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ASPECTS OF THE BROOD REDUCTION PROCESS OF

THE FIORDLAND CRESTED PENGUIN

*Eudyptes pachyrhynchus*

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A thesis  
submitted in partial fulfilment  
of the requirements for the Degree  
of  
Master of Applied Science  
in  
Lincoln University

by  
Stephen M. Phillipson

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1991



Abstract of a thesis  
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**ASPECTS OF THE BROOD REDUCTION PROCESS OF  
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The brood reduction process of tawaki, or Fiordland crested penguin, *Eudyptes pachyrhynchus* was studied on Taumaka Island (Open Bay Islands) from July to November 1988. During the study I made observations on adults, eggs and chicks from both manipulated nests, where I swapped eggs to produce clutches of equivalent sized and aged eggs, and natural nests, where parents' retained their own eggs. I observed adult behaviour, egg laying, egg incubation and egg hatching to determine how the initial asymmetries between chicks in a brood were produced, and observed chick and adult behaviours to determine the process of brood reduction for tawaki. I also assessed the implications that brood reduction would have on a management strategy for the species.

The initial size difference between offspring was created by the female who laid two, different sized, eggs. The parent undertaking the first incubation of the eggs did not produce a fully vascularised brood patch until after the second, and larger, (B) egg was laid. This meant that the smaller - first laid - (A) egg was unlikely to begin developing before the B egg was laid and consequently unlikely to hatch significantly earlier.

In both natural and manipulated nests, B eggs typically hatched first. First hatched chicks were usually fed before the second egg hatched. This increased further the difference in mass between the two chicks. I determined that, starvation of chicks, resulting from the brood reduction process, was the largest cause of chick mortality and that significantly more larger chicks of a brood survived to the fledging stage.

For the first five days after hatching, when chicks were not physically coherent, the female would preferentially feed one of the chicks. Which of the two chicks she fed determined the pattern of brood reduction. If the larger chick was favoured the smaller chick starved to death soon after hatching. These nests were typified by high begging rates for the small chick and low levels of interference interactions between chicks during feeding. If the smaller chick was favoured it would begin to grow and the brood would coexist for a longer period, although the smaller chick would still starve to death. These nests were typified by even begging levels and much higher levels of interference interactions between chicks during feeding. Overt aggression between chicks, or between chicks and adults was not witnessed.

Because brood reduction is an integral part of the tawaki breeding system, any species management strategy should concentrate on increasing adult survival rather than increasing reproductive output.

**Key words:** Fiordland crested penguin, *Eudyptes*, brood reduction, infanticide, management, behaviour, egg dimorphism, chick asymmetries.

## CONTENTS

	Page
Abstract	i
Contents	iv
List of figures	vii
List of tables	viii
Preface	ix
1. General introduction	1
1.1 An introduction to infanticide	1
1.2 The crested penguins	5
1.3 The conservation of tawaki	6
2. The creation of asymmetries between offspring	9
2.1 Introduction	9
2.2 Methods	13
2.2.1 Study method	14
2.2.2 Data exclusion	16
2.3 Results	17
2.3.1 Clutch size, egg size and laying order	17
2.3.2 Incubation and hatching	18
2.4 Discussion	22

3.	The brood reduction process of tawaki	26
3.1	Introduction	26
3.2	Methods	28
3.2.1	Study site	28
3.2.2	Nests used in the study	28
3.2.3	Monitoring of natural and manipulated nests	29
3.2.4	Behavioural observations	30
3.3	Results	32
3.3.1	The effect of the study method on chick mortality	32
3.3.2	Effects of manipulation	32
3.3.3	Factors associated with the survival of a chick	34
3.3.4	Differences between coexistence groups	34
	a. Begging	40
	b. Feeding	40
	c. Interference interactions	45
3.3.5	Adoption of chicks	45
3.4	Discussion	49
4.	Conservation of tawaki	56
4.1	Clutch manipulation	56
4.1.1	Adult response to manipulations	57
4.1.2	The effect of manipulation on the viability of eggs	58
4.2	The transfer of chicks	58
4.3	Natural constraints on a manipulative breeding programme	60
4.4	The broader perspective	61



5.	General discussion	62
5.1	The creation of asymmetries	62
5.2	The brood reduction process	65
5.3	Implications for a tawaki conservation strategy	66
5.4	Afterword	67
	Acknowledgements	69
	References cited	

**LIST OF FIGURES**

Figure		Page
1	Number of chicks dying per day as a result of the brood reduction process.	35
2a	Growth of S and NS chicks from group 1 nests.	37
2b	Growth of S and NS chicks from group 2 nests.	37
3a	Relative proportions of begging at different ages shown by S and NS chicks from group 1 nests.	41
3b	Relative proportions of begging at different ages shown by S and NS chicks from group 2 nests.	41
4a	Relative proportions of feeds received at different ages by S and NS chicks from group 1 nests.	42
4b	Relative proportions of feeds received at different ages by S and NS chicks from group 2 nests.	42
5a	Cumulative proportions of the total feeds received by S and NS chicks from group 1 nests.	44
5b	Cumulative proportions of the total feeds received by S and NS chicks from group 2 nests.	44
6	A comparison of the total number of interference interactions occurring in group 1 and group 2 nests.	46
7a	Relative proportions of interference interactions initiated by S and NS chicks from group one nests.	47
7b	Relative proportions of interference interactions initiated by S and NS chicks from group 2 nests.	47

**LIST OF TABLES****Table**

1	The fate of 51 eggs from natural nests.	20
2	How observed levels of begging, feeding and interference behaviours differed from statistically generated expected values.	39

## PREFACE

### 1. Objective of this Study

The overall objective of this study was to examine the offspring reduction process of tawaki or Fiordland crested penguin *Eudyptes pachyrhynchus*. In particular I concentrated on collecting data on:

- a. the creation of the asymmetries between offspring,
- b. the mechanism of reduction used.

The results from this study were intended to fill two roles:

- i. to contribute to the body of information on infanticide among birds,
- ii. and to provide biological information relevant to the conservation of the species.

### 2. Structure of the Thesis

Chapter one is intended to give the reader the background information on:

- a. the history, theories, and possible functional roles of infanticide,

- b. the conservation status of tawaki and the current gaps in our knowledge of their ecology and biology.

Chapters two and three were written in the form of papers which, with minor modifications, will be submitted for publication. This format was chosen to allow the reader to concentrate on the subject matter of each chapter without having to continually cross-reference small sections from other chapters. Because these two chapters were written in this format, ideas, theories and literature which are reviewed in the general introduction (chapter one) are sometimes repeated in the introductions of chapters two and three. To avoid excessive repetition throughout both chapters I have minimised the overlap of the methods and results sections by cross referencing between chapters.

In chapter four, I have presented and discussed information from chapters two and three that would be relevant to management of tawaki populations. I have also presented observations and results from the manipulation process used in the study, which had no place in the subject matter of chapters two and three, but which would have relevance to a manager involved with the conservation of this species.

Chapter five is a general discussion in which I have considered the combined results and conclusions from chapters two and three, and discussed these in the overall context of avian brood reduction. In chapter five I also discussed the implications of this overview as it relates to management strategies for tawaki.

# CHAPTER 1

## GENERAL INTRODUCTION

### 1.1 An Introduction to Infanticide

Infanticide, among animals was regarded initially by biologists and social scientists as a maladaptive or pathological trait of the individuals involved (Blaffer Hrdy and Hausfater, 1984). This attitude was based largely on moral principles i.e. killing one's offspring is deemed an immoral practice in human (at least western) society, and theoretical considerations i.e. infanticide seemed counter to basic evolutionary theory which emphasised the maximisation of reproductive output (Blaffer Hrdy and Hausfater, 1984). The general acceptance of infanticide by the scientific community was linked closely with the development of the theoretical concepts of kin selection and inclusive fitness as evolutionary processes (Hamilton, 1964a and 1964b). Once the principle of infanticide became accepted and the phenomenon studied it became apparent that it was a widespread practice among animals from a large number of taxa (reviewed in Blaffer Hrdy and Hausfater, 1984).

Studies of infanticide in the breeding system of birds revealed that the most common infanticidal process was that of brood reduction i.e. a reduction in the number of offspring through the death of chicks, and that the demise of the surplus chick/s was

- 
1. Infanticide is defined by Mock (1984a) as: *behaviour that makes a direct and significant contribution to the immediate death of an embryo or newly hatched (or born) member of the performer's own species.*

caused primarily primarily by its sib/s i.e. siblicide (Mock, 1984a). Typically the chicks which initiated and survived the siblicidal process were larger, older, or both larger and older than the chick/s which were eliminated. Most theoretical studies of the adaptive value of avian infanticide have concentrated on the brood reduction process (O'Connor, 1978; Stinson, 1979; Dickins and Clark 1987).

The most popular of these theoretical studies is that of O'Connor (1978). O'Connor proposed that in siblicidal species the surviving sib/s trade off some of their indirect fitness to increase their own chances of survival and future reproduction. He proposed that the survivors lost some degree of indirect fitness because the genes that they shared with the eliminated chick/s would not be transmitted to the next generation by the eliminated chick/s, yet the survivors may have increased their own chances of surviving to reproduction by being able to appropriate a larger share of the food gathered by the parent/s, especially during periods of food shortage. According to O'Connor the situation is complicated further since the parents and offspring should have different genetic interests in the surplus chick. Parents should view each sibling as being equally valuable because each contains an equivalent proportion of the parents' genes. However, since a sib only shares half (on average) of its genes with its other sib/s it should consider itself to be more important. Theoretically this should cause some parent-offspring conflict over the distribution of parental investment i.e. the parents should invest in each chick equally while each sib should try to appropriate the greater share of the parental investment for itself. O'Connor developed this theme into a model which predicted under which conditions of food shortage the surplus chick/s should die as a result of siblicide, parentally induced infanticide or even suicide.

O'Connor (1978) supported his theory by using actual, or derived, data from other studies in his model and comparing the predicted with the actual outcome. Although many of the results appeared to support his model some serious criticisms of his use of data have been made (Clark and Wilson, 1981) and some subsequent studies have revealed that other parent-offspring strategies commonly exist that seem counter to O'Connor's theory (Drummond, Gonzalez and Osorno; 1986).

Lack (1947, 1954) is generally accepted as being the first person to suggest a functional role for brood reduction. He suggested that the process of hatching asynchrony, which produced different sized chicks in a brood, was an adaptation which allowed parents to adjust, secondarily, the number of offspring to the available food supply through the selective starvation of smaller chicks. This explanation has provided the basis for the widely accepted 'brood reduction hypothesis' (e.g. Ricklefs, 1965; Clark and Wilson, 1981; Slagsvold, Sandvik, Rofstad, Lorensten and Husby, 1984; Stokland and Amundsen, 1988). The hypothesis proposes that hatching asynchrony, egg-size dimorphism, egg quality, hatching pattern, or any combination of these, are mechanisms by which birds can produce asymmetries among chicks and so adjust their reproductive effort to match prevailing environmental conditions. This is thought to apply mainly to those bird species which breed in unpredictable or variable habitats.

However, studies of the infanticidal processes among various bird species have shown that, while many results were consistent with, and could be explained by, the brood reduction hypothesis (Howe, 1976; Hahn, 1981; Braun and Hunt, 1983), others were inconsistent (Emlen, Demong and Emlen, 1989; Mock, Lamey and Ploger, 1987;



Stokland and Amundsen, 1988; Simmons, 1988) or could be equally well explained by alternative hypotheses e.g. the predation and peak load hypotheses (Hussel, 1972) and nest failure hypothesis (Clark and Wilson, 1981).

One of the infanticidal patterns which was found to deviate from that predicted by the brood reduction hypothesis was obligate brood reduction (Clark and Wilson, 1981; Mock, 1984a). Obligate brood reductionist species regularly (Simmons (1988) suggests greater than 90% of the time) produce more chicks than they can raise to independence (Mock, 1984a; Simmons, 1988; Anderson, 1990).

The obligate brood reduction pattern differs from that predicted by the brood reduction hypothesis in the following ways.

1. One of the major assumptions of the brood reduction hypothesis is that the birds adjust their brood size because of the unpredictability of their habitat e.g. unpredictable peaks in food abundance. The regularity with which brood reduction occurs in obligate reductionists suggests that the environment remains relatively stable (at least in terms of the human life span) and is, therefore, predictable (Mock, 1984a).
2. Research has indicated that the reduction process is such an integral part of the breeding system of, at least, some obligate brood reductionist species that even when food was made abundant to the chicks the reduction process still took place (reviewed in Mock, 1984a; Mock *et al.*, 1987; Simmons, 1988).

A number of alternative explanations for the presence of surplus chicks in a brood have been mooted (reviewed in Mock, 1984a). The most widely accepted of these is the so called insurance hypothesis (Ingram, 1959; Lack, 1968). According to this hypothesis the function of the surplus offspring is to replace the expected survivor/s of the brood i.e. the largest/eldest chick/s, should they fail to hatch or grow normally.

## 1.2 The Crested Penguins

One notable group of obligate infanticidal birds are the crested penguins, genus *Eudyptes*. The crested penguins are notable because they demonstrate some intriguing anomalies to the pattern of brood reduction typically seen in obligate brood reductionist species.

1. In all of the crested penguin species a clutch of two, markedly dimorphic, eggs is laid with the first laid (or A) egg being the smallest and the second (B) egg the larger (Warham, 1974b; Slagsvold *et al.*, 1984). This is the reverse of the typical egg laying pattern for brood reductionists where the larger eggs are laid first (Slagsvold *et al.*, 1984).
2. The crested penguins show a range of obligate infanticidal processes from two species where all surplus offspring are lost through clutch reduction (offspring reduction through egg loss), to one species which loses surplus offspring through a combination of clutch and brood reduction, to two species which use pure brood reduction (see the introduction to chapter three for specific details).

Because of these anomalies the breeding processes of the crested penguins are of interest to scientists working in the field of infanticide e.g. Mock, 1984a; Johnson, Bednarz and Zack, 1987.

