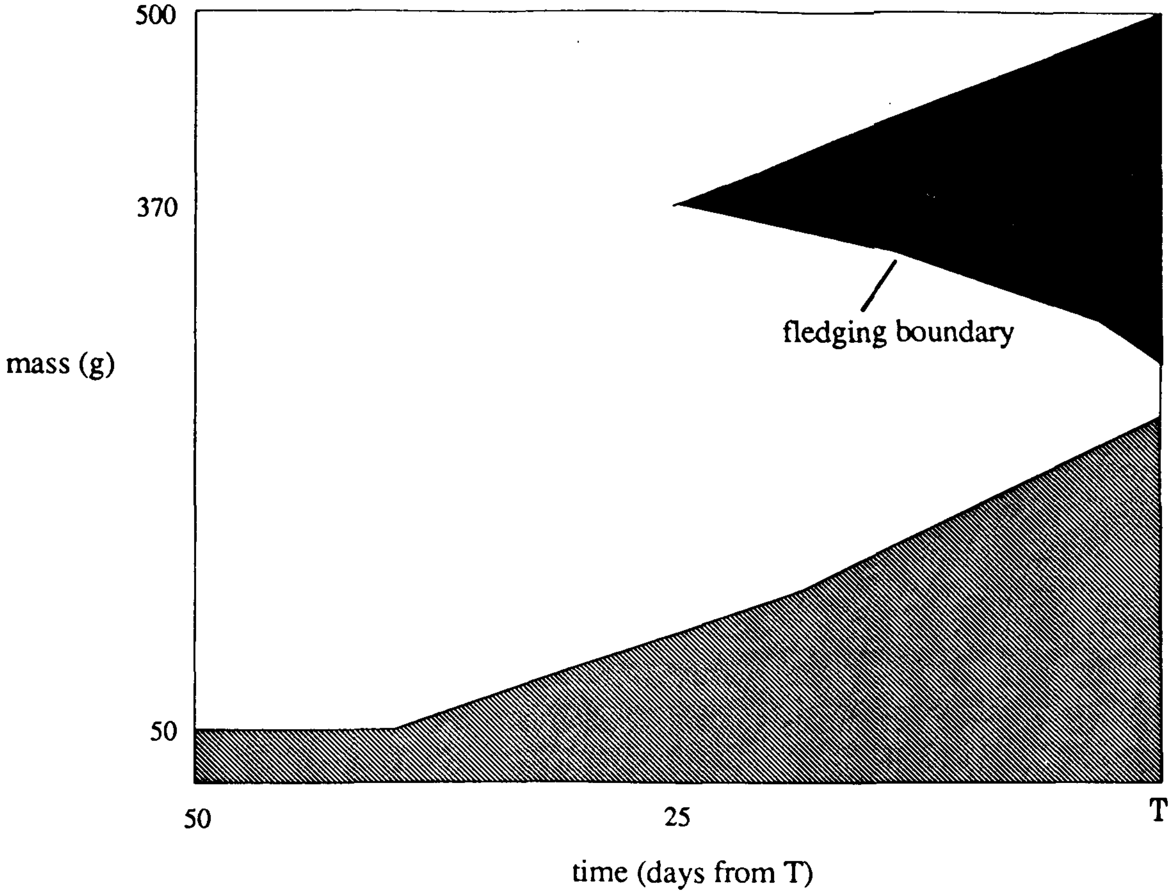

Figure 4.3. Decision matrix for the Rhinoceros Auklet version of the fledging model. For every mass/time pair nestlings can stay in the nest (blank area), stay in the ocean (solid area), or have zero fitness (hatched area). Nestlings move through mass/time according to the growth rate functions (see text) and fledge when they cross the fledging boundary. The optimal fledging mass declines over the season.

Cassin's Auklet version

I modified the dynamic fledging model using Cassin's Auklet parameters but using the same equations (Table 4.1). In cases where parameters were unknown, I set values consistent with the Rhinoceros auklet model. Juvenile growth rate was set at ~1% of x_{max} in both models. The same terminal fitness coefficient γ was used for both models, because there was no a priori reason to change it. Some parameters had to be estimated from other studies. I assumed the value for critical fledging mass, x_c, estimated for Cassin's Auklets on the Farallon Islands, California by Ainley et al. (1990), was similar for the Triangle Island population. This would be true if x_c was the crucial size to fledge successfully and forage effectively.

Changing the parameters did not change the assumptions of the fledging model. Daily nestling and juvenile mortality rates are size independent, daily mortality rates are greater at sea than in the nest, the growth function in the nest is a logistic curve, the growth function in the nest is deterministic, growth rate at sea is constant until adult mass is reached, growth rate at sea is greater than growth rate in the nest, and fitness is dependent on the mass attained at the end of the season and the optimal time to fledge is that which maximizes fitness. However, daily juvenile mortality rate is only marginally greater than nestling growth rate. Compared to Rhinoceros Auklets, Cassin's Auklet nestlings grow faster in the nest than in the ocean, as indicated by their higher r_n value. In the Rhinoceros Auklet based model, x_c is 50% of adult mass whereas in the Cassin's Auklet model, depending on what value is used for adult mass (within individuals, adult mass varies over the season), x_c is ~70-75% of adult mass.

The resulting decision matrix shows a horizontal fledging boundary (Fig. 4.4). Similar to the Rhinoceros Auklet version, nestlings should not fledge until ~25 days before the time horizon and the 'stay' region is bounded on the right by the nestling growth rate function. Any nestling hatched to the right of this curve will not reach the

Table 4.1. Parameter values for the Cassin's Auklet version of the fledging model. Nest growth function: $g_n(x) = r_n x(1 - x / K_n)$; terminal fitness function: $\Phi(x) = \gamma(x - x_c)$. The following equation was used to calculate daily mortality rate, $1 - M = e^{-\mu t}$, M = mortality per t time units, μ = mortality per time unit (Ydenberg 1989).

Parameter	Definition	Value	Reference
x_{min}	minimum mean mass (hatching mass)	20 g	Triangle Island 1994
x_{max}	maximum mean mass (adult mass)	190 g	Triangle Island 1994
x_c	critical terminal mass	135 g	Ainley et al. 1990
γ	terminal fitness coefficient	.007	consistent with Rhinoceros Auklet model
r_n	intrinsic nest growth rate	.13	Triangle Island; Ainley et al. 1990[1]
K_n	asymptotic nest mass	160 g	Triangle Island 1994; Ainley et al. 1990[a]
μ_n	daily nestling mortality rate	.00099	Triangle Island 1994[b]
μ_o	daily juvenile mortality rate	.001	estimated[c]
$g_o(x)$	daily juvenile growth rate	2 gd^{-1}	1% of adult mass; consistent with Rhinoceros Auklet model

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[a] In Ainley et al. 1990, r_n ranges from .107 to .159; asymptote (K_n) varies from 160.7 g to 169.0 g.

[b] Mortality due to starvation was excluded. Nestlings that were found dead in the burrow were considered starved; nestlings were considered depredated if the nestling could not be found. Predation accounted for 8 deaths out of the 179 nestlings. To calculate the daily nestling mortality rate, M = .04469 and t = 46 days.

[c] See footnote 1 on page 82.

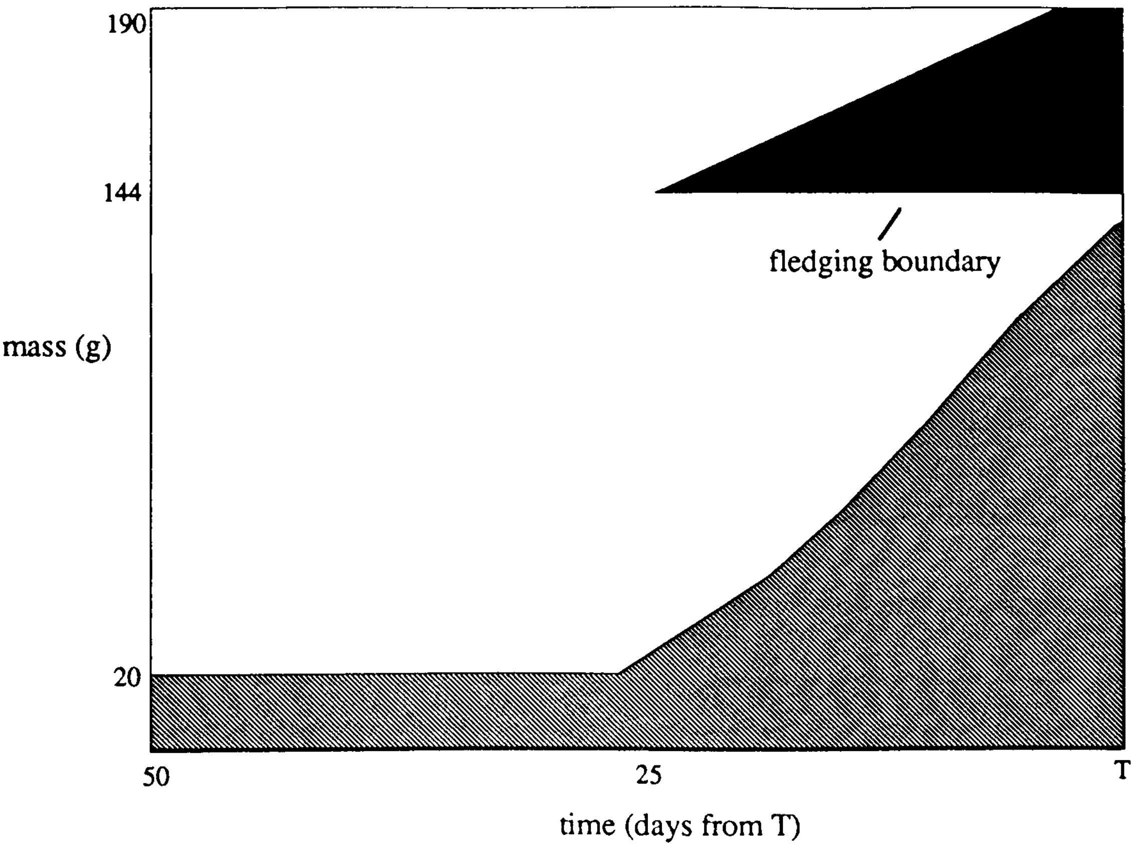

Figure 4.4. Decision matrix for the Cassin's Auklet version of the dynamic fledging model. For every mass/time pair nestlings can stay in the nest (blank area), stay in the ocean (solid area), or have zero fitness (hatched area). Nestlings move through mass/time according to the growth rate functions (see text) and fledge when they cross the fledging boundary. The optimal fledging mass does not decline over the season.

critical terminal fledging mass and will have zero fitness. The 'fledge' region is bounded at the top by the ocean growth function.

