THE PROVISIONING OF NESTLINGS BY PARENT RHINOCEROS AUKLETS

(CERORHINCA MONOCERATA)

by

**Douglas Frank Bertram**

**B.Sc., University of Victoria, 1984**

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biological Sciences

© Douglas Frank Bertram 1988

SIMON FRASER UNIVERSITY

January 1988

APPROVAL

Name:     Douglas Frank Bertram

Degree:   Master of Science

Title of Thesis:

The Provisioning of Nestlings by Parent Rhinoceros
Auklets, (Cerorhinca monocerata).

Examining Committee:

Chairman:

Dr. R.C. Ydenberg, Assistant Professor,
Senior Supervisor

Dr. A.S. Harestau, Assistant Professor

Dr. K. Vermeer, Research Scientist, Canadian
Wildlife Service

Dr. B.D. Roitberg, Assistant Professor,
Biological Sciences Dept., Simon Fraser
University,  Public Examiner

Dr. N.A.M. Verbeek, Associate Professor,
Biological Sciences Dept., Simon Fraser
University, Public Examiner

Date Approved     JAN 15 1988

Title of Thesis/Project/Extended Essay

The Provisioning of Nestlings by Parent Rhinoceros Auklets

(Cerorhinca monoceata)

_____

_____

_____

Author

(signature)

_Doug Bertrum_
(name)

_15 January, 1988_
(date)

# ABSTRACT

Parental provisioning of nestling rhinoceros auklets (Cerorhinca monocerata) was studied on Lucy Island, B.C. from 1985 to 1987. There was considerable inter-year variation in the amount of food delivered as chicks aged. In 1985 the amount of food delivered to chicks in the latter half of their nesting period dropped off sharply and continued to decline until fledging. A similar reduction in provisioning was noted for chicks of the same age range in 1986, although the rate of decline was much less than in 1985. In 1987 no decline in provisioning occurred with chick age, although the data combined for all years indicate that this trend is significant. No consistent differences were observed in the size of food loads delivered to early and late hatched chicks of the same age, suggesting that a seasonal decline in food availability was not the cause of the reduced pre-fledging feeding rate. I suggest the decline in provisioning is the manifestation of a parental life history tactic in which adults increase their probability of survival by making fewer visits to the colony when chicks are older.

Chick growth rates decreased from 1985 to 1987. Independent evidence suggests that growth rates of nestling rhinoceros auklets can act as an indicator of marine feeding conditions. Inter-annual differences in the amount of food delivered as chicks aged are hypothesized to result from variations in food availability, inferred from the measurements of chick growth

rate.

Chick exchange experiments in 1986 did not induce parents to change the amount of food delivered to either larger or smaller foster chicks. In a more extensive experiment in 1987, parents delivered less to small foster chicks and more to larger chicks when young and middle aged chicks were exchanged. As in 1986, parents did not respond to foster chicks of the middle to late age range by changing food deliveries. These results are discussed in terms of parent-offspring conflict.

# ACKNOWLEDGEMENTS

To my father

## TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER I

## GENERAL INTRODUCTION

Life history characteristics in seabirds have been well documented (e.g. Lack, 1968). Single-egg clutches, long incubation spells and extended periods between chick feedings, slow embryonic and posthatching growth and great variability in chick weight are traits shared by seabird families in three avian orders: the Procellariiformes, Pelecaniformes and Charadriiformes. These features have often led ecologists to infer that food resources for reproduction in pelagic seabirds, especially tropical species, are sparse, distant, variable and unpredictable (Ricklefs, 1985).

A great deal of attention by avian ecologists has focused on the slow and prolonged development of chicks. It has been explained by at least five hypotheses. The energy limitation hypothesis, associated primarily with Lack and his co-workers, suggests that slow growth is an adaptation that reduces energy requirements of the chick in the face of a restricted food supply (Lack, 1968; Ashmole, 1971; Harris, 1977; Nelson, 1977). The precocity of development hypothesis states that slow growth rate is a by-product of selection for the early development of mature function in many tissues (Ricklefs, 1979a; Ricklefs and White, 1981; Shea and Ricklefs, 1985). A third hypothesis states that due to the high survival and potentially long lives of many seabirds, adults are selected to invest relatively little in any single breeding attempt in order to safeguard their reproductive

future. Chicks grow slowly as a result (Williams, 1966b; Goodman, 1974). Ricklefs (1979a) proposes that the ratio of certain essential nutrients to energy in the diet may not be enough to support rapid chick growth. Ricklefs reasoned that by slowing growth, a chick reduces the ratio of nutrients necessary for growth to total energy required for growth and maintenance. Shea and Ricklefs (1985) address this hypothesis but conclude that it was unlikely to be true since closely related species with similar diets exhibit both rapid and slow growth. Finally, it has been suggested that slow growth may be an outcome of relaxed selection for rapid growth, due to the absence of sibling competition in single-egg nesters (Werschkul and Jackson, 1979).

These five hypotheses about slow growth can be divided into two groups. Lack's energy limitation hypothesis, and Williams' life history hypothesis both imply that parents provision according to a schedule that has evolved to maximize their own fitness, and that the slow growth of their chicks is a by-product of selection on adult behaviour. In contrast, Ricklefs' hypotheses and the sibling competition hypothesis of Werschkul and Jackson (1979) imply that parental provisioning has evolved primarily in response to selection pressures on the chick.

Lack's energy limitation hypothesis implies that parents are working as hard as they can in a food limited system to provision their chicks. The limit to provisioning rate is viewed

2

as being set by selection for parental ability. Twinning experiments show that adults usually fail to rear both chicks. Other experiments, involving the removal of one of the parents, showed that a lone parent could not rear a chick. Both types of experiment have been widely considered as evidence in support of Lack's hypothesis (Alcidae: see Birkhead and Harris, 1985; Procellariiformes: Rice and Kenyon, 1962; Harris, 1966). In a recent cross-fostering experiment Shea and Ricklefs (1985) substituted the eggs of the large (175 g) sooty tern (Sterna fuscata) into the nests of the smaller (150 g) but closely related gray-backed tern (S. lunata). Adult gray-backed terns worked much harder than usual, increasing food deliveries to their foster chicks by 30%. Shea and Ricklefs (1985) reason that twinning represents too large a demand on parental work load, and for this reason earlier studies failed to demonstrate the ability of adults to work harder than they normally do. Based on their finding that adult gray-backed terns can increase their provisiong effort in excess of normal rates, Shea and Ricklefs rejected Lack's energy limitation hypothesis.

Ricklefs (1979a) proposes an alternative hypothesis. The idea is based on his discovery (Ricklefs, 1973, 1979a,b) of a general inverse relationship between growth rate and the acquisition of mature function by tissues. Muscle cells that differentiate for thermogenesis or mobility are removed from the pool of proliferating cells thus lowering the growth rate. Ricklefs (1979a; Ricklefs and White, 1981) reasons that there are often selective pressures for precocial development in

3

seabirds (mobility, thermogenesis) leading in turn to a slow growth rate. Consequently, parents are able to easily meet the needs of their chick.

However, there are other reasons why seabird parents may work at a level below their capacity. The cost of reproduction (see Reznick, 1985 for a review) or William's principle (c.f. Sargent and Gross, 1986) states that natural selection favours animals that maximize their lifetime reproductive success, subject to the trade-off between reproductive effort (e.g. chick provisioning) and somatic effort (the proportion of resources devoted to the parent's own growth and survival and hence potential future reproduction). Given this life history perspective the following statement by Shea and Ricklefs (1985) can be addressed. They write "Increased foraging rate may stress adult gray-backed terns or expose them to increased risk of death and therefore decrease lifetime expected reproduction. If this were true, slow chick growth could be selected in order to ensure high adult survival (Williams, 1966a; Goodman, 1974). Although adult stress and risk are difficult to measure, the fact that gray-backed terns sustained high rates of food delivery for more than a month argues against this hypothesis". The dismissal of the adult survival hypothesis based on the fact that foster parents were able to work harder for a long time overlooks the way in which reproductive costs may be incurred. For example, the foster parents may have sacrificed body condition in order to maintain high feeding rates. Nur (1984a, b) has shown that in the blue tit, Parus caeruleus, weight loss

4

during the nestling period increased linearly as feeding frequency increased, that females that fed most often were lightest and that the lightest females were least likely to survive to the following year. However, the costs incurred by reproducing need not be physiological (Lima, 1987). Costs can take the form of any risk that jeopardizes survival, such as the risk of predation or injury. Charnov (1986) depicts the relationship between adult survival and parental resource gathering effort as a trade-off with survival decreasing as effort increases. In species that are long lived and have low mortality outside the breeding season, there should be strong selection to reduce the chance of mortality during a breeding season. This view would predict that parents should not work as hard as they can to raise a single chick, if in doing so they risk their future.

In iteroparous species rearing a single young, such as most seabirds, the parents face a trade-off between their single present offspring, and their reproductive future. The level of investment in any individual chick (i.e. year) will depend on the marginal costs and benefits of additional effort. Parents may increase investment when the expected fitness benefit (a fitter chick) compensates the expected cost arising from the risks they undertake and resources they expend. Consequently, we can in general expect that the interests of both offspring and parents will play a role in shaping the provisioning schedule. From this perspective chicks grow slowly due to a low rate of parental provisioning, and yet parents have the ability to

5

increase the provisioning rate.

The aim of this thesis is to examine the explanatory power of Lack's energy limitation hypothesis, Ricklefs' precocial growth hypothesis, and the life history perspective to account for the provisioning pattern observed in a temperate, colonial, burrow-nesting seabird, the rhinoceros auklet (<u>Cerorhinca monocerata</u>).

I compared chick growth in three large colonies on the British Columbia coast in 1984-86. The main part of my study focused on parental provisioning and chick growth on one colony in the years 1985-87. I measured the provisioning rate in each of these years, and considered the data on growth and provisioning in relation to the predictions made by the three hypotheses. As further tests I conducted a supplementary feeding experiment in 1985 and a series of fostering experiments in 1986 and 1987.

# CHAPTER II

## GENERAL METHODS

### Study Species

A member of the Alcidae, the rhinoceros auklet is actually a puffin (tribe Fraterculini), related to the tufted (Lunda cirrhata), horned (Fratercula corniculata) and Atlantic puffins (Fratercula arctica; Storer, 1945; Strauch, 1985). Despite its common name the rhinoceros auklet is not a true auklet (tribe Aethiini). Rhinoceros auklets are confined to the Pacific Ocean with colonies in Japan, Alaska, British Columbia, Washington, Oregon and California (see Vermeer, 1979). Its breeding biology and natural history have been documented in a number of studies (Richardson, 1961; Leschner, 1976; Wilson, 1977; Summers and Drent, 1979; Vermeer, 1979; Hatch, 1984; Wilson and Manuwal, 1986). The rhinoceros auklet is colonial and piscivorous, and lays a single egg clutch in a burrow. Egg laying occurs between 30 April to 7 May in Washington state (Wilson and Manuwal, 1986) and between 5 June and 20 July in Alaska (Hatch, 1984). Eggs are incubated from 39 to 52 days with an average of 45 days and following hatching, the downy chicks are brooded, on average, for four days (Wilson and Manuwal, 1986). Rhinoceros auklets "fly" underwater to catch fish which they feed their chicks. A parent may deliver one very large fish (up to 55 g, pers. obs.) or up to 20 smaller fish carried cross-wise in its bill. In British Columbia, Pacific sandlance (Ammodytes hexapterus) is

7

the dominant prey species although Pacific herring (Clupea harengus) and rockfish (Sebastes spp.) are also common prey, among a variety of others (see Vermeer and Westrheim, 1984). Prey composition may vary within seasons (eg. Vermeer, 1980), between years, and between colonies (see Vermeer and Westrheim, 1984; Bertram and Kaiser, in prep). Parents provision their chicks at night (but see Thorenson, 1983). Adults remain on the colony during the dark hours and depart before sunrise (see Wilson and Manuwal, 1986). Parents generally make one trip each to the burrow every night, although Richardson (1961) reports instances of three visits to a single burrow in one night. Some nights however, neither parent visits and chicks receive nothing (pers. obs.). Growth rates of rhinoceros auklet nestlings are among the slowest in the Alcidae. Chicks fledge at 51-80 percent (250-400 g) of adult weight (Vermeer and Cullen, 1979; pers. obs.) between 45-60 days of age. The young complete their development at sea following fledging. Band returns suggest that rhinoceros auklets from British Columbia winter in the waters off California and Oregon (e.g. Kaiser et al., 1984).

## Study Site

My study was conducted on the Lucy Islands (54° 18' N; 130° 37' W), an archipelago of small, low-lying, heavily forested islands located in Chatham Sound, 18 km west of Prince Rupert, British Columbia. Approximately 21,000 breeding pairs of rhinoceros auklet nest on the islands, spread over most of the

larger treed islands (Figure 2.1). The flora and fauna on Lucy Island are described by Bertram and Kaiser (in prep.). The islands have no mammals, other than a pair of river otters (Lutra canadensis). The otters have never been recorded preying on auklets. Avian predators, however, are relatively common. Although they do not breed on the Lucy Islands, up to 30 bald eagles (Haliaeetus leucocephalus) have been seen on the colony at one time. Eagles have been disrupted from warm carcases at night (pers. obs.) and I infer that they prey directly on rhinoceros auklets (see also DeGrange and Nelson, 1982).

As part of an intercolony comparison, data were collected in 1984-86 at two other rhinoceros auklet colonies. Pine Island (50° 58' N; 127° 41' W) is heavily forested and low-lying, with an estimated 50,000 breeding pairs. It is 10 km from the north-east end of Vancouver Island, and is immediately adjacent to the Storm Islands, where an estimated 60,000 pairs breed. Triangle Island (50° 52' N; 129° 05' W), the outermost of the Scott Island Group, is an exposed, treeless, steep-sloped island 40 km from the north-west tip of Vancouver Island. It is B.C.'s largest seabird colony and contains about 20,000 breeding pairs of rhinoceros auklets among a half million pairs of other seabird species.
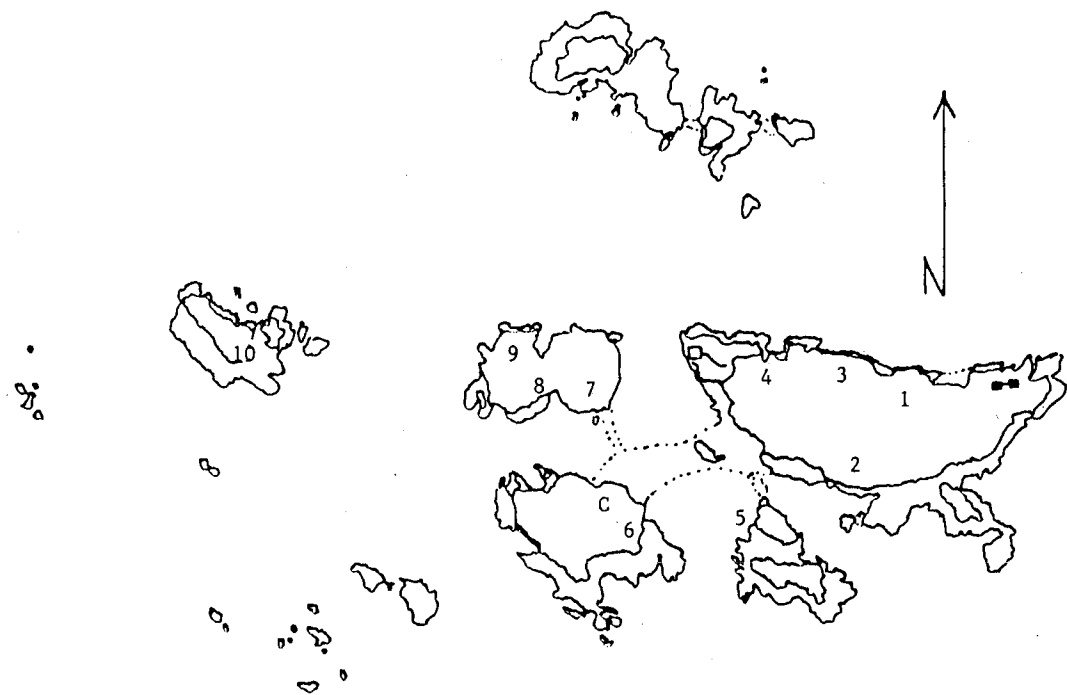
Figure 2.1: The Lucy Islands archipelago (1:12400) showing the
10 study areas, and the location of the camp (C).

## Study Methods

In each year (1985-87) I arrived on the colony in late June and departed in late August. I made my camp in the forest on an uninhabited island where the nesting density of birds was relatively low. Each day I visited a series of rhinoceros auklet burrows to perform tasks pertaining to various experiments (see below). Rhinoceros auklet nesting burrows on the Lucy Islands range from one to five m in length. Many are intricate, with branching tunnels and multiple entrances. The tunnels range from one cm to over one m deep, and frequently go under roots or open into underground caverns at the base of trees. I excavated burrows using a trowel and a pair of pruning clippers to cut through small roots. Consecutive holes were dug along each burrow until the nest chamber was discovered. The access holes were always recovered with sticks or cedar shingles and dirt. Incubating adults tended to desert their nests if disturbed too often, but once the egg hatched the parents were very resistant to disturbance. Burrows were assigned a number and marked with flagging tape. Permanent aluminum tags were also placed at the entrance to each burrow. Chicks were removed and weighed to the nearest two g on an OHAUS Lume-o-gram electronic balance (model D1001 or D1001 0A). To determine the age of chicks, the wing lengths of a sample of known-age chicks were measured in 1985. The flattened wing was measured from the wrist to the fleshy tip, pin or feather tip, depending on the age of the chick. Wing length is a reliable indicator of age since it varies little

11

between fast and slow growing birds (in terms of weight gain) within or between seasons (Asbirk, 1979; Vermeer and Cullen, 1979). I studied chick growth by visiting burrows every fifth day from the initial encounter until fledging, or until I left the colony. To facilitate comparisons of chicks of the same age at different times in the season, I grouped chicks that were of the same age (within five days) on 31 July. I refer to the age of a nestling on 31 July as the standard age. Chicks were ringed with red plastic bands to denote previous handling and fitted with U.S. Fish and Wildlife stainless steel bands after reaching 200 g. In 1986 and 1987 I attempted to establish groups of early and late hatched chicks separated by about 10 days. A 10 day period was chosen because it was the longest period of time between which I could assign the greatest number of chicks to early and late hatched groups.

I visited burrows in 10 areas among the islands although the majority of chicks were located in areas 1 and 2 (Figure 2.1). Most areas could be reached on foot at low tide except for area 10 which required a Zodiac boat.

I collected food samples by capturing adults at night as they visited the colony with fish for their young. Samples from individual adults were referred to as "bill loads", and were placed in separate plastic bags for later identification and measurement.

A second method for examining the food of nestlings involved fitting chicks with nylon hoods equipped with drawstrings to

12

prevent removal (Hatch, 1984). I used two sizes of hoods, depending on the size of the nestling. All hoods had breathing holes cut at the level of the nostril. Parents visiting hooded chicks left the fish intended for the chick in the burrow. The morning following hooding, these fish were located, measured and then fed to the chicks. I called these fish a "burrow load" (Hatch, 1984). A burrow load could be composed of one, two, or occassionally three bill loads. (Sometimes parents did not visit, and so a burrow load could be zero). In 1985 16 of the hooded chicks apparently wandered out of their burrows to their demise. One hood was later found near the burrow entrance among a downy feather pile - the pluck site of a bald eagle. To avoid this problem in 1986 and 1987 hooded chicks were tethered in the nest chamber by a 15 cm piece of nylon mason cord attached to a bird band on the leg, and secured to a peg which was firmly planted in the ground. This method proved very successful in preventing wandering and appeared to have no adverse affects on chicks or provisioning by adults.

Burrow loads were plotted against chick age in each year. A second degree polynomial equation was fitted to these data, and referred to as a 'provisioning curve'. In this study (Chapter 3) and in other studies of Alcids (eg. Ashcroft, 1979; Harris and Hislop, 1978; Hudson , 1979; Cairns, 1987; Emms, 1987) chicks often received progressively less food in the later phase of development as they approached fledging. A second order polynomial provides an equation flexible enough to describe all of the shapes of provisisioning curves that have been observed.

In addition, the $X^2$ term of a second order polynomial provides a measure of the rate of decline in the provisioning rate as chicks age, a phenomemom particularly important in developing the ideas in this thesis.

I also constructed composite growth curves, as outlined by Ricklefs and White (1975), in order to facilitate comparisons between Lucy, Pine and Triangle Islands between years. This technique involves locating a sample of nestlings from a wide developmental range and measuring their wing lengths and weights on the same day. After a short period of development (I chose 10 days) the nestlings are remeasured. Using wing length to estimate age, a mass-age relationship or composite growth curve representing a hypothetical chick is constructed. I chose to fit straight lines to the composite growth data from each year.