Published studies of offspring reduction among the crested penguin species have concentrated mostly on either clutch reduction in macaroni penguins, *Eudyptes chrysolophus chrysolophus* (Williams, 1989; Brown, 1988; Williams, 1981, 1980a) or the egg loss aspects of the reduction process in rockhopper penguins, *Eudyptes chrysocome* (Brown, 1988; Williams, 1980a, 1980b, 1981; Burger and Williams, 1979). The reduction processes of the other crested penguin species have either not been studied directly or the studies are yet to be published.

### **1.3 The Conservation of Tawaki**

The sea has had, and continues to have, a profound influence on many of the physical aspects of the islands of New Zealand. The predominance of the sea is also reflected in the composition of our native avifauna where the number of seabird species out numbers our terrestrial species (Robertson, 1985). In pre-human times, when birds were the dominant terrestrial vertebrates of New Zealand, the coasts and inland areas of the three major islands (North, South and Stewart islands) abounded with nesting seabirds. Even after the arrival of the Maori people huge numbers of petrels and shearwaters (*Procellariidae*) continued to nest on the coasts and far inland to the alpine zones of our major islands e.g. Best (1977); Falla (1934) and Stead (1927).

However, the ecological changes associated with the arrival of the European peoples e.g. the extensive modification of native vegetation communities for agriculture and the introduction of new bird species, mammalian predators and diseases, have dramatically changed the distribution of our nesting seabirds so that comparatively few species still nest on the main islands. Among the remaining mainland nesting seabirds are three species of penguin, korara or little blue penguin *Eudyptula minor*, hohio or yellow-eyed penguin *Megadyptes antipodes* and tawaki or Fiordland crested penguin.

Of these three penguin species the tawaki is probably the least known. No doubt the comparative anonymity of tawaki is related to the remoteness of its breeding areas. The known geographic range in which tawaki nest extends southward from the remote areas of South Westland, including the Open Bay Islands; down the coast of Fiordland and eastward along the southern coast of the South Island as far as Green Islets; and as far south as Solander Island, the west coast of Stewart Island and a number of other smaller islands in this area (Warham, 1974b, 1975). Young birds i.e. pre-breeders, have also turned up in such places as the south coast of Australia and the Falkland Islands (Warham, 1975; T. Lamey pers. comm., 1988).

Although the distributional limits of tawaki are relatively well known (Warham, 1974a; Waas and Miskelly, in press) the population size and trends in population number remain unknown. The lack of this type of baseline information makes it difficult to accurately assess the conservation status of tawaki. However, the current opinion seems to be that, at least on the mainland i.e. on the South Westland and Fiordland coast of the South Island, tawaki is a threatened species (Bell, 1986). Bell (1986)

records the main threats to tawaki as being predation in mainland colonies by introduced mammalian predators such as stoats *Mustela erminea* (Warham, 1974a) and domestic dogs *Canis familiaris*. However, as the interactions of tawaki with its various predators, native and introduced, have never been studied, the overall importance of predation is unknown.

Should the need for active management of the species be required it is possible that the manipulation of breeding to increase reproductive output could be used as a management tool. If this were so, then the reproductive processes of tawaki would need to be understood to ensure that any manipulation was effective.

Studies of the general biology of the tawaki remained largely anecdotal (Henry, 1903; Sutherland, 1920 and 1923) until 1966 when John Warham included tawaki in a more general study of the breeding biology of *Eudyptid* penguins (Warham, 1974b). Since then studies on egg formation (Grau, 1982) and aspects of diet (van Heezik, 1989) are the only studies to have been published for the species. Although the study by Warham (1974b) provided valuable information on many aspects of tawaki biology, it lacks the detail necessary to formulate a manipulative breeding programme. My study was designed to provide some of that detail in two important areas:

1. Aspects of the incubation, hatching and brood reduction processes and how they interact to produce the surviving offspring.
2. Information on, and lessons learned from, the manipulation of eggs and chicks.

## CHAPTER 2

### THE CREATION OF ASYMMETRIES BETWEEN OFFSPRING

#### 2.1 Introduction

Infanticide is a process in which the death of offspring is caused primarily by members of the victim's own species and often own family (Mock, 1984a). Studies of the breeding processes of various animal species have shown that infanticide, or offspring reduction, occurs in a range of animal groups (Blaffer Hrdy and Hausfater, 1984) including birds (Mock, 1984a).

Studies of avian infanticide have shown that it may serve one of a number of functions. In its most extreme form all the chicks in a brood may be killed to promote the onset of a new breeding effort e.g. wattled jacanas *Jacana jacana* (Emlen *et al.*, 1989). However, in its most common form it appears to function as a method for parents to secondarily adjust the number of offspring in a clutch or brood in response to one, or more, limiting environmental factors (Lack, 1947, 1954; Ricklefs, 1965; Mock 1984; Slagsvold *et al.*, 1984). These environmental factors range from the immediate and often highly variable, such as food availability e.g. (Howe, 1976), to more long term factors such as availability of breeding sites (Simmons, 1988).

Although the apparent functions of offspring reduction may be diverse, the processes used by the infanticidal bird species show many similarities. The most commonly seen, or typical, pattern of infanticide is for offspring to be lost through brood reduction i.e.

chick death (Mock, 1984a). The process of brood reduction is usually facilitated by asymmetries in the size and/or age of offspring which assist the bigger - and usually older - chicks to eliminate, or out compete, their siblings e.g. larger chicks can prevent the smaller from feeding (Safriel, 1981), directly attack them (Meyberg, 1974), eject them from the nest (Braun and Hunt, 1983) or even eat them (Meyberg, 1974). Typically asymmetries between offspring are created by the parent birds through such mechanisms as laying dissimilar sized eggs (Slagsvold *et al.*, 1984), incubating early eggs before the clutch is complete and inducing asynchronous hatching (Clark and Wilson, 1981), or more commonly a combination of these two factors.

One of the few groups of birds to depart significantly from this general pattern of offspring reduction is the crested penguins, genus *Eudyptes*. The six species of crested penguins are all reported to be obligate offspring reductionists (Warham, 1975) i.e. they consistently produce more offspring than they can raise to independence (Mock, 1984a; Simmons, 1988). However, a range of infanticidal processes occur in this genus, from obligate clutch reduction (the death of surplus offspring at the egg stage), as reported for Macaroni Penguins *Eudyptes chrysolophus chrysolophus* (Gwynn, 1953; Warham, 1971; Williams, 1980; Brown, 1988) and possibly erect-crested penguins *Eudyptes sclateri* (Richdale, 1941); through a combination of clutch and brood reduction, as reported for rockhopper penguins, *Eudyptes chrysocome* (Gwynn, 1953; Williams, 1980; Strange, 1982); to obligate brood reduction, as seen in Snares crested penguins *Eudyptes robustus* (Warham, 1974a) and tawaki or Fiordland crested penguin *Eudyptes pachyrhynchus* (Warham, 1974b). Two other features of their breeding system set the crested penguins apart from the more typical brood reductionists:

- i. They lay markedly dissimilar sized eggs with the differences in egg size within a clutch being among the most extreme known for any bird species (Slagsvold *et al.*, 1984).
- ii. The first laid egg (subsequently called the A egg) is smaller than the second laid egg (B egg). This is the reverse of the typical pattern of egg size with laying order seen in offspring reductionists (Gwynn, 1953; Slagsvold *et al.*, 1984).

In the clutch reducing crested penguin species the relative size of offspring is fixed during egg laying and this in turn appears to determine which of the two offspring will hatch and which will be lost as an egg. However, among the brood reducing crested penguin species, which typically hatch both eggs, the magnitude of asymmetries between chicks in a brood can, potentially, be influenced by factors operating during the incubation and hatching phases of offspring production.

Among the many species of small passerines that show the same egg laying habit as crested penguins i.e. an increase in egg size as laying of a clutch progresses, incubation usually begins with the laying of the first egg which causes the chicks to hatch asynchronously (Clark and Wilson, 1981; Howe, 1976). The smaller, first hatched chicks are fed before their larger sibs hatch and so differences in size between sibs is ameliorated. All three of the brood reducing crested penguins show a different incubation and hatching pattern to that described above. Both rockhopper and Snares crested penguins appear to hatch B eggs before the A eggs (Williams, 1980; Brown, 1988; Lamey, in press, but see Warham, 1974a), while tawaki have been reported to hatch either A or B eggs first Warham (1974b). Therefore, the crested penguins



maintain, or increase, the asymmetries between sibs in a manner similar to other, more typical, brood reductionist species.

Some of the finer details of the incubation and hatching processes that produce this pattern of hatching among rockhopper penguins have been reported (Burger and Williams, 1979; Brown 1988), however, similar information for the other two species, Snares crested penguin and tawaki, remains unavailable.

The purpose of this study was to observe the egg laying, incubation and hatching processes of tawaki, or Fiordland crested penguin, to determine some of the factors which affected these processes and how they interacted to produce the patterns of chick asymmetry seen in tawaki broods.

## 2.2 Methods

Field work was conducted during the austral winter and spring (July - November) of 1988 on Taumaka Island which is one of the Open Bay Islands located 5km off the coast of South Westland, South Island, New Zealand (43° 50'S, 168° 53' E). Taumaka is a small island (approx. 700m x 200m and up to 25m in elevation) which is vegetated primarily by a densely tangled cap (up to 4 metres deep) of the epiphyte vine kiekie *Freycinetia banksii*, surrounded by a fringe of the salt resistant shrub *Hebe elliptica*. The island lacks introduced mammalian predators, has no permanent human residents, and shows minimal human modification of the environment.

The tawaki nested in scattered groups over most parts of the island. Most of the breeding groups/colonies were concentrated on the north-western side of the island where gently sloping limestone shelves provided relatively easy landing sites and access to nesting areas. The location of nests could be classed into three broad categories:

- a. in the open but with the nests pressed up against rocks;
- b. under overhangs and boulders, in rock fissures, or in caves;
- c. under dense tangles of kiekie.

The majority of nests found on Taumaka were category 'c' type nests. The tawaki nesting under the kiekie usually formed large aggregations (estimated group sizes ranged between 30 - 100+ pairs of birds) of regularly spaced nests centered around streams. The streams were used for access and for bathing and drinking. The a and

b category nests were usually located at the very edge of the coastal vegetation. The number of birds occurring in each of these sites seemed to rely on the extent of cover available. I never found more than 13 pairs together but the variable proximity of other nesting groups makes it meaningless to suggest an overall breeding group size.

Nests used in this study were mostly of types a and b. These nests were chosen because they were visible from a distance (which lessened the disturbance to the birds when observations were taking place), easily accessible and because several nests could usually be observed at the same time.

### **2.2.1 Study Method**

Of the 114 nests initially located, 81 in which two, or more, eggs were laid were selected for this study. Study nests were allocated to one of three categories:

1. Natural nests (n = 27). Natural nests were treated in the following ways:
  - a. The adult birds were banded with individually numbered stainless steel flipper bands.
  - b. Eggs were marked, using various coloured Stephens' brand "Vivid" marker pens, with a unique letter number combination to enable individual identification of eggs.

Natural nests were used to evaluate the normally occurring events that influenced egg survival to hatching and also to serve as a control for the manipulated nests.

2. Manipulated nests ( $n = 23$ ). These were treated in the following ways:

- a. The adult birds were banded.
- b. Each nest received two eggs of approximately equal size (maximum difference of 5g) and state of incubation (maximum difference two days). The first day of incubation was defined as the day the natal nest contained two eggs. Neither egg placed in a manipulated nest was from the host nest nor were the eggs from the same donor nest. This last measure was to ensure that eggs and adults were not closely related.

Ten manipulated nests received two A eggs (A+A nests), nine received two B eggs (B+B nests), 11 received an A and a B egg (A+B nests), and two received a B and a C egg (B+C nests; third eggs laid in a nest were designated as C eggs). The timing of the transfer of eggs was designed to avoid dislodging the developing embryos of the youngest eggs while ensuring that the older eggs were more than two weeks away from hatching and so probably not communicating with or being imprinted on the incubating adults.

Manipulated nests were used to evaluate whether relative size of eggs or some other features associated with being an A or B egg were influencing egg hatching or survival.

3. Control nests ( $n = 31$ ). In control nests eggs, chicks and adults were not handled or marked.

These nests were used to test for any indirect effects on egg survival or hatching due to marking and handling of eggs or adults from the other two nest categories.

Daily checks were made of all the manipulated and natural nests. During the check the following was recorded: sex of the incubating parent; the number of eggs, with any new eggs being marked and weighed (using Pessola or Salter brand spring balances); the position of individual eggs relative to the incubating parent i.e. did it lie to the posterior or anterior end of the parent's brood patch; signs of eggs hatching; and any additional observations. If eggs were missing the immediate area would be investigated to try to locate the missing egg, or its remains, and ascertain the cause of death.

Control nests were visited at approximately weekly intervals (tide and weather permitting). During the initial visit to the control nests the location of the nests was mapped to allow recognition of individual nests during subsequent visits. In ensuing visits the nests were checked for the number of eggs or chicks they contained, by gently lifting the incubating adult with a stick.

### **2.2.2 Data Exclusion**

When analysing the effect of handling on egg mortality I did not include data from nests that lost eggs as a direct result of human activity related to the study (nine eggs). Eight of these eggs were lost to weka *Gallirallus australis* (an endemic flightless rail introduced to the island in the early 1900's) which stole unattended eggs. One egg was pecked by the adult tawaki as it was being returned to the nest.

## 2.3 Results

In the following tests not all eggs or nests in a category were available for each test.

### 2.3.1 Clutch Size, Egg Size and Laying Order

Of the 114 nests located at the pre-egg laying stage 13 (11.4%) became one egg nests, 97 (85%) became two egg nests, 3 (2.6 %) had three eggs laid in them (third eggs were designated as C eggs) and one control nest was found to contain 4 eggs (possibly the eggs of two or more females). In two nests C eggs appeared after one of the other eggs disappeared and in the third nest the female laid a third egg. The relative frequency of one and two egg nests found in this study approximates that found by Warham (1974b), however, Warham never found more than two eggs in a nest.

The mass of A eggs (mean = 99.6g, sd = 9.2g, n = 67) was significantly less than that of B eggs (mean = 118g, sd = 9.4g, n = 65), ( $F(1, 130) = 129.75, p < 0.001$ ). B eggs were approximately 16% heavier than A eggs (mean difference = 15.93%, sd = 4.77%; median = 16.5%, min = 2.78%, max = 26.83%). A similar result was obtained by Warham (1974b) during his study of tawaki.