Sensitivity of the model to growth and mortality parameter values

For the Rhinoceros Auklet and Cassin's Auklet versions of the fledging model, parameters were varied systematically and the resulting changing shape of the fledging boundary were solved analytically. These analyses were done using Maple software, which is good for solving systems of equations. This approach has benefits over programming, primarily because Maple solves for the optimal fledging mass over continuous time, whereas Quick Basic must discretize time. Also, the output from Maple is easier to interpret since it can produce an equation for the fledging boundary.

The fledging boundary occurs exactly where the fitness gained from fledging equals the fitness gained by staying in the nest one more day before fledging. Let fitness gained from fledging at a particular mass and time be:

$$F_n(x,t) = (1-\mu_o)^{T-t}\gamma(x + g_o(T-t) - x_c)$$

μ_o = daily juvenile mortality rate
γ = fitness coefficient
g_o = daily juvenile growth rate
T = time horizon
x_c = critical mass

Let fitness gained from fledging at $(t+1)$ days be:

$F_n(x,t) = (1-\mu_n)(1-\mu_o)^{T-t-1}\gamma(x + r_n x(1 - x / K_n) + g_o(T - t - 1) - x_c)$

μ_n = daily nestling mortality rate
μ_o = daily juvenile mortality rate
γ = fitness coefficient
r_n = nestling growth constant
K_n = nestling asymptote
g_o = daily juvenile growth rate
T = time horizon
x_c = critical mass

When $F_o(x,t) = F_n(x,t)$, a nestling does just as well whether it fledges or stays for one more day. When all parameters are defined based on Rhinoceros Auklets, the solution is a parabola, and mass is a function of time (Fig. 4.5a). Ideally, one would solve optimal fledging mass as a function of a unknown parameter, but there is more than one value of fledging mass for some parameter values. When interpreting the equation, only a certain range should be looked at. If $T = 45$, then the important range of t is 0 - 45 days. Unlike the dynamic model, this analytical model lets juveniles grow larger than adult mass. This extends the duration of the seasonal effect farther than is realistic. The area $t < .5(x - x_{max}) + T$ defines the area in which nestlings cannot reach adult mass, and over this range, the fledging boundary is realistic.[2] Over the relevant range of t, the fledging boundary has a negative slope (Fig. 4.5b). This is the prediction of a seasonal fledging mass decline, which is a unique feature of Ydenberg's model. The solution of the fledging boundary using Cassin's Auklet parameters is also a parabola, but at t = 0 - 45 days, the slope is negligible (Fig. 4.6). In a following section, the conditions necessary to get a negative slope will be investigated.

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[2] Given that the point ($x = x_{max}$, $t = T$) and the slope (2 gd^{-1}) of this line are known, the equation of the line is $x_{max} = 2T + b$, where b is the intercept. Solving for b and rearranging to make t a function of x, $t = .5(x - x_{max}) + T$.

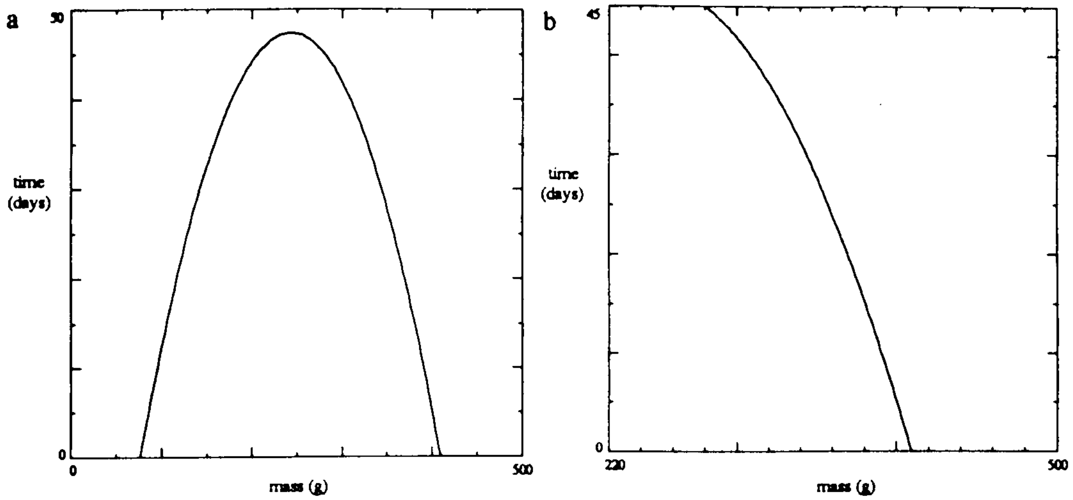

Figure 4.5. Fledging boundary for Rhinoceros Auklets, solved using an analytical model. In (a), the whole parabola, $t = -.002x^2 + .831x - 53.6$, is shown. In (b), since the time horizon (T) in the model was 45 days, only 45 days are shown. As in the dynamic model, fledging mass decreases as T is approached.

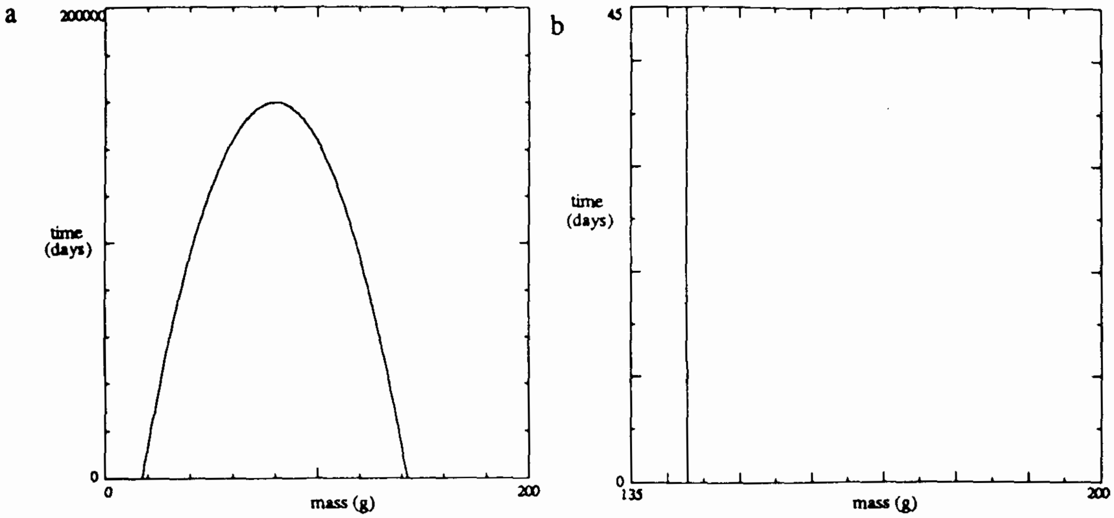

Figure 4.6. Fledging boundary for Cassin's Auklets, solved using an analytical model. In (a), the whole parabola, $t = -40.6x^2 + 6494x - 99924$, is shown. In (b), since the time horizon (T) in the model was 45 days, only 45 days are shown. Over this range of t, fledging mass does not decline noticeably with increasing time.

To analyze how the position and shape of the fledging boundary is affected by growth parameter values, only one parameter was varied at a time. In the Rhinoceros Auklet version, r_n was varied from .03 - .20; K_n was varied from 330 - 430 g. In the Cassin's Auklet version, r_n was varied from .05 - .20; K_n was varied from 140 - 190 g.

In the Rhinoceros Auklet version, with increasing r_n, the slope of the fledging boundary decreased (Fig. 4.7). With faster growth, nestlings fledge heavier. With increasing K_n, the slope of the fledging boundary remained the same but the elevation increased (Fig. 4.8). Optimal fledging mass therefore increased with K_n. In the Cassin's Auklet version, fledging mass also increased with r_n and K_n, but fledging mass did not decline over the season (Fig. 4.9, 4.10).

The influence of the relative magnitude and actual magnitude of juvenile mortality rates was analyzed. In Rhinoceros Auklets, $\mu_o = 20\mu_n$; in Cassin's Auklets, $\mu_o = 1.01\mu_n$. In both the Rhinoceros Auklet and Cassin's Auklet versions of the model, μ_o was defined as $1.01\mu_n$, $10\mu_n$, and $20\mu_n$. When $\mu_o = 1.01\mu_n$, the slope of the fledging boundary was level for both species; when $\mu_o = 20\mu_n$, the slope was negative for both species. Figure 4.11 shows this result for Cassin's Auklets. The actual magnitude of mortality had unexpected consequences on the slope of the fledging boundary, even though the relative mortality between the nest and ocean was kept the same. For Rhinoceros Auklets, nestling mortality rate was defined as $(.05\mu_o)$. With decreasing μ_o, the slope of the fledging boundary became level (Fig. 4.12).