A second technique used to study · growth rates within and between seasons on Lucy Islands involved measuring the weights of chicks every five days from the time of discovery until fledging or until I departed from the colony. I refer to this technique as 'sequential growth' measurements.

# CHAPTER III

## PROVISIONING BY PARENTAL RHINOCEROS AUKLETS

### INTRODUCTION

The provisioning of nestlings in the Alcidae has usually been studied by recording either feeding frequencies or bill loads, but rarely both (e.g. rhinoceros auklet - Cody, 1973; Vermeer and Westrheim, 1984; Wilson and Manuwal, 1986; Atlantic puffins - Cody, 1973; Corkhill, 1973; Nettleship, 1972; Wehle, 1983; Barrett et al., 1987). A complete data set has been provided by Ashcroft (1979) for Atlantic puffins on Skomer, Wales. She found that food delivery increased until the chicks were 24-28 days old and decreased thereafter until fledging at about 40 days of age (Figure 3.1). Other researchers studying Atlantic puffins have found similar results. Harris and Hislop (1978) noted that older young receive less food, since bill load weight remains constant throughout the breeding season and feeding frequency declines. Hudson (1979) reported a steady decline in the quantity of food delivered to Atlantic puffin chicks after about 26 days of age. Information on nestling provisioning has also been provided for members of the genus Cepphus. Emms' (1987) study of pigeon guillemots (Cepphus columba) showed a decrease in delivery rates in the second half of the fledging period, and noted that this reflected a true decline in feeding rate since the size of fish delivered did not increase. In the black guillemot (Cepphus grylle) estimated
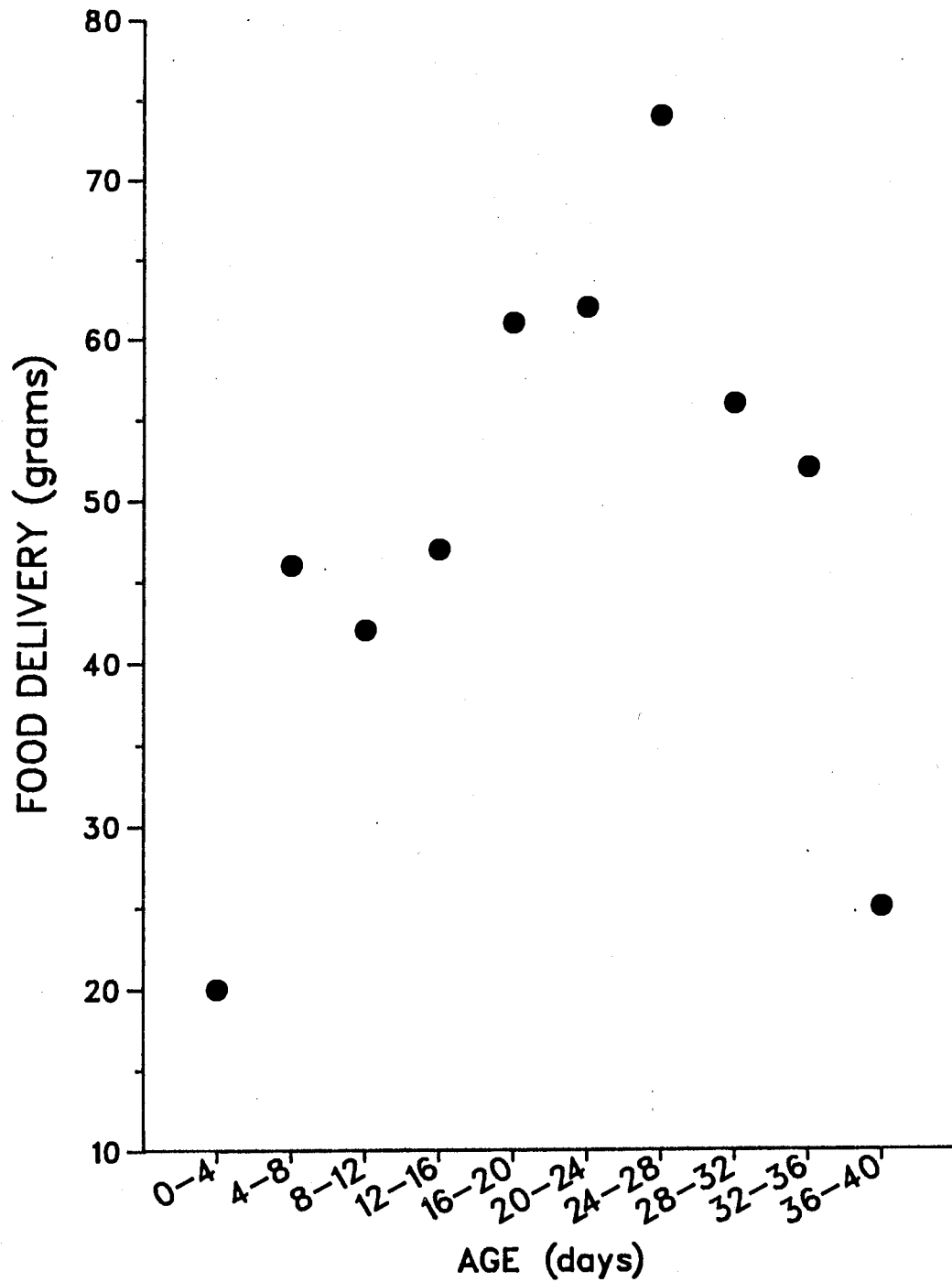
Figure 3.1: Mean weight of food (fish) delivered to wild
Atlantic puffin nestlings in relation to age. Drawn
from data in Ashcroft (1979).

daily food delivery rose from 80-85 g for three day old chicks, to 140 g for chicks 25 days old, then declined from this point to about 130 g until fledging at approximately 35 days old (Cairns, 1987).

In the Procellariiformes, seabirds with a breeding biology similar to many of the Alcidae, greatly reduced feeding rates during the latter part of the chick rearing period have been associated with the prolonged period of weight recession prior to fledging exhibited by many species (Lack, 1968).

These studies indicate that a decline in feeding rate is widespread among seabirds. Anecdotal observations of the rhinoceros auklet also suggest a decrease in feeding frequency before fledging (Richardson, 1961). There are a number of possible explanations for this apparent decline in the provisioning rate of older chicks.

*The Environmental Hypothesis*

The first and probably most commonly invoked explanation is that this phenomenon is a reflection of marine feeding conditions. This hypothesis suggests that the availability of food close to the breeding colony is reduced, either because of seasonal trends in the abundance of prey species, or because birds feeding in the immediate vicinity of the colony exhaust food supplies (e.g. Burger, 1980). Consequently, older chicks tend to be fed at a lower rate. The idea that food supplies decline has also been used to account for other aspects of

seabird breeding biology, such as the seasonal decline in egg and chick weights among razorbills and murres (Birkhead and Nettleship, 1982). These ideas clearly stem from Lack's original energy limitation hypothesis - the idea that parents are working as hard as they can to provision chicks, and that provisioning rate therefore directly reflects ocean feeding conditions. The prediction of this hypothesis to be tested in this chapter is that if there is a seasonal decline in food availability or abundance, chicks hatched later in the season should receive less food at each developmental stage than early hatched chicks. Chapter 4 will examine the growth of 'early' and 'late' hatched chicks.

*The Precocial Growth Hypothesis*

A second explanation for the decline in provisioning rate is based on Ricklefs' (1979a) precocity of development hypothesis for slow growth in seabirds. Under this scenario, the parental provisioning rate reflects chick needs rather than the vagaries of the environment. Therefore the decline in provisioning rate late in the chick rearing period reflects the decreasing energy demands of the nestling. There is some evidence that energetic demands decrease. In the pigeon guillemot the daily energy requirement (BMR plus energy stored in body components) increases to about 1670 KJ/day at 20 days old and then declines to 1255 KJ/day at fledging (Koelink, 1972). Similarly, in the dark-rumped petrel (<u>Pterodroma</u> <u>phaeopygia</u> <u>sandwichensis</u>), the energy budget reaches a peak of about 600 KJ/day in the middle

of the developmental period, then falls to 400 KJ/day by fledging at approximately 110 days old (Simons and Whittow, 1984). Further support for the idea of reduced energy demand by older nestlings comes from work on experimental feeding of Atlantic puffin chicks. Harris (1978) and Hudson (1979) showed that nestlings fed ad lib consumed a constant amount of food, on average, until they reached 30 days old after which intake dropped sharply until fledging. However, it should be noted that while wild chicks were fed at a diminishing rate, the quantity of food consumed by captive chicks during the same period was much greater at all times than their wild-fed counterparts (Hudson, 1979).

The precocial growth hypothesis explains the decline in provisioning rate on the basis of declining chick needs, and it implies that parents can easily meet the needs of their chick. Consequently, this hypothesis predicts that provisioning of chicks should be similar in all years. If ocean feeding conditions are poor in a given year, parents can increase their work effort to satisfy their offspring's requirements.

*The Parental Tactic Hypothesis*

A third explanation for the decline in provisioning rate is that it represents a parental tactic. This idea is based on the theory of life history evolution (Williams, 1966a; Stearns, 1980) which postulates that natural selection will favor behaviours which maximize lifetime reproductive success. Thus, natural selection has led to the evolution of a set of

reproductive decision rules for breeding birds, which in turn lead parents to decrease the provisioning rate to nestlings late in the developmental period.

The theory of parent-offspring conflict (Trivers, 1974) shows that young are selected to demand more investment than parents are selected to give. The theory predicts parents should invest increasingly less in offspring as they approach independence thereby forcing offspring to look after themselves. This is because the returns on parental investment in terms of enhancing offspring survival decline as chicks complete their development. Davies (1976, 1978) referred to this progressive reduction in investment as parental 'meanness', analogous to weaning in mammals. Implicit in the idea of changes in the parental provisioning rate as a reproductive tactic is the understanding that the final outcome in any given breeding season may be different, depending on environmental conditions (Davies, 1978).

The objective of the research described in this chapter is to examine parental provisioning of nestling rhinoceros auklets, both within and between seasons, in an effort to evaluate the validity of the three above hypotheses. My general approach involved comparing provisioning rates of 'early' and 'late' nesting birds within each season, to see if late nestlings were fed less, which would suggest a seasonal deterioration in feeding conditions.

METHODS

The principal technique used in this part of the study was hooding, which allowed me to obtain burrow loads delivered by parents to rhinoceros auklet chicks on any given night. In 1985 a wide developmental range of nestlings (24 day span) was used in the hooding study. The experiment began with 45 chicks but in the course of the study 16 nestlings were lost. In 1986 and 1987 I attempted to establish distinct samples of 'early' and 'late' hatching birds with about a 10 day spread between the two groups. In 1986 the early sample consisted of 19 birds of roughly the same age, although due to a shortage of chicks the late sample was small (nine) and the age range large (15 days). In 1987 I established distinct 'early' and 'late' samples, exhibiting a 10 day spread in age with little variation in age within each group. There were 16 birds in the early group and 17 in the late.

Experimental chicks were hooded once every five nights from the onset of the experiment until they fledged. Chicks were hooded in the evening between 1700 and 2200 hrs. The following morning the nestlings were unhooded and the uningested fish collected by systematically checking all tunnels of the burrow through previously formed access holes. Following washing and measurement of the fish, chicks were fed their intended meal. In 1985 fish from burrow loads were measured from snout to tail notch on a fish plate (a piece of metric graph paper sandwiched between two sheets of clear plexiglass). Using a weight-length

regression from samples collected the same year, the total weight of fish in the load was later calculated. The same method and regression equations were used in 1986. In 1987, in addition to measuring fish length, the entire burrow load was weighed to the nearest two g. Comparison of the weights estimated using the two methods indicated no significant difference between them.

To estimate the number of bill loads in a burrow load, we collected bill loads by capturing adults on the colony at night as they returned with fish for their young. Sampling was never conducted in an area where experiments were underway, and I tried to separate repeat samples from the same area by about one week to reduce disturbance to the birds.

For each year a provisioning curve was established by using a second degree polynomial equation to describe the relationship between burrow load and chick age. The burrow load data from all years were also pooled and subjected to this curve-fitting routine. To test for differences between burrow loads fed to chicks of similar age, early and late in the season, I compared groups of chicks of different standard ages (see General Methods). I ranked the burrow loads fed to chicks in these different standard age groups over five day increments from 10 days old to fledging. Then choosing the widest developmental range that encompassed the greatest range of standard age groupings, I compared burrow load rank in relation to standard age using Friedman's method for randomized blocks (outlined by Sokal and Rohlf, 1981, pp. 445-447). If later hatched chicks are

fed smaller loads than early hatched chicks, the rankings of burrow loads should be consistently low for nestlings with the smallest standard ages. Tests for differences in bill loads throughout the season were conducted using ANOVA followed by a Student-Newman-Keuls multiple range test if necessary. Unless stated otherwise the significance level for all tests was 0.05.

## RESULTS

A frequency histogram of all 790 burrow loads collected from 1985 to 1987 is shown in Figure 3.2. Burrow loads range in size from zero to 116 g although the modal load is about 30 g, the average size of a bill load (see below).

There were considerable differences in the pattern of burrow load deliveries as chicks aged between years. In 1985 burrow loads increased with chick age and peaked at around 30 days of age, after which they steadily declined (Figure 3.3). In 1986 the burrow loads delivered to young chicks were larger and remained roughly constant until chicks were about 45 days old, after which they declined (Figure 3.4). In 1987 there was no decline in the size of burrow loads as chicks approached fledging (Figure 3.5). The provisioning curves (second order polynomial equations fitted to the relationship between burrow load and chick age) are shown for each year in Figure 3.6. (The provisioning curves were fitted to all the data, and not to the group means shown in Figures 3.3-3.5). The decline in burrow loads near the end of the season in 1985 and 1986 are shown to