The smaller egg was laid first in 96 out of 97 two egg nests i.e one reversal, Warham (1974b) also recorded one reversal. In the three nests where third eggs were laid the C egg was smaller than the A or the B egg in one case, larger than the preceding two eggs in the second case and unknown in the third case (a control nest).

### 2.3.2 Incubation and Hatching

The laying to hatching period of A eggs (mean = 36.1 days, sd = 1.1, n = 30) and B eggs (mean = 31.9 days, sd = 1.0, n = 33) was significantly different (Kruskal-Wallis  $X^2$  approximation  $p < 0.001$ , n = 64). This indicates that either differential speed of development of A and B egg embryos occurred or incubation did not begin until after the second egg was laid. If incubation began with, or after, the laying of the B egg, as suggested by Warham (1974b), then the mean incubation to hatching time for A eggs (31.9 days, sd = 1.2) and B eggs (31.9 days, sd = 1.4) was not significantly different (Kruskal-Wallis  $X^2$  approximation  $p > 0.05$ , n = 62).

During egg laying I observed that adult birds adopted a semi-prone position over the first laid egg. Although different from the fully prone position - commonly seen after egg laying was complete - the semi-prone position appeared to cover the egg and bring it in contact with the brood patch region. I also observed that brood patch formation of adults occurred after egg laying was complete. De-feathering of the brood patch was not obvious in the adult, usually male, undertaking the first incubation shift until two or three days after the second egg was laid. Even then it was still not fully vascularised, as indicated by it becoming a deep purple colour, for another three to four days.

During incubation it was found that neither A nor B eggs occupied the rear incubation position significantly more often than the other (Kolomogorov-Smirnov statistic = 0.02,  $p > 0.05$ , n = 66 nests). The relative frequency of A or B eggs occurring in the front or rear incubation positions was highly variable between the nests observed.

In manipulated nests 60 out of 77 eggs (78%) hatched, in natural nests 38 out of 51 eggs (75%) hatched and in control nests 52 out of 58 (90%) hatched. A comparison of the hatching success among the three nest categories showed no significant difference (Pearson's  $X^2_2 = 4.61$ ,  $p > 0.05$ ,  $n = 186$  eggs). This suggests that the handling of eggs in the natural and manipulated nests did not cause any significant increase in embryo mortality from that in control nests.

The hatching success of A and B eggs from natural and manipulated nests also showed no significant difference (Freeman-Tukey  $X^2$  approximation = 1.17,  $p < 0.88$ ,  $n = 121$ ).

This confirms that:

- a. the transportation of eggs from manipulated nests did not cause any significant increase in the mortality of A or B eggs from that found in natural nests;
- b. that the overall mortality rate of A and B eggs was not significantly different, which indicates that clutch reduction did not occur during the incubation or hatching periods.

The fate of 51 eggs from natural nests can be seen in table 1.



	A EGGS	B EGGS
HATCH	17	20
INFERTILE	1	5
FLOODED OUT	1	1
EJECTED	3	1
ADULT DAMAGE	1	1

Table 1. The fate of 51 eggs from natural nests.

In natural nests A or B eggs were equally likely to pip first (Binomial  $p < 0.5$ ,  $p(\text{of pipping first}) = 0.5$ ,  $n = 7$ ) but B eggs usually hatched first (Binomial  $p < 0.02$ ,  $p(\text{hatching first}) = 0.5$ ,  $n = 18$ ). The B egg would usually hatch one or more days before the A egg (Binomial  $p < 0.05$ ,  $p(\text{hatching on same or different days}) = 0.5$ ,  $n = 18$ ). In manipulated A+B nests the B egg hatched first in 7 out of 10 cases (not a significant result, Binomial  $p < 0.17$ ,  $p(\text{hatching first}) = 0.5$ ,  $n = 10$ ) and the eggs all hatched one or more days apart (Binomial probability  $< 0.001$ ,  $p(\text{hatching on same or different days}) = 0.5$ ,  $n = 10$ ). In 14 manipulated nests with two A or two B eggs the eggs usually hatched one or more days apart (10 out of 14) although this result was not statistically significant (Binomial  $p < 0.09$ ,  $p(\text{hatching on same or different days}) = 0.5$ ,  $n = 14$ ). Therefore, in A+B nests (natural and manipulated) the B egg usually hatched first, at least a day before the A egg.

In natural nests the mass of newly hatched chicks from B eggs was greater than that of newly hatched chicks from A eggs (Kruskal-Wallis  $X^2$  approximation  $p < 0.002$ ;  $n = 38$ ).

In manipulated nests the mass of newly hatched chicks from A or B eggs was not significantly different (Kruskal-Wallis  $X^2$  approximation  $p < 0.34$ ,  $n = 16$ ). However, in both natural and manipulated nests B egg chicks were significantly heavier by the time the A egg chicks hatched (both Kruskal-Wallis  $X^2$  approximation probabilities  $< 0.001$ ). That B egg chicks from manipulated nests went from a newly hatched mass approximately the same as that of A egg chicks to being significantly larger by the time A eggs actually hatched illustrates that the first hatched B egg chicks were fed and increased in mass before the A egg chicks hatched.

The initial size difference between the offspring within natural tawaki nests resulted from the female laying two, markedly dissimilar sized eggs. Typically the first laid A egg was the smaller and the second laid B egg the larger egg of the clutch. This pattern was also observed by Warham (1974b). Although the difference in mass between the eggs in tawaki clutches is the smallest of any of the crested penguin species (Warham, 1975), it still rates among the most extreme intra-clutch differences in egg size to be found among bird species (Slagsvold *et al.*, 1984).

Incubation of the eggs did not begin until after the completion of laying (Warham, 1974b; this study). Warham (1974b) suggested that the primary reason for the delay in incubation was that the incubating adult birds did not settle properly on the A egg and bring it into contact with the brood patch. My observations suggested that the major determinant affecting the onset of incubation was the timing of brood patch development by the incubating parents. The males - who generally incubate the eggs for the first 13 days after laying (Warham, 1974b, this study) - did not fully develop their brood patch until after the second egg was laid. Similar timing of brood patch formation has been reported for yellow-eyed penguins *Megadyptes antipodes* (Farner, 1958) and many other bird species (reviewed in Clark and Wilson, 1981). Burger and Williams (1979) found that rockhopper penguin clutches were not heated until after the second egg was laid but concluded that this was not related to the timing of brood patch formation.

Most obligate brood reductionists exaggerate the differences in mass between their chicks through asynchronous hatching of broods. Typically this is caused by the adults incubating the clutch before the final egg is laid e.g. South Polar skua *Stercorarius maccormicki* (Young, 1963), common grackle *Quiscalus quiscula* (Howe, 1976) and blue-footed booby *Sula nebouxii* (Drummond *et al.*, 1986). The pattern of increasing egg size with laying order seen in tawaki, however, precluded the possibility of exaggerating the difference in the mass of chicks by incubating the first laid egg. If tawaki had used this typical incubation pattern they would have, in fact, ameliorated the difference between the two offspring. However, by beginning incubation after the B egg was laid tawaki reduced the possibility of the A egg hatching first and so ensured that the relative difference in mass between the two eggs would be reflected in the mass of the newly hatched chicks. It is also possible that the A egg embryo was disadvantaged by being allowed to cool before being incubated.

Rockhopper penguins have been reported to further enhance the survival, and perhaps rate of development, of their B eggs by preferentially incubating them in the rear incubation position i.e. to the rear of the A egg and closest to the posterior of the incubating adult (Burger and Williams, 1979; Brown, 1988). During this study I found that tawaki did not preferentially position the B egg in either incubation position.

During this study it was usual for both eggs in a clutch to hatch, with the B egg hatching before the A egg. This differs from the pattern found by Warham (1974b) who found that either egg was likely to hatch first. Rockhopper penguins and Snares crested

penguins, the only other crested penguin species known to - at least sometimes - hatch two eggs (Burger and Williams, 1979; Lamey, in press, but see Warham, 1974a), are reported to have a similar hatching pattern to that of the tawaki observed during this study.

A study of the metabolic rates of developing embryos in macaroni and rockhopper penguin eggs (Brown, 1988) showed that the A eggs of both species took longer to develop and hatch than B eggs. This was found to be due to inherent differences in the rates of embryonic metabolism, which appeared to be unrelated to egg size and incubation temperature regime. During this study of tawaki, however, it was observed that either A or B eggs from natural nests were likely to pip first. Assuming that pipping indicates the readiness of an egg to hatch this implies that the embryo development of A and B eggs may have been equivalent.

Despite the apparent randomness of A or B eggs pipping first in natural nests, B eggs usually hatched one day or more before A eggs (this was the general pattern for both natural and manipulated nests with A and B eggs). My interpretation of these results was that B eggs were able to hatch faster than A eggs yet either egg was able to use cues from its hatching nest mate to initiate its own hatching process. Communication between embryos affecting the synchronisation of hatching, and the ability of some chicks to hatch faster than their nest mates are both events known to occur in other bird species (reviewed in Drent, 1975).

At the completion of hatching the typical tawaki nest contained two, dissimilar sized

chicks, with the largest and oldest chick originating from the B egg. In natural and manipulated A+B nests the initial size difference between the chicks, which was determined primarily by their egg mass, was increased further when the first hatched B chick (i.e. the chick from the B egg) was fed before the second chick hatched. The magnitude of the influence this factor had on relative mass of chicks in a brood can be gauged from observations of manipulated A+B nests. In these nests the food received by the B chick before the A egg hatched gave it a significant gain in mass over the A chick whereas if the chicks had hatched at the same time there would have been no significant difference in mass.

The results of this study show that physiological, and perhaps behavioural, factors associated with the incubation and hatching phases of chick production in tawaki work to increase the initial differences in offspring size created during egg laying. The pattern of hatching asynchrony and the degree of chick asymmetry observed in tawaki nests during this study were similar to those reported for the other, more typical, brood reductionist species.

## CHAPTER 3

### THE BROOD REDUCTION PROCESS OF TAWAKI

#### 3.1 Introduction

Infanticide, or offspring reduction, is an integral part of the breeding system of many bird species (Mock, 1984a). Among avian taxa the contribution that offspring reduction makes to pre-fledging mortality of eggs and/or chicks is highly variable. In some species offspring reduction is facultative, allowing parents to adjust their brood size in response to environmental factors e.g. food shortage (Howe, 1976). At the other extreme are the obligate infanticidal species where one, or more, of the offspring always die and where these deaths seem to be unconnected to immediate environmental stress e.g. brown boobies *Sula leucogaster* (Dorward, 1962) and many raptor species (Edwards and Collopy, 1983). Where obligate offspring reduction occurs it may be the biggest cause of pre-fledging mortality within a species (Mock, 1984a).

The process of offspring reduction has been studied in a wide range of bird families e.g. raptors (Meyburg, 1974; Edwards and Collopy, 1983; Simmons, 1988), gulls (Braun and Hunt, 1983; Hahn, 1981), passerines (Howe, 1976), herons (Fujioka, 1985; Mock, 1984b) and pelicans (Evans and McMahon, 1987; Cooper, 1980). However, few published studies have dealt specifically with the processes of reduction used by penguins although the phenomenon probably occurs, at least occasionally, in eleven penguin species (Lamey, 1989; in press).

The crested penguins, genus *Eudyptes*, are probably the most well known of the infanticidal penguins. All of the species in this genus lay markedly dissimilar sized eggs, lay their largest egg first - which is the reverse of the typical egg laying pattern seen in brood reductionists - and are obligate offspring reductionists (Warham, 1975; Slagsvold *et al.* 1984). Another feature of infanticide among the crested penguins is the diversity of offspring reduction methods used within the genus. These range from brood reduction (infanticide by chick loss), as used by Snares crested penguin *Eudyptes robustus* (Warham, 1974b; C.M. Miskelly, pers. comm.; Lamey, in press), rockhopper penguins *Eudyptes chrysocome* (Williams, 1980; Strange, 1982) and tawaki or Fiordland crested penguins (Warham, 1974b); through to clutch reduction (infanticide by egg loss) as used by macaroni penguins *Eudyptes chrysolophus chrysolophus* (Warham, 1975; Williams, 1980; Williams, 1989), royal penguins *Eudyptes chrysolophus schlegeli* (Warham, 1975), and erect crested penguins *Eudyptes sclateri* (Richdale, 1941; C.M. Miskelly pers. comm. 1990). Most of the published studies on infanticide among the crested penguins have concentrated on either clutch reduction in macaroni penguins (Williams, 1989; Brown, 1988; Williams, 1981, 1980a) or the egg loss aspects of the reduction process in rockhopper penguins (Brown, 1988; Williams, 1981, 1980a, 1980b; Burger and Williams, 1979).

The purpose of this study was to investigate the process of brood reduction of tawaki and in particular to ascertain the factors which determine which chick survives brood reduction. To do this I investigated both physical and behavioural aspects of adult birds and chicks during the chick rearing phase of breeding.



## **3.2 Methods**

### **3.2.1 Study Site**

The study site is described in the methods section 2.2 of chapter two.

### **3.2.2 Nests Used in the Study**

Only nests that successfully hatched two chicks were used in this study. The nests were from one of three possible treatment categories, control nests, natural nests or manipulated nests. The treatment associated with each of these nest categories is fully described in chapter two (section 2.2.1). The main purpose for manipulating the eggs of the 'manipulated' nests was to ameliorate differences in size and age of chicks at hatching and so remove the initial hierarchy between the chicks in a nest. In manipulated nests it was expected that:

- a. parent birds would raise more sets of twins if there was no initial size/age hierarchy:
- b. the period of chick coexistence in nests would be extended and this would amplify factors associated with the formation of a hierarchy between chicks.

### 3.2.3 Monitoring of Natural and Manipulated Nests

From hatching onwards nests were checked on a daily basis for newly hatched, dead or missing chicks. New chicks were weighed, if the new chick was the second to hatch in a nest both chicks were weighed (all chick weights were measured with Pessola spring balances). Each chick was individually marked by toe nail clipping and had a small amount of non-toxic stock marker sprayed on the throat section of their white ventral down. Chicks marked in these ways were regularly re-marked as the spray marker wore off quickly and toe nails grew at a fast rate. An attempt was made to assess if any of the colours used on the chicks were affecting the survival of, or parent attitude toward, the chicks. Unfortunately the result was not statistically testable. However, my subjective opinion is that the colours used had no recognisable effects.