Sensitivity of the model to the shape of the juvenile growth rate function

In the Rhinoceros Auklet version of the fledging model, the ocean growth function was modified to determine the sensitivity of the model's predictions to the shape of this function. This was done using a Quick Basic program. First, I found a function that exactly mimicked the step function used in the model:

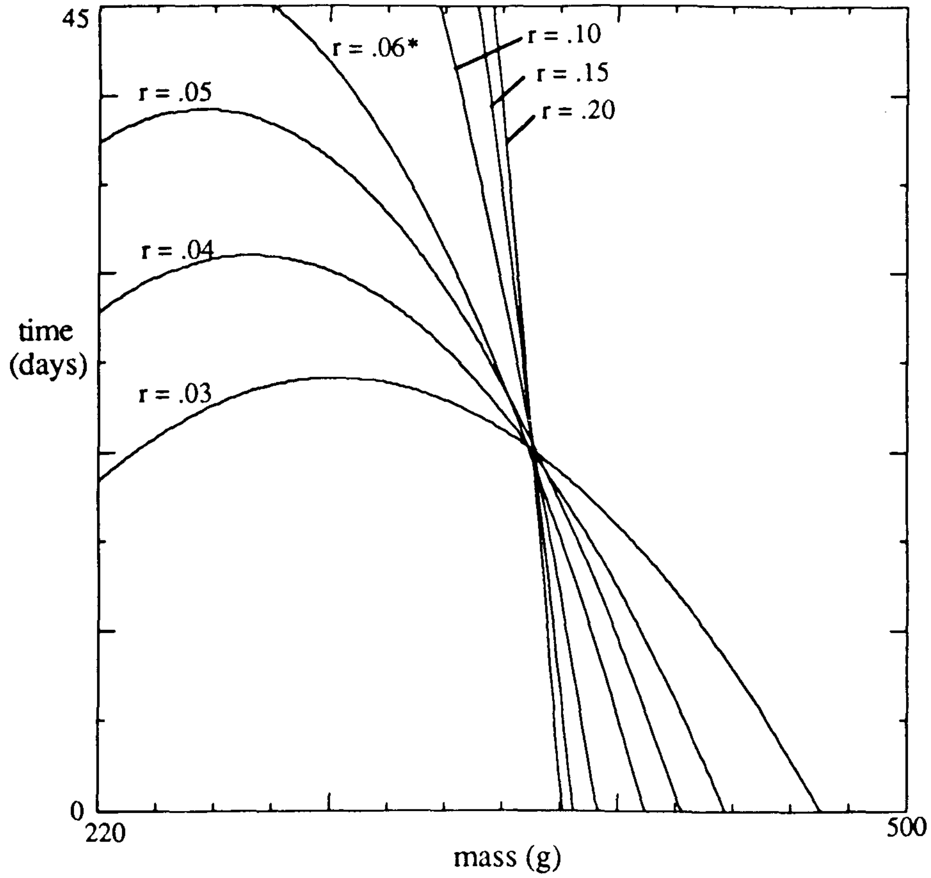

Figure 4.7. Change in the position and slope of the fledging boundary when the nestling growth rate constant, r_n, is varied in the Rhinoceros Auklet version of the fledging model. With increasing r_n, the slope of the fledging boundary decreases. According to the growth rate functions, at $r_n < .054$, the maximum growth rate in the nest is lower than the growth rate in the ocean. This probably explains why nestlings are predicted to fledge at low masses when $r_n < .06$. The systematic change in r_n is not linear. The asterisk indicates the original value of r_n used in the model.

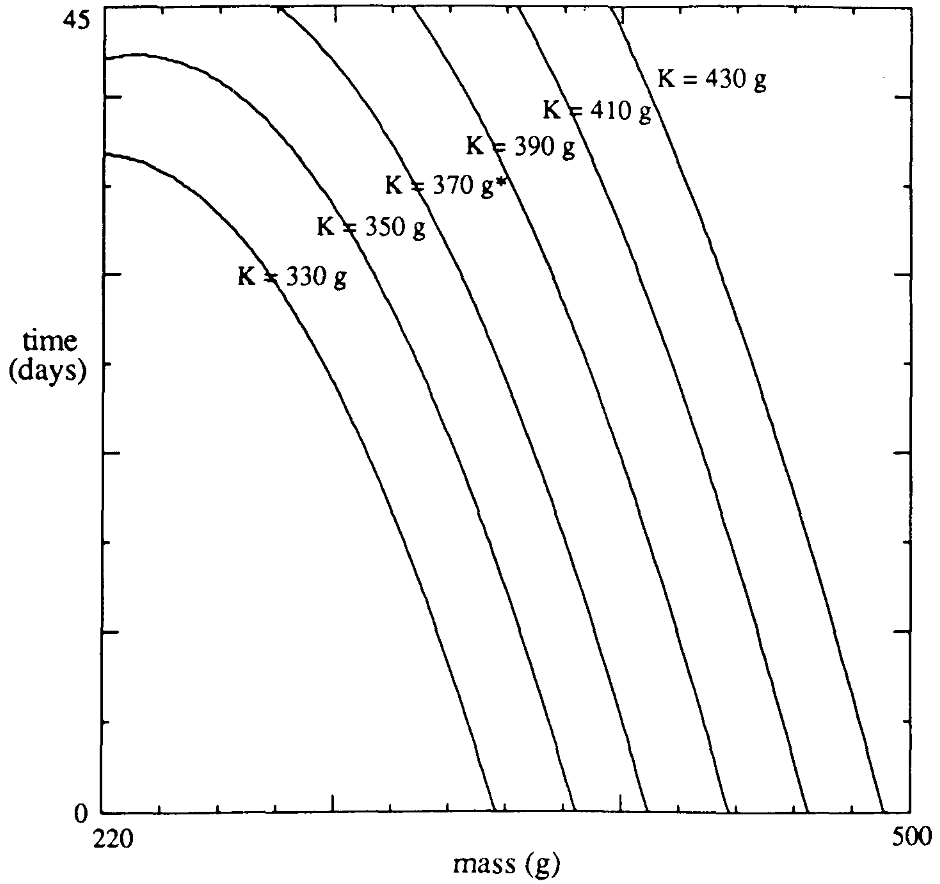

Figure 4.8. Change in the position of the fledging boundary when the nestling asymptote, K_n, of the nestling growth function is varied in the Rhinoceros Auklet version of the fledging model. With increasing K_n, the elevation of the fledging boundary increases but the slope does not change. For $K_n < 350$ g, the pattern breaks down, probably because when $K_n < 333.3$, the maximum growth rate in the nest is lower than the growth rate at sea. The asterisk indicates the original value of K_n used in the model.

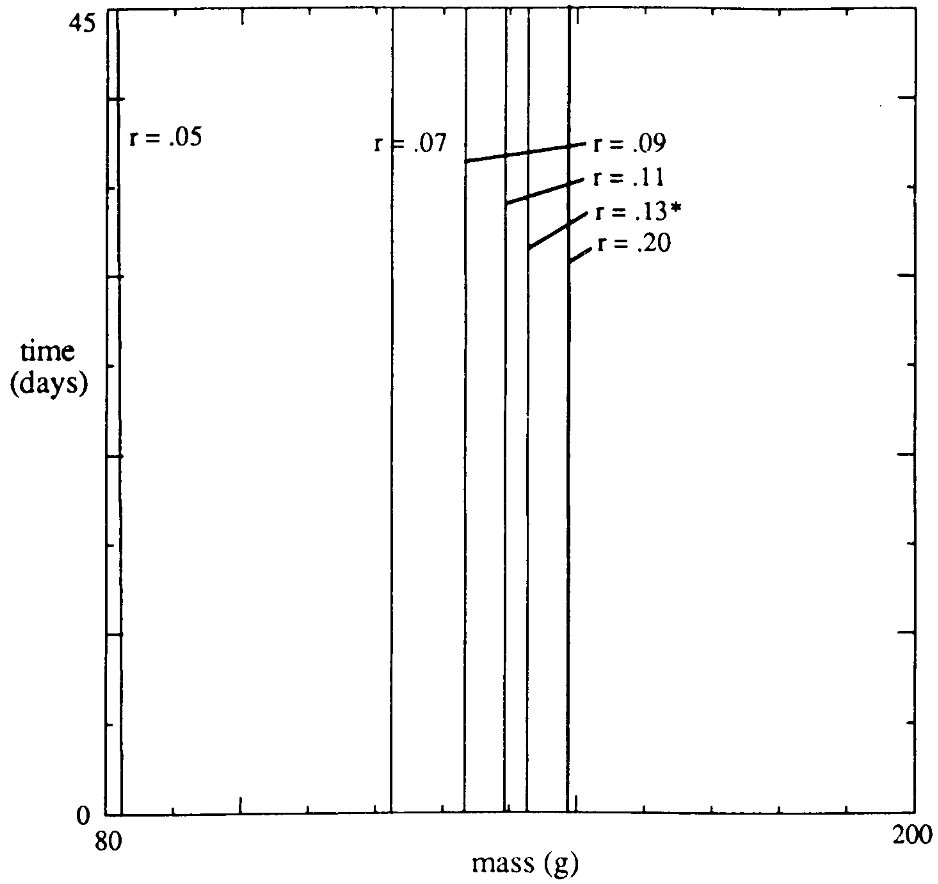

Figure 4.9. Change in the position of the fledging boundary when the nestling growth rate constant, r_n, is varied in the Cassin's Auklet version of the fledging model. With increasing r_n, nestlings fledge heavier. According to the growth rate function, at $r_n < .05$, the maximum growth rate in the nest is lower than the growth rate in the ocean. This probably explains why the predicted fledging mass is so low for nestlings with $r_n = .05$. The asterisk indicates the original value of r_n used in the model.