23
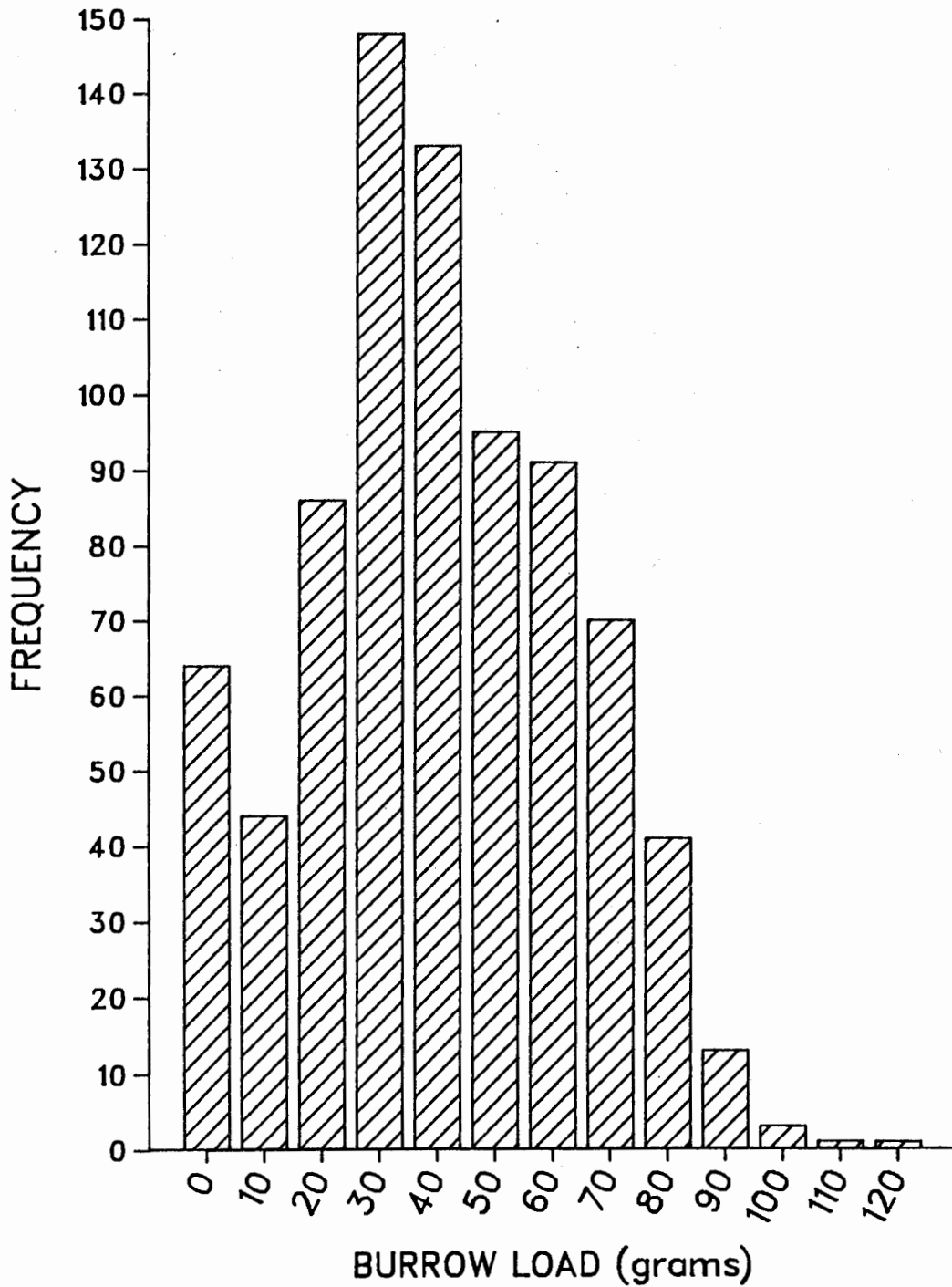
Figure 3.2: Frequency histogram of all 790 burrow loads delivered to hooded chicks in 1985-87. The burrow loads are grouped into blocks of 10 grams each, the numbers along the axis (except zero) represent the midpoint of the group. Zero represents burrow loads ranging from zero to five g.
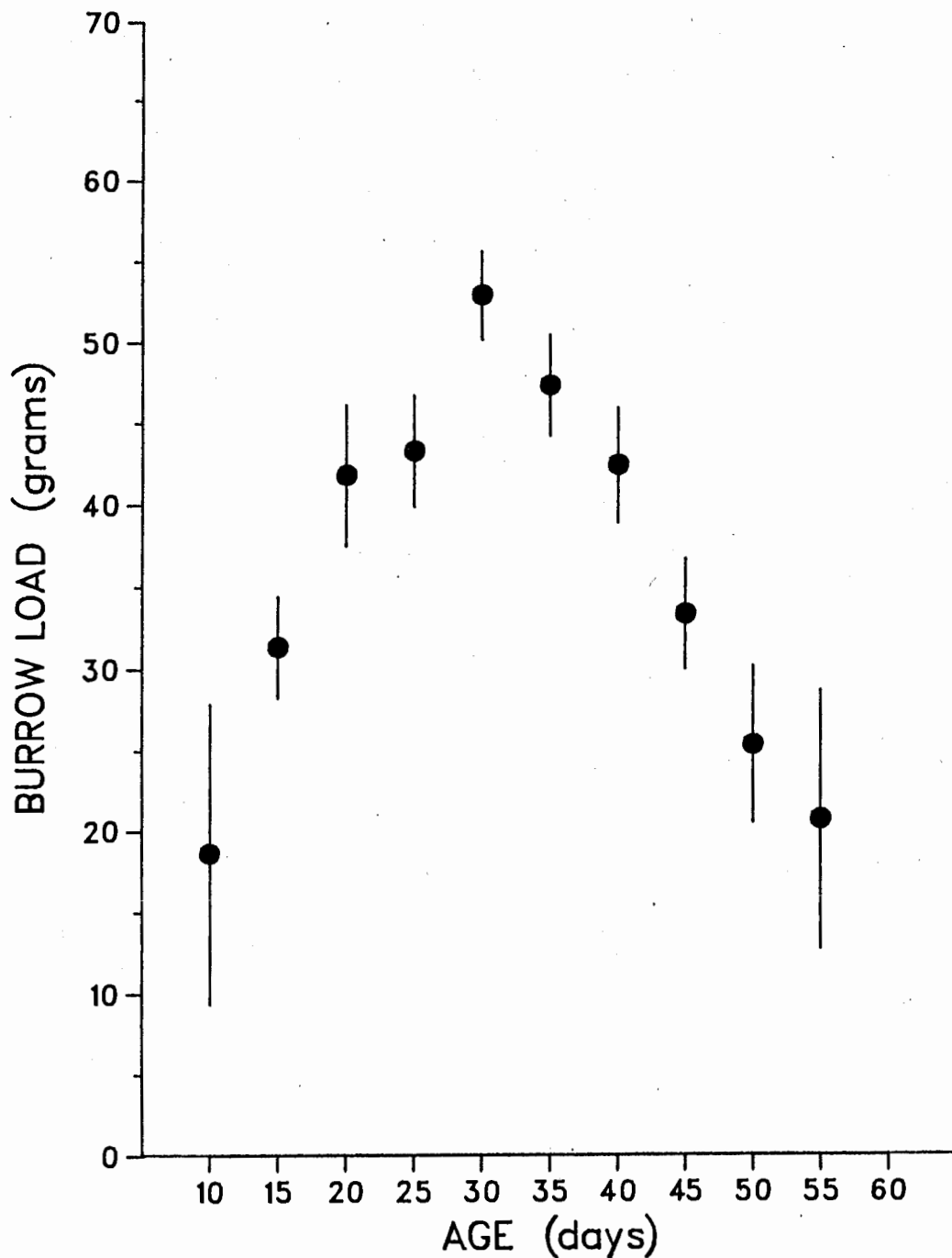
Figure 3.3: Burrow loads (mean +/- S.D.) delivered to hooded chicks in relation to their age in 1985. The loads are grouped into five day age intervals. The numbers along the axis represent the midpoint of the interval.
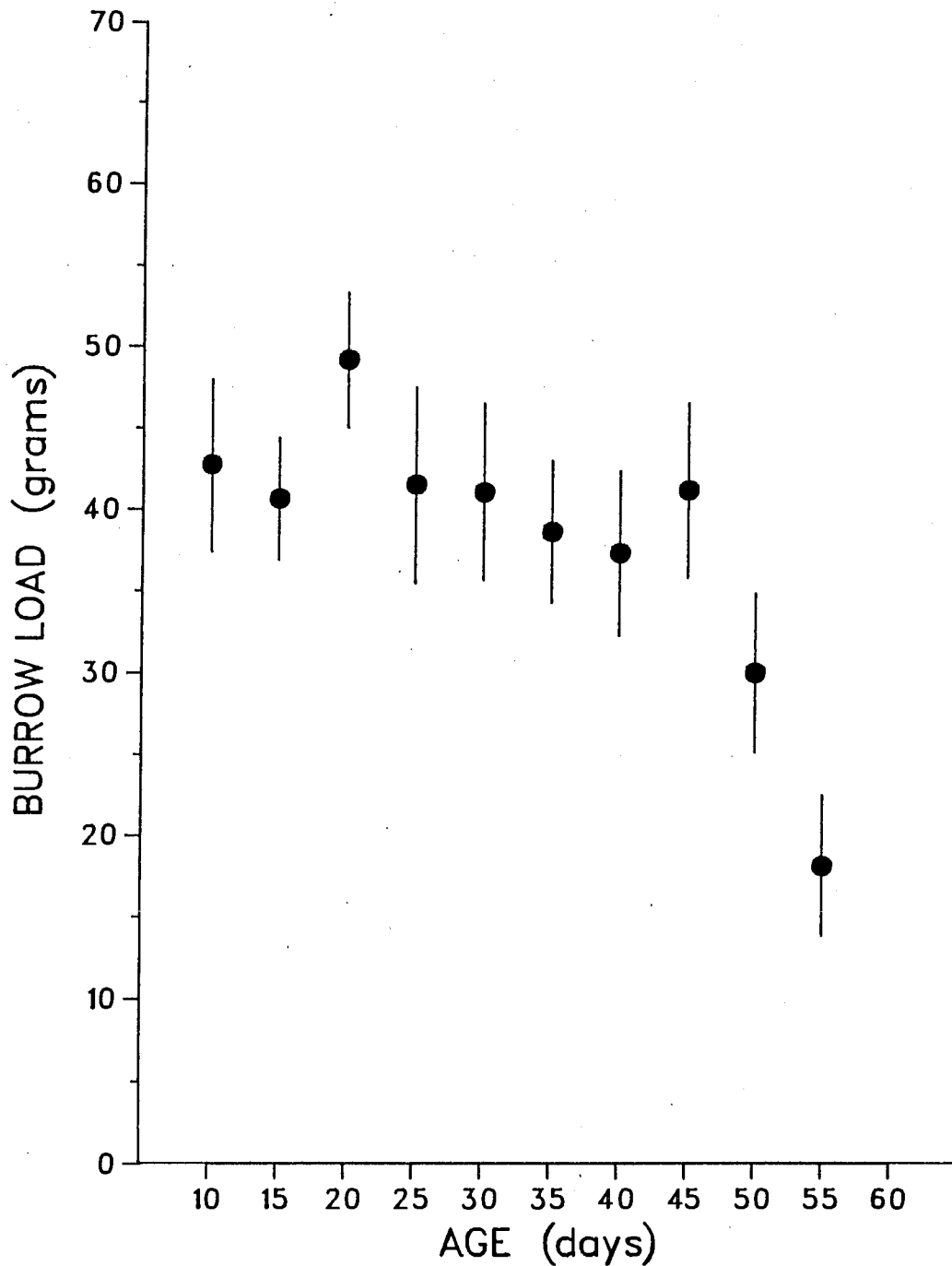
Figure 3.4: Burrow loads (mean +/- S.D.) delivered to hooded
chicks in relation to their age in 1986. The loads
are grouped into five day age intervals. The numbers
along the axis represent the midpoint of the
interval.
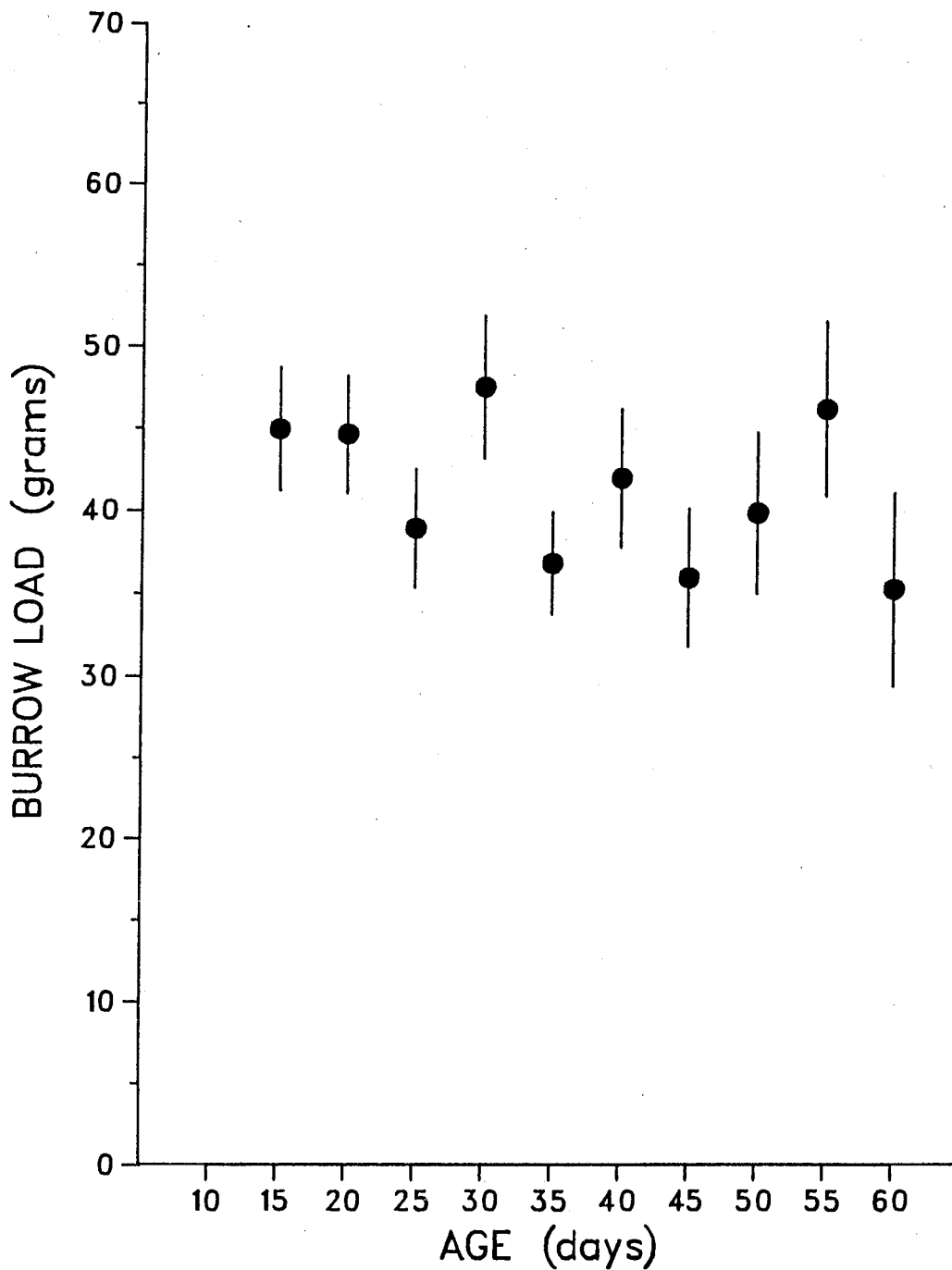
Figure 3.5: Burrow loads (mean +/- S.D.) delivered to hooded chicks in relation to their age in 1987. The loads are grouped into five day age intervals. The numbers along the axis represent the midpoint of the interval.
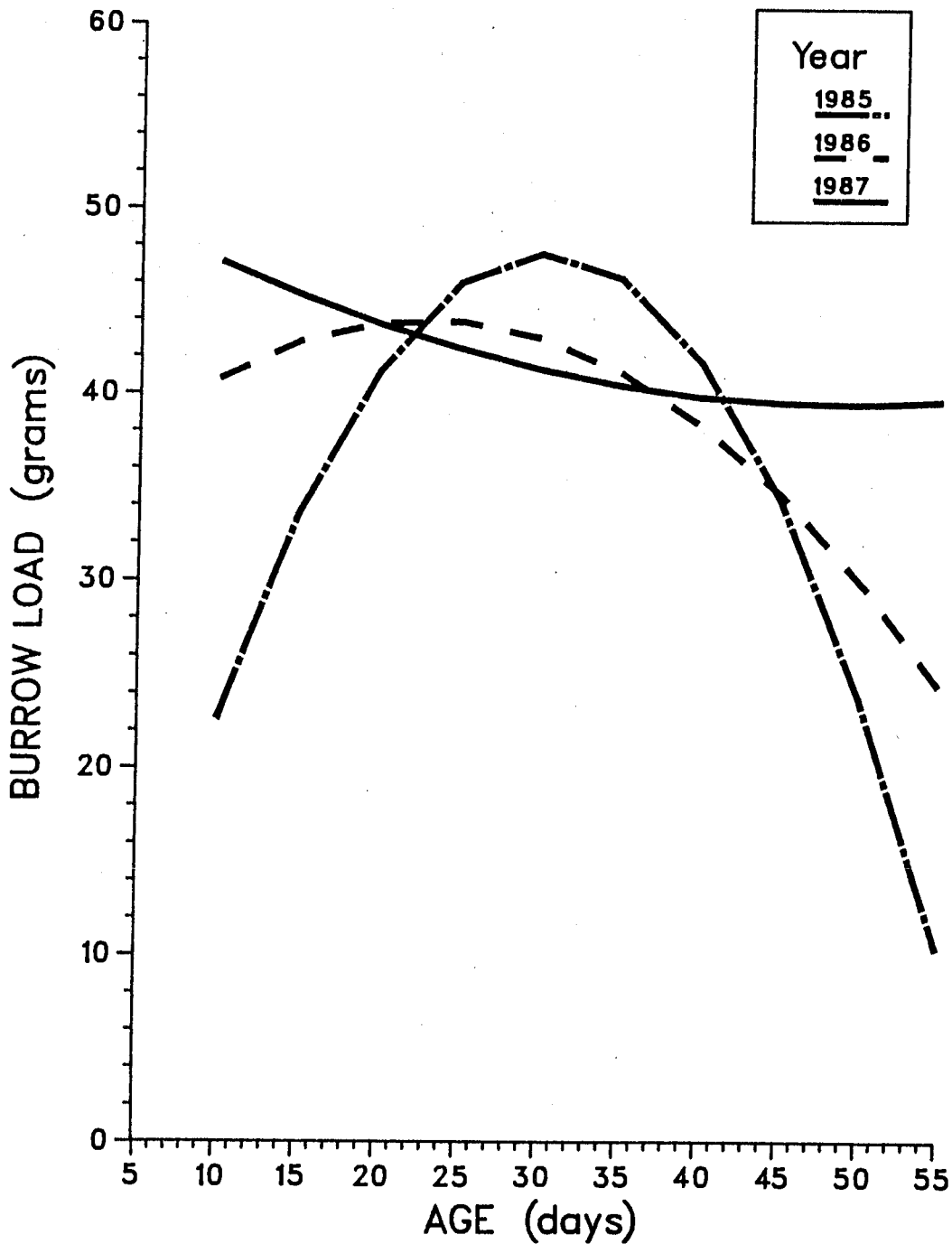
Figure 3.6: Provisioning curves (second order polynomials fitted
to the relationship between burrow load and chick
age) in 1985-87. Coefficients of each curve are
given in Table 3.1.

be real effects by the significant negative quadratic parameter of the polynomial equations (Table 3.1). The provisioning curves account for 13.2, 4.5, and 0.1 percent of the variation in 1985, 1986, and 1987, respectively. Adding the $X^2$ coefficient increases the sum of squares from 2551 to 19830 in 1985, from 4370 to 6396 in 1986, and from 1096 to 1262 in 1987. The increase is significant in 1985 ($F = 38.7$, $df = 1,285$, $P < 0.0005$; see Sokal and Rohlf, 1981, pp. 633-635 for a description of the test statistic). In 1986 and 1987, however, the increase in the amount of variance accounted for by adding the $X^2$ term is not significant (1986: $F = 2.6$, $df = 1, 207$, $P < 0.1$; 1987: $F = -0.87$, $df = 1, 291$, $P >> 0.25$). The $X^2$ coefficients differ significantly between years: (1985-86, $t = -51.3$, $df = 496$, $P < 0.001$; 1986-87, $t = -30.8$, $df = 501$, $P < 0.001$).

I used Friedman's method for randomized blocks to test for differences in the provisioning of 'early' and 'late' hatched chicks. Table 3.2a shows the complete data set for 1985 with the subset of points used in the analysis enclosed by a box. The ranking of burrow load with standard age showed no consistent trend, indicating that there is no difference in the weight of burrow loads fed to chicks of the same age 'early' and 'late' in the season. The same result was also obtained in 1986 and 1987 (Table 3.2b, c).

In order to perform a more powerful analysis, I combined data from all years (Tables 3.2d, e) and repeated Friedman's analysis. Table 3.2d shows the ranking of burrow loads delivered

Table 3.1: Coefficients of parameters of second order polynomials fitted to the relationship between burrow loads delivered to chicks at different ages (provisioning curves) in different years. * = significantly different from zero with $\alpha = 0.05$ for one tailed tests.

| Year | Quadratic Parameters | | | | | | |
|------|-----------|------|-------------|------|--------------|--------|-----|
| | Intercept (a) | S.D. | Age ($\bar{X}$) | S.D. | Age$^2$ ($\bar{X}^2$) | S.D. | n |
| 1985 | -8.2 | 9.9 | 3.69 * | 0.64 | -0.061 * | 0.009 | 287 |
| 1986 | 34.0 * | 9.6 | 0.87 | 0.64 | -0.019 * | 0.009 | 209 |
| 1987 | 51.5 * | 9.6 | -0.49 | 0.59 | 0.005 | 0.008 | 294 |
| 1985-7 | 30.9 * | 5.6 | 0.97 * | 0.36 | -0.018 * | 0.005 | 790 |

Table 3.2: Ranks of burrow loads delivered to chicks of different standard ages at various developmental stages in 1985 (a), 1986 (b), 1987 (c) and for all years combined (d, e). The box in each table encloses data used in the analysis (Friedman's method for randomized blocks) of burrow load size delivered to chicks of same age on different dates (standard ages).

a) 1985

| Standard Age (days) | Chick Age (days) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 |
| 22.6-27.5 | 3 | 2 | 5 | 3 | 1 | 1 | 5 | - | - | - |
| 27.6-32.5 | 1 | 3 | 4 | 5 | 5 | 5 | 1 | 4 | 1 | - |
| 32.6-37.5 | 2 | 4 | 2 | 2 | 4 | 2 | 2 | 3 | 3 | - |
| 37.6-42.5 | - | 1 | 3 | 4 | 2 | 3 | 3 | 1 | 4 | 2 |
| 42.6-47.5 | - | - | 1 | 1 | 3 | 4 | 4 | 2 | 2 | 1 |

b) 1986

| Standard Age (days) | Chick Age (days) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 | 35 | 40 |
| 12.5-17.5 | 1 | 1 | 2 | 1 | 2 | - | - |
| 17.6-22.5 | 4 | 2 | 1 | 3 | 3 | - | - |
| 22.6-27.5 | 2 | 5 | 4 | 4 | 4 | 1 | 1 |
| 27.6-32.5 | - | 4 | 5 | 2 | 1 | 3 | 3 |
| 32.6-37.5 | 3 | 3 | 3 | 5 | 5 | 2 | 2 |

Table 3.2: Continued.

c) 1987

| Standard Age (days) | Chick Age (days) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 |
| 32.6-37.5 | 2 | 1 | 2 | 2 | 1 | 1 | 2 | 2 |
| 42.6-47.5 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 1 |

d) 1985-87 combined

| Standard Age (days) | Chick Age (days) | | |
|---|---|---|---|
| | 20 | 25 | 30 |
| 12.5-17.5 | 2 | 1 | 1 |
| 17.6-22.5 | 1 | 2 | 2 |
| 22.6-27.5 | 7 | 3 | 3 |
| 27.6-32.5 | 6 | 6 | 7 |
| 32.6-37.5 | 5 | 4 | 4 |
| 37.6-42.5 | 4 | 7 | 5 |
| 42.6-47.5 | 3 | 5 | 6 |

e) 1985-87 combined

| Standard Age (days) | Chick Age (days) | | | | |
|---|---|---|---|---|---|
| | 20 | 25 | 30 | 35 | 40 |
| 22.6-27.5 | 5 | 1 | 1 | 1 | 4 |
| 27.6-32.5 | 4 | 4 | 5 | 5 | 1 |
| 32.6-37.5 | 3 | 2 | 2 | 2 | 2 |
| 37.6-42.5 | 2 | 5 | 3 | 3 | 3 |
| 42.6-47.5 | 1 | 3 | 4 | 4 | 5 |

to chicks 20 to 30 days old with standard ages ranging from 15-45 days old. The results indicate a significant relationship ($X^2$ = 13.14, df = 6, P < 0.05) showing that late hatching chicks receive smaller burrow loads than early hatching ones. This result is largely attributable to the extremely small loads delivered to the four chicks with standard ages of 15 and 20 days. (Recall that the sample of 'late' chicks in 1986 was small and highly variable in age). When I examined the burrow loads fed to the two chicks in each of these age categories, it became apparent that in three of the four birds, burrow loads at any developmental stage never exceeded the weight of commonly observed bill loads (see below). This suggested that those chicks were being fed by only one parent. When the chicks in these standard age groups were removed and the analysis repeated with the addition of a nestling 35-40 days old on 31 July (Table 3.2e) there was no significant relationship between load weight ranking for same age chicks over the season.

This conclusion may be further investigated by estimating the power of a test comparing burrow loads in different standard age groups. The power is the likelihood that a true difference between groups can be detected, and is the opposite of the probability of a type II error, $\beta$ (Power = $1-\beta$). I followed the procedure outlined by Sokal and Rohlf (1981; p. 263) for calculating the power of a simple one-way analysis of variance. The procedure is outlined in Appendix 1. It is clear from these relatively crude calculations that the power of the test is very low, and hence it is likely that if a difference of the

33

magnitude I estimate does exist, I would not have been likely to detect it with the procedure I used.

The sampling of bill loads varied in frequency, intensity and timing over the three years. Pacific sandlance was the dominant prey species throughout the season in all years (see Vermeer and Westrheim, 1984). In 1985 there was a significant difference in the size of bill loads delivered to the colony on different nights (F = 5.97, df = 2, 71, P = 0.004) with the middle sample (26 July) larger than the earlier or later samples (Table 3.3). In 1986, the year with the widest spread in sampling dates and most intense collecting, no difference in bill load mass over the season was detected. In 1987, bill loads on 18 July were larger than in the other samples. Overall, there was no significant difference between the mass of bill loads between years (Table 3.3).

## DISCUSSION

The overall domed shape of the provisioning curves in 1985 and 1986 (Figure 3.6, Table 3.1) match that observed by other researchers (e.g. Ashcroft, 1979; Harris and Hislop, 1978; Cairns, 1987). In general, the decline in the load weight in the later phase of development is more marked than the initial rise (Table 3.1).