Dead chicks were removed from the nest, had their identity checked and were weighed. If chicks were missing, the immediate area and neighbouring nests were checked (on two occasions chicks were found in neighbouring nests, both of which were returned to their original nests). Chicks not found were presumed dead.

Prior to the chicks forming creches, pairs of chicks were weighed at irregular intervals. This weighing regime was adopted for two reasons:

- a. it was found that daily weighing caused undue disturbance to the guarding males and their chicks (males guard the chicks from hatching until they form creches (Warham, 1974b; this study)).
- b. to reduce the chances of chicks becoming hypothermic during the frequent periods of heavy rain and strong winds.

After the chicks had creched chicks were only weighed when they were banded. This was because weighing chicks in creches caused extensive disturbance to all the chicks in the creche and the surrounding adults.

#### **3.2.4 Behavioural Observations**

After a series of preliminary observations on nests with chicks it was decided to use the one-zero time sampling method (Martin and Bateson, 1987) to record behavioural interactions between chicks and between chicks and adults. Additional notes on chick and adult behaviours were also made during the observation periods. A nest under observation would be watched continuously from the time the female began to feed the chicks for one hour or until the female finished feeding and left the nest (females almost exclusively feed the chick/s until they fledge (Warham, 1974b)). Previous observations of tawaki females feeding chicks showed that a majority of the feeding was performed in the first hour after arrival. The observation period was divided in to 15 second sample intervals and each chick would be scored if it performed one, or more, of a number of previously defined activities during the sample interval.

A sample interval of 15 seconds was chosen to ameliorate the two major problems with one-zero sampling i.e. that it fails to accurately record either duration or frequency of events (Altmann, 1974; but also see Tyler, 1979 and Smith, 1985). As a test of the accuracy of the sampling method at recording feeding frequency, I recorded frequency of feeding during a number of one hour observations as well as recording feeding by the one-zero sampling method. A comparison of the results showed that there was no significant difference (Pearson's  $X^2$   $p < 0.97$ ; 14 observation periods compared).

The behaviours defined for the one hour observations were chicks begging, chicks feeding and four types of interference interactions between the chicks. The interference interactions were:

1. "Lay-backing", where one chick would lean backwards against its nestmate often pinning it to the female.
2. "Shoving", where the chick would lean sideways against its nestmate.
3. "Neck-crossing", where a chick would lay its neck across that of its nestmate usually forcing it down to the floor of the nest.
4. "Shunting", where the chick would push its nestmate from behind.

### 3.3 Results

#### 3.3.1 The Effect of the Study Method on Chick Mortality

A comparison of the frequency of surviving and non-surviving chicks (from one and two egg nests) among natural, manipulated and control nests showed no significant difference (Pearson's  $X^2$   $p > 0.05$ ,  $n = 144$  chicks). This indicates that the study method did not induce additional mortality to chicks from natural and manipulated nests.

#### 3.3.2 Effects of Manipulation

During the study 22 natural and 25 manipulated two chick nests were monitored. Of the 44 chicks from natural nests, 23 survived to fledge, 13 died of starvation attributable to brood reduction, 2 died from starvation when the female failed to return to the nest and feed chicks, 3 died of hypothermia and 3 died of unknown causes. Of the 50 chicks from manipulated nests, 24 survived to fledge, 21 died as a result of brood reduction, 2 died from starvation when the female failed to return to the nest and feed chicks, 1 was killed by neighbouring birds when it approached their nest and 2 died of unknown causes. A comparison between natural and manipulated nests of the number of chicks that survived, the number that died as a result of brood reduction and the number that died from other causes showed no significant difference (Pearson's  $X^2$   $p > 0.05$ ,  $n = 94$ ). This indicated that the unnatural mixture of age and weight of chicks in manipulated nests caused no significant changes in the patterns

of chick mortality and/or survival from those seen in natural nests.

The time period between the hatching of the first and second eggs in a nest (hatching interval), the difference in mass between chicks at the time the second chick hatched (initial mass disparity) and the time period chicks coexisted in the nest were compared between manipulated and control nests. The hatching interval was not significantly different between natural and manipulated nests (Kruskall-Wallis Nonparametric ANOVA  $X^2$  approximation  $p > 0.05$ ,  $n = 32$ ; natural nests median = 1 day, minimum value = 0, maximum = 2; manipulated nests median = 1 day, minimum = 0, maximum = 4). The initial mass disparity was not significantly different between manipulated and natural nests (Kruskall-Wallis Nonparametric ANOVA  $X^2$  approximation  $p > 0.05$ ,  $n = 27$ ; manipulated nests mean = 26.72g, sd = 33.67g; natural nests mean = 32.00g, sd = 21.31g). The number of days that chicks coexisted was not significantly different between manipulated and natural nests (Kruskall-Wallis Nonparametric ANOVA  $X^2$  approximation  $p > 0.05$ ,  $n = 31$ ; manipulated nests median = 9, minimum = 3, maximum = 30; natural nests median = 5.5, minimum = 2, maximum = 29 (disregarding one nest where both chicks fledged)).

Because significant differences could not be detected between natural and manipulated nests for any of the factors tested, data from both nest categories were pooled for subsequent tests. However, not all nests were available for each of the tests.

### 3.3.3 Factors Associated with the Survival of a Chick

A contingency analysis of hatching order, relative size of the chicks (at the time the second chick hatched) and survivorship of chicks showed that all of these factors were significantly interrelated (Freeman-Tukey  $\chi^2$   $p < 0.001$ ,  $n = 68$ ). It was found that chicks which survived to fledge were typically the biggest chick of a pair and had hatched first (22 of 34 surviving chicks). Of the remaining 12 surviving chicks 9 were bigger than their nest mate and hatched at the same time; one was bigger and hatched second; one was equal in size and hatched first; and one was smaller and hatched at the same time.

A comparison of the factors associated with surviving and non-surviving chicks from A+B nests showed that the surviving chick was typically from the B egg (20 out of 22 nests, Binomial  $p < 0.001$ ; assuming the probability of survival for A and B chicks is 0.5). In natural nests this was an expected result since B eggs are usually larger than A eggs (Warham, 1974a), however, in manipulated A+B nests the initial mass disparity between the A chicks and B chicks resulted from asynchronous hatching (see chapter two for details).

### 3.3.4 Differences Between Coexistence Groups

A graph of the number of chicks, of a given age, that died as a result of brood reduction (fig. 1) indicated that a range of different brood reduction processes were possibly occurring. To investigate this, nests were divided into two arbitrary groups.

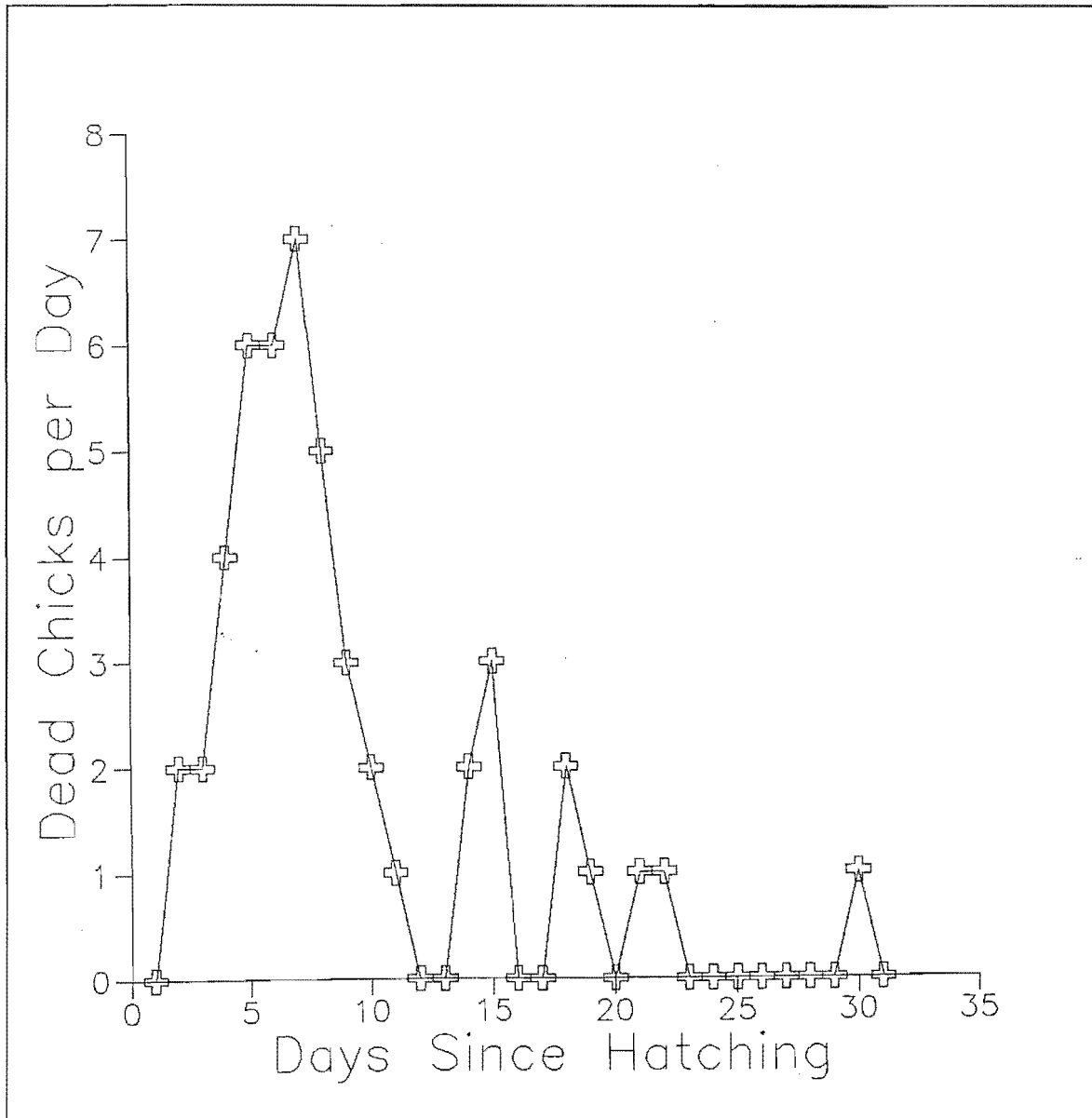


Figure 1. Number of chicks dying per day as a result of the brood reduction process.



Nests where chicks coexisted for 12 or fewer days were labelled as group 1, those nests where coexistence was greater than 12 days were labelled as group 2.

In group 1 nests the non-surviving chicks (NS chicks) lived for approximately six to seven days (mean = 6.29 days, sd = 2.21; median = 6 days, min = 2, max = 11; mode = 7 days; n = 38). In group 2 nests the non-surviving chicks lived for approximately 18 days (mean = 18.27 days, sd = 4.77; median = 18 days, min = 14, max = 30; mode = 15 days; n = 11).

Hatching interval and initial mass disparity were compared between nests in the two coexistence groups. Initial mass disparity was not significantly different between nests in the two groups (Kruskall-Wallis Non-parametric ANOVA  $p > 0.05$ , n = 31; group 1 mean = 20.75g, sd = 29.69g, n = 9; group 2 mean = 33.44g, sd = 29.93g, n = 22). Hatching interval also was not significantly different (Kruskall-Wallis Non-parametric ANOVA  $p > 0.05$ , n = 26; group 2 median = 1 day, min = 0, max = 4, n = 8; compared with group 1 median = 1.5 days, min = 0, max = 4, n = 18). This result indicates that the longer periods of chick coexistence seen in group 2 nests were not the result of pairs of chicks being closer together in size or age than those pairs of chicks in group 1 nests.

The growth rates, up to nine days of age, for chicks that survived brood reduction (S chicks) and those that died as a result of brood reduction (NS chicks) from the two coexistence groups can be seen in figures 2a and 2b. A pair-wise comparison of the mass of chicks from the coexistence groups showed that the NS chicks from group

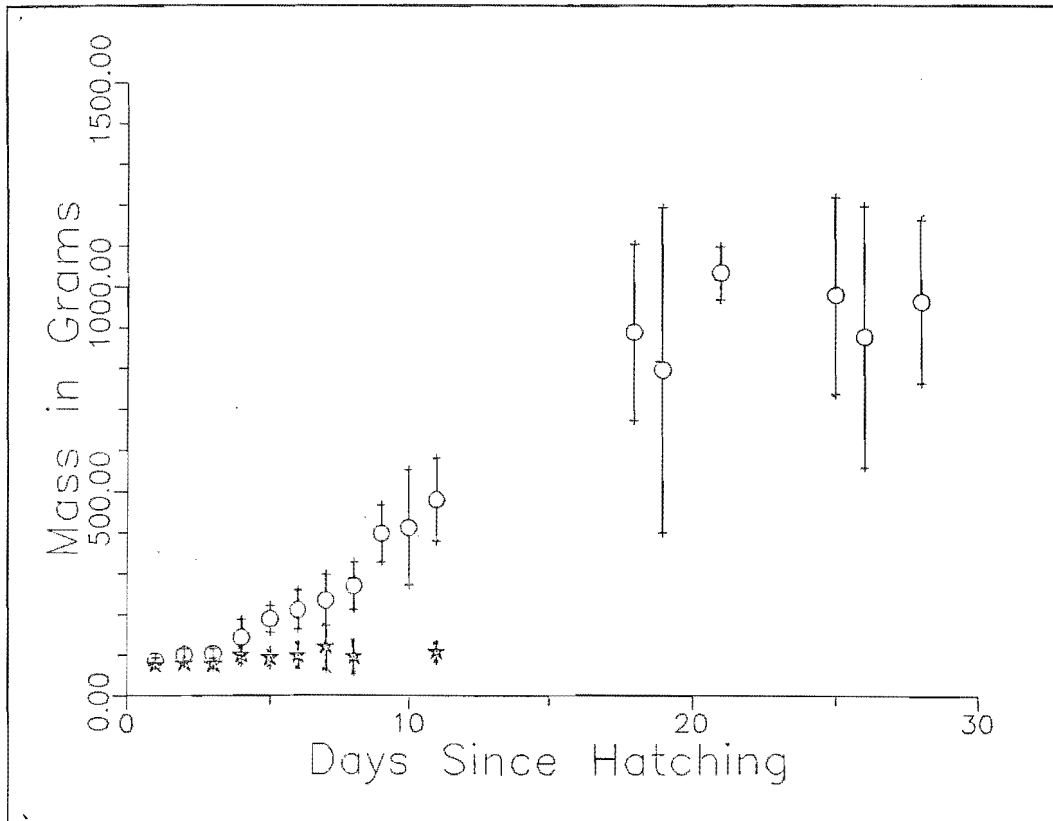


Figure 2a. Growth of S (circles) and NS (stars) chicks from group 1 nests. Plot shows mean values and 95% confidence intervals.