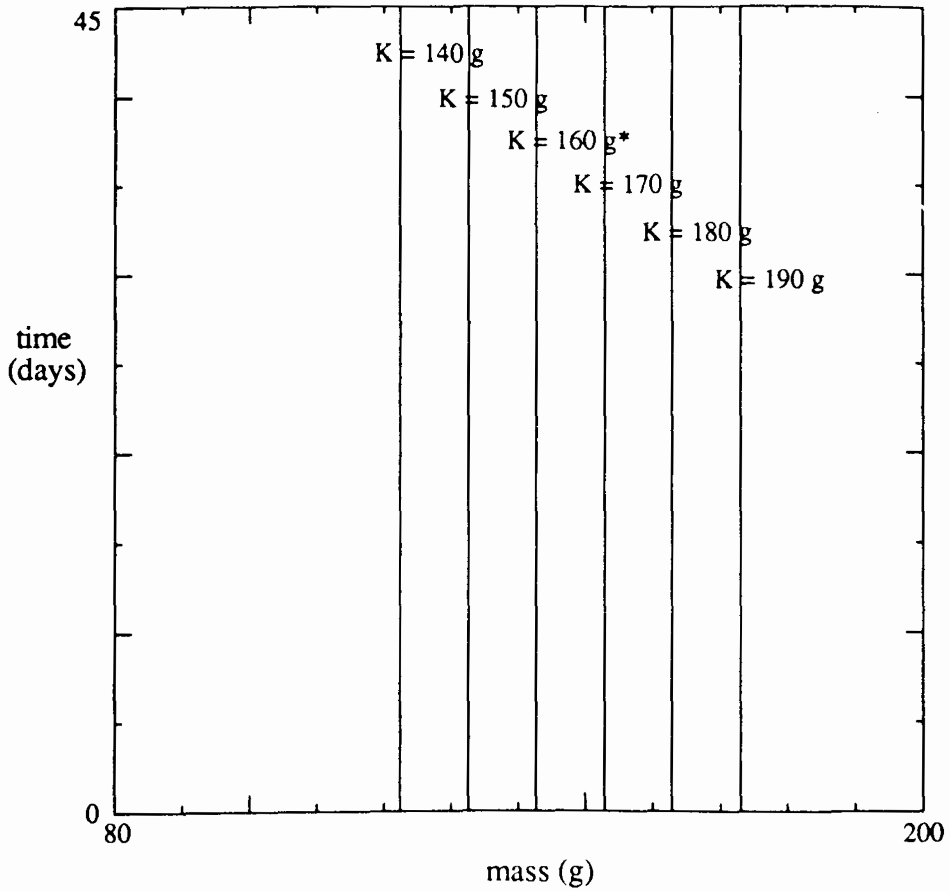

Figure 4.10. Change in the position of the fledging boundary when the nestling asymptote, K_n, is varied in the Cassin's Auklet version of the fledging model. With increasing K_n, nestlings fledge heavier, but there is no seasonal effect. The asterisk indicates the original value of K_n used in the model.

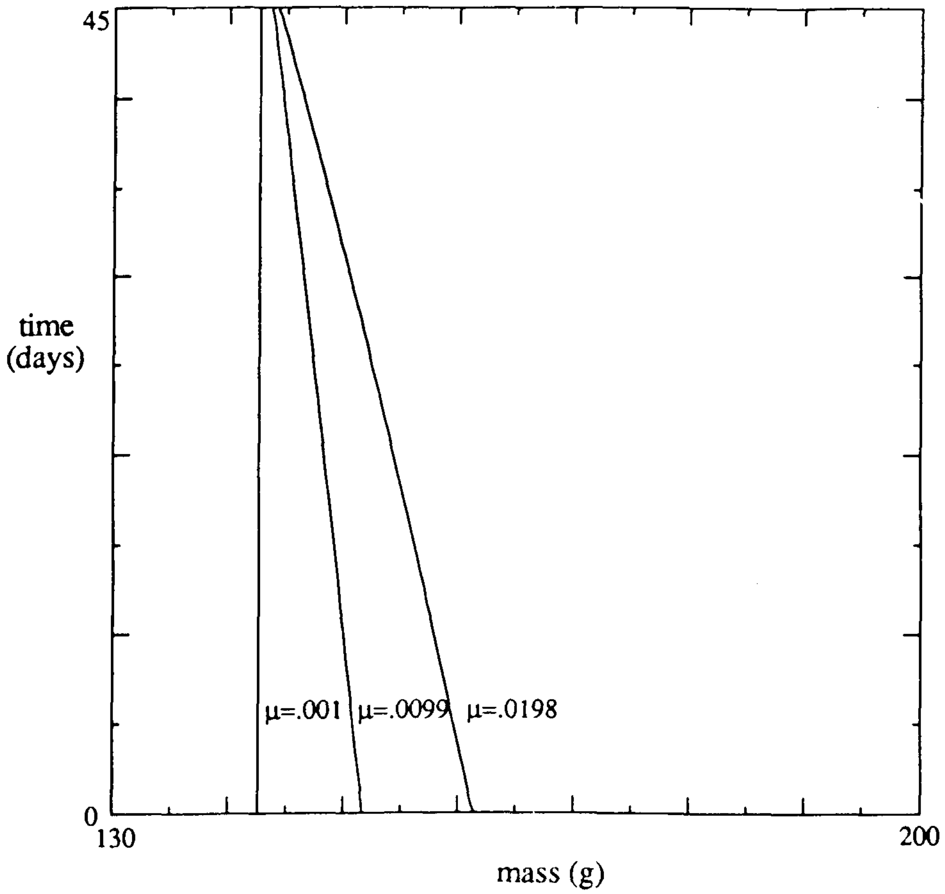

Figure 4.11. The influence of relative mortality rates on the position of the fledging boundary for Cassin's Auklets.. Juvenile mortality (μ_o) was defined as 1.01μ_n, 10μ_n, and 20μ_n. The values used for μ_o are shown. With increasing μ_o, the seasonal fledging mass decline becomes more pronounced.

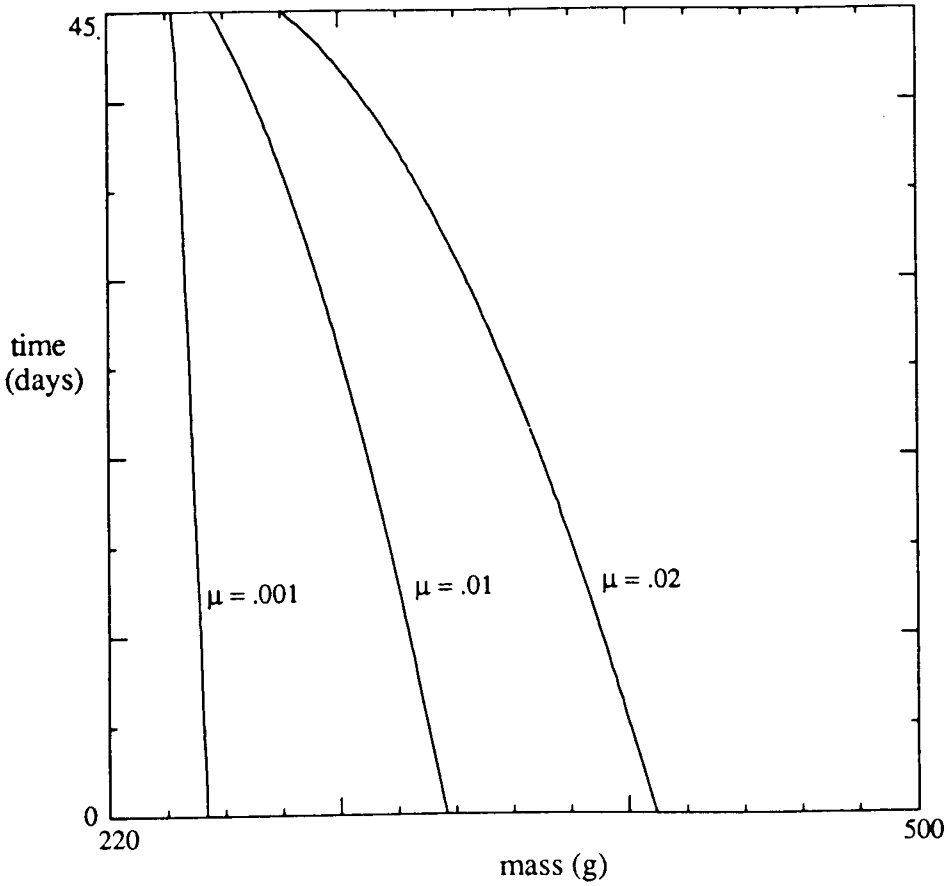

Figure 4.12. Influence of the magnitude of juvenile mortality (μ_n) on the position of the fledging boundary in the Rhinoceros Auklet version of the fledging model. Nestling mortality was defined as $.05\mu_o$. When the magnitude of μ_n is low, the fledging boundary is horizontal.

$$\frac{dx}{dt} = a(1 - a^{-b(-x+c)})$$

$a = 5$; $b = 20$; $c = 500$

units: x (g); t (days)

The constant a is the linear ocean growth rate, b changes the shape of the function, and c is adult mass. When b is decreased, growth rate decreases monotonically with increasing mass (Fig. 4.13). When $b > .01$, the predictions of the model do not change. However, when $b < .01$, the predictions change, even though the tradeoffs between nest and ocean growth rates appear to be unchanged.

A logistic growth function was also used to describe juvenile growth. I defined the juvenile growth rate constant, r_o, as .0444 such that the maximum growth rate in the nest equalled the maximum growth rate at sea. Since there is a higher asymptote in the ocean, the maximum growth rate occurs at a larger mass in the ocean than in the nest. At low masses, nest growth is higher. This modification caused the fledging boundary to lie above the nest asymptote. Therefore, nestlings do not fledge until they reach the horizon.