Results from the analysis of the size of burrow loads delivered to chicks hatching on different dates (Table 3.2)

Table 3.3: Analysis of variance and multiple range tests of bill loads (g) collected on different dates throughout the season (JL = July, AU = August). The same letter beside the mean indicates no significant difference in load weight based on a Student-Newman-Keuls multiple range test (MRT). * = groups significantly different with $\alpha$ = 0.05.

| Year | MRT | Load | S.D. | Min | Max | n | Date | | F | P |
|------|-----|------|------|-----|-----|-----|------|-----|------|-------|
| 1985 | a | 27.9 | 12.8 | 7 | 60 | 15 | JL | 10 | | |
| | b | 34.5 | 9.3 | 16 | 53 | 49 | | 26 | 5.97 | 0.004 * |
| | a | 24.1 | 8.1 | 13 | 39 | 10 | AU | 9 | | |
| | overall | 31.8 | | | | | | | | |
| 1986 | a | 33.9 | 9.9 | 12 | 70 | 61 | JL | 14 | | |
| | a | 36.3 | 9.4 | 17 | 74 | 72 | | 28 | | |
| | a | 31.7 | 11.3 | 14 | 62 | 39 | AU | 6 | 1.87 | 0.135 |
| | a | 33.0 | 12.5 | 14 | 70 | 40 | | 12 | | |
| | overall | 34.1 | | | | | | | | |
| 1987 | a | 31.6 | 8.5 | 16 | 48 | 63 | JL | 14 | | |
| | b | 39.8 | 9.0 | 26 | 54 | 12 | | 18 | | |
| | a | 33.8 | 8.3 | 19 | 56 | 30 | | 25 | 3.70 | 0.014 * |
| | a | 34.9 | 7.2 | 22 | 46 | 26 | AU | 3 | | |
| | overall | 33.5 | | | | | | | | |

indicated no seasonal effect. However, the power of my statistical tests was probably quite low (Appendix 1). As a result, the possibility of a seasonal effect cannot be ruled out. In any case, these effects are probably small compared to the effect of chick age on parental provisioning. This agrees with the results of Hatch's (1984) study of the rhinoceros auklet. Hatch (1984) found that provisioning by parents varied with the age of the chick, but not with the time of the season. The inability of this and other studies, to detect a seasonal effect on the size of burrow loads, suggests that Lack's energy limitation hypothesis is insufficient to account for the observed decline in feeding rate to chicks in the late stages of development.

The provisioning curves vary from a distinct dome shape in 1985, to almost flat in 1987 (Figure 3.6, Table 3.1). If parents were provisioning their young according to chick energy demand then I would expect the shape of the curves to be similar in all years. Ricklefs and White (1981) argue that the growth rate of slow growing nestling sooty terns could be doubled by adults increasing their provisioning effort by only 5%. Additionally, Shea and Ricklefs (1985) demonstrated that adult gray-backed terns, which also rear a single, slowly growing chick, are capable of increasing food delivery by at least 30% - enough to rear successfully a foster chick of the larger, closely related sooty tern. Provisioning curves should therefore look similar from year to year if adults are provisioning chicks based on the chick's energetic needs and if parents can increase their

36

delivery of food as easily as Ricklefs and White (1981) claim. The fact that the provisioning curves differed between years suggests that the precocial growth hypothesis is insufficient to account for the decline in feeding rate as chicks approach fledging.

What accounts for the decline in feeding rate? There was no consistent pattern of bill load size over the season (Table 3.3) in this and other studies on the rhinoceros auklet (Leschner, 1976; Wilson, 1977) or in the Atlantic puffin (Harris and Hislop 1978; Ashcoft, 1979). The variation shown in Table 3.3 is consistent with the observation that bill loads are known to vary widely from day to day in the rhinoceros auklet (Hatch, 1984). Although Vermeer and Westrheim (1984) report that bill loads were significantly smaller early than late in some seasons on Lucy, Pine and Triangle Islands, no differences among late season samples (when chicks are generally older) were detected. Therefore, one can infer that the decline in provisioning rate in the late chick rearing period is a result of a reduction in feeding frequency, rather than of a reduction in bill load size. This is what Ashcroft (1979) and Harris and Hislop (1978) report for the Atlantic puffin.

That the provisioning rate changes due to visitation frequency rather than due to changes in bill load size makes intuitive sense if visits to the colony to provision chicks are dangerous for adult birds, and hence pose a threat to their reproductive future. In fact, Nettleship (1972) reports that the

size of meals delivered to Atlantic puffin chicks in two habitats was the same, but that the frequency of feeding was lower in the habitat where the risk of predation on adults by gulls was greatest. Harris (1980) notes that adult mortality due to gull predation during the three month breeding season in the Atlantic puffin colony on Dun, Scotland, approaches 5% - the normal loss of adults for a whole year. Predation by bald eagles on rhinoceros auklets has been recorded by DeGrange and Nelson (1982) and has been inferred (eagles disturbed from carcases) by myself and co-workers on Lucy Islands throughout the season. Watanuki (1986) demonstrated that Leach's storm petrels in Japan reduce their activity in moonlight when predation rate by gulls is relatively high. In addition to the risk posed by predators, I have found rhinoceros auklets dead in the forest on Lucy Island, probably as a result of breaking their necks on trees as they made their aerial descents in the dark. Similarly, workers on Triangle Island, B.C., where there are no trees, have found dead auklets in driftwood piles at the base of steep slopes. These birds were apparently unable to clear the debris during departure flights (Moira Lemon, pers. comm.). Death from crashing into obstacles has also been reported by Jewett et al. (1953) and Richardson (1961).

The theory of parent-offspring conflict (Trivers, 1974) predicts that conflict should increase as chicks age. As a result there should be selection for parents to wean chicks. In face of this conflict the potential risks associated with visiting the colony are likely to be important factors that

influence the frequency with which parents visit their chick as it grows older. Assuming predation risk remains constant throughout the breeding season, visits to feed chicks approaching independence are likely less beneficial than visits to younger chicks, since the marginal increment in chick survival resulting from each visit will likely be smaller. In the rhinoceros auklet, chicks fledge at 50-80 percent of adult weight and 45-60 days of age, and complete their development at sea. The decision of when to fledge will depend on the provisioning rate, and the point at which parents wean chicks should depend on the likelihood of postfledging chick survival on the ocean (see Chapter 6). As I will show in the next chapter, there seem to be significant variations in the availability of food from year to year (Chapter 4). These variations may influence the postfledging survival of chicks. Thus, viewing the decline in nestling provisioning rate as the manifestation of a flexible parental tactic appears to be the only hypothesis of the three capable of explaining the variations in the pattern of feeding during development observed in this study. In the next two chapters I investigate other lines of evidence to further test this hypothesis.

# CHAPTER IV

# CHICK GROWTH

## INTRODUCTION

The slow growth rate of pelagic seabird nestlings has long been viewed as an adaptation to a limited food supply that reduces energy requirements during development (Lack, 1968). Results from twinning experiments show that adults usually fail to rear both chicks (rhinoceros auklet: Summers and Drent, 1979; other Alcidae: see Birkhead and Harris, 1985, for a summary; Procellariiformes: Rice and Kenyon, 1962; Harris, 1966). Similar results have been obtained from experiments involving the removal of one parent. These studies suggest that parents are working at maximum capacity to raise young, and they are cited as evidence for Lack's hypothesis. Ricklefs and White (1981) cite further support for Lack's energy limitation hypothesis by comparing the patterns of energy utilization by chicks of closely related pelagic and nearshore species. They report energy requirements of slow growing pelagic sooty terns level off at an early age in contrast to the rapidly growing nearshore common tern, (<u>Sterna</u> <u>hirundo</u>), which exhibits a marked peak at a much higher level midway through the growth period.

An experimental test of Lack's energy limitation hypothesis was performed by Shea and Ricklefs (1985). They substituted a chick of the larger sooty tern into the nest of a gray-backed tern and reasoned that if the parents could successfully rear

sooty tern chicks the energy limitation hypothesis would have to be rejected. The authors discovered that gray-backed foster parents were capable of increasing food deliveries by at least 30%, indicating that they are not normally working at maximum capacity; Lack's hypothesis was therefore rejected. As an alternative, Shea and Ricklefs advocated the idea that slow growth in seabirds was a result of selection for precocity of development in nestlings. Ricklefs (1979a) speculated that in crowded colonies of tropical seabirds early mobility (i.e. precocity) carried a premium for young to escape predation or avoid intraspecific aggression. This scenario suggests that growth rate is at its maximum, constrained by selection for precocial development. Furthermore, since adults can vary their provisioning effort, Shea and Ricklefs' hypothesis implies that nestling growth rate should remain the same from year to year regardless of fluctuations in ocean feeding conditions.

Changes in the availability of food have been cited as one of the main causes of the decline in the number of Atlantic puffins in Britain during this century (Harris, 1978). To test the idea that food shortage has been responsible for the decline in numbers and poor reproductive success of puffins on St. Kilda Harris (1978) conducted a supplementary feeding experiment and compared the results to an identical experiment on the Isle of May, where puffin numbers have been increasing and conditions are apparently favorable. Harris found that chicks raised on unlimited food ate far more than either control chicks given the same amount as wild nestlings, or chicks given 50 g in addition

41

to the amount controls received. As a result of their different diets chicks raised on unlimited food grew faster and reached heavier weights than controls. Young given an extra 50 g were lighter than ad lib birds, but still attained heavier weights than controls. Harris reports that the differences were less marked on the Isle of May than on St. Kilda, and concluded that adults on St. Kilda were having difficulty rearing young, apparently due to a food shortage. A similar supplementary feeding experiment by Hudson (1979) shows that chicks fed ad lib grew faster than those given an extra 50 g per day. However, this latter group did not grow faster than control birds. According to Case (1978) the critical test of the precocity of development hypothesis for slow growth would be to provide nestlings with additional food. An increase in growth rates resulting from greater intake would indicate that the rate of growth is not constrained by the developmental pattern. The elevated growth rates of puffins in supplementary feeding experiments indicate that slow growth in these birds is unlikely to have been a result of selection for precocial development.

The rhinoceros auklet is particularly interesting to evolutionary ecologists because it has the slowest growth rate and widest range of fledging weights reported for any of the Alcidae. Chick growth in rhinoceros auklets has been studied for a number of years on three colonies in Washington state (Wilson and Manuwal, 1986) and one main colony in B.C. (Vermeer, 1979). The substantial inter-colony and inter-year differences in chick growth and diet have commonly been ascribed to ocean feeding

42

conditions by these researchers. While this conclusion is consistent with the energy limitation hypothesis, it appears inconsistent with the view of slow growth as a result of selection for precocial development. This view holds that parents are able to increase their effort, compensating for a reduced availability of food, and thereby keeping the intake rate of the chick at the required level. However, parents may be unable to compensate for the full range of ocean feeding conditions experienced, and as a result growth rates may reflect ocean feeding conditions (e.g. Ricklefs et al., 1984), in especially poor years. A recent study of Atlantic puffins in Norway that relates developmental characteristics such as growth rate and fledging weight to the level of herring (Clupea harengus) stocks, provides some direct support for this concept (Barrett et al., 1987).

Many seabird researchers have compared growth rates of early and late hatching nestlings. Under Lack's energy limitation hypothesis differences between these groups of nestlings reflect a seasonal change in food availability. In contrast, the precocial growth hypothesis predicts that growth rates should be similar throughout a season since parents can compensate for fluctuations in marine feeding conditions by adjusting provisioning effort. The results of Chapter 3 suggested that a seasonal decline in the availability of food, if it occurred, is unlikely to be large, and so the observed growth rates should remain constant.

One of my goals in this part of the study was to investigate the relationship between chick growth rate and amount fed in order to determine if chicks were growing at the maximum possible rate as predicted by the precocial growth hypothesis. Secondly, by studying growth rates within and between years I tested the prediction of the precocial growth hypothesis that growth rates should be largely the same throughout and between seasons.

## METHODS

*Supplementary Feeding Experiment*

I performed a supplementary feeding experiment in 1985. I used wild chicks for the study and obtained food samples using the hooding technique. The experiment consisted of four treatments:

1. Deprived nestlings were hooded every fifth night and denied the meal their parent(s) had delivered during that night (their intended meal).

2. Fed birds were fed an extra meal every fifth day, taken from a deprived bird earlier the same day. The fed bird was then hooded, left overnight, and fed its intended meal the following morning.

3. Hood Control birds were visited every fifth night, hooded and given their intended meal the following day.

4. Control birds were not hooded but were weighed and measured every fifth day.

I established 15 groups, each containing one chick randomly assigned to each of the four experimental treatments. Birds within each group were within five days of age of one another and were from the same area in the colony, or the next closest area. Food obtained from a 'deprived' chick was always assigned to a 'fed' chick in the same group. Chick weight was taken between 1700-2300 hrs, before hooding, accurate to within two g. Measurements were taken from the start of the experiment until I left the colony on 18 August, 1985.

For the growth measurements in 1986 and 1987, I attempted to establish distinct 'early' and 'late' samples of nestlings separated by about 10 days. These birds were hooded every five days, using the same technique as in 1985, and their body size measured until I departed from the colony in late August. The morning following hooding, each chick was fed its intended meal.

*Chick Growth*

To describe the growth of chicks, previous researchers studying rhinoceros auklets have usually fitted Gompertz equations to a data set combining measurements from many chicks (e.g. Vermeer, 1979; Wilson and Manuwal, 1986). I chose to obtain an estimate of growth rate for each individual chick, in order to be able to perform statistical comparisons between groups of birds. However, data over the complete developmental period were lacking for many chicks either because I discovered them well after hatching, or because I left the colony before birds fledged. In addition, visual inspection of growth data

45

indicated that many birds did not exhibit weight gain patterns similar to the Gompertz curve. Some birds showed erratic patterns of weight gain involving periods of slow followed by rapid growth, while others gained weight in a linear fashion throughout development. Wilson (1977) has pointed out that estimates of asymptotic weight derived from the Gompertz equation were generally higher than he observed for wild birds. For these reasons the Gompertz equation did not seem adequate for my purposes. Instead, I estimated the rate of growth of each bird when it was between 10 and 40 days old. I used the BMDP statistical package (Engelman et al., 1979) to regress weight gain on age between 10 and 40 days and obtained the slope of each line (growth rate in g/day) for each bird.

Peak weights were established using the following criteria. If a bird fledged, the highest weight attained was called peak weight. If the bird reached a peak late in the developmental period then exhibited a weight recession, but did not fledge during my stay, the highest weight was considered to be the peak. If the bird resided in the burrow for over 55 days the highest weight in this late stage of development was considered peak weight.

Growth rates and peak weights of birds in different categories within years were compared using ANOVA followed by a Student-Newman-Keuls (SNK) multiple range test. Growth parameters of chicks from the hood control treatment in 1985 were compared with the hooded chicks from 1986 and 1987.

As part of a comparison of nestling growth and diet between the three largest rhinoceros auklet colonies in British Columbia (Lucy, Pine and Triangle Islands), I constructed composite growth curves in 1984-86 as outlined by Ricklefs and White (1975). Chicks encompassing a wide range of development were measured on each island in early July, and again 10 days later. On Lucy Island in 1985 and 1986, chicks used to construct the composite curve were used only for that purpose, or were control birds in the supplementary feeding experiment. A composite growth curve was also constructed in 1987 on Lucy, but all of the birds used were from the hooding study. (No composite growth curves were constructed on Pine and Triangle Islands in 1987). Growth rates were estimated by fitting a straight line to the full data set from each island in each year.

## RESULTS

Rhinoceros auklet chicks weigh between 46 and 64 g at hatching (mean = 54.5, S.E. = 1.1, n = 24). At this early stage of development nestlings are particularly susceptable to starvation and will die if not fed within three days. I often found dead hatchlings surrounded by fresh fish which had presumably been delivered too late. Adults feed chicks in the burrow until fledging at 45-60 days. Weight gain is generally linear throughout most of the developmental period although it often slows and sometimes declines before fledging. There is,

however, considerable variability in growth rates as exhibited by a sample of four control chicks from 1985 (Figure 4.1).

The relationship between growth rates (X) and peak weight (Y) is linear (Y = 259 + 16.2X) and significant (F = 83.15, df = 1,53; P < 0.0005). The combined data for all chicks in all years is plotted in Figure 4.2.

*Supplementary Feeding*

There were significant differences in growth rates between the treatments in the supplementary feeding experiment in 1985 (Table 4.1a). 'Control' chicks grew fastest followed by 'fed' chicks, 'hood controls' and finally 'deprived' birds. The 'deprived' birds grew significantly slower than birds in either the 'fed' or 'control' treatments but did not differ from the 'hood controls'. No differences between peak weights of birds in any treatment were observed although the ranking was similar to the growth rate data with 'control' birds reaching the highest weights followed by 'fed' chicks (Table 4.1b).