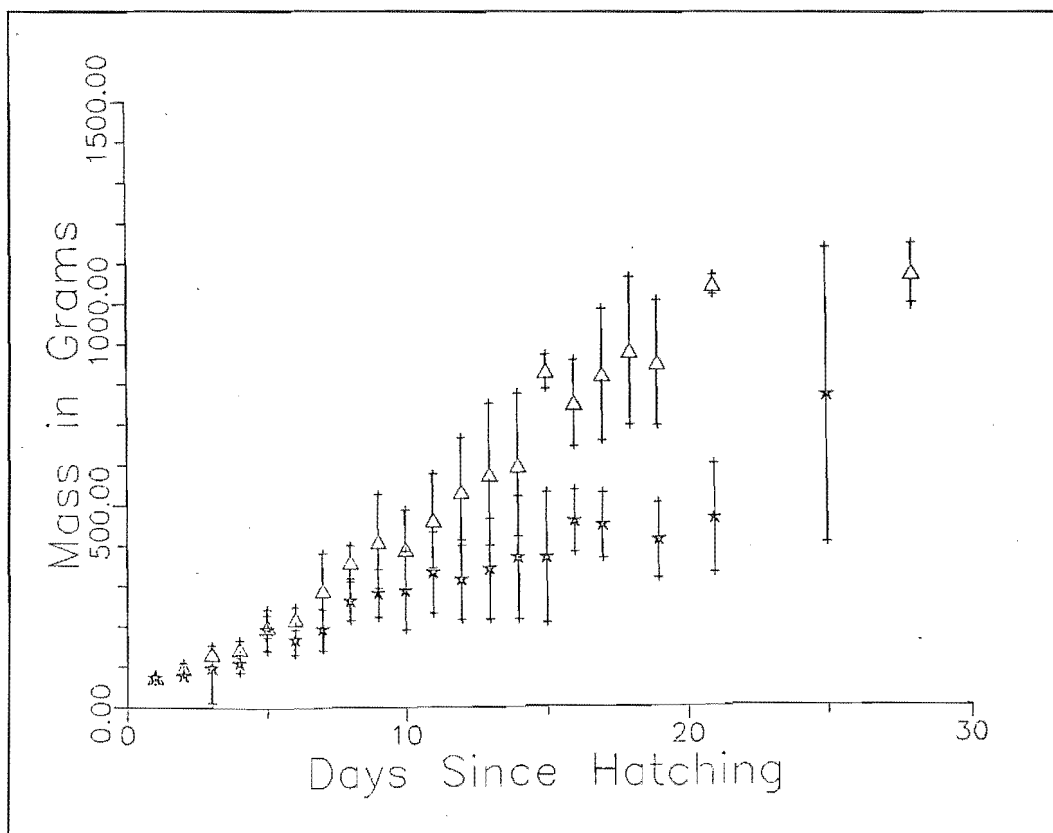


Figure 2b. Growth of S (triangles) and NS (stars) chicks from group 2 nests. Plot shows mean values and 95% confidence intervals.

1 nests were significantly lighter than S and NS chicks from group 2 nests and significantly lighter than survivors in group 1 nests (Tukey (HSD)  $p < 0.05$ ). This clearly is due to the group 1 NS chicks showing little or no increase in mass with age before death.

A log-linear model was used to compare the number of 15 second sample intervals in which begging, feeding and interference behaviour took place between eventual survivors and non-survivors from the two different coexistence groups. Only observations for the first 4 days of coexistence were used to try to ensure that most of the behaviours of the chicks observed were not modified extensively by being in the final stages of starvation. Observations in which NS chicks were obviously near death (typified by them not attempting to beg or feed and just remaining under the female during feeding sessions) were not used. All of the variables tested were found to be significantly interrelated (Freeman-Tukey  $X^2$  approximation  $p < 0.001$ ,  $n = 10$  nests; 6 group 1 nests and 4 group 2 nests). A summary of the results can be seen in table 2. Because the data for each group were obtained from a small number of nests these results should be viewed with some caution.

		COEXISTENCE GROUP		
		GROUP 1 (0-12)	GROUP 2 (13-30)	
B E H A V I O U R	BEGGING	SURV	LESS**	LESS**
		NSRV	MORE**	N SIG
	FEEDING	SURV	N SIG	N SIG
		NSRV	LESS**	MORE**
	INTERFERE	SURV	MORE**	N SIG
		NSRV	LESS**	N SIG

KEY:

GROUP = Coexistence Category.  
 (1-2) = Number of days chicks coexisted.  
 SURV = Surviving chicks.  
 NSRV = Non-surviving chicks.  
 MORE = Occurred more often than expected.  
 LESS = Occurred less often than expected.  
 \*\* = Significant at 0.01 probability level.  
 N SIG = No sig. difference at 0.05 level.

Table 2. How observed levels of begging, feeding and interference behaviours differed from statistically generated expected values. The comparison is between survivors and non-survivors from group 1 and group 2 nests, during the first four days after hatching.

Many of the following results are based on small sample sizes and some of the observations are serial comparisons i.e. from the same nests on different days. Because of this, statistical tests were not used to test some of the data sets from group 2 nests and some comparisons are based on visual assessment of graphical data.

Because of this, statistical tests were not used to test some of the data sets from group 2 nests and some comparisons are based on visual assessment of graphical data.

#### **a. Begging**

The results from table 2 indicate that the S chicks from group 1 and 2 nests generally begged less often than the NS chicks during the first 4 days of coexistence. This trend was more conspicuous in group 1 nests than in group 2 nests (fig. 3a and 3b) and probably was related to the different feeding patterns (discussed later) of chicks from the two nest groups. In both nest groups the overall levels of begging seemed to increase with the age of the chicks.

#### **b. Feeding**

A comparison of the number of sample intervals in a sample period during which feeds were received by S and NS chicks in group 1 nests showed that S chicks were fed in significantly more sample intervals (Wilcoxon's Signed Rank Test one tail exact  $p = 0.006$ ,  $n = 12$  observations from 8 nests). Figure 4a shows the relative proportions of sample intervals in which S and NS chicks in group 1 nests received feeds.

A different pattern was seen among group 2 nests (fig. 4b). In these nests the NS chicks initially were fed in proportionally more sample intervals than the S chicks but the situation reversed as the chicks grew older.

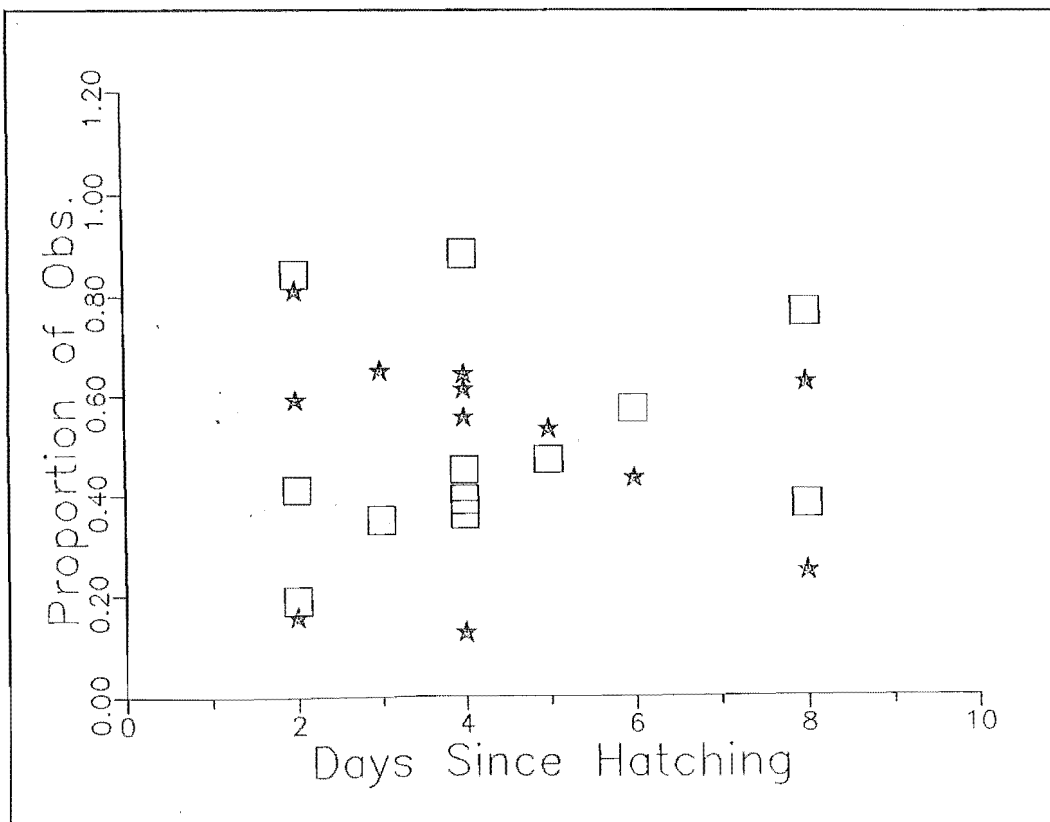


Figure 3a. Relative proportions of begging at different ages shown by S (squares) and NS (stars) chicks from group 1 nests.

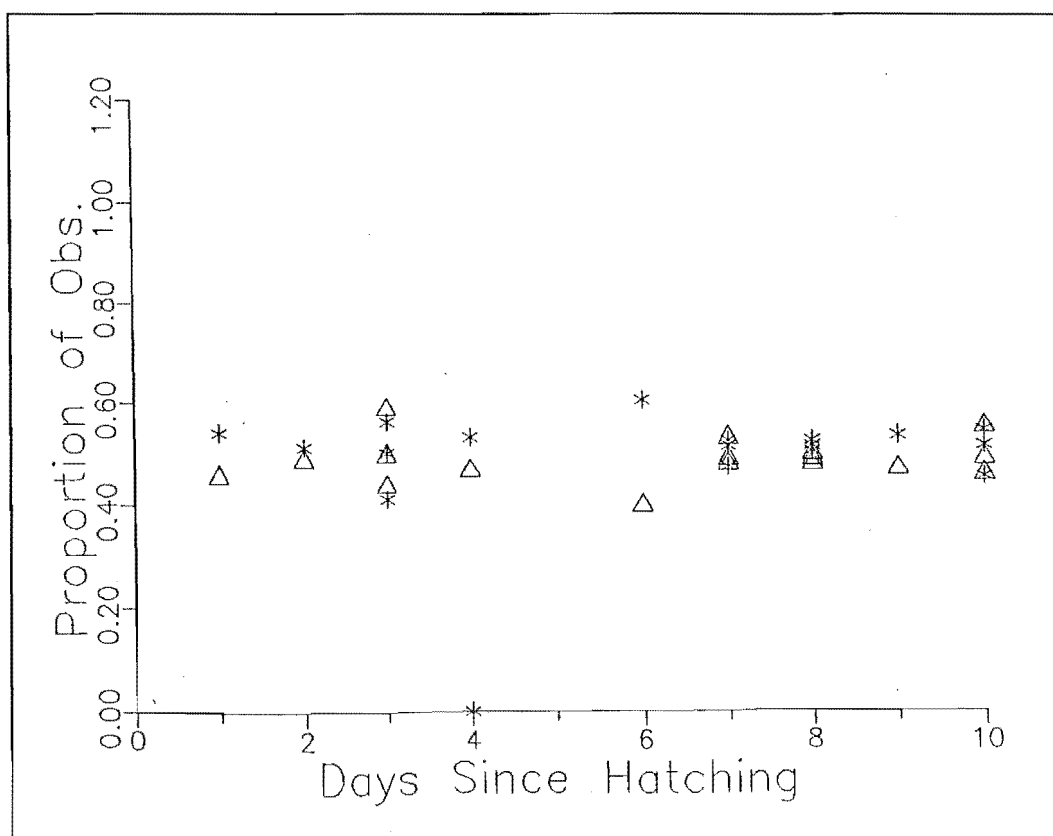


Figure 3b. Relative proportions of begging at different ages shown by S (Triangles) and NS (asterisks) chicks from group 2 nests.