Conditions necessary to produce a negatively sloped fledging boundary

To observe an appreciable negative slope, the parabola describing the fledging boundary must have a low elevation, such that the origin lies at a lower value of t. The position of t is determined by the equation, $-b^2/4a + c$, where a is the coefficient for the squared term, b is the coefficient for the linear term, and c is the constant.[3] If no parameter values are specified, a, b, and c are defined as:

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[3] The equation for the parabola is $t = ax^2 + bx + c$. Taking $dt/dx = 2ax + b = 0$ will solve for the value of x at which t is a maximum. The maximum occurs at $x = -b/2a$ and $t = -b^2/4a + c$.

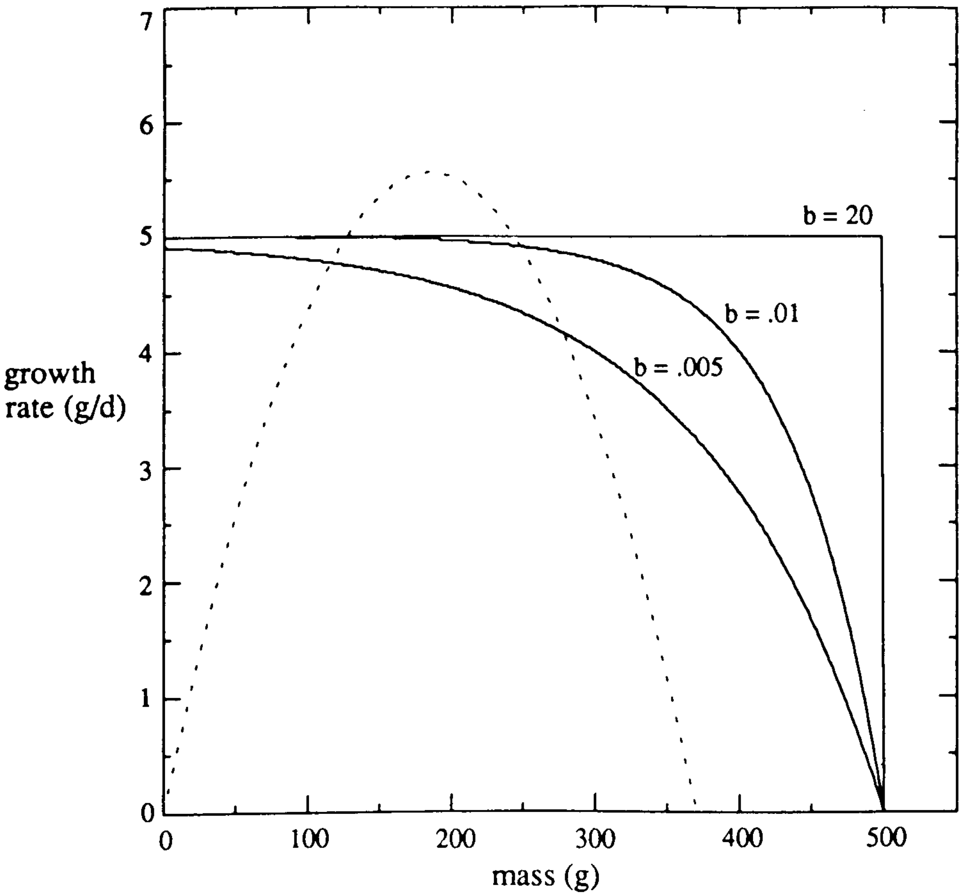

Figure 4.13. Comparison of growth rate functions in the nest (dotted line) and at sea (solid lines) for Rhinoceros Auklets. The ocean growth function is $dx/dt = 5(1 - 5^{-b(-x+500)})$, in which *b* is varied (see text for explanation). When $b = 20$, this equation mimics the growth rate step function used in Ydenberg's (1989) model, in which growth rate is constant until adult mass is reached. By decreasing *b*, ocean growth rate becomes a monotonically decreasing function of mass, which is a more realistic description of ocean growth rate.

$$a = \frac{-(1-\mu_n)r_n K_n}{(\mu_o - \mu_n)g_o}$$

$$b = \frac{(1-\mu_n)r_n}{(\mu_o - \mu_n)g_o}$$

$$c = \frac{(1-\mu_n)(g_o T - g_o - x_c) - (1-\mu_o)(g_o T - x_c)}{(\mu_o - \mu_n)g_o}$$

All the parameters, except for thc terminal fitness coefficient, influence the height of the parabola. Similar to Ydenberg et al.'s (1995) claim, the model's predictions do not depend on a strong relationship between mass at the end of the season and subsequent fitness. The influence of the parameters on the shape of the fledging boundary is complicated. Rather than determine what parameter values are necessary to produce an appreciable negative slope, what conditions are necessary to produce a negative slope? The orientation of the parabola (concave up or concave down) depends on the sign of a. If a is positive, the parabola will be concave up and the fledging boundary will be negative. If a is negative, the parabola will be concave down and the fledging boundary will be positive. Given that $r_n > 0$, $K > 0$, $g_o > 0$, $0 < \mu_n < 1$, and $0 < \mu_o < 1$, a is only positive when $\mu_o > \mu_n$.

Werner-type fledging model based on Cassin's Auklets

The optimal mass to fledge in Cassin's Auklets was modelled without time-constraints, in the style of Werner (1988). The model assumptions include state specific growth and mortality rates, a positive relationship between state (mass) and fitness, and a stable population size (Werner 1986). In this model, the fitness criterion differs from that in the dynamic fledging model. In this case, nestlings maximize their growth rate while minimizing their risk of mortality at every time step. In the dynamic fledging model, fitness is measured only once, at the end of the season. In this model, state-dependent growth and mortality functions are required for the nest and ocean habitats. Two models will be presented; the first will use the same functions used in the dynamic fledging model and the second will use biologically more realistic functions. The solutions were determined using Maple software.

Model 1

The first model used functions identical to those in the Cassin's Auklet version of the fledging model:

1. mass-specific growth rate in the nest: $\frac{dx}{dt} = r_n x(1 - \frac{x}{K_n})$

   $r_n = .13$; $K_n = 160$ g

   units: x (g); t (days)

2. mass-specific growth rate at sea: $\frac{dx}{dt} = 2$

   units: x (g); t (days)

3. mass-specific mortality rate in the nest: $\frac{d\mu}{dt} = .00099$

   units: μ (mortality due to predation); t (days)

4. mass-specific mortality rate at sea: $\frac{d\mu}{dt} = .001$

   units: μ (mortality); t (days)

Mortality rate vs. growth rate curves were constructed for the nest and ocean habitats. The optimal habitat choice minimizes mass-specific mortality rate vs. growth rate (μ/g) (Werner 1988). The optimal mass to switch habitats (fledge) occurs when μ/g is the same in the nest as it is in the ocean. Using these functions, optimal fledging mass was 143 g. When r_n and K_n were solved as functions of optimal fledging mass, optimal fledging mass increased with increasing r_n or K_n (Fig. 4.14). When the magnitude of juvenile mortality was increased, optimal juvenile mass increased (Fig. 4.15). As long as

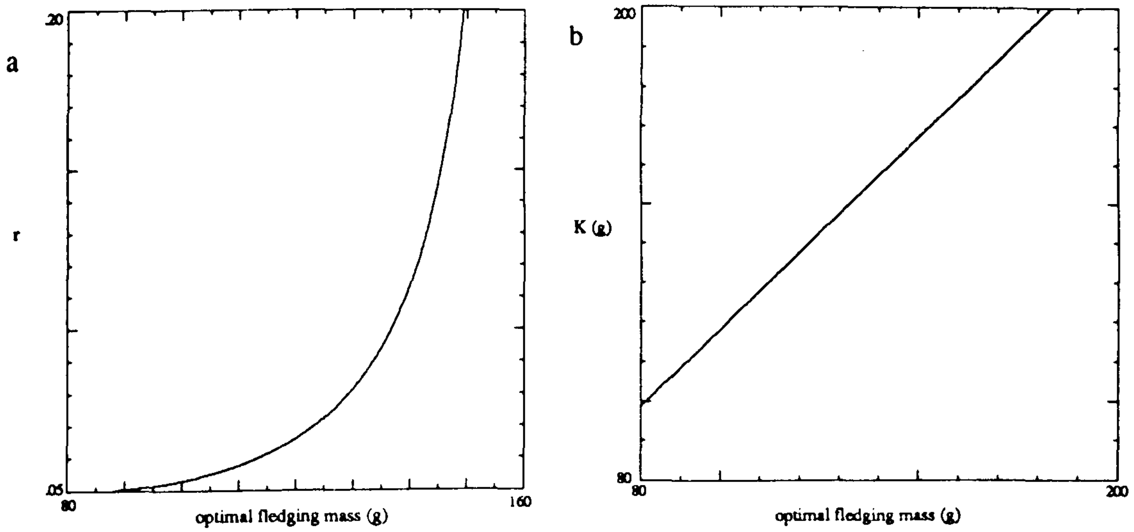

Figure 4.14. Effect of r_n (a) and K_n (b) on the predicted fledging mass in the Cassin's Auklet version of the Werner-type model. Predicted fledging mass increases with r_n or K_n. In (a), the equation is $r_n = 1584/(800x - 5x^2)$. In (b), the equation is $K_n = 10^8x^2/(-1.52*10^9 + 10^8x)$. The ranges of the variables chosen are based on the following properties of the model. When $r_n < .05$, the optimal habitat to be in when mass < 80 g is the ocean. This occurs because the maximum nestling growth rate, at 80 g ($.5K_n$), is less than the juvenile growth rate. Adult mass is 200 g, and nestling cannot grow bigger than 160 g. The upper range of r_n was chosen because above this value, optimal fledging mass asymptotes at 160 g.