*Intra-year Comparisons*

In 1986 the 'early' group consisted of 17 birds with standard ages of 32.6-37.5 days. Due to a shortage of chicks that year I was able to assign only nine birds, of varying ages, to a late sample. The standard ages of those nine birds ranged from 15-30 days. In addition, the four chicks in the 15 and 20 day standard age groups were eliminated from the analysis because it was believed that most of them were being fed by only
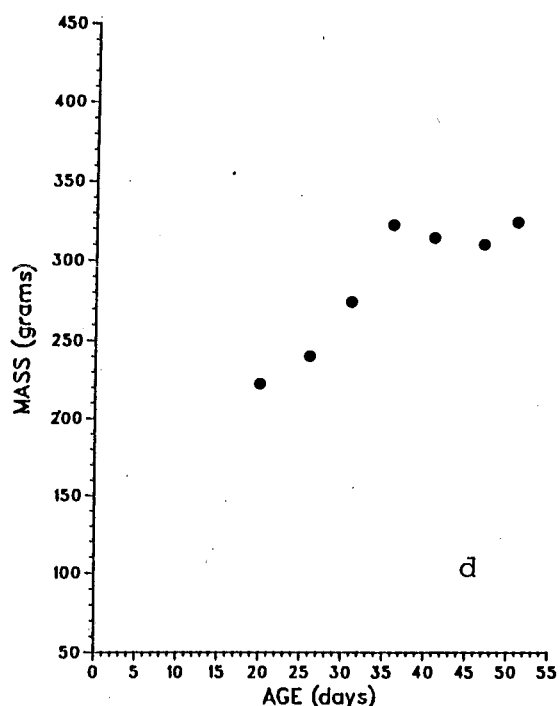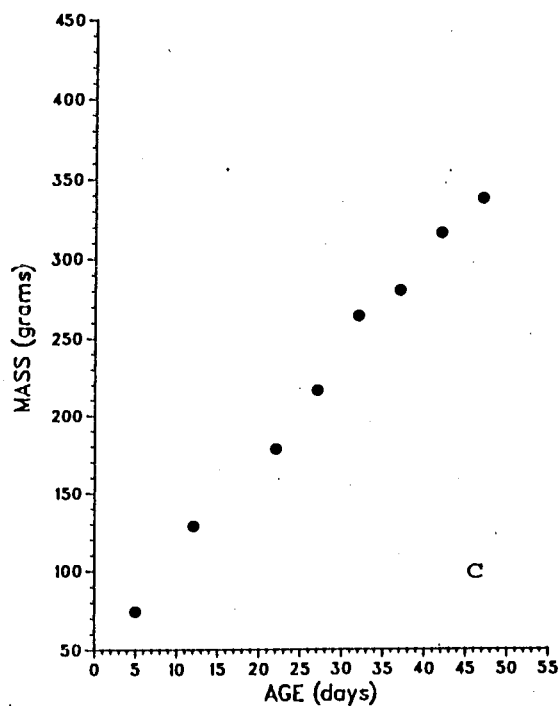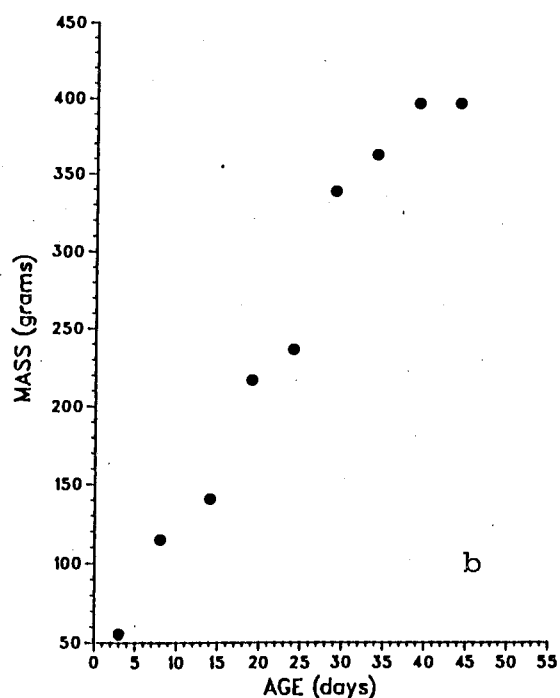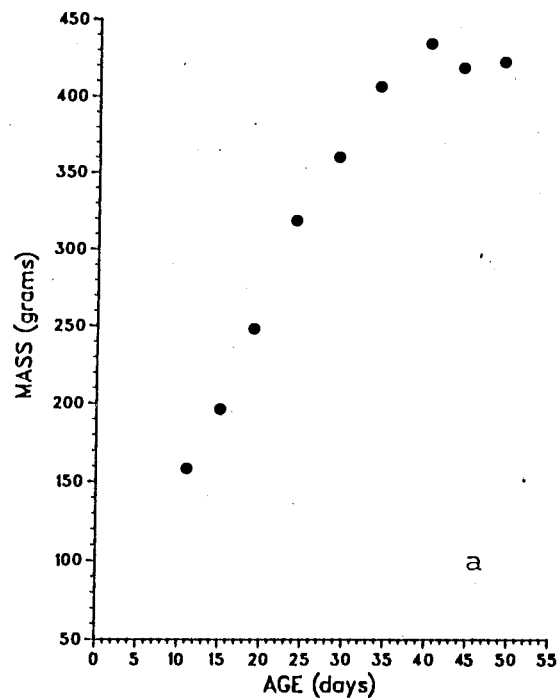
Figure 4.1: Variability in the growth of a sample of four (a, b, c, d) control chicks weighed once every five days in 1985.
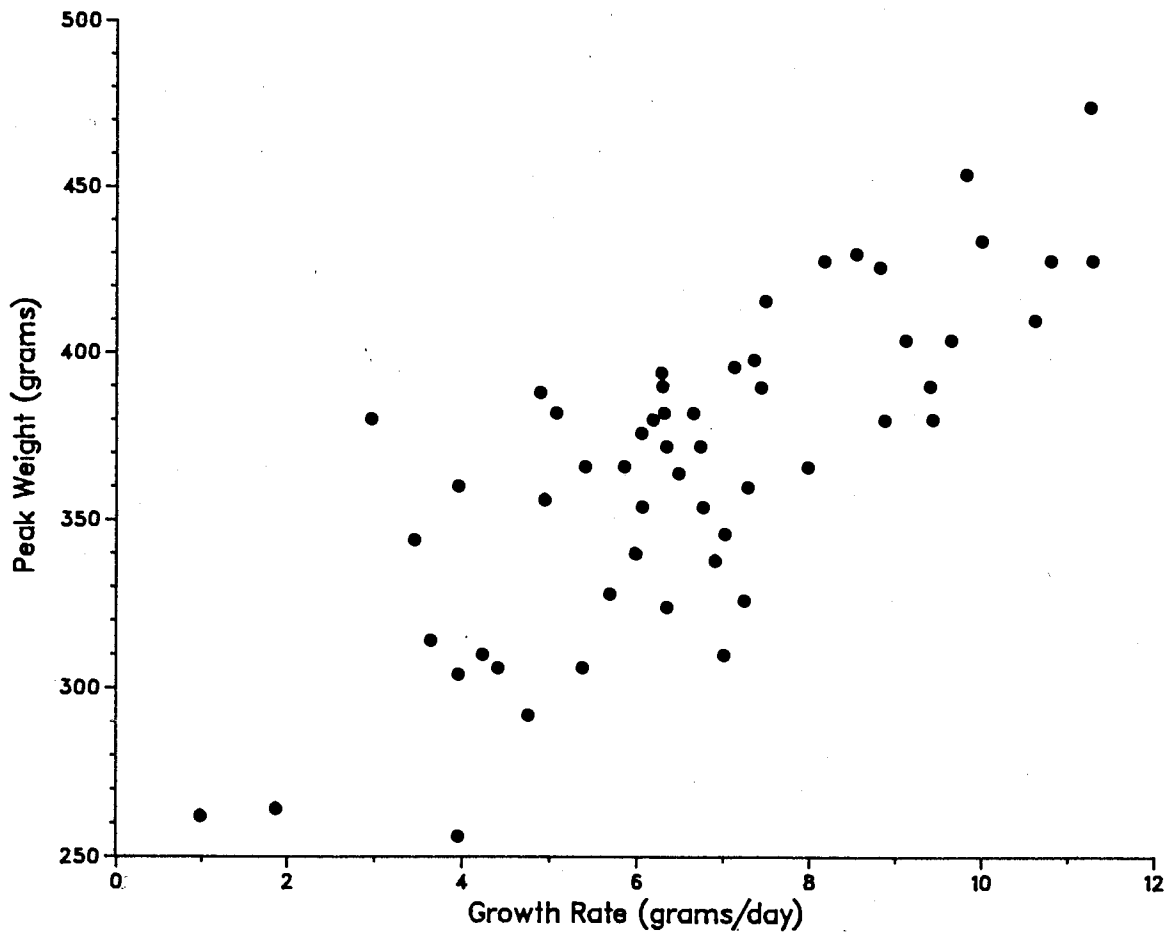
Figure 4.2: The relationship between growth rates and peak weights for birds from all four treatments in 1985 and for hooded birds in 1986 and 1987. Note that peak weights could not be obtained for all birds for which growth was measured.

50

Table 4.1: Comparison of growth rates (a) and peak weights (b) for chicks in different treatments of the supplementary feeding experiment in 1985. Differences were tested using ANOVA followed by a Student-Newman-Keuls multiple range test (MRT). In the MRT different letters represent significantly different rates of growth. * = significant difference among groups with $\alpha$ =0.05.

a)  Growth Rate

| Treatment | Mean Growth Rate[1] | MRT | S.D. | n | F | P |
|---|---|---|---|---|---|---|
| Deprived | 6.47 | b | 1.48 | 13 | | |
| Hood control | 7.10 | a,b | 2.57 | 14 | 4.47 | 0.007 * |
| Fed | 8.35 | a | 1.78 | 15 | | |
| Control | 8.82 | a | 1.67 | 15 | | |

[1]From linear portion of curve between 10 and 40 days old (g/day)

b)  Peak Weight

| Treatment | Mean Peak Weight (g) | S.D. | n | F | P |
|---|---|---|---|---|---|
| Deprived | 371.0 | 80.6 | 2 | | |
| Hood control | 369.0 | 30.6 | 5 | 1.63 | 0.214 |
| Fed | 381.8 | 40.1 | 9 | | |
| Control | 417.0 | 45.8 | 8 | | |

one parent (see Chapter 3). No difference between growth rates in the remaining standard age groups were found (Table 4.2a). Peak weights could not be compared between 'early' and 'late' nesters since no data were available for the late sample.

Sixteen 'early' and 17 'late' nesting chicks were hooded and measured every five days in 1987. There was no significant difference in growth rate between these two groups (Table 4.2b), and the magnitude of the peak weights could not be compared since there were only two values for late nesting birds.

*Inter-year Comparisons*

All chicks in the sequential growth study were hooded and fed their intended meal the following day in 1986 and 1987. To standardize methodology, only hood control chicks from 1985 were used in the comparison of growth rates and peak weights between years. Since no difference was found between growth rates of 'early' and 'late' hatched chicks in 1986 or 1987 (Tables 4.2a, b) these samples were combined within each year. Nestlings grew significantly faster in 1985 than in 1986 or 1987, the latter two years showing no difference (Table 4.3a). Although peak weights increase linearly with growth rates (Figure 4.2), no significant differences in peak weights were detected between years (Table 4.3b). However, many of the nestlings in 1986 and 1987 remained in the nest for over 55 days and thus had more time to reach higher weights than conspecifics in 1985.

Table 4.2: Intra-year comparisons of growth rates for hooded chicks in different standard age groups in 1986 (a) and 1987 (b). The comparisons were made by ANOVA. Growth rate was estimated from sequential data.

a) 1986

| Standard Age (days) | Mean Growth Rate[1] | S.D. | n | F | P |
|---|---|---|---|---|---|
| 22.5-27.5 (late) | 4.55 | 2.41 | 4 | | |
| 27.6-32.5 | 3.76 | 1.24 | 2 | 2.18 | 0.139 |
| 32.6-37.5 (early) | 5.79 | 1.39 | 17 | | |

[1]From linear portion of curve between 10 and 40 days old (g/day)

b) 1987

| Standard Age (days) | Mean Growth Rate[1] | S.D. | n | F | P |
|---|---|---|---|---|---|
| 32.5-37.5 (late) | 5.50 | 1.19 | 17 | 0.96 | 0.346 |
| 42.5-47.5 (early) | 5.79 | 1.81 | 16 | | |

[1]From linear portion of curve between 10 and 40 days old (g/day)

Table 4.3:　Inter-year comparison of nestling growth rates (a) and peak weights (b) on Lucy Islands using ANOVA followed by a Student-Newman-Keuls multiple range test (MRT). Different letters in the MRT test represent different growth rates. Growth was estimated from sequential data.

a)　Growth Rate

| Year | Mid Point Standard Age | Mean Growth Rate[1] | MRT | S.D. | n | F | P |
|------|------|------|-----|------|-----|------|------|
| 1985 | 35 | 7.10 | a | 2.58 | 14 | | |
| 1986 | 35 | 5.40 | b | 1.66 | 23 | 5.68 | 0.004 * |
| 1987 | 40 | 5.25 | b | 1.52 | 33 | | |

[1]From linear portion of curve between 10 and 40 days old (g/day).

b)　Peak Weight

| Year | Mid Point Standard Age | Peak Weight (grams) | Still in Burrow After 55 Days (%)† | S.D. | n | F | P |
|------|------|------|------|------|-----|------|------|
| 1985 | 35 | 396.6 | 20 | 30.6 | 5 | | |
| 1986 | 35 | 335.4 | 71 | 42.1 | 14 | 2.05 | 0.144 |
| 1987 | 40 | 360.4 | 71 | 40.3 | 17 | | |

†Fledged or peak weight after 55 days old.

The slopes of the composite growth curves show the same ranking between years as the sequential growth data although their magnitudes differ (Table 4.4). No hooded birds were used in constructing the curves in 1984, 1985 or 1986, whereas all of the birds used in 1987 were part of the hooding study. The slope of this composite growth curve will therefore be underestimated since hooded birds tend to grow more slowly than unhooded ones (Table 4.1a).

## DISCUSSION

The supplementary feeding experiment indicates that the three treatments involving hooding had an effect on chick growth rate (Table 4.1a). In general hooded birds grew more slowly than control birds. Hooding may interfere with the normal physiological routine of digestion, retarding growth rate as a result. Within the hooding treatments, fed chicks grew faster than hood controls which, in turn, grew faster than deprived chicks. It is noteworthy that the magnitude of additional food given to chicks (amount fed/day, on average) in the fed group was much less than was alloted to the supplementary fed Atlantic puffin chicks in studies by Harris (1978) and Hudson (1979). These authors supplied chicks with upwards of 50 g per day in comparison to approximately 50 g every fifth day in my study. Moreover, Atlantic puffins are smaller than rhinoceros auklets by approximately 130 g. In my experiment, supplementary feeding served mostly to offset the effects of hooding (Table 4.1a).

Table 4.4: Nestling growth rates on Lucy Islands estimated from the slopes of composite growth curves from 1984-87. Shown are the percentage of hooded chicks used in the construction of a composite curve, the age range of chicks used, and the dates of measurement.

| Year | Growth Rate[1] | n | Hooded Birds (%)† | Age Range (days) | July Date |
|------|------|----|------|------|------|
| 1984 | 7.3 | 38 | 0 | 1 - 30 | 4 - 16 |
| 1985 | 10.6 | 30 | 0 | 7 - 40 | 5 - 18 |
| 1986 | 8.1 | 22 | 0 | 10 - 39 | 7 - 18 |
| 1987 | 5.4 | 33 | 100 | 14 - 36 | 10 - 22 |

[1]Linear regression on entire data set (g/day).
†Percentage of hooded birds used in the study.

However, among hooded birds the effects of additional food were successful in elevating growth rate.

The precocial growth hypothesis predicts similar growth rates between individuals, something I did not observe (Figure 4.1). In addition, the fact that there were significant differences in growth rates between years suggests that the slow growth of rhinoceros auklet chicks has not evolved as a by-product of selection for precocity.

The sample of 'late' hatched birds in 1986 was small and moreover, those birds were not of the same standard ages (Table 4.2a). No significant difference in growth rates between the groups was observed. In 1987 when discrete 'early' and 'late' samples were obtained I could find no difference in growth rate between the two groups (Table 4.2b). Wilson and Manuwal (1986) report that rhinoceros auklets from inshore Protection Island, Washington, "tended to grow better than those hatched late in the season", although this was not found in the coastal Destruction Island population. In that study the hatching period was divided into thirds ranging from 8-13 days. Early birds (n = 6-12) were those that hatched in the first third while late birds hatched in the last third. Wilson and Manuwal, however, do not present data on growth rates per se, but only peak and fledging weights. Vermeer and Cullen (1982) present data on growth in early and late hatched rhinoceros auklet chicks on Triangle Island, B.C. Although no statistical comparisons could be performed their figure indicates no differences in growth

rate until 34 days old, after which the growth rate of the latest hatched birds declines. This difference was ascribed to a "decrease in quality and availability of the bird's prey availability later in the season" (Vermeer and Cullen, 1982). The results from 1986 and 1987 on Lucy Island do not suggest a seasonal decline in food availability during the season, at least within the period that my 'early' and 'late' groups were nesting. This result is supported by the lack of differences between weights of burrow loads delivered to chicks of the same age 'early' and 'later' in the season (Table 3.2). As pointed out by Gaston (1984), seasonal decline in growth rates and fledging weights may be colony-specific, "reflecting seasonal changes in food that are peculiar to particular marine areas".

The significant differences between nestling growth rates in various years is of interest in terms of the information this result may convey about inter-year fluctuations in ocean feeding conditions. Inter-year variations in growth reported for rhinoceros auklets and tufted puffins on Triangle Island have been attributed to changes in marine feeding conditions, particularly the availability of pacific sandlance between years (Vermeer, 1980; Vermeer et al., 1979). Similarly, researchers working in Washington state attributed differences in growth rates between years on Destruction and Protection Islands to changes in feeding conditions (Leschner, 1976; Wilson, 1977). Slow growth of tufted and horned puffins on Buldir Island in Alaska has been associated with poor feeding conditions by Wehle (1983). Among Atlantic puffins, slow chick growth, retarded

fledging and low fledging weights as a result of food shortages have been reported by Nettleship (1972), Harris (1980) and Barret et al. (1987). This latter study is the most convincing since it examines 12 colonies over a three year period and presents evidence which suggests a direct relationship between the level of herring stocks and breeding success.

Independent evidence for inter-year differences in marine feeding conditions around Lucy Island comes from the comparison of composite growth curves on Lucy, Pine and Triangle Islands. This comparison indicates that chick growth rates derived from composite curves on each colony all vary in the same direction from year-to-year, suggesting a coastal, marine phenomenon (Table 4.5; Bertram and Kaiser, in prep). On all colonies chick growth rates were fastest in 1985. Ricklefs and White (1975) suggested that the composite growth curve may be an indicator of the environment at a particular time. This means that inferences about marine feeding conditions based on a composite curve constructed in July should not be used to speculate about feeding conditions in August. I suggest that this is part of the reason for the greatly different slopes of the composite curves on Lucy Islands in 1986 and 1987 (Table 4.4). The sequential growth rates for these years are more similar (Table 4.3). In 1986, the composite growth curve used data from 7-18 July, a period in which burrow loads were relatively high. As a result the composite curve for 1987 is shallower than in 1986. Using hooded chicks to create the composite curve in 1987 probably led to an additional decrease in the estimate of the growth rate.

Table 4.5:   Growth rates (g/day) for rhinoceros auklet chicks
             from the intercolony comparison in British Columbia
             (from Bertram and Kaiser, in prep.) Growth rate is
             estimated from the slope of the single composite
             curve constructed on each colony in each year.
             Sample sizes are given in parentheses.

| Colony | 1984 Mean | S.D. | 1985 Mean | S.D. | 1986 Mean | S.D. |
|---|---|---|---|---|---|---|
| Lucy | 7.3 | 0.5 | 10.6 | 0.5 | 7.9 | 0.6 |
| | (38) | | (30) | | (38) | |
| Pine | 6.0 | 0.2 | 7.1 | 0.5 | 5.7 | 0.4 |
| | (66) | | (53) | | (58) | |
| Triangle | 6.0 | 0.4 | 7.7 | 0.3 | 6.7 | 0.4 |
| | (53) | | (49) | | (40) | |

The effect of hooding can be accounted for by multiplying the composite growth rate by 1.24 (the ratio between growth rate of control/hood control birds in 1985, Table 4.1a). When this is done the composite growth rate in 1987 becomes 6.7 (5.4 x 1.24), still poorer than in 1986. The composite growth curve data as well as the sequential growth rate data both suggest that feeding conditions were best in 1985 when growth was fastest, and poorer in the years when growth rates were slower (Tables 4.3a, 4.4).

In summary, growth rates varied more widely between than within years. The lack of a decline in growth rate late in the season lends further support to the conclusion reached in Chapter 3 that the decline in nestling provisioning observed in 1985 and 1986 is not due to a seasonal deterioration of the food supply. The large changes in growth from year to year is not consistent with Ricklefs' (1979a) precocial growth hypothesis, which predicts that parental birds should be able to compensate for changes in the food supply by adjusting their effort so that chick growth is kept at the optimum level. Finally, the fact that growth on all three colonies changed together supports the idea that changes in marine conditions on a coastal scale were responsible for the growth changes. Conditions seemed best in 1985 and poorest in 1987.

# CHAPTER V

## INFLUENCES ON PARENTAL PROVISIONING

INTRODUCTION
‾‾‾‾‾‾‾‾‾‾‾‾

Parental investment theory (e.g. Williams, 1966b) is
concerned with how much effort parents should invest in their
young. Parental investment is defined as 'any investment by the
parent in an individual offspring that increases the offspring's
chance of surviving at the cost of the parent's ability to
invest in other offspring' (Trivers, 1974). Trivers (1974)
showed that there will be disagreement between parent and
offspring over the amount of investment expended on each young,
and he coined this phenomenon parent-offspring conflict. In the
rhinoceros auklet, provisioning can be regarded as an investment
since it increases an offspring's chance of survival, but at the
cost of decreasing the probability that an adult will be able to
invest in young in future years. This cost arises due to the
risk of predation (or death from collision) associated with each
visit an adult makes to the colony. In most seabird species
adult survivorship is greater than 90%. As such the costs of
investment into a single young are likely to feature strongly in
the tactics that adults use when raising young, since lifetime
reproductive success may be greatly reduced by only a slight
decrease in the survival chances of the adult (Goodman, 1974).·

A number of studies have addressed the question of whether
the chick or adult determines the feeding regime in Atlantic

puffins. When Harris (1983) removed nine chicks that averaged 31 days old from their burrow and replaced them with chicks 3-23 days younger, he found no difference in the peak or fledging weights or fledging age of exchanged chicks. However, no data on the amount fed to these birds was presented. A similar experiment with puffins was performed by Hudson (1979) who exchanged seven chicks "about 20 days old". Age and weight differences between the exchanged chicks were not reported. Hudson monitored the feeding rate of fostering parents and concluded that parents fed the chick according to their previous feeding schedule, not according to the chick's age. When chicks of the larger tufted puffin were substituted into rhinoceros auklet burrows, the foster chicks grew more slowly than usual (Vermeer and Cullen, 1979). While this suggests that adult rhinoceros auklets did not respond to the greater demands of tufted puffin chicks, the exchange was not conducted to test that hypothesis. The foster parents may have been working harder than they normally do, but the fact that their rhinoceros auklet foster parents provisioned only at night could have precluded the tufted puffin chicks (which are usually fed many times throughout the day) from growing faster. In a recent study (Ricklefs, 1987) rotated a number of Leach's storm petrel chicks through a smaller number of burrows to produce "chick equivalents of food requirements" varying incrementally from one to two. Adults did not respond to increased food demand and Ricklefs postulates that the average amount of food delivered daily by each parent is determined independently of food demand

of the chick, and that chicks attain a mass that balances food intake against food requirement, which varies in direct relation to mass. An intriguing result of this study was that after termination of the experiment underweight birds increased in mass quickly when returned to their natal burrow. No data on feeding rate during this period were provided.

In this section I investigate factors that influence parental provisioning of nestlings by rhinoceros auklets in relation to Lack's energy limitation hypothesis, Ricklefs precocial growth hypothesis, and the parental tactic hypothesis (the life history perspective). Lack's hypothesis suggests that since parents are working at capacity to feed young, they will not be able to respond to an experimentally induced increase in chick demands. Alternatively, Ricklefs' hypothesis implies that parents can easily respond to increased chick demands. The life history perspective posits that parents can increase work effort but that they normally keep it low in order to safeguard their reproductive future. Parents will increase their provisioning effort only when the fitness returns exceed the extra costs they will incur. I examined parental response to chick demand at various stages of development, by conducting a series of fostering experiments. I assume that energetic needs and thus demand, increase with chick age. Young rhinoceros auklets fledge at 50-80 percent of adult weight, and thus complete 50-20 percent of their growth at sea. Thus the energetic demands are likely to increase throughout the whole nesting period, since the chick still has a substantial proportion of its growth to

complete at the time it fledges.