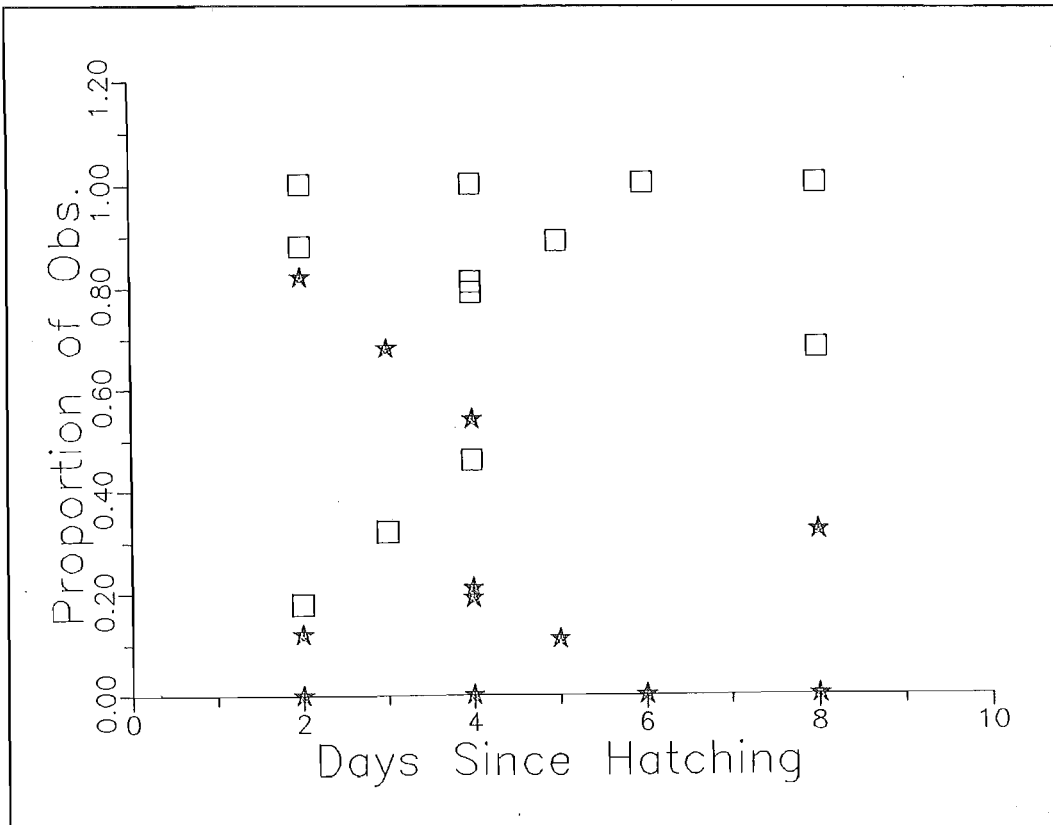


Figure 4a. Relative proportions of feeds received at different ages by S (squares) and NS (stars) chicks from group 1 nests.

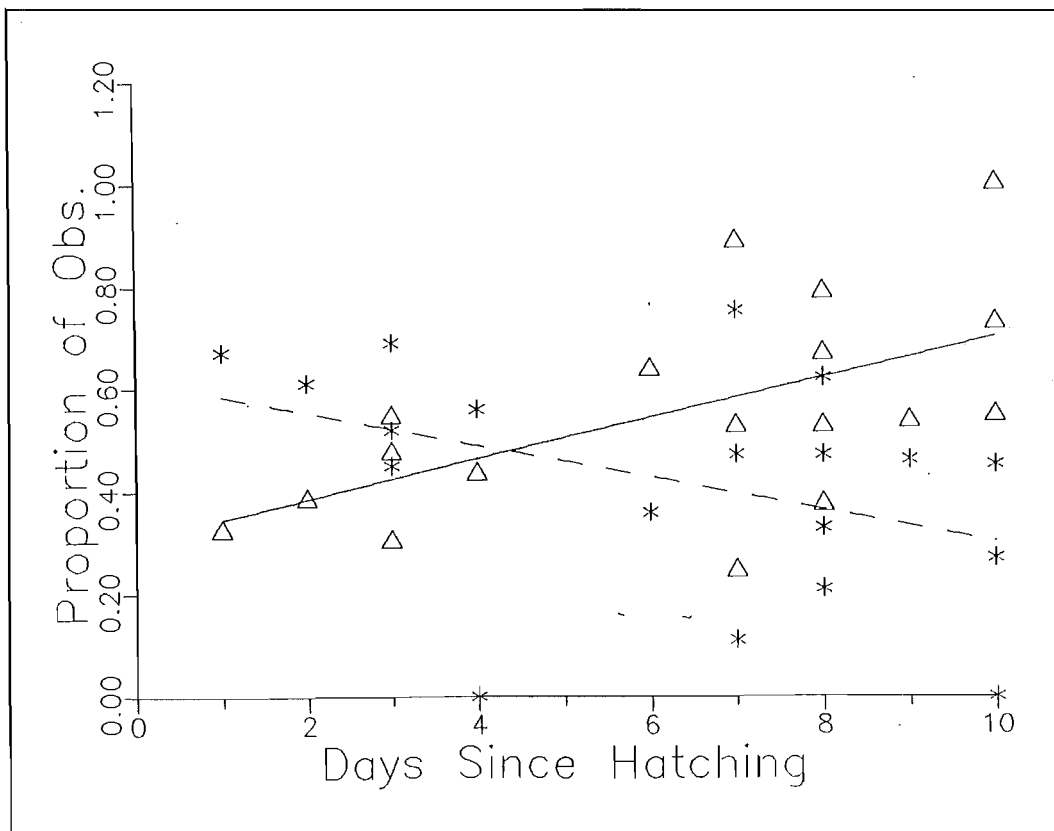


Figure 4b. Relative proportions of feeds received at different ages by S (triangles) and NS (asterisks) chicks from group 2 nests. Least squares lines show trends in the data for S (solid line) and NS (dashed line) chicks.

To ascertain whether females from group 2 nests were delivering more food to the chicks during feeding bouts than females from group 1 nests, I compared the number of sample intervals in a sample period during which feeding occurred.

Comparisons were made between randomly selected pairs of observation periods (one observation each from a group 1 and a group 2 nest) with chicks of similar age i.e. first hatched chicks in each nest of the same age. Although group 2 nests usually had the greater number of feeding intervals per session (in 10 out of 14 cases) no significant difference was found between the level of feeding of the two groups (Wilcoxon's signed rank test, 1 tailed exact  $p = 0.105$ ,  $n = 14$  comparisons).

To see if there was any bias in the order in which food was delivered to S and NS chicks I compared the number of sample intervals in which feeds were received by each chick in relation to the number of sample intervals in which feeds were given by the female. The test was performed separately for group 1 and 2 nests. No significant differences in the timing of food delivery were found between S and NS chicks in either group 1 or 2 nests (Kolmogorov - Smirnov  $X^2$  approximation both  $p > 0.05$ ,  $n = 12$  sample periods for group 1 and  $n = 24$  sample periods for group 2). However, a visual comparison of the feeding order of S and NS chicks from group 1 and 2 nests (fig. 5a and 5b) showed that in group 1 nests, S chicks did tend to receive many of their feeds earlier in the feeding session than NS chicks, while the timing of delivery was more evenly matched between the chicks in group 2 nests. The statistical comparison of the order of food delivery to S chicks from group 1 and 2 nests,



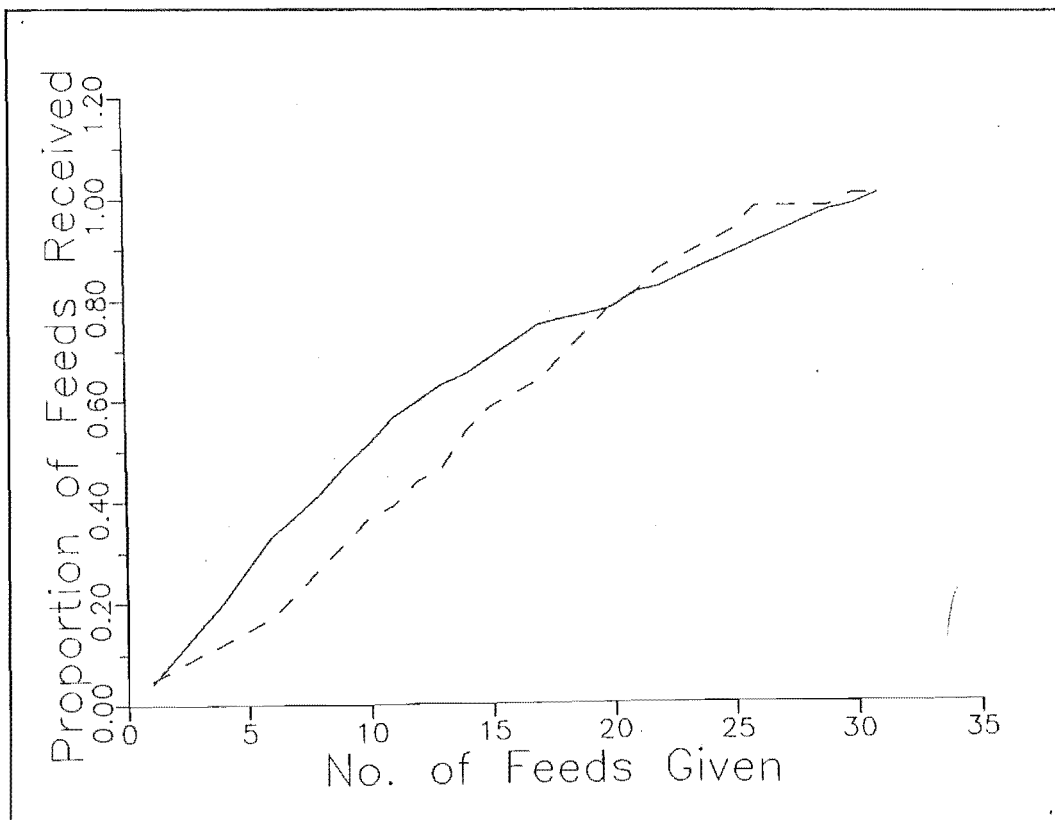


Figure 5a. Cumulative proportions of the total feeds received by S (solid line) and NS (dashed line) chicks from group 1 nests.

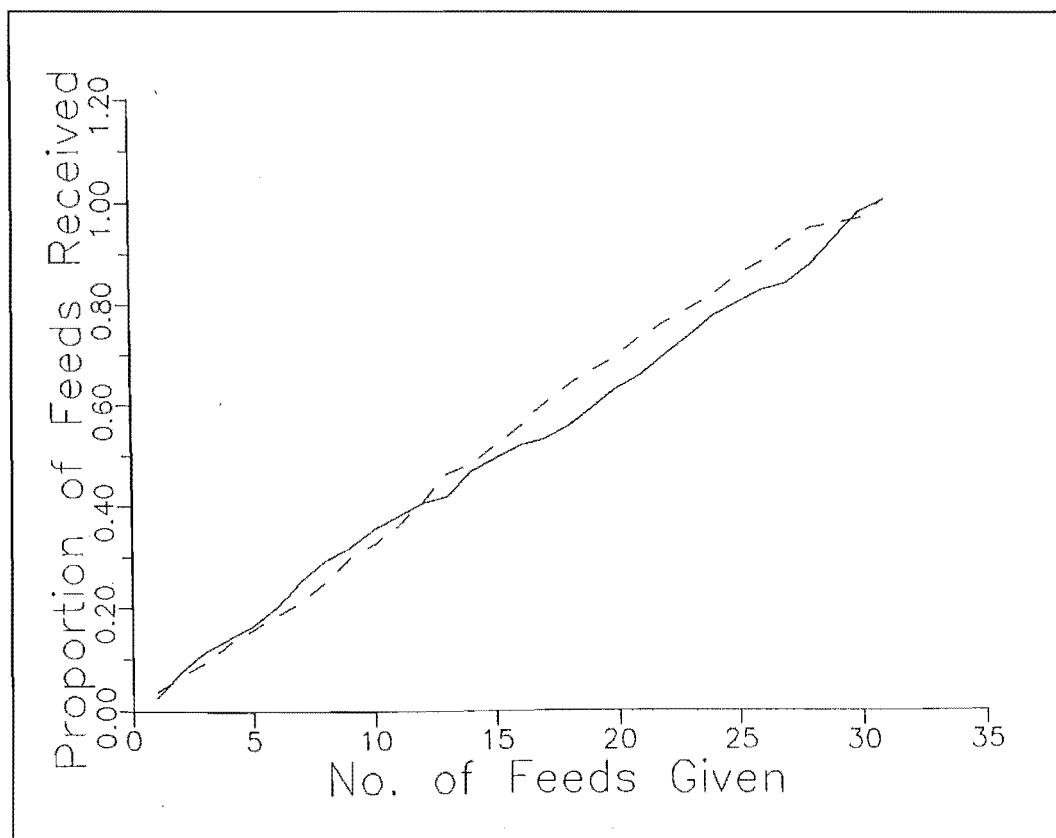


Figure 5b. Cumulative proportions of the total feeds received by S (solid line) and NS (dashed line) chicks from group 2 nests.

showed that S chicks from group 1 nests received most of their feeds significantly earlier in the feeding session than the S chicks from group 2 nests (Kolmogorov - Smirnov  $X^2$  approximation  $p < 0.05$ ,  $n = 12$  sample periods for group 1 and  $n = 24$  sample periods for group 2).

### **c. Interference Interactions**

The different patterns in the level of interference behaviours observed in the two nest groups can be seen in fig. 6. One of the most noticeable trends in the data is that the overall level of interference interactions in both nest groups remained fairly similar until the chicks were around 5 days old at which point the level of interactions appeared to escalate in group 2 nests.

The within nest group patterns in interference interactions also differed between the two groups. In group 1 nests (fig. 7a) the S chicks almost always initiated more interference interactions during feeding than did the NS chicks (Wilcoxon's Signed Rank Test one tailed exact  $p = 0.019$ ,  $n = 12$  observations from 8 nests). In group 2 nests a more complex pattern was seen for which I offer no explanation (fig. 7b).