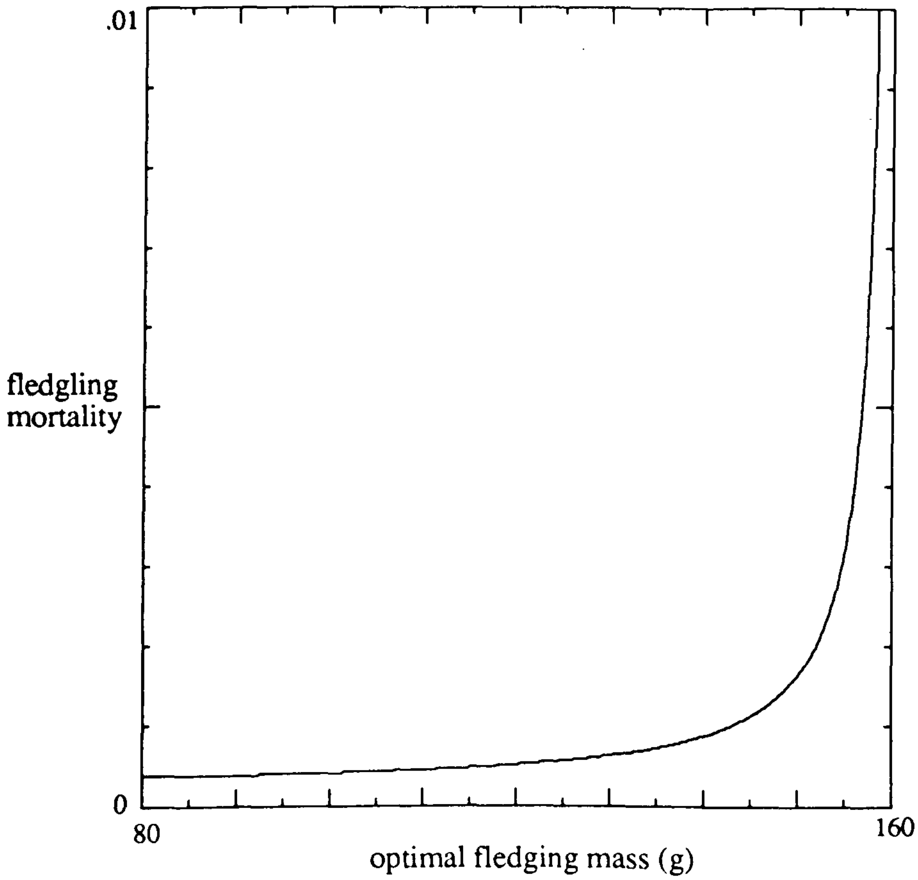

Figure 4.15. Influence of juvenile mortality rate (μ_o) on the optimal fledging mass in the Cassin's Auklet version of the Werner-type model. With increasing $_o$, optimal fledging mass increases. Low values of μ_o have a greater influence on optimal fledging mass than do high values of μ_o. The function is $\mu_o = -2.437/(x(x-160))$.

the relative magnitude of the mortality between the nest and ocean was the same, the magnitude of mortality did not affect optimal fledging mass.

Model 2

The second model used biologically more realistic functions for growth and mortality (Fig. 4.16).

1. mass-specific growth rate in the nest:

$$\frac{dx}{dt} = r_n x \frac{(K_n - x)}{K_n}$$

$r_n = .13$; $K_n = 160$ g

units: x (g); t (days)

This function is the same as that used in the Cassin's Auklet version of the dynamic fledging model.

2. mass-specific growth rate at sea:

$$\frac{dx}{dt} = r_o (x - a) \frac{K_o - x}{K_o}$$

$r_o = .13$; $a = 50$ g, $K_o = 190$ g

units: x (g); t (days)

The constant a moves the function to the right so if nestlings fledge at less than 50 g, they will lose mass. I assumed that the growth rate function is logistic, with the maximum growth rate occurring at a mass greater than in the nestling growth rate function.

3. mass-specific mortality rate in the nest:

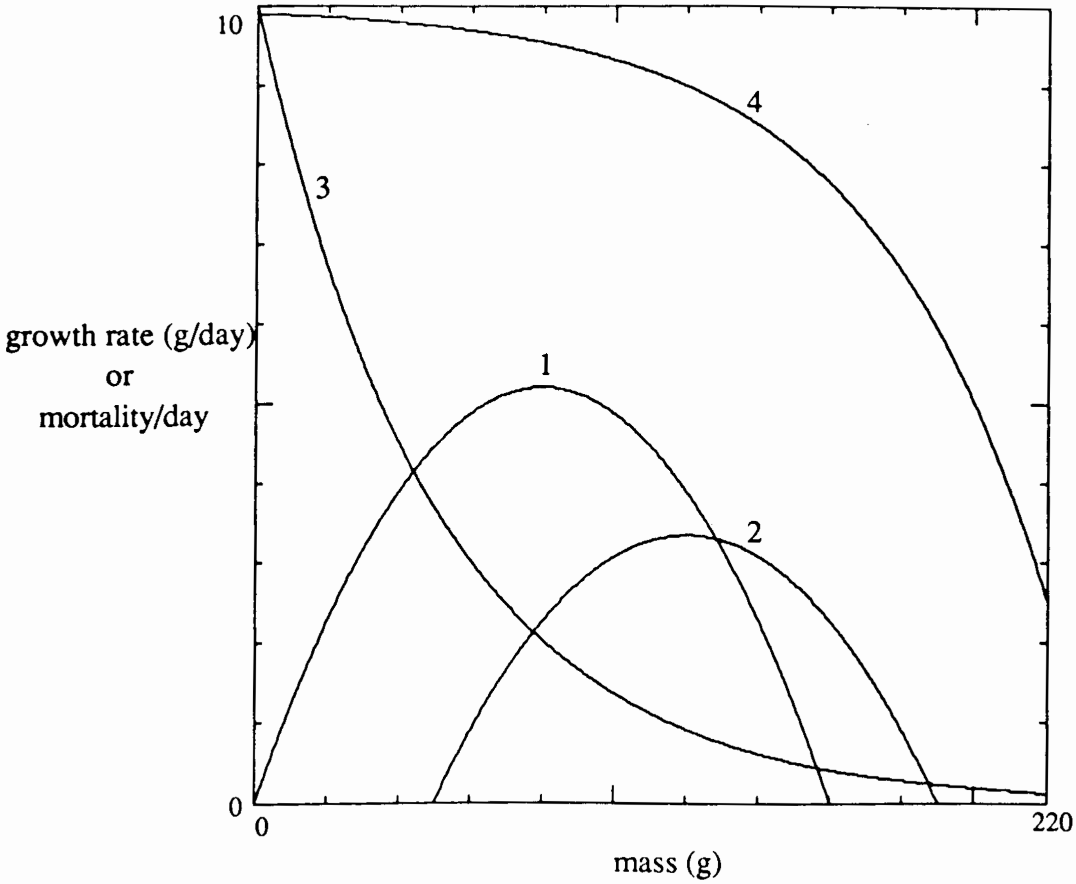

Figure 4.16. Mass-specific growth and mortality rates in the nest and at sea for Cassin's Auklets. The following functions are described in the text: 1 = growth rate in the nest, 2 = growth rate at sea, 3 = mortality rate in the nest, and 4 = mortality rate at sea.

$$\frac{d\mu}{dt} = ae^{-b\mu}$$

$a = 10$; $b = .02$

units: μ (mortality); t (days)

The parameters for this exponential function were estimated from Triangle Island (Fig. 4.2). Mortality due to predation and starvation are included.

4. mass-specific mortality rate at sea:

$$\frac{d\mu}{dt} = -ce^{d(\mu-f)} + g$$

$c = 5$; $d = .02$; $f = 200$; $g = 10$

units: μ (mortality); t (days)

This function lets mortality be greater at sea than in the nest and lets mortality be lower for large nestlings. The implicit assumption is that being bigger has survival advantages.

Mortality rate vs. growth rate curves were constructed for the nest and ocean habitats (Fig. 4.17). Three asymptotes occur at nest asymptotic mass, $x = 160$ g, at ocean asymptotic mass, $x = 190$ g, and at $x = 50$ g, below which juveniles lose weight. Using the 'minimize μ/g rule,' nestlings should fledge at 159 g. Both r_n and K_n were solved as functions of optimal fledging mass (Fig. 4.18). With increasing r_n or K_n, the optimal fledging mass increased, but this was more pronounced with K_n. Adult mass was defined as $K_n + 30$ and the effect of varying K_n was determined. Changing K_n and K_o simultaneously did not differ from the effect of K_n on optimal fledging mass (Table 4.2).