## METHODS

*Chick Manipulations*

In 1985 I had an opportunity to conduct a simple manipulative experiment. It is worth outlining here as it motivated the experiments described below. As described earlier (Chapter 2) chicks hooded in 1985 were not tethered in the nest chamber and sometimes wandered out of their burrows, hooded, never to be seen again. This happened to one of the 'hood control' chicks on 23 July. This vacant spot was filled with a chick that we had found starving on 11 July and had taken into camp and fed. At the time of the substitution this bird was 29 days old, but weighed only 200 g, about 100 g less than wild chicks its age. We called this bird "Manipuchick" and continued to hood it on the same schedule as the natal chick. The rationale for the substitution was that Manipuchick was starving and thus should exhibit greater feeding demands than a healthy chick. According to Lack's hypothesis, the foster parents cannot increase their effort in response to the additional demand. Ricklefs' hypothesis predicts they can and will, and the life history perspective predicts a conditional response (see below).

In 1986 I performed two chick fostering experiments. The first was an exchange of young (early developmental stage, n = 14) and middle aged (mid developmental stage, n = 14) nestlings. Chicks for this experimental group were approximately 10 days

65

different in age. I exchanged chicks between burrows attempting to keep the weight difference between exchanged chicks constant. Chicks of equal age and weight (n = 16) were also exchanged, serving as a control for the effect of the change. I began the early-mid fostering study on 14 July. Each day for six days prior to the exchange, all chicks (n = 44) were weighed to the nearest two g between 1700 and 2300 hrs. Individual chicks were always weighed using the same scale and, if possible, at the same time of day. Regardless, weighing time was recorded to the nearest quarter hour.

Following weighing on the sixth day, the exchange of chicks was carried out by transporting nestlings between natal and foster burrows in nylon or cloth bird bags. Chicks were tethered into their new burrow for the first night to prevent desertion, and to allow the nestling to become familiar with its new surroundings and foster parents. The following day birds were untied and weighing continued as before for another six days. Weight gain from one day to the next was used to estimate the amount fed to chicks (burrow load) between two successive weighings using the technique described below and in Appendix 2. The mean burrow load on five nights before and five nights after the exchange (the loads on the night of the exchange and the following night were not used) were compared in relation to the difference in weight and age of the exchanged chicks. Thus, comparisons were made between the same parents before and after the substitution. This procedure is important. In all populations there is variation among individuals, and so some

66

individuals are of higher quality than others (e.g. Coulson and Porter, 1985). Therefore, in manipulative experiments, comparisons between nesting pairs are bound to obscure real effects unless sample sizes are large enough to compensate for inter-individual variation. To control for the variation in quality, individuals or pairs should be compared with themselves before and after a manipulation.

The second fostering experiment in 1986 commenced on 30 July and involved exchanging middle aged (mid developmental stage, n = 14) chicks with chicks in the late stages of development (n = 14). The procedure was identical to the early-mid fostering experiment, although the number of burrow loads collected before and after the exchange was more variable. No comparisons were made where less than three food loads could be estimated in both the pre- and post-exchange periods.

The fostering experiments were repeated in 1987, with larger samples and comparisons between parents before and after the exchange included up to seven burrow loads. I did not include in the analysis burrow loads delivered to chicks the night of the exchange, or on the two following nights. Due to time constraints, only the loads delivered on the night of the exchange and the following evening were eliminated in the mid-late experiment. This gave the parents two possible nights to encounter the substitute chick in their burrow, rather than three. The early-mid exchange experiment commenced on 10 July while the mid-late experiment began on 30 July.

Ricklefs et al. (1985) described a technique to estimate the amount of food delivered to nestling petrels based on the relationship of weight gain over 24 hrs, and the sum of positive mass increments due to feeding at intervals during the night between the two weighings. I chose a more direct technique for two main reasons. Ricklefs' et al. were able to measure all of their birds in the same two hour period in each day. Given that there were other daily activities to carry out, and the intricate and dispersed nature of the accessible burrows on Lucy Islands I thought it unlikely that a field team could match the accurate weighing schedule achieved by Ricklefs et al. (1985). Therefore I needed a technique that could account for the considerable daily weight loss exhibited by rhinoceros auklet chicks (Vermeer and Cullen, 1982) while allowing a more flexible daily weighing routine. Secondly, given my other activities, I would have had difficulty in finding an adequate sample of burrows to conduct nightly weighings since burrows would have to be located outside of other experimental areas to prevent nocturnal disturbance. To satisfy these requirements, in 1986 I raised six chicks in camp (Permit BC PC 86/09) on a known diet and measured their weight at intervals throughout the day. In this way I could manipulate the quantity of food chicks received and relate it to the weight loss that occurred through the day. Chicks were raised in artificial burrow holes in the ground about 1 m long, 20 cm wide and 20 cm deep. The holes were covered with arborite and dirt, and a 3 cm diameter plastic pipe

provided ventilation.

The six chicks were provisioned according to a schedule based on a latin square design, with six food levels ranging from zero to the the maximum burrow load (110 g) observed. The experiment was divided into four, six day blocks, each separated by a few days. In blocks 1 and 4 the six food levels were 0, 19, 38, 57, 76 and 95 g. For blocks 2 and 3, the food levels were 0, 22, 44, 66, 88 and 110 g. (The difference in feeding levels between blocks is related to the fact that chicks are fed more in the middle of their nesting period). Before each block commenced, individual chicks received a feeding of the maximum size for that block. Chicks were fed previously frozen meals consisting primarily of sandlance that had been collected from adults returning to the colony. We fed chicks between 2300-0100 hrs. Each day the "camp chicks" were weighed at 1000, 1400, 1600 and 2200 hrs, to the nearest 2 g.

Six camp chicks were also raised in 1987 (Permit number BC PC 87/12) with some modifications to the previous procedure. The birds were kept in the same spot although the holes were lined with bottomless, wooden boxes (300 cm x 20 cm x 20 cm) with removable lids. The boxes had 10 half inch diameter holes on the sides near the top for ventilation. Chicks were fed with the same frequency with which burrow loads of various sizes were delivered to known-age chicks in 1985. The experiment was divided into four blocks of 7-8 days each, with only one separation of two days between blocks 1 and 2. The six chicks

were randomly assigned to three groups. Within each block, two chicks were assigned to each of three feeding sequences. Although the feeding order and size of loads in 1987 differed from 1986 the average amount of food per night was very similar between years.

*Camp Chick Growth Model*

Using the camp chick growth data I developed a model which incorporated weight on day X at time $t_1$, and weight the following day (X+1) at time $t_2$ to estimate the amount of food a chick had received during the night between the two weighings. In the model, feeding was assumed to occur at midnight (when camp chicks were fed) and weight loss during the day was assumed to be linear. Feeding in the colony usually peaks around midnight. Visual inspection of data for camp chick weight loss throughout the day suggests exponential weight loss in the early part of the day levelling to a linear decline in the late afternoon and evening. Since the camp chick model was intended to estimate meal sizes of wild chicks weighed after 1700 hrs, the assumption of linear weight decline was justified. The derivation of the model is shown in Appendix 2. The constants in the final equation were obtained by multiple regression of the amount of fish (g) fed to camp chicks on the four variables derived from weighings of those birds at 1400, 1800 and 2200 hrs.

I used the same basic model to analyze the two camp chick data sets (1986 and 1987) although in 1987 I incorporated the

70

exact time that camp chicks were fed. I assumed a midnight feeding for wild birds during the early-mid fostering experiment, and the feeding time for the mid-late exchange in 1987 was assumed to be at 2315 hrs since adults tended to arrive at the colony earlier as the season progressed.

## RESULTS

*Manipuchick*

Following substitution of Manipuchick into the burrow of the lost chick, the foster parents increased the size of the food deliveries sharply. Before the natal chick was lost, the size of food loads delivered was not significantly different than loads brought to 16 control chicks of similar age at the same time. However, the loads brought to Manipuchick were significantly larger ($t = 17.0$; $df = 48$; $P < 0.001$) than loads delivered during the same time to wild chicks of the same age as the natal chick (Figure 5.1). This rules out a seasonal change for the increase in load size delivered to Manipuchick. The mean increase in burrow load (38 g) corresponds closely to the size of one bill load in 1985 (32 g), suggesting that the increase is due to one extra parental visit per night.

*Camp Chicks*

The six chicks grew from an average of 167 (range 144-196) g to 318 (range 290-338) g during the experiment in 1986 and progressed from an average of 130 (range 116-148) g to 290
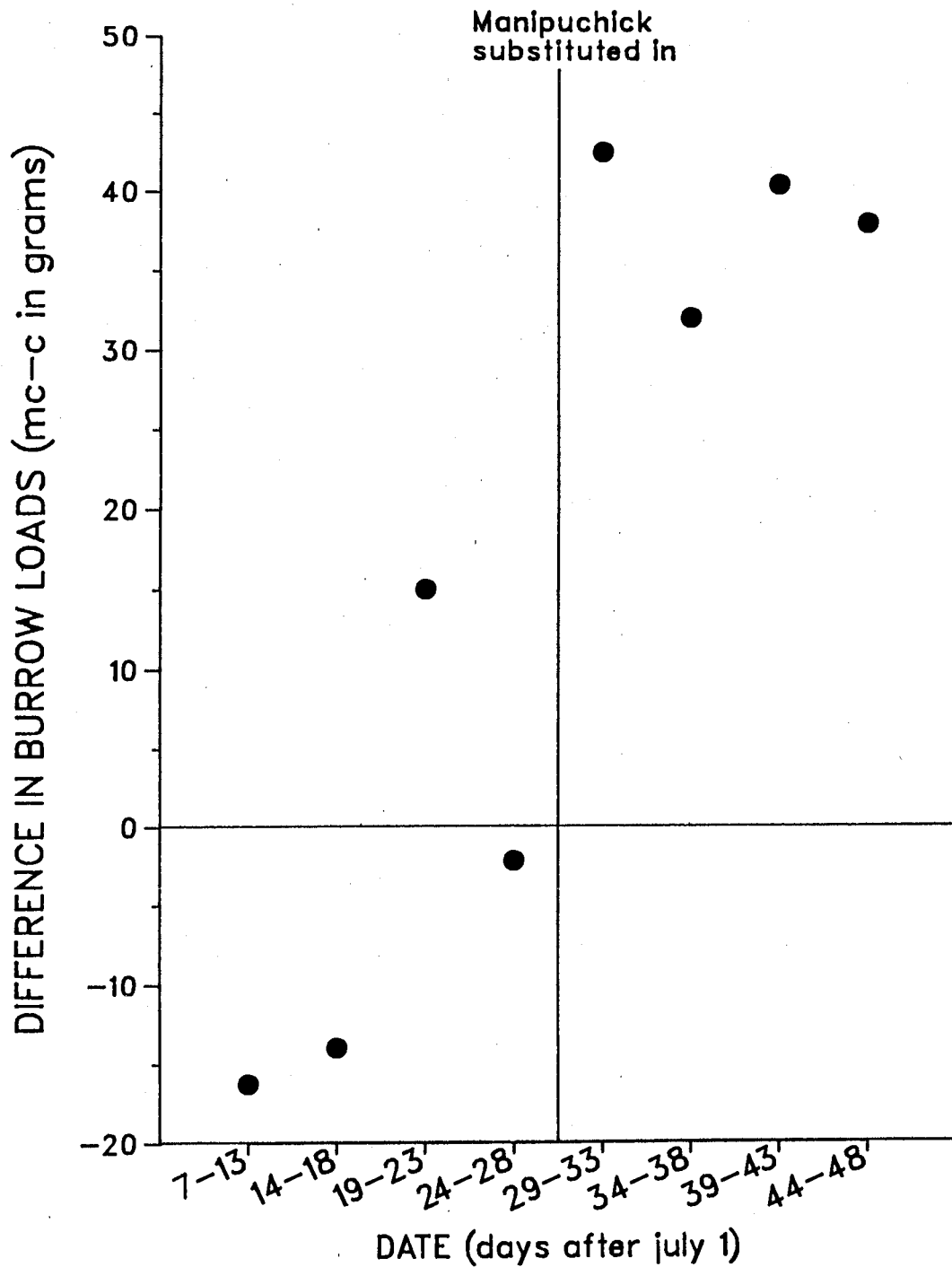
71

Figure 5.1: Comparison of burrow loads delivered by foster parents (mc) to their natal chick and Manipuchick, with loads brought concurrently to control chicks (c, n = 16) of the same age as the natal chick. Manipuchick was substituted into the burrow on 25 July.

(range 272-312) g in 1987. The amount of food predicted to have been consumed by the camp chick growth model was highly correlated with the true amount fed in both years (1986: r = 0.844; 1987: r = 0.887). The model equations for both years are provided in Appendix 2.

*Fostering Experiments*

Table 5.1 summarizes the number of estimated burrow loads before and after the exchange and the number, age and weight of the chicks used in the fostering experiments. The average weight of burrow loads fed to all chicks in each treatment (experimental and control) before and after the exchanges in both years are shown in Table 5.2.

Unfortunately in 1986, the electronic scale used to weigh most of the nestlings in the early-mid fostering experiment was found to be defective in the last two days of the post-exchange monitoring. The scale consistently underestimated weights and the deviation from true weights increased with increasing weight. Since I do not know when the malfunction ocurred the data are suspect and the results are not presented.

Making sure to calibrate my scales regularly in 1987, I performed the same early-mid fostering experiment and obtained a significant result. When the difference in mean load after and before the exchange was compared for parents that received a foster chick larger than their own young with control parents, it was evident that experimental foster parents increased food

Table 5.1: Number of estimated burrow loads before (Bef.) and after (Aft.) the exchange and the means and standard deviations of weights and ages of various groups of chicks on the exchange day in the early-mid (a) and mid-late (b) fostering experiment in both years. Controls = Cont.; Experimental chicks = Exp. Note that some chicks were lost during the experiment and as a result the sample may be smaller than initially.

| | | | Number of Chicks Exch. | | Mean Number of Loads | | Age of Chick | | | | | | Weight | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | Date | Cont. | Exp. | Bef. | Aft. | Cont. | S.D. | Early | S.D. | Mid | S.D. | Cont. | S.D. | Early | S.D. | Mid | S.D. |
| a) | 1987 | JL 17 | 14 | 28 | 6.9 | 7.0 | 24.8 | 2.7 | 17.1 | 1.5 | 26.3 | 1.1 | 235.3 | 62.9 | 165.9 | 33.6 | 265.6 | 34.6 |
| b) | 1986 | AU 6 | 9 | 11 | 4.9 | 5.0 | 40.0 | 2.7 | 31.6 | 5.1 | 43.7 | 3.0 | 304.9 | 26.1 | 273.6 | 52.8 | 335.4 | 36.0 |
| | 1987 | AU 7 | 9 | 24 | 6.9 | 6.1 | 35.1 | 7.0 | 28.3 | 3.8 | 42.8 | 2.0 | 317.8 | 67.3 | 262.0 | 36.7 | 347.4 | 36.5 |

Table 5.2:   Means of burrow loads (g, estimated using the camp
            chick growth model) delivered to control and
            experimental chicks before and after the exchange in
            the early-mid and mid-late fostering experiments in
            1986 and 1987. Larger indicates that parents
            received a larger foster chick and smaller indicates
            a smaller substitute. Before and after refer to the
            exchange date.

| Chick Developmental Stage | Treatment | 1986 | | 1987 | |
|---|---|---|---|---|---|
| | | Before | After | Before | After |
| Early - Mid | Control | - | - | 53.9 | 59.8 |
| | Larger | - | - | 43.9 | 59.0 |
| | Smaller | - | - | 59.4 | 56.5 |
| Mid - Late | Control | 59.8 | 56.8 | 62.6 | 60.4 |
| | Larger | 57.1 | 63.8 | 57.0 | 56.7 |
| | Smaller | 61.8 | 62.2 | 64.7 | 61.0 |

loads in response to a larger chick (t = 2.93, df = 25.9, P = 0.0072). Parents receiving a foster chick smaller than their own offspring delivered less than control parents (t = 3.36, df = 21.1, P = 0.003). These results are depicted in Figure 5.2, showing the difference in load size after and before the exchange in relation to differences in weight and age of natal and foster chicks.

Parents did not change the amount of food delivered in either the 1986 or 1987 mid-late chick exchange (Table 5.2; Figure 5.3, 5.4).

DISCUSSION

*Fostering Experiments*

When early and mid-sized chicks were exchanged in 1987, parents responded by delivering more food to older, larger chicks and less to younger, smaller foster chicks (Figure 5.2a, b). This is the first clear evidence that alcid parents will work harder than they usually do when rearing young. When chicks in the middle and late developmental stages were exchanged foster parents did not alter their previous feeding regime (Figures 5.3, 5.4).

Why do parents respond differently to increased demands of their chicks in early and late stages of development? Lack's energy limitation hypothesis provides no explanation, since it holds that parents are working at maximum capacity, and
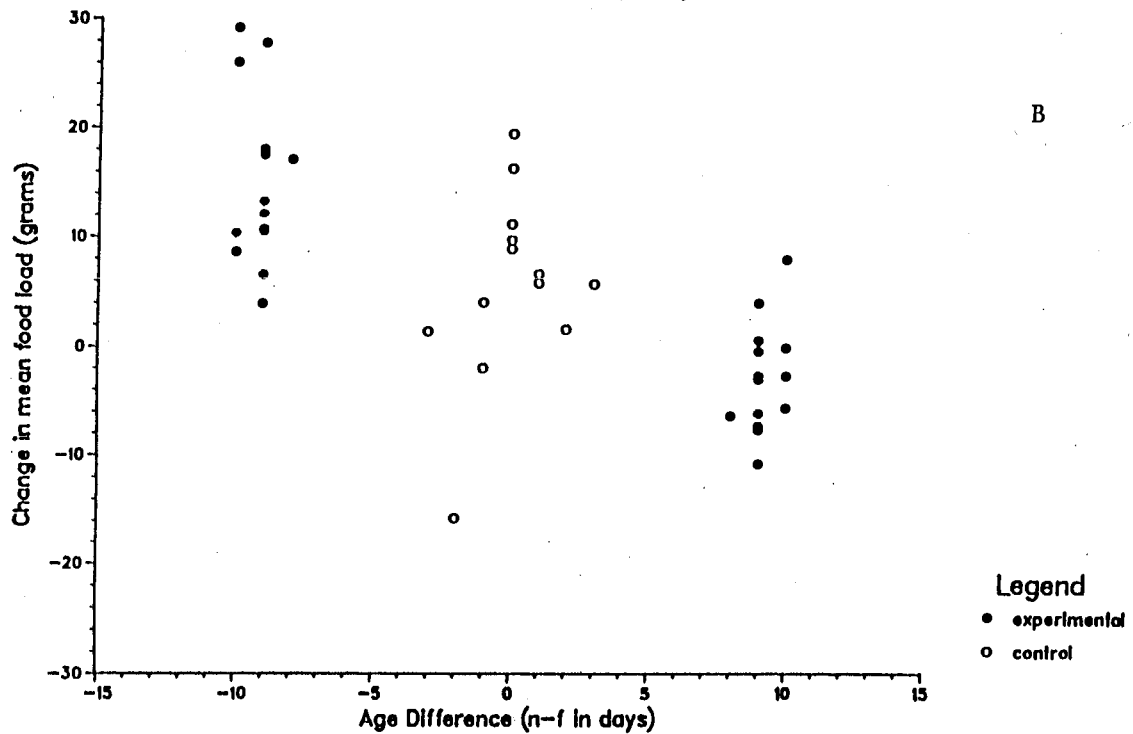
76

Figure 5.2: Differences between mean food loads delivered by
parents after and before the exchange of chicks,
versus the difference in weight (A) and age (B) of
natal (n) and foster (f) chicks in the early-mid
fostering experiment in 1987.