#### **3.3.5 Adoption of Chicks**

In two cases during the course of the study NS chicks from group 2 nests were found in the nests of other penguins. In the first case the chick was found in a neighbour's nest where the adult birds were still incubating eggs. The chick had been fed by its

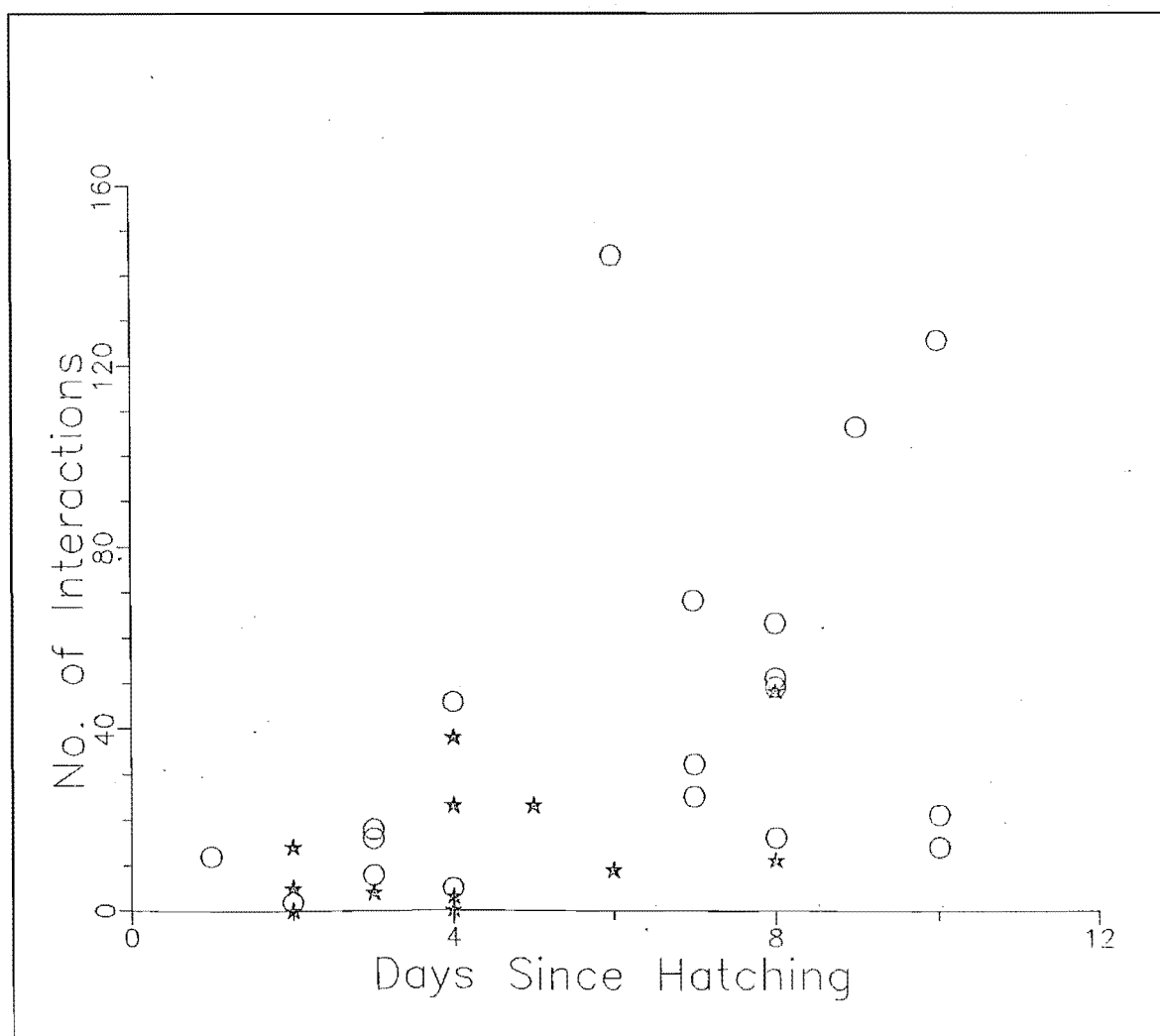


Figure 6. A comparison of the total number of interference interactions occurring in group 1 (stars) and group 2 (circle) nests.

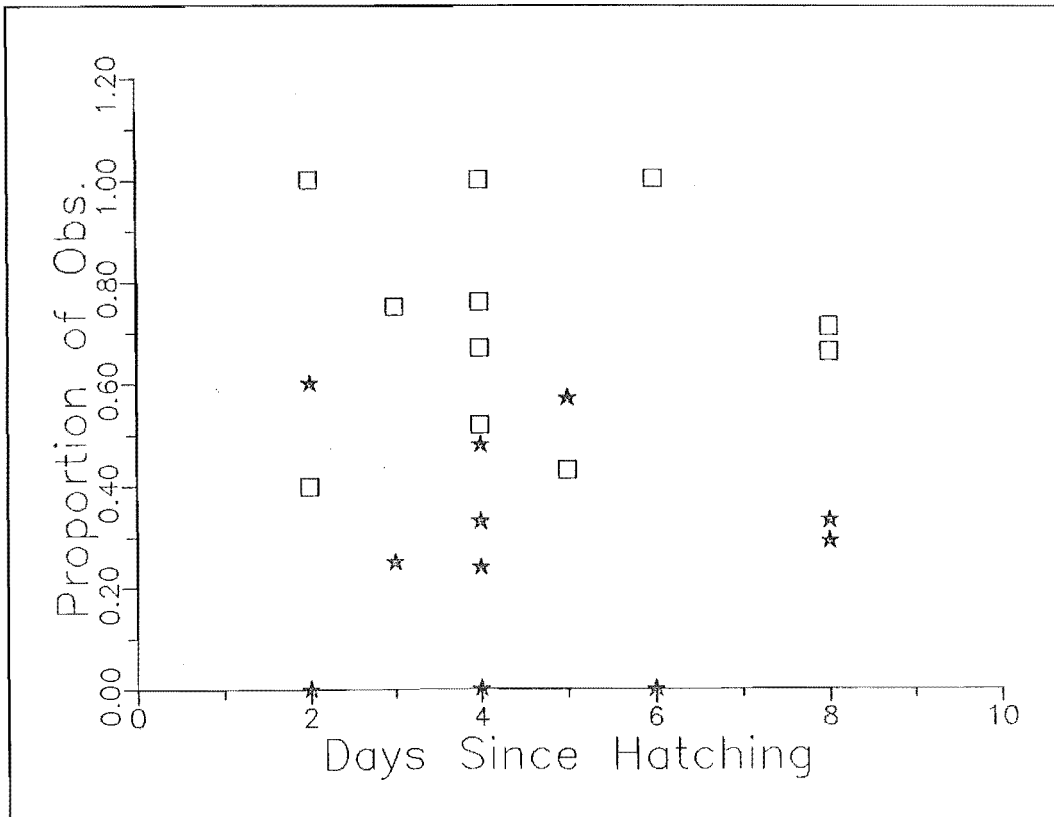


Figure 7a. Relative proportions of interference interactions initiated by S (squares) and NS (stars) chicks from group 1 nests.

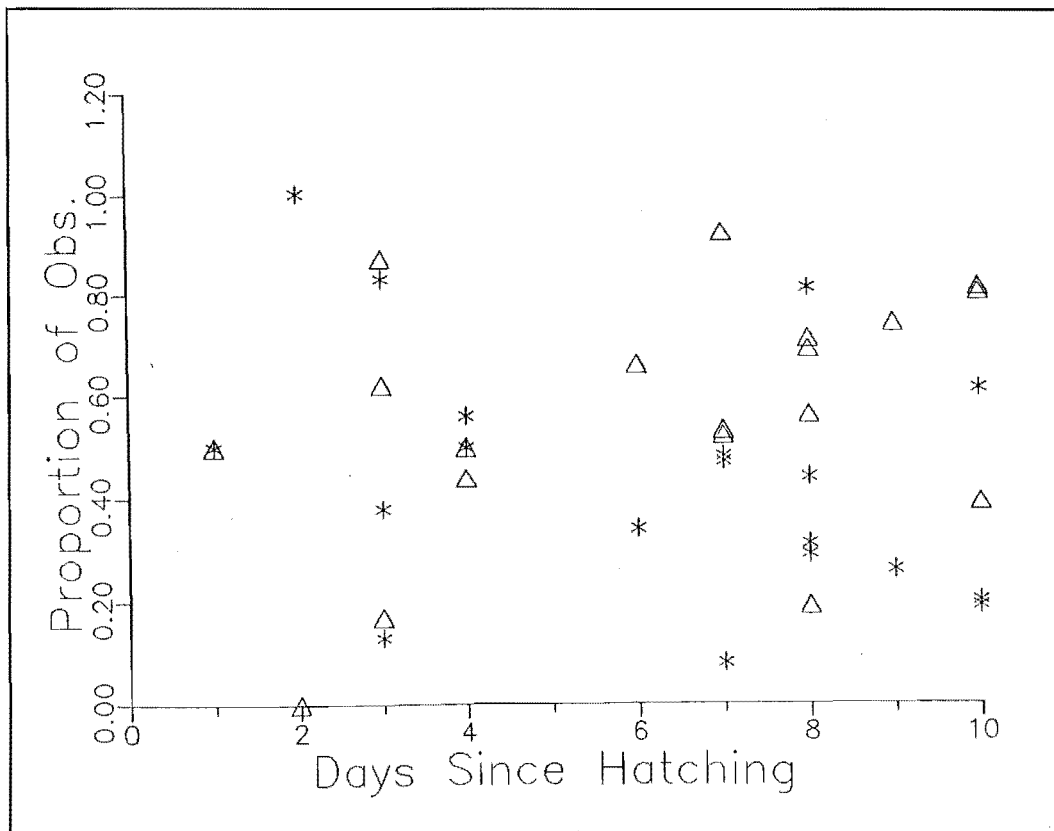


Figure 7b. Relative proportions of interference interactions initiated by S (triangles) and NS (asterisks) chicks from group 2 nests.

new parents and would have no doubt become the survivor in this brood had it not been returned to its natal nest. In the second case the chick was found in a neighbour's nest that contained two chicks smaller than it. Again I have no doubt the adopted chick would have been the survivor in this brood had it not been returned to its natal nest. Given the mobility of the chicks I presume that they made their own way into their foster nests.

### 3.4 Discussion

During this study it was found that chick starvation - resulting from the brood reduction process - was the major cause of death among tawaki offspring. This is consistent with observations on chick death reported by Warham (1974a). The regularity with which one of the chicks in a brood died as a result of the brood reduction process generally confirms Warham's conclusion that tawaki, like the other crested penguins, seldom (Warham states "never") fledge two offspring despite laying two eggs (Warham, 1974a; 1975). Therefore, tawaki can be classified as obligate brood reductionists (using the criteria of Simmons (1988)).

As mentioned previously, the typical mode of brood reduction observed by Warham (1974a) and during this study was for the smallest chick of a brood to starve to death. Although the process of reduction involved the chicks competing for access to food I never observed any aggressive<sup>1</sup> interaction between chicks in a brood nor between chicks and parents. This feature appears to be common to all crested penguin species in which brood reduction occurs (Lamey, in press) but is unusual among other obligate brood reductionist species (Edwards and Collopy, 1983; Mock, 1984a; Simmons 1988). Typically, mechanisms of brood reduction are based on a dominance hierarchy between chicks in a brood which is created and maintained by some degree of aggressive interaction e.g. white boobies *Sula dactylatra* and brown boobies (Dorward, 1962; Nelson, 1978), various eagle species (Meyburg, 1974) and American

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1. I define "aggressive interaction" to be one where hostility occurs between individuals i.e. deliberate blows, which are intended to injure or intimidate, are directed at the other individual.

white pelican *Pelecanus erythrorhynchos* (Evans and McMahon, 1987). Often brood reduction in these species is by siblicide with the dominant chick either directly killing its sib or using intimidation to prevent it from obtaining essential resources (Edwards and Collopy, 1983; Mock, 1984a).

In tawaki the size hierarchy in broods from natural nests resulted from a combination of differential egg size, the A or first laid egg being the smallest (Warham, 1974a; chapter 2) and asynchronous hatching, with the B eggs typically hatching first (details in chapter 2; but see Warham, 1974a). Hence chicks which were eliminated through brood reduction (NS chicks) were typically the second to hatch and were from the smallest, first laid egg (A egg).

In manipulated A+B nests the non-surviving (NS) chick was typically from the A egg and hatched second; in manipulated A+A or B+B nests the NS chick was typically from the second hatched egg. In the few manipulated nests where chicks were of equal weight and hatched on the same day, a size hierarchy quickly developed and the smallest chick eventually died. The pattern of the biggest - and usually first hatched - chick being the most likely survivor of the brood reduction process is common among infanticidal bird species e.g. oyster catcher *Haematopus ostralegus* (Safriel, 1981), laughing gull *Larus atricilla* (Hahn, 1981), South Polar skua *Stercorarius maccormicki* (Young, 1963) and blue-eyed shag *Phalacrocorax atriceps* (Shaw, 1985).

Despite the uniformity in the mode of brood reduction seen during this study it was noticeable that the period over which tawaki broods coexisted varied (fig. 1). It

appeared that the length of time a pair of chicks coexisted was not affected by my manipulations, nor was it determined purely by physical factors associated with the chicks themselves i.e. the period of coexistence did not relate to either similarity of mass or degree of asynchrony in the timing of hatching, but was the product of a combination of behavioural and physical factors. Observations on broods from either end of the coexistence continuum revealed the following patterns.

In the initial zero to five days after hatching the chicks from both nest groups showed poor coordination and motor skills. Chicks would beg in any direction and often at any object e.g. tall rocks or the adult's flipper, interference interactions were haphazard and often misdirected, and feeding appeared to be controlled by the female who often had to encourage chicks to feed and would guide them to her bill (usually by delicately grasping their bills). During the small number of observations made on nests with chicks that had been hatched less than 5 days, it was often noted that females would selectively feed one of the brood while consistently ignoring the other chick.

In group 1 nests it appears that the S chicks were selectively fed the most food by the female (fig. 4a) while NS chicks were fed the least. The S chicks also tended to receive most of their feeds near the beginning of feeding sessions while NS chicks were generally fed later (fig. 5a), however, this difference in pattern was not statistically significant. The S chicks showed a steady increase in mass while the NS chicks usually failed to increase in mass before dying (fig. 2a).



Proportionally, NS chicks usually begged in more sample intervals than the S chicks but were fed less often. I suggest that the comparative levels of begging between S and NS chicks probably reflected the degree of satiation of the chicks. However, it is possible that the adult females were using begging levels as cues to discriminate between individual offspring when feeding them i.e. persistent begging may have indicated the smallest/weakest chick.

Although the group 1 NS chicks were fed little, or no, food they survived for around six days after hatching. This probably reflected the time it took to deplete their internal yolk reserves. Adelle penguin chicks, *Pygoscelis adeliae*, have been shown to survive for 6-7 days after hatching by using their yolk reserves alone (Reid and Bailey, 1966).

The timing of the peak in brood reduction in the group 1 nests occurred at the time the chicks' physical coherency improved (which seemed to coincide with their eyes opening (Warham, 1974a)). The weakened state, or death of, the NS chick meant that the S chick faced little, or no, competition during feeding sessions and consequently the level of interference interactions remained low in group 1 nests.