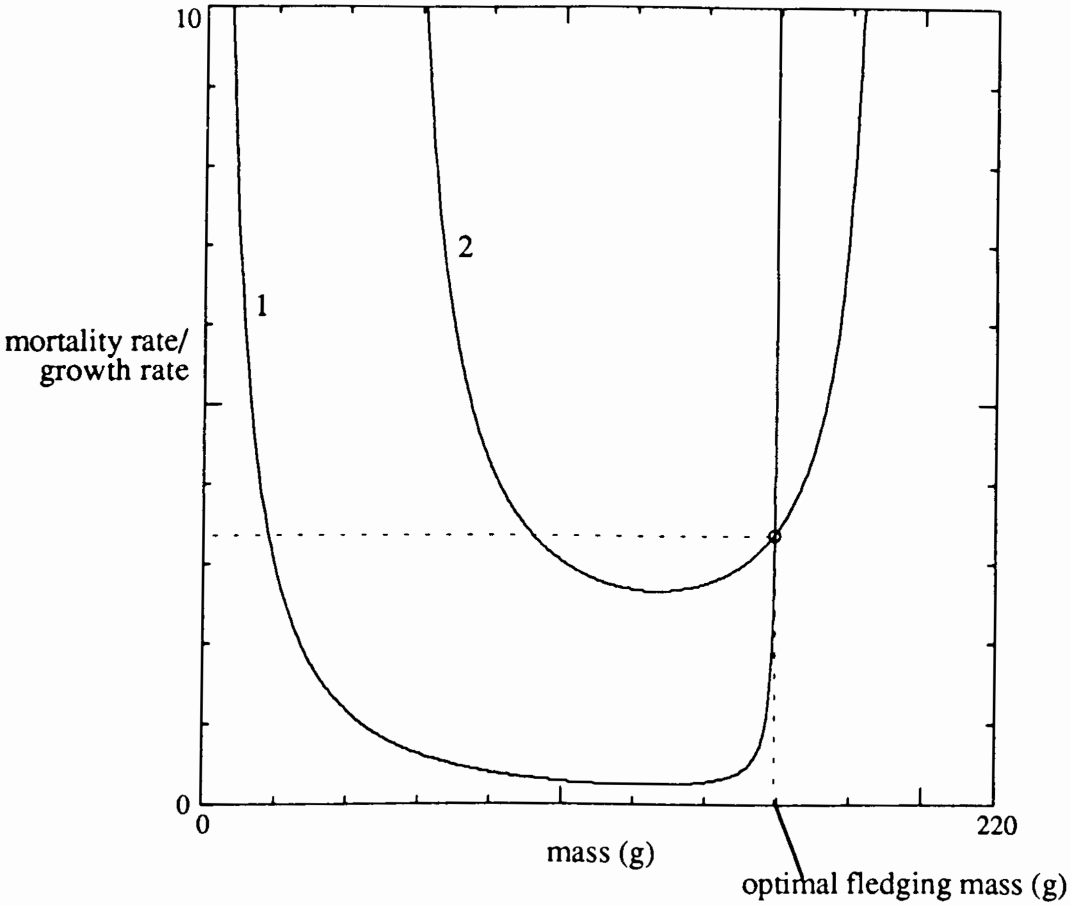

Figure 4.17. Mass-specific mortality rate divided by mass-specific growth rate in the nest (1) and at sea (2), based on curves in Fig. 16. According to the minimize μ/g rule, nestlings should fledge at 159 g.

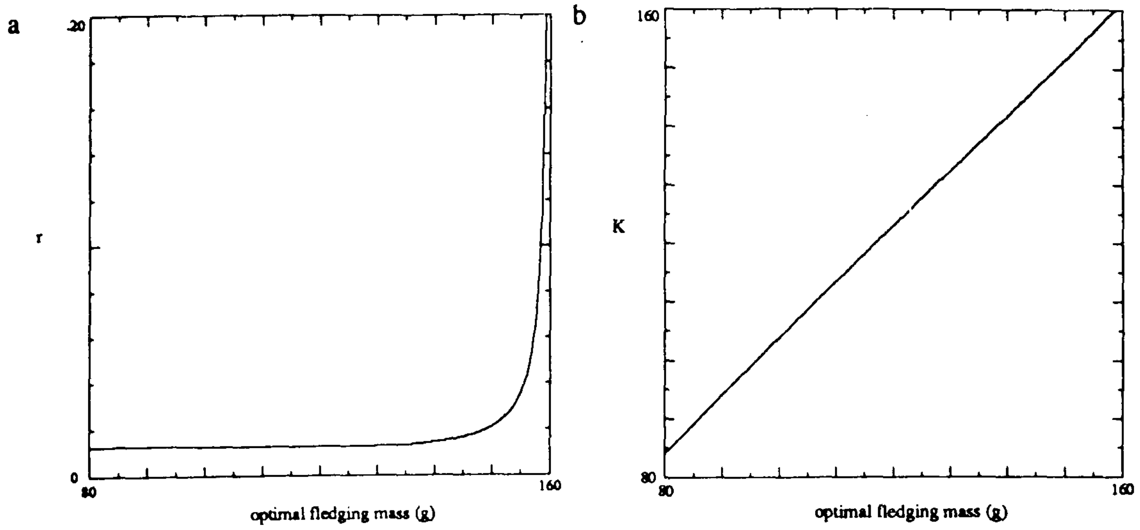

Figure 4.18. Influence of r_n (a) and K_n (b) on optimal fledging mass in the Cassin's Auklet-based Werner-type model using biologically realistic functions. With increasing r_n and K_n, optimal fledging mass increases. In (a), low values of r_n have a greater impact on optimal fledging mass than high values. In both (a) and (b) the equation given by Maple is extremely complicated, and for this reason is not presented.

Table 4.2. Effect of changing both K_n and K_o on the predicted fledging mass in the Cassin's Auklet version of the Werner-type model using biologically realistic functions.. The effect of varying K_n and K_o simultaneously on optimal fledging mass does not differ from the effect of K_n on optimal fledging mass. The asterisk indicates the values used in the original model.

K_n (g)	K_o (g)	Predicted fledging mass (g)	K_o (g)	Predicted fledging mass (g)
140	170	139	190	138
150	180	149	190	149
160*	190*	159	190	159
170	200	169	190	169
180	210	179	190	180
190	220	189	190	190

The 'minimize μ/g rule,' is not the only rule nestlings could employ to maximize their fitness. For example, if nestlings employed a different rule, such as maximizing growth rates in the nest and at sea, optimal fledging mass would be 110 g.

Discussion

The fledging model developed by Ydenberg (1989) and Ydenberg et al. (1995) makes a general prediction about how fledging behaviour should vary over the season and with nestling growth rate. Fledging mass is predicted to decline with fledging date and fast-growing nestlings are predicted to fledge heavier than slow-growing nestlings. Since growth rate is deterministic, a nestling of a given mass will be a specific age. Therefore, fast-growing nestlings will also fledge younger. Modelling exercises show that the seasonal fledging mass decline, predicted for Common Murres and Rhinoceros Auklets, is not predicted for Cassin's Auklets, although the relationship between growth rate and fledging mass still holds. The observations of Cassin's Auklet fledging behaviour on Triangle Island conformed to the predictions of the Cassin's Auklet version of the model. Fledging mass did not decline over the season but fast-growing nestlings fledged heavier and younger than slow-growing nestlings (Ch. 2). A Werner-type model made the same predictions about how fledging behaviour should vary with growth rate. This simpler model was less sensitive to the shape of the growth and mortality functions than the dynamic model.

The decision matrix produced by the dynamic model has limited utility for predicting the optimal fledging mass at every time period. For example, in both models, fledging does not occur until 25 days before the end of the season. In reality, fledging probably occurs over a much greater time range. This result can be understood by considering the deterministic restrictions placed on nestling growth rate in the model. According to the nestling growth function, nestlings cannot grow bigger than the asymptote and there is no limit on fledging age. Early in the season, a nestling at the asymptote will remain at the asymptote, according to the growth function, until reaching the fledging boundary. In reality, the fledging decision must also consider the parents' perspective (Clark and Ydenberg 1990; Ydenberg 1989). The colony is dangerous for parents and they are probably trading off their own mortality against the survival prospects of their nestlings (Ydenberg 1989). It is unlikely that parents will continue to feed nestlings to keep them at asymptotic size. To corroborate this, once nestlings reach an asymptotic mass, they begin to lose mass. Although the reasons for the mass loss are not completely understood, change in parental behaviour, such as reducing the provisioning rate, is probably important.

If early hatched nestlings 'decide' to remain in the nest until reaching the fledging boundary, parents could respond in either of two ways. If parents stopped or reduced provisioning, nestlings would lose weight until it became beneficial to fledge. Alternatively, parents could delay breeding so nestlings growing along a typical trajectory would hit the fledging boundary sooner. Both tactics would reduce the predation costs paid by parents by reducing the total number of visits to the colony.

If time-limitation does not affect the fledging strategy when nestlings are far from the time horizon, a stronger seasonal fledging mass decline may be observed in colonies with short breeding seasons. This would apply to Rhinoceros Auklets but not to Cassin's Auklets, since the model does not predict a seasonal fledging mass decline for Cassin's Auklets.

In the Rhinoceros Auklet version of the dynamic fledging model, fledging mass declines over the season (Ydenberg et al. 1995). This can be understood in terms of the asset protection principle (Clark 1993). Large body size is an asset to a nestling because fitness increases with mass. To protect this asset, nestlings avoid the risky habitat and stay in their relatively safe burrows longer (while growing bigger) before fledging. Late in the season, the benefits of accruing more growth at sea presumably outweighs the mortality cost, and nestlings fledge lighter (and younger). In contrast, the fledging boundary in the Cassin's Auklet fledging model was horizontal, suggesting that fledging behaviour is time-invariant.

The lack of a predicted seasonal fledging mass decline for Cassin's Auklets is most likely caused by two effects. First, the slope of the fledging boundary is strongly affected by the relative magnitude of juvenile mortality compared to nestling mortality. In Cassin's Auklets, juvenile mortality is only marginally greater than nestling mortality, thus, a lack of a negatively sloped fledging boundary is not surprising. However, the magnitude of mortality also influences the slope (Fig. 4.12). Even if the ocean is relatively more dangerous, if mortality is generally low, a horizontal fledging boundary would be predicted. In Ydenberg et al. (1995), the value used for juvenile mortality was .02 and for nestling mortality, .001. With this mortality rate, a negative slope is predicted. In contrast, in Harfenist (1991), Rhinoceros Auklet juvenile mortality rate was calculated as .003 and nestling mortality rate was .0003. Using these values, a horizontal slope is predicted, due to the low magnitude of mortality. Estimates of mortality from mark-recapture data are combinations of mortality due to starvation, mortality due to predation, and emigration. The fledging model treats mortality as the probability of death per day, for a particular growth trajectory. Therefore, mortality due to starvation should not be included when estimating mortality to test the model. When using mortality due to predation only, the fledging boundary becomes more level.