Figure 5.3: Differences between mean food loads delivered by
parents after and before the exchange of chicks,
versus the difference in weight (A) and age (B) of
natal (n) and foster (f) chicks in the mid-late
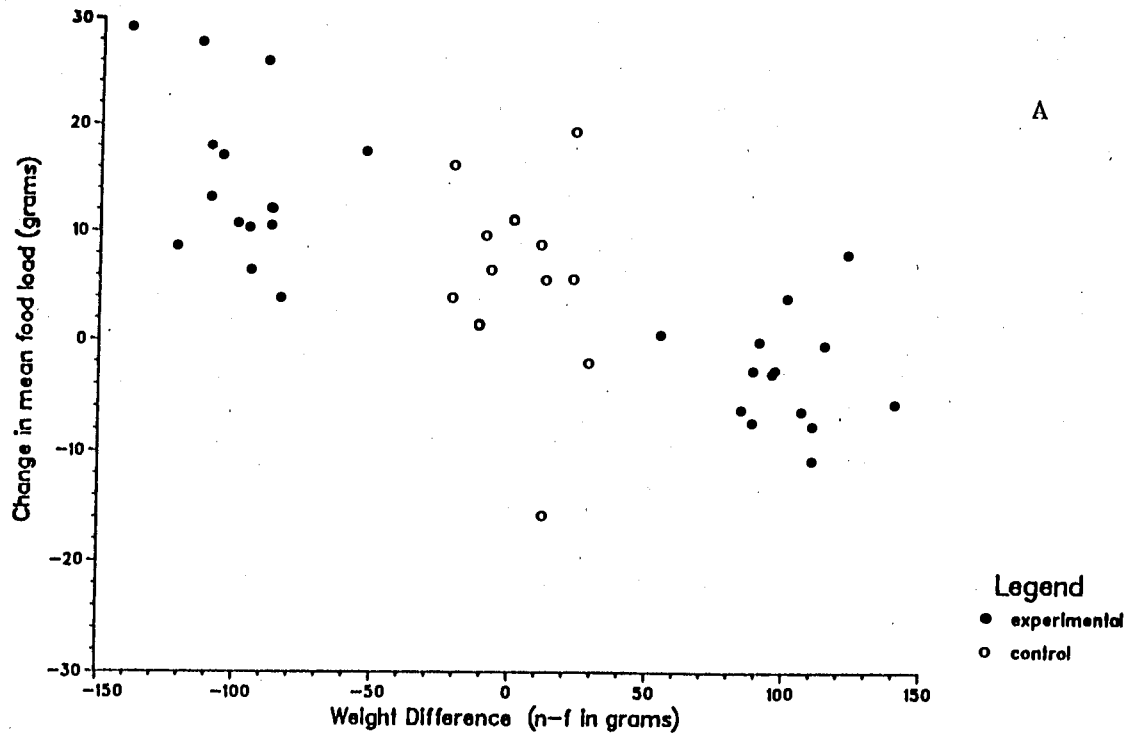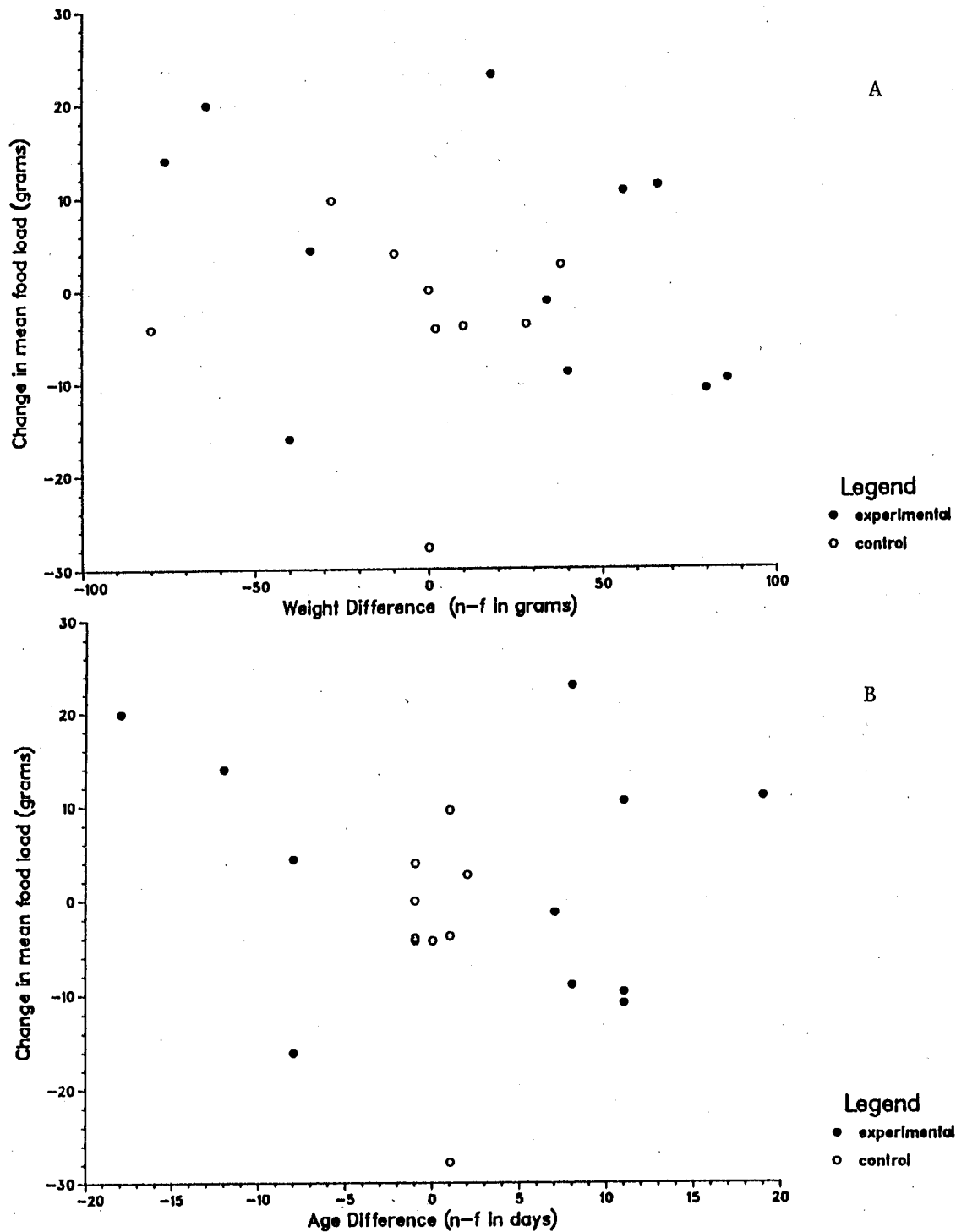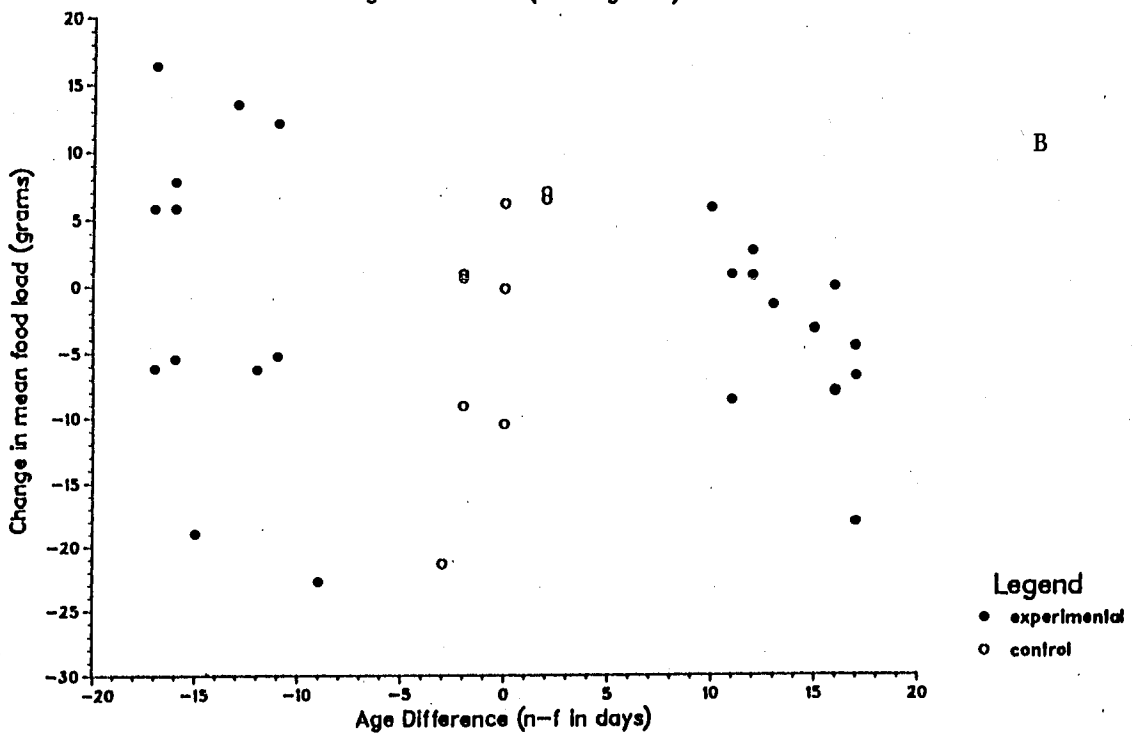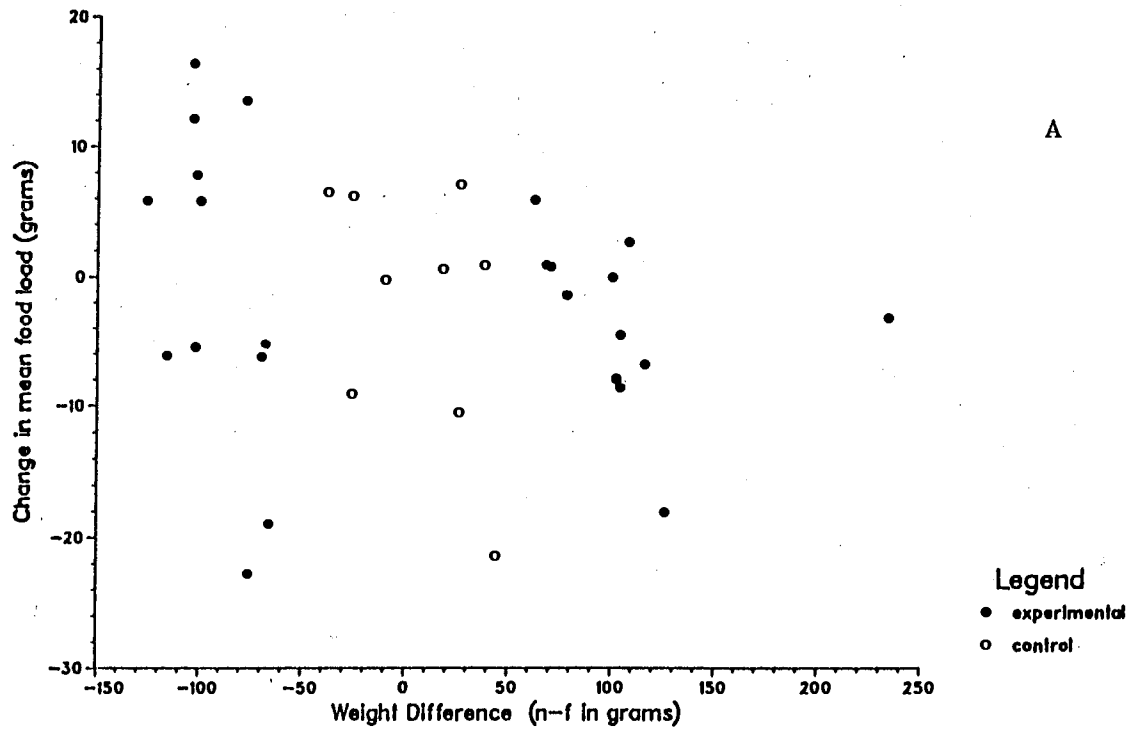fostering experiment in 1986.

Figure 5.4: Differences between mean food loads delivered by
parents after and before the exchange of chicks,
versus the difference in weight (A) and age (B) of
natal (n) and foster (f) chicks in the mid-late
fostering experiment in 1987.

therefore can never increase food delivery. Under the precocial growth hypothesis of Ricklefs, parents can increase their work effort as occurred in the early-mid exchange in 1987, but it cannot account for the lack of response to foster chicks in the late stages of development.

Can the results from the fostering experiments be explained by viewing chick provisioning as a parental tactic? The theory of parent-offspring conflict proposes that offspring are selected to secure more investment from their parents than parents are selected to give. That there may be conflict between adults and young over provisioning in the Alcidae is neatly illustrated by Hudson's (1979) work with Atlantic puffins. He showed that chicks offered an extra 50 g of food per day or fed ad lib ate far more than wild birds of the same age. However, the weights of the birds in his three feeding groups did not differ significantly for the first part of the study (when chicks were 10-23 days old) suggesting that the wild parents were meeting chick demands during this period. I suggest that early in development the marginal return on a unit of parental investment is relatively high, but declines as the chick approaches maturity. The reason is that the growth rate of the chick slows late in the nestling period (Vermeer and Cullen, 1979). Therefore the parent's investment is being expended less on chick growth and to an increasing degree on maintenance. If the survival of the chick depends on the size at which it fledges (Perrins et al., 1973; c.f. Harris and Rothery, 1985), the parent's return (i.e. the probability of a surviving chick)

80

is therefore declining because the cost (risk) of each visit is constant, while the benefit (growth, i.e. increased survivorship) declines. Predation risk does affect the willingness of parents to provision as shown by Nettleship (1972). He demonstrated that Atlantic puffins breeding on sloped habitat fed young more frequently than parents with burrows on level habitat where the rates of predation and kleptoparasitism were higher. Similarly, Harris (1980) reported that Atlantic puffins nesting in high density areas enjoyed greater reproductive success than those in low density areas, where the risk of predation from gulls was considerably higher.

Survival after fledging may also be influenced by ocean feeding conditions. When conditions are poor there should be greater benefit to an adult for a unit of investment in the chick than when conditions are good, because the chick will need to be relatively larger before it can fledge and move to the open sea to complete its development.

The above argument is consistent with Trivers' (1974) view that parent-offspring conflict should increase as the period of parental investment continues. In addition, it can be used to explain the results of the fostering experiments. Parents responded to the demands of chicks in the early-mid range because the marginal return on increased investment was still high. However, by the time the chicks were exchanged in the mid-late experiments the marginal return had declined and parents should ignore chick demands. Rather, during this period,

parents should feed nestlings on a trajectory determined by ocean feeding conditions.

*Manipuchick*

The exchange involving Manipuchick in 1985 was essentially similar to a mid-late exchange. At 29 days old Manipuchick was placed in a burrow previously occupied by a 40 day old chick. However, unlike the mid-late fostering experiments in 1986 and 1987, the foster parents increased their provisioning rate to Manipuchick (Figure 5.1). In the fostering experiments the exchanged chicks were all in good condition, whereas Manipuchick was at least 100 g below the average weight for chicks of a similar age in 1985.

Another hypothesis for the increased feeding rate to Manipuchick is that its foster parents were especially experienced and were therefore able to respond to the demands of the chick. Before the substitution occured the natal chick was one of the largest in the colony for its age, and was among the earliest hatched birds. In the following years the chick in the same burrow (and I assume the same parents) was the earliest hatched bird, and the first chick to fledge in all of the monitored nests, further suggesting that its parents were of higher quality and better able to rear offspring than other parents in the population.

Summarizing, the fostering experiments showed that adult rhinoceros auklets are capable of increasing their provisioning

rate in response to chick needs, but that they did not always choose to do so. They responded when chicks were exchanged in the first half of the nestling period, but not in the second half. Then they fed their foster chick as they would have their natal chick. This pattern is consistent with the idea that parents respond only when the fitness benefits of doing so exceed the costs.

# CHAPTER VI

## GENERAL DISCUSSION AND CONCLUSIONS

In Chapter 3 I showed that there were marked differences between the provisioning curves in the three years. They ranged from an inverse 'U' shape in 1985, to almost flat in 1987 (Figure 3.6, Table 3.1). I dismissed the precocial growth hypothesis as an explanation for the decline in provisioning rate to older nestlings because it predicts that provisioning curves should exhibit similar shapes between years. Burrow loads delivered to early and late hatched nestlings of the same age were of similar sizes, suggesting that there was no strong seasonal decline in food availability during those periods (Table 3.2). However, due to the low power of my tests the possibility of a seasonal effect cannot be ruled out as an explanation for the decrease in provisioning rate observed. I proposed that the provisioning rate of nestlings was the outcome of a parental tactic which may have evolved as a result of selection pressures imposed by the significant mortality risk associated with visiting the colony. This is consistent with the inference that provisioning rate varies with the number of visits adults make to the colony, rather than with fluctuations in bill load size.

In Chapter 4 I showed that growth rates, even within a year, may be highly variable (Figure 4.1). The precocial growth hypothesis predicts similar growth between individuals. I found no difference in the growth rate of 'early' and 'late' hatched

nestlings within years, which supports the idea of no seasonal decline in feeding conditions (Table 4.2). The supplementary feeding experiment showed that provisioning rate has an influence on growth rates (Table 4.1). Although I was unable to increase the rate of growth (perhaps due to my methodology), studies of the closely related Atlantic puffins show that additional food increases the rate of weight gain (e.g. Harris, 1978; Hudson, 1979). According to Case (1978) this finding refutes the main prediction of the precocial growth hypothesis.

Growth on widely separated colonies as measured by composite growth curves, rose and fell in unison between years, suggesting variation in feeding conditions over a large geographic region (Table 4.5, Bertram and Kaiser, in prep). This result led me to infer that ocean feeding conditions were best in 1985 and poorest in 1987 when the slopes of composite growth curves from Lucy were highest and lowest, respectively.

Chapter 5 showed that adults responded to foster chicks in early stages of development by working harder, but ignored demands from foster chicks in the late developmental stages. The fact that adults were capable of increasing work effort refutes Lack's energy limitation hypothesis. Conversely, Ricklefs' precocial growth hypothesis is insufficient to account for the lack of response by parents to older chicks. When the inevitable conflict between parent and offspring over reproductive effort was considered, the results were consistent with the idea that variations in the rate of provisioning are parental tactics.

Why does the shape of the provisioning curve vary between years (Figure 3.6, Table 3.1)? I discussed the use of chick growth rates as estimates of ocean feeding conditions and presented indirect evidence in Chapter 4 that feeding conditions deteriorated from 1985 to 1987. In the year when chick growth was fastest (1985), presumably indicating superior feeding conditions, the steepest decline in provisioning rate in the late pre-fledging stage was observed (Table 6.1). In contrast, there was no decline in the provisioning rate in 1987 when growth rate was slowest, suggesting marginal feeding opportunities. The rate of decline in provisioning and growth rates were both intermediate in 1986.

Life history theory is the study of trade-offs. It assumes that increasing reproductive effort yields the benefits of increased offspring survival at the cost of reducing parental survival, and that natural selection has led to the optimization of levels of effort relative to these costs and benefits (e.g. Stearns, 1980). I suggest that the variation in provisioning curves between years is the result of a parental tactic which manifests itself differently depending on various trade-offs imposed by yearly changes in ocean feeding conditions. For chicks, the colony is a safe place because they are underground where no predators can reach them. Growth rate, however, is slow there because provisioning is controlled by parents who only visit at night. In contrast, growth rate is potentially faster on the ocean because food is always available. Life on the ocean, however, is likely more dangerous than life in the

Table 6.1: Comparison of the decline in the provisioning rate as measured by the coefficient of the squared term in the quadratic equations of Table 3.1, in relation to growth rates derived from composite and sequential data.

| Year | Quadratic Parameter Age ($X^2$) | Growth Rate (g/day) | | |
|------|------|------|------|------|
| | | Composite | Sequential | MRT† |
| 1985 | -0.061 | 10.6 | 7.10 | a |
| 1986 | -0.019 | 8.1 | 5.40 | b |
| 1987 | 0.005 | 5.4 | 5.25 | b |

†Student-Newman-Keuls multiple range test;
 Different letters signify differences.

burrow. Assuming that there is some survival benefit to reaching maximum weight before the first winter (Perrins et al., 1973), chicks should evaluate these trade-offs in deciding when to leave the burrow. Since chick survival is an important factor in determining the reproductive success of the adult, the parent can influence the chick's fledging decision by adjusting provisioning rate. I propose that when ocean feeding conditions are good (as in 1985) adults should be selected to decrease provisioning rate to chicks late in their development by reducing the number of feeding trips to the colony (by feeding every second night for example), thus making it profitable for chicks to fledge earlier (Davies, 1976; 1978). The selective agent acting on parental behaviour is likely predation risk, since reducing the number of visits to the colony increases the probability that the adult will survive to breed again. Alternatively, when feeding conditions at sea are poor (as in 1987) parents will be selected to invest more in their chicks before fledging in order to improve their survival prospects and, as such, parents should not decrease provisioning rates as chicks approach fledging.

This hypothesis is consistent with the observation that parental feeding in oystercatchers (Haematopus ostralegus) ceased earlier in habitats where food was obtained relatively easily by foraging juveniles than where it was more difficult to procure (Norton-Griffiths, 1969). Davies (1978), studying the acquisition of independence in passerine fledglings, suggested that parents might adopt a strategy which involved adjusting the

rate of reduction of investment to postfledging young according to independent estimates of feeding conditions.