Although the prediction of the seasonal fledging mass decline is sensitive to the parameter values, the prediction of a positive relationship between growth rate and fledging mass is robust. With increasing growth rate, caused either by an increase in r_n or K_n, nestlings fledge heavier. Since the growth is deterministic, fast-growing nestlings also fledge younger. For Rhinoceros Auklets, the position of the fledging boundary was affected differently by r_n and K_n. It is therefore important to know whether intraspecific variation in growth rate is due to variation in r_n, K_n, or both. If the variation is due to r_n, then the seasonal effect will be more pronounced for slow growers. If the variation is due to K_n, a seasonal fledging mass decline is predicted for all nestlings. An important point is that the model predicts multiple fledging boundaries when there is variation in growth rates, not a single fledging boundary. For Cassin's Auklets, regardless of whether intraspecific variation in growth rates are caused by variation in r_n or K_n, a negative relationship between fledging mass and hatching date would occur only if growth rates declined with hatching date.

The Werner-type model of fledging behaviour for Cassin's Auklets has benefits over the dynamic model because it is less sensitive to the parameter values and to the shape of the growth rate functions. In both versions of this model, a positive relationship between growth rate and fledging mass was predicted. Variation in K_n had a linear effect on fledging mass whereas only low values of r_n had a strong effect on fledging mass. When biologically more realistic growth and mortality functions were used in the Werner-type model, the optimal fledging mass more closely matched observed fledging mass (162 ± 12g (151)). The value of adult mass does not affect the optimal fledging mass as long as adult mass is larger than nestling asymptotic mass. Therefore, the hypothesis that nestlings fledge at a constant proportion of their final size is not supported. The insensitivity of the model to the shapes of the growth and mortality functions stresses the importance of the basic underlying tradeoffs between habitat and mass specific growth and mortality rates. The underlying tradeoffs in the dynamic model are the same, but the inclusion time-limitation complicates the model.

The difference between the optimal fledging mass in the Werner-type and dynamic fledging models probably arises from the different methods of calculating fitness. In the dynamic model, fitness, or survival to breeding age as a function of mass, is calculated at the end of the season. In the Werner-type model, fitness is calculated daily. If time-limitation is unimportant, calculating fitness daily would not differ from calculating the cumulative fitness at the end of the season.

A potential problem with the structure of these fledging models could affect their interpretation. The existence of a growth asymptote limits nestling mass. If the model is used to fit data collected on fledging behaviour, then the selective forces molding the particular fledging strategies seen among the Alcidae cannot be inferred. This is because the shape of the growth rate function may be the result of selection acting to optimize fledging behaviour, not a constraint on fledging behaviour. The model can only suggest the importance of size- and habitat-specific growth and mortality rates on the fledging strategy.

The prediction of a seasonal decline in fledging mass is not robust to violations of the model's assumptions. A negatively sloped fledging boundary is always predicted as long as juvenile mortality is higher than nestling mortality, but the magnitude of mortality influences the steepness of this slope. Using a more realistic ocean growth function, for example, letting growth rate decrease monotonically with mass, complicates the tradeoffs and eliminates the prediction of a seasonal fledging mass decline. Harfenist's (1991) observations support a time-limited fledging strategy, but when her parameters are used in the model, a horizontal fledging boundary is predicted. Rather than discounting the model as a explanation for a seasonal decline in fledging mass because of its sensitivity, experimental manipulations can test whether time-limitation is important. The prediction of a positive relationship between growth rate and fledging mass is robust in both the dynamic and Werner-type models.

Chapter V

General summary

The observed phenology and reproductive success of Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island were comparable to previous studies. Hatching dates ranged from 6 May-7 June with peak hatching occurring on 18 May; fledging dates ranged from 13 June-23 July with peak fledging occurring on 1 July. Hatching success was .79 and fledging success was .88.

Some interesting results were obtained concerning egg and nestling mortality. Most of the egg loss occurred after the peak of hatching, indicating that rodents might be specializing on eggs at this time. Most of the nestling mortality occurred in young chicks; there was no direct evidence of predation on nestlings.

Egg size had a slight effect on nestling growth rates, but this was potentially confounded with the effect of parental quality on growth rates. Egg size did not decline over the season. The most interesting result from the analysis of egg size variation was the site effect. Although more study is required, the presence of smaller eggs in the sites at the fringe of the densest part of the colony suggests differences in habitat or parental quality may be important.

The presence and effect of ticks on Cassin's Auklets has not been documented. Ticks were prevalent in areas of the colony with rock or soil; ticks were virtually absent from burrows dug in sand. Tick abundance adversely affected nestlings. Nestlings with a high tick loads had slower rates of wing growth and shorter fledging wing lengths and fledged older.

Nestling growth rates were comparable to previous studies. When a logistic growth curve was fit to the growth data, $r_n = .13$ and $K_n = 166$ g. Mass recession prior to fledging was observed in most nestlings regardless of whether they grew fast or slow.

Both phenotypic and experimental evidence supported a causal relationship between growth and fledging behaviour. In comparison to slow-growing nestlings, fast-growing nestlings generally reached a higher peak mass at a younger age and fledged at a higher mass and younger age. A handling effect, namely a reduction in growth rates, was observed in nestlings that were measured more frequently. Frequent handling is therefore a manipulation of nestling growth rates. Nestlings that were handled more frequently reached peak mass at an older age and fledged at an older age.

Since growth rates declined with hatching date, correlated variation in fledging behaviour was expected. Although fledging age increased with hatching date, fledging mass did not decrease with hatching date. Possibly later in the season, parents compensated for slow growth by feeding nestlings for a longer period of time until they reached optimal fledging mass. If this were the case however, a positive relationship between growth rate and fledging mass would not have been observed.

The variation in growth rates showed a strong seasonal trend. Over most of the season, growth rates declined but at the end of the season, growth rates increased. The cause of the seasonal decline in growth rates could not be determined with either phenotypic or experimental evidence. The experiment that manipulated hatching date had methodological complications and the low sample size precluded the detection of significant effects. Natural variation in age-specific growth was very sensitive to day to day effects, which suggests the importance of fluctuating environmental conditions on growth. However, the analysis of age-specific growth did not support or refute the hypothesis that declining food availability caused the observed seasonal decline in growth rates.

One hypothesis drawn from the results of the experiment is that parents compensate for a forced delay by increasing provisioning rates. This reaction was not anticipated prior to designing the experiment, but the results do indicate that delayed nestlings grew faster than controls. An ultimate explanation for this is that parents consider their own risk of mortality when making provisioning decisions. If mortality is directly proportional to the number of visits to the colony, parents that are forced to incubate eggs longer may compensate by making fewer provisioning trips. By increasing the size of food loads, nestlings would grow faster and fledge younger, which effectively reduces the required number of provisioning visits.

The data did not support the hypothesis of time-constrained fledging behaviour. Modelling exercises showed that the prediction of a significant seasonal decline in fledging mass is sensitive to the parameter values used in the habitat-specific growth and mortality functions. Although a negative sloping fledging boundary is always predicted as long as mortality is greater at sea than in the nest, the both the relative and actual magnitude of mortality affect the slope. When mortality is generally low, or when the sea is only marginally more dangerous than the nest, the slope of the fledging boundary is negligible. In Cassin's Auklets, nestling and juvenile mortality are low and juvenile mortality is only marginally greater than nestling mortality. These two conditions resulted in a fledging boundary with a negligible negative slope.

The dynamic fledging model also predicted that faster-growing nestlings should fledge heavier and younger (Ydenberg 1989). This prediction was robust and was corroborated with field evidence, but was sensitive to the shape of the nestling growth function. A model disregarding time-limitation predicted the same relationship between growth and fledging behavior. This model had advantages over the dynamic model. The magnitude of nestling and juvenile mortality did not influence optimal fledging mass; only the relative difference in nestling and juvenile mortality was important. The trade off between habitat-specific growth and mortality can be easily visualized in this model, and probably as a result, the effect of modelling biologically realistic growth and mortality functions can be interpreted.

The results and conclusions have been drawn from only one field season. Possibly, 1994 was an atypical year in terms of nestling growth and fledging behaviour. Where possible, I compared my results to previous studies of Cassin's Auklets. In general, reproductive success, breeding phenology, and all components of the growth curve were comparable between years and studies. My objective was to study the effects of environmental conditions and nestling growth patterns on fledging behaviour. The real question is whether these effects on fledging behaviour are consistent between years and studies.

If fledging behaviour doesn't vary as predicted given a set of environmental conditions, perhaps the fledging strategy does not respond to small scale temporal fluctuations in environmental conditions. This would be true if the fluctuations cannot be detected by nestlings or adults. For example, nestling mortality could generally be lower than juvenile mortality when compared over many years. If nestling mortality was higher than juvenile mortality in one year, it is questionable whether fledging behaviour would match predictions for that year. The missing information is how environmental variation is transformed into phenotypic variation (the reaction norm) (Stearns 1989). Also missing is how the environment and genotype interact to produce the phenotype. Inter-colony and intra-annual comparisons would certainly help to elucidate how flexible the fledging strategy is in relation to environmental conditions. Also, more data would increase the power to detect how environmental conditions influence fledging behaviour.

Unfortunately, previous studies on Cassin's Auklets often did not focus on these questions and there is clearly a lack of data for comparison. From Ainley et al. (1990), the only data I can compare are the general seasonal patterns in growth and fledging behaviour, which they combined for eight years. Little inter-annual variation was evident in the shape of the growth trajectory, but asymptotic mass (calculated by fitting a logistic curve to the growth data) declined with hatching date. Since there was a seasonal decline in asymptotic mass, growth rates (measured during the linear growth phase) probably declined with hatching date, but this information is not presented. A negative relationship between fledging mass and fledging date was observed, and in contrast to what I found, fledging age decreased with hatching date. No information was presented on how nestling growth affects fledging mass and age. This is an insufficient amount of data to determine whether the effect of nestling growth on fledging behaviour was typical for Cassin's Auklets. Also, the effect of environmental conditions on fledging behaviour is mostly theoretical. The most critical missing information is how environmental conditions on the colony and at sea differ between colonies, years, and over the season, and how this affects fledging behaviour.

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