When viewed in the context of life history theory, the most parsimonious explanation for slow growth rates in the rhinoceros auklet appears to be that a low rate of chick provisioning has resulted due to selection for high adult survival. On Lucy Islands the main cost of reproduction to rhinoceros auklets is likely to be the risk of predation or injury associated with visiting the colony. Parents should be selected to increase their work effort only when there is the potential for gain in terms of reproductive success (e.g. when conditions for growth of young at sea are poor) and I suggest that this evaluation on the part of the parents resulted in the provisioning curve varying its shape from year to year. A greater understanding of the trade-offs imposed by the various costs and benefits involved in parental provisioning, as well as an understanding of the fitness interests of the parent and chick, will aid in the construction of a general theory for the phenomenon of slow growth and parental provisioning not only in temperate alcids such as the rhinoceros auklet, but also in tropical seabirds.

# LITERATURE CITED

Asbirk, S. 1979. The adaptive significance of the reproductive pattern in the black guillemot Cepphus grylle. Videnskabelige Meddelelser Dansk Naturhistorisk Forening 141: 29-80.

Ashcroft, R. E. 1979. Survival rates and breeding biology of puffins on Skomer Island, Wales. Ornis Scandinavica 10: 100-110.

Ashmole, N.P. 1971. Seabird ecology and the marine environment. (pp. 223-286) In: D.S. Farner and J.R. King, (Eds.). Avian Biology. Vol. 1. Academic Press, New York.

Barrett, R. T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N.Rov and W. Vader. 1987. The food, growth and fledging success of Norwegian Puffin chicks Fratercula arctica in 1980-1983. Ornis Scandinavica 18: 73-83.

Birkhead, T.R. and D.N. Nettleship. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres Uria lomvia. Ecology 63: 300-306.

Birkhead, T.R. and M.P. Harris. 1985. Ecological adaptations for breeding. (pp. 205-231) In: The Atlantic Alcidae: the evolution, distribution and biology of the auks inhabiting the atlantic ocean and adjacent waters. D.N. Nettleship and T. Birkhead (Eds.). Academic Press, London.

Burger,J. 1980. The transition to independence and postfledging parental care in seabirds. (pp. 367-447) In: Behavior of Marine Animals. J. Burger, B. Olla and H. Winn (Eds.). Plenum Press, New York.

Cairns, D.K. 1987. The ecology and energetics of chick provisioning by black guillemots. Condor 89: 627-635.

Case, E. L. 1978. On the evolution and adaptive significance of postnatal growth in terrestrial vertebrates. Quarterly Review of Biology 53: 243-281.

Charnov, E.L. 1986. Life history evolution in a "recruitment population": why are adult mortality rates constant? Oikos. 47: 129-134.

Cody, M.L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31-44.

Corkhill, P. 1973. Food and feeding ecology of puffins. Bird Study 20: 207-220.

Coulson, J.C. and J.M. Porter. 1985. Reproductive success of the Kittiwake Rissa tridactyla: the roles of clutch size, chick growth rates and parental quality. Ibis 127: 450-466.

Davies, N.B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (Muscicapa striata). Behavior 59: 280-295.

Davies, N.B. 1978. Parental meanness and offspring independence: an experiment with hand-reared great tits, Parus major. Ibis 120: 509-514.

DeGrange, A.R. and J.W. Nelson. 1982. Bald eagle predation on nocturnal seabirds. Journal of Field Ornithology 53: 407-409.

Emms, S.K. 1987. The adaptive significance of the pattern of nesting dispersion in the pigeon guillemot. M.Sc. thesis. Simon Fraser University, Burnaby.

Engelman, L. J.W. Frane and R.I. Jennrich. 1979. BMDP Biomedical Computer Programs P-Series. W.J. Dixon and M.B. Brown (Eds.) University of California Press, Berkeley.

Gaston, A.J. 1985. Development of the young in the atlantic alcidae. (pp. 319-354) In: The Atlantic Alcidae: the evolution, distribution and biology of the auks inhabiting the Atlantic ocean and adjacent waters. D.N. Nettleship and T. Birkhead (Eds.). Academic Press, London.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. American Naturalist 108: 247-268.

Harris, M.P. 1966. Breeding biology of the Manx shearwater . Ibis 108: 17-33.

Harris, M.P. 1977. Comparative ecology of seabirds in the Galapagos Archipelago. (pp. 65-76) In: B. Stonehouse and C. M. Perrins, eds. Evolutionary ecology. Macmillan, London.

Harris, M.P. 1978. Supplementary feeding of young puffins Fratercula arctica. Journal of Animal Ecology 47: 15-23.

Harris, M.P. 1980. Breeding performance of puffins, Fratercula arctica, in relation to nest density, laying date and year. Ibis 122: 193-209.

Harris, M.P. 1983. Parent-young communication in the puffin, Fratercula arctica. Ibis 125: 109-114. 224 pp.

Harris, M.P. and J.R.G. Hislop. 1978. The food of young puffins. Journal of Zoology 185:213-236.

Harris, M.P. and P. Rothery. 1985. The post fledging survival of young puffins Fratercula arctica in relation to hatching date and growth. Ibis 127: 243-250.

Hatch, S.A. 1984. Nesting diet and feeding rates of rhinoceros auklets in Alaska. (pp. 106-115) In: Marine Birds: their feeding ecology and commercial fisheries relationships. D.N. Nettleship, G.A. Sanger and P.F. Springer (Eds.). Proceedings of the Pacific Seabird Seabird Group Symposium, Seattle, January 1982. Canadian Wildlife Service Special Publication.

Hudson, P.J. 1979. The parent-chick fledging relationship of the puffin, Fratercula arctica. Journal of Animal Ecology 48: 889-898.

Jewett, S.G., W.P. Taylor, W.T. Shaw and J.W. Aldrich. 1953. "Birds of Washington State". University of Washington Press, Seattle.

Kaiser, G.W., D. Bertram and D. Powell. 1984. A band recovery for the rhinoceros auklet. Murrelet 65: 57.

Koelink, A.F. 1972. Bioenergetics of growth in the pigeon guillemot. M.Sc. thesis, University of British Columbia, Vancouver.

Lack, D. 1968. "Ecological Adaptations for Breeding in Birds". Methuen, London.

Leschner, L. 1976. The breeding biology of rhinoceros auklet on Destruction Island. M.Sc. thesis, University of Washington, Seattle.

Lima, S.L. 1987. Clutch size in birds: a predation perspective. Ecology 68: 1062-1070.

Nelson, J.B. 1977. Some relationships between food and breeding in the marine Pelecaniformes. (pp. 77-88) In: Evolutionary Ecology. B. Stonehouse and C.M. Perrins (Eds.). Macmillan Press, London.

Nettleship, D.N. 1972. Breeding success of the common puffin [Fratercula arctica (L.)] on different habitats at Great Island, Newfoundland. Ecological Monographs 42: 239-268.

Norton-Griffiths, M. 1969. The organization, control and development of parental feeding in the oystercatcher, (Haematopus ostralegus). Behaviour 34: 55-114.

Nur, N. 1984a. The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. Journal of Animal Ecology 44: 731-742.

Nur, N. 1984b. Feeding frequencies of nestling blue tits (Parus caeruleus): costs, benefits and a model of optimal feeding frequency. Oecologia (Berlin) 65: 125-137.

Perrins, C.M., M.P. Harris and C.K. Britton. 1973. Survival of manx shearwaters, Puffinus puffinus. Ibis 115: 535-548.

Reznick, D. 1985. Cost of reproduction: an evaluation of the empirical evidence. Oikos 44: 257-267.

Rice, D.W. and K.W. Kenyon. 1962. Breeding cycles and behavior of Layson and black-footed albastross. Auk 79: 517-567.

Richardson, F. 1961. Breeding biology of the rhinoceros auklet on Protection Island, Washington. Condor 63: 456-473.

Ricklefs, R.E. 1973. Patterns of growth in birds. 2. Growth and mode of development. Ibis 115: 177-201.

Ricklefs, R.E. 1979a. Adaptation, constraint and compromise in avian postnatal development. Biological Review 54: 269-290.

Ricklefs, R.E. 1979b. Patterns of growth in birds. 5. A comparative study of development in the starling, common tern and Japanese quail. Auk 96: 10-30.

Ricklefs, R.E. 1985. Pelagic seabird reproduction and the marine environment. 1985 Meeting. A.O.U. Abstracts, Arizona.

Ricklefs, R.E. 1987. Response of adult Leach's storm-petrels to increased food demand at the nest. Auk 104: 750-756.

Ricklefs, R.E. and S.C. White. 1975. A method for constructing nestling growth curves from brief visits to seabird colonies. Bird Banding 46: 135-140.

Ricklefs, R.E. and S.C. White. 1981. Growth and energetics of chicks of the sooty tern (Sterna fuscata) and common tern (S. hirundo). Auk 98: 361-378.

Ricklefs, R.E., D. Duffy and M. Coulter. 1984. Weight gain of blue-footed booby chicks: an indicator of marine resources. Ornis Scandinavica 15: 162-166.

Ricklefs, R.E., C.H. Day, C.E. Huntington and J.B. Williams. 1985. Variability in feeding rate and meal size of Leach's storm-petrel at Kent Island, New Brunswick. Journal of Animal Ecology 54: 883-878.

Sargent, C.S. and M.R. Gross. 1986. Williams' Principle: An explanation of parental care in teleost fishes. (pp. 275-293) In: The behavior of teleost fishes. T.J. Pitcher, (Ed.). Croom Helm, London.

Shea, R.E. and R.E. Ricklefs. 1985. An experimental test of the idea that food supply limits growth rate in a tropical pelagic seabird. American Naturalist 126: 116-122.

Simons, T.R. and G.C. Whittow. 1984. Energetics of breeding dark-rumped petrels. (pp. 159-181) In: Seabird Energetics. G.C. Whittow and H. Rhan (Eds.). Plenum Press, New York.

Sokal, R.S. and F.J. Rohlf. 1981. Biometry. 2nd Edition. W.H. Freeman, San Francisco.

Stearns, S. 1980. A new view of life-history evolution. Oikos 35: 266-281.

Storer, R.W. 1945. Structural modifications in the hind limb of the Alcidae. Ibis 87: 453-456.

Strauch, J.G. 1985. The phylogeny of the alcidae. Auk 102: 520-539.

Summers, K.R. and R.H. Drent. 1979. Breeding biology and twinning experiments of Rhinoceros Auklets on Cleland Island, British Columbia. Murrelet 60: 16-27.

Thorenson A.C. 1983. Diurnal activity and social displays of rhinoceros auklets on Teuri Island, Japan. Condor 85: 373-375.

Trivers, R.L. 1974. Parent-offspring conflict. American Zoologist 14: 249-264.

Vermeer, K. 1979. Nesting requirements, food and breeding distribution of rhinoceros auklets, Cerorhinca monocerata, and tufted puffins, Lunda cirrhata. Ardea 67: 101-110.

Vermeer, K. 1980. The importance of timing and type of prey to reproductive success of rhinoceros auklets, Cerorhinca monocerata. Ibis 122: 343-350.

Vermeer, K. and L. Cullen. 1979. Growth of rhinoceros auklet and tufted puffins, Triangle Island, British Columbia. Ardea 67: 22-27.

Vermeer, K. and L. Cullen. 1982. Growth comparison of a plankton and a fish feeding alcid. Murrelet 63: 34-39.

Vermeer, K. and S.J. Westrheim. 1984. Fish changes in diets of nestling rhinoceros auklets and their implications. (pp. 95-105) In: Marine Birds: their feeding ecology and commercial fisheries relationships. D.N. Nettleship, G.A. Sanger and P.F. Springer (Eds.). Proceedings of the Pacific Seabird Group Symposium, Seattle, Janurary 1982. Canadian Wildlife Service Special Publication.

Vermeer, K., L. Cullen and M. Porter. 1979. A provisional explanation of the reproductive failure of tufted puffins, Lunda cirrhata, on Triangle Island, British Columbia. Ibis 121: 348-353.

Watanuki, Y. 1986. Moonlight avoidance behavior in Leach's storm-petrels as a defense against slaty-backed gulls. Auk 103: 14-22.

Wehle, D.H.S. 1983. The food, feeding and development of young tufted and horned puffins in Alaska. Condor 85: 427-442.

Werschkul, D.F. and J.A. Jackson. 1979. Sibling competition and avian growth rates. Ibis 121: 97-102.

Williams, G.C. 1966a. "Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought". Princeton University Press, Princeton, N.J.

Williams, G.C. 1966b. Natural selection, costs of reproduction and a refinement of Lack's principle. American Naturalist 100: 687-690.

Wilson, U.W. 1977. A study of the biology of the rhinoceros auklet on Protection Island, Washington. M.Sc. thesis, University of Washington, Seattle.

Wilson, U.W. and D.A. Manuwal. 1986. Breeding biology of the rhinoceros auklet in Washington. Condor 88: 143-155.

# APPENDIX 1: AN ESTIMATE OF THE POWER OF THE ANALYSIS IN TABLE 3.2

Sokal and Rohlf (1981; p. 263) show that the sample size n, required to find a given minimum difference d, with probability P, between samples with standard deviation S, is

$$n \geq 2 \, (S/d)^2 (t_{\alpha[\nu]} + t_{2(1-P)[\nu]})^2$$

where $\nu$ is the degrees of freedom and $\alpha$ the significance level. Rearranging shows that the difference d, which can be detected with a given sample size n is

$$d \geq \sqrt{((2(t_{\alpha[\nu]} + t_{2(1-P)[\nu]})^2 S^2)/n)} \quad (1)$$

The hypothesis to be tested is that there exists a true decline in the amount parent rhinoceros auklets provision to chicks of a given standard age as the season advances. The average sample size of a cell in Tables 3.2a-d is 7-8. The mean burrow load observed is approximately 40 g, with a standard deviation of approximately 20. I estimate that the size of the true change, if it exists, is approximately 1 g/day (and therefore 5 g per 5 day block used). Setting $\alpha = 0.05$, I used formula (1) to calculate how large a difference would be detected with 80% certainty. In a comparison with two samples of eight observations each, a difference of 31 g would be detected with 80% certainty. The test is obviously not very powerful, not surprising in light of the large co-efficient of variation.

However this overestimates the true minimum difference detectable, because Friedman's analysis is more powerful than

the simple two sample comparison. (In effect, it makes many such comparisons). In spite of this the basic conclusion that the tests are relatively low power seems unlikely to change very much.

# APPENDIX 2: THE CAMP CHICK GROWTH MODEL

The model was designed to yield an estimate of the amount of food eaten by a chick on a certain night given the weight of the bird at time T before the feeding, and the weight of the same bird at time U following the feeding.

The fostering experiments in 1986 and 1987 were performed in order to compare the size of burrow loads delivered by parents to their natal chick and to a foster chick. Data collection for these experiments involved weighing the chicks for a series of consecutive days before and after the exchange and noting the time of each weighing. This information was used in the model in order to estimate the size of nightly feedings.

In 1986 and 1987 I raised six chicks in camp on a known diet. By weighing these birds at intervals throughout the day I was able to establish a model relating weight at known times on consecutive days to the amount fed to the chicks during the night between two weighings. A diagramatic representation of the model is shown in Figure App.2.1. After weighing at time $t_1$, chicks lose weight until they are fed (I assumed at midnight), at which time their weight increases incrementally. Chicks then lose weight until the weighing the following day. Assuming weight loss is linear the equations can be rearranged so that the amount fed to a chick can be described given $W_{t-1}$, $T_i$, $W_t$ and $U_i$ as outlined in equation 5, below.
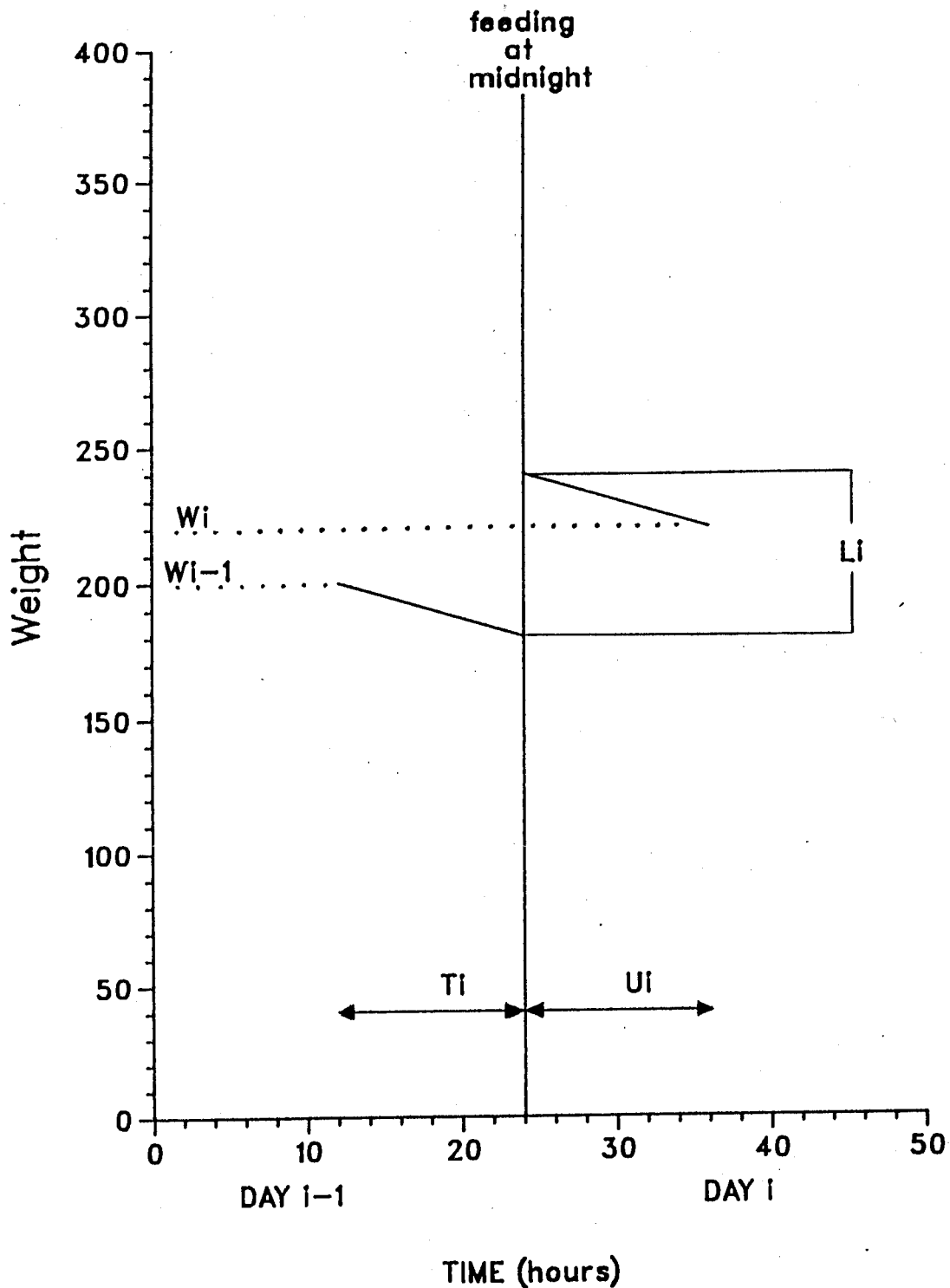
98

Figure App.2.1: A diagramatic representation of the camp chick
growth model. The angled lines represent the
weight loss before (-a) and after feeding (-b).
The variables are described in the text.

The model derivation is shown below.

$W_i$ = weight on day i.

$W_{i-1}$ = weight on day i-1.

$L_i$ = amount fed during night between $W_{i-1}$ and $W_i$

$T_i$ = time from weighing on day $W_{i-1}$ until midnight feeding

$U_i$ = time between weighing on day $W_i$ and midnight feeding

$$W_i = [W_{i-1}e^{-aT_i} + L_i]e^{-bUi} \qquad (1)$$

$$W_i = W_{i-1}e^{-aT_i-bU_i} + L_ie^{-bU_i} \qquad (2)$$

$$L_ie^{-bU_i} = W_{i-1}e^{-aT_i-bU_i} + W_i \qquad (3)$$

$$L_i = W_ie^{-bU_i} - W_{i-1}e^{-aT_i} \qquad (4)$$

Assume linear decrease in weight loss (therefore -a = -b)

$$L_i = W_i(c_1 + c_2U_i) + W_{i-1}(c_3 + c_4T_i) \qquad (5)$$

where $c_1$ - $c_4$ are constants. Rearranging yields

$$L_i = c_1W_i + c_2W_iU_i + c_3W_{i-1} + c_4W_{i-1}T_i \qquad (6)$$

The constants in equation 6 are obtained by regressing the four variables against $L_i$, the amount fed.

In 1986 the equation is

$L_i = 23.1 + 1.37W_i + 0.0286W_iU_i - 1.95W_{i-1} + 0.0294W_{i-1}T_i$

In 1987 the equation is

$L_i = 13.8 + 1.25W_i + 0.0238W_iU_i - 1.69W_{i-1} + 0.0232W_{i-1}T_i$