In contrast, it was the NS chicks in group 2 nests (i.e. nests where chicks coexisted for more than 12 days) which initially received the greater proportion of feeds during the first 5 days after hatching (fig. 4b), and they began to increase in mass at a similar rate to the S chicks (fig. 2b). During the first 10 days of coexistence, the proportional levels of begging were much more even between the chicks (compared with group 1 nests) and no obvious bias in feeding order was seen (fig. 5b). Although the S chicks

apparently received fewer feeds than NS chicks they still increased in mass and maintained their relative mass advantage over the NS chicks. This may be the result of an increased quality or quantity of food per feed given to S chicks although I have no data to test this hypothesis. As the group 2 chicks grew older the proportion of the feeds received by the NS chick fell while that received by the S chick began to increase (fig. 4b). This change in feeding rates was closely associated with the increase in coherency of movements and development of motor skills in the growing chicks. Five days after hatching the S chicks became more directed in their movements and were able to take advantage of their greater mass to disrupt the feeding of the NS chick and also to dominate the delivery of food (by assuming and maintaining the best feeding position relative to the female). Because the chicks in group 2 nests were actively competing for food the level of interference interactions generally increased to a greater level than that seen in group 1 nests. The asymmetry in mass between chicks in the group 2 broods continued to increase with age until the NS chicks ceased to increase in mass and then died.

Data on periods of chick coexistence in Snares crested penguin (Warham, 1974b; C.M. Miskelly, pers. comm.) and rockhopper penguins (Strange, 1982; but see Williams, 1980) suggest that variations in the brood reduction process, perhaps similar to those seen in tawaki, may also occur in these two species. However, no behavioural studies of the brood reduction process for these two species have been published as yet.

When considering the variability in the brood reduction process of tawaki it was apparent that certain physical and behavioural characteristics associated with the

female exerted a strong influence on that process. In natural nests, the female created the initial asymmetry between the eggs that was maintained through to hatching. Because she was the sole provider of food to the newly hatched brood, her behaviour, during the first five days of feeding at least, dictated the initial distribution of food between the chicks. This action, in turn, appeared to control the timing, but not the outcome, of the brood reduction process.

In the published accounts of brood reduction in avian species there are few references to adults selectively feeding chicks (Horsfall, 1984; Braun and Hunt, 1983) although this may change as more species are studied intensively. In most brood reductionist species adults often appear to play a passive role in the brood reduction process e.g. blue-footed booby *Sula nebouxii* (Drummond, Gonzalez and Osorno, 1986) and American white pelican (Evans and McMahon, 1987), except in some cases when they may reduce sibling aggression by splitting the brood, with each parent feeding only one chick e.g. Western Grebe *Aechmophorus occidentalis* (Nuechterlein, 1981) and South Polar skua (Young, 1963). Therefore, it is of interest to look at the consequences of preferential feeding on the brood reduction process of tawaki.

In group 1 nests the preferential feeding of the S chick resulted in an increasing difference in mass between the S chick and its nest mate. This not only conferred a competitive advantage to the S chick, but also weakened or eliminated the NS chick before it was physically coherent enough to compete for food. The group 1 females benefited from their actions by not expending food on doomed chicks.

In the group 2 nests the preferential feeding of the NS chick allowed it to increase in mass at a similar rate to the S chick. Consequently chicks coexisted in a nest for longer periods and actively competed for food. Therefore, the elimination of the NS chick was more dependent on the actions of the S chick than in group 1 nests. The adult females from group 2 nests expended more energy than those from group 1 nests by providing food to the doomed chick, but possibly accrued at least two benefits. Firstly they may have benefited from the extended period of chick coexistence by having the "insurance" (Lack, 1968; Warham, 1975) value of the second chick for a longer period i.e. if the larger chick died some time after hatching the smaller chick would still be available to replace it. The second possible benefit to the parents was that they stood a chance of their smaller chick being adopted by neighbouring adults who could possibly raise and fledge it for them. Adoption occurred on two occasions during this study. In both cases I have no doubt that the adopted chick would have out competed the host brood and fledged. However, the rarity of adoption suggests that this was probably a chance event rather than a regular breeding strategy.

The results of this study confirm that tawaki are obligate brood reductionists and that the typical mode of brood reduction is for the smaller of the two chicks in a brood to starve to death. Although variation in the brood reduction mechanism was found to occur, this only altered the timing of brood reduction and not the outcome. Although some possible benefits to chicks and adults from the variations in the brood reduction process are suggested, I did not directly address these questions in this study.

## CHAPTER 4

### CONSERVATION OF TAWAKI

In the general introduction to the thesis (chapter one) I identified some of the gaps in our knowledge about tawaki, how these affected our understanding of their conservation status and how this would limit our ability to actively manage the species, should this become necessary.

During this study I gathered detailed information on some aspects of the natural breeding process of tawaki and was able to evaluate whether human presence or handling of adults, eggs or chicks affected the birds' reproductive output. Additionally I was able to assess the effect of manipulating clutches of eggs and broods of chicks to try to increase fledging success.

Much of this information has been presented in chapters two and three of the thesis. In this chapter, however, I discuss it in the context of tawaki conservation.

#### **4.1 Clutch Manipulation**

During this study I manipulated 25 clutches of eggs (details of the manipulation procedure are contained in chapter two, section 2). Of the 25 pairs of adults involved in the manipulation 23 accepted and incubated the eggs they received. In two cases the incubating adult deserted the nest after receiving the manipulated eggs. Two of the four deserted eggs were damaged and eaten by weka, the other two intact eggs

were transferred to single egg nests, not used in the study, where they were incubated successfully .

#### **4.1.1 Adult Response to Manipulations**

A majority of the adult birds on nests that received eggs remained on the nest during the transfer and would attack my hand as I removed or placed eggs inside their nest bowl. Once the transfer was complete the birds would rearrange the eggs then adopt the typical incubation position. In some cases incubating birds would leave the nest and return after the egg transfer was complete. In these cases we would remain close to the nest - but out of sight - and guard the eggs against attacks by weka.

In general the birds would accept anything placed in their nest. Because of the distance involved between groups of nests and the different numbers of useable nests in a group we sometimes had to take more eggs than we could replace. In these cases we used stones from avocado pears as dummy eggs rather than leave nests empty. The stones were considerably smaller than the smallest of the penguin eggs and more spherical. However, in all cases the eggs were accepted by the incubating adults. On receiving the stones the incubating adult would peel off the brown tomentum of the seed and then incubate the peeled seed. Later when we were placing eggs back into these nests the adults would actively defend the avocado seeds with the same intensity with which they guarded their own eggs.

The two nests where the birds deserted their new clutch were next to each other. Both adults deserted their nest at our approach and took some time to return after the egg transfer. The birds then deserted their nests again some time in the two hours following the transfer.

During the manipulation of the eggs and at all other times when I was checking or weighing eggs or chicks I always used slow but deliberate movements approaching the nests and handling the contents.

#### **4.1.2 The Effect of the Manipulation on the Viability of Eggs**

Results presented in chapter two indicated that our handling and moving eggs during manipulation did not cause a decrease in viability of those eggs. However, it is worth emphasising that the age at which eggs are moved may be critical. In consultation with New Zealand Department of Conservation staff (Christchurch Regional Office) it was decided that eggs less than 10 days old should not be moved as this could, potentially, dislodge the developing embryo. This whole topic of egg transfers is one area that should be investigated further as this particular decision regarding tawaki eggs was not based on evidence.

#### **4.2 The Transfer of Chicks**

My information on the transfer of chicks between nests comes from two sources, observations on natural transfers and a small number of manipulations I performed on broods during, but outside of, the study.

In the two cases of natural transfers, chicks from nests used in this study were found settled and being fed in neighbouring nests (details in chapter three). In both cases the chick which had migrated was the chick from an A egg - or was the smallest in a brood - and came from a nest where it had coexisted with its sib/nestmate for more than 10 days.

During the course of the study I performed three chick transfers. In the first two transfers I moved single 4-5 day old A egg chicks, who were close to starving to death, into nests where adults were incubating two obviously infertile eggs. In one case the incubating male immediately accepted the chick and even tried to feed it. However, at that point the male had been fasting for some weeks and so had no food to regurgitate. The female of the pair immediately began feeding the chick on her return and it eventually fledged. In the second case the incubating male accepted the chick but I believe that the chick was too close to starvation and died before being fed by the returning female. In the third case I transferred single young (1-2 days old) chicks between two adjacent nests. Both sets of incubating parents accepted the new composition of their broods and the chicks underwent the typical pattern of brood reduction.

I conclude that parent birds will readily accept young chicks in their nest whether they have hatched them or not. In the cases described above I suspect adults accepted the chicks because chicks and parents had not imprinted upon each other. I suspect that the same transfers would probably not work with older chicks or with parents who had an older brood of their own.



### 4.3 Natural Constraints on a Manipulative Breeding Programme

The observations on tawaki made during this study indicate at least two natural constraints that would apply to a manipulative breeding programme.

The first - and probably most significant - of these is that only one chick can be raised successfully in a nest (see chapter three for details). Of the 114 pairs of breeding adults initially located for this study only one pair raised two chicks to, at least, the creche stage. Warham (1974a) never observed a pair of tawaki fledging two chicks during the five years of his study. Even in the manipulated nests of this study where chicks of the same age and mass were produced asymmetries would soon develop between the chicks and the smaller of the two would starve to death.

The second constraint is that females will only lay two to three eggs at the most (but see Warham, (1974b)). This means that egg production can not be increased significantly by continually removing eggs from laying females. Given that only one chick per nest will be raised by the parents it is probable more eggs would be laid than could be raised anyway.

Given the constraints listed above I would suggest that a manipulative breeding programme should concentrate on ensuring that all of the available breeding adults are incubating at least one viable egg. This could be done by taking viable A eggs from clutches and fostering these on pairs with infertile eggs or those who have lost eggs.

#### **4.4 The Broader Perspective**

Our knowledge of the ecology of tawaki is minimal, as is our understanding of the ecology of many of our seabirds. The little information that we do possess is heavily biased toward the terrestrial aspects of the tawaki's existence and in particular its breeding process. If we are to take the conservation of tawaki - or any seabird species - seriously our approach must be a more integrated one and include the interaction of tawaki with the marine environment.

The level of species management outlined in this chapter should only occur as a last resort. Under a well designed conservation strategy any major population problems of a species would be identified at an earlier stage, and appropriate steps taken to rectify the situation (if possible). Unfortunately it is unlikely that such a proactive programme will be formulated for this species and the only time it will receive the attention it deserves is if it joins the long list of our threatened, endangered and disappearing animal and plant species.

## CHAPTER 5

### GENERAL DISCUSSION

The breeding pattern of tawaki is the result of a complex interaction of environmental, morphological, physiological and behavioural factors. During this study I identified, or confirmed the presence of, a number of factors from the latter two classes and looked at how they interacted to contribute towards the tawaki's breeding pattern.

In this chapter I review the information presented in the preceding chapters and discuss it in the broader context of avian offspring reduction. I also discuss the implications that the tawaki breeding strategy could have on any conservation strategies developed for it.

#### 5.1 The Creation of Asymmetries

In chapter two I looked at the creation and maintenance of asymmetries between tawaki siblings. My study confirmed Warham's (1974a) observation that the initial difference between the offspring was created by the female who laid an A egg approximately 16% smaller than the second laid B egg. Two aspects of this laying pattern are of great interest to biologists involved with the study of avian infanticide, the degree of egg size dimorphism e.g. Slagsvold *et al.*, (1984) and the order in which the two eggs are laid e.g. Johnson, Bednarz and Zack (1987), Lamey (in press).

Among the crested penguin species tawaki show the least degree of egg dimorphism (Warham, 1975), yet the differences in egg size are among the most extreme to be found among bird species (Slagsvold *et al.*, 1984). The only other bird group to show a similar degree of egg dimorphism is the large raptors (Slagsvold *et al.*, 1984) all of which are also obligate brood reductionists (Simmons, 1988).

Theories as to why this degree of egg dimorphism has arisen in crested penguins invariably relate to possible evolutionary scenarios involving a change in foraging conditions e.g. Lack (1968), Williams (1981a). Unfortunately all of these theories currently are untestable.

Although the egg laying pattern of the crested penguins is considered unusual among offspring reductionists, the increase of egg size with laying order in a clutch is not an uncommon phenomenon, especially among small passerines (Howe, 1978, Clark and Wilson, 1981; Slagsvold *et al.*, 1984). Typically, these passerines hatch their eggs asynchronously i.e. the first laid eggs produce the first chicks (Clark and Wilson, 1981). The pattern of egg laying and chick hatching demonstrated by this group is considered to be a mechanism by which parents can ameliorate size differences between chicks that would otherwise result from asynchronous hatching e.g. Howe (1978). Clearly this is not the case with crested penguins. In those species which hatch both eggs, the B, or second laid egg, hatches first. Consequently the asynchrony favours the B egg chick by allowing it to further increase the disparity in mass between it and its smaller, second hatched sib.

During this study of tawaki it was found that the asynchrony in hatching appeared to be related to:

- a. the timing of brood patch formation of the parent, usually male, which undertook the first incubation period on the eggs,
- b. inherent differences between the developing embryos.

I found that the brood patch of the incubating adults did not develop until after the second egg was laid. This delay in the formation of the brood patch prevented effective incubation of the eggs until after the clutch was complete. I also found that, although either egg in a clutch was likely to pip first, the B egg would hatch a day or more before the A egg. My interpretation of this result was that chicks from B eggs were able to hatch faster than chicks from A eggs and that either chick was able to use cues from its hatching nestmate to initiate its own hatching process.

These observations lead me to conclude that - despite their atypical egg laying pattern -the tawaki studied on Taumaka Island produced the patterns of asynchronous hatching of eggs and asymmetry in size of hatched chicks seen in other, more typical, obligate brood reductionist bird species.

## 5.2 The Brood Reduction Process

At the completion of hatching tawaki nests typically contained two different aged and sized chicks. In chapter three I showed that the typical mode of brood reduction was for the smaller of the two chicks to starve to death. This is the most common mode of brood reduction seen in infanticidal bird species (Mock, 1984a).

However, while the outcome of the brood reduction process of tawaki was predictable i.e. the larger of the two chicks was almost always the survivor, the process was quite variable. I found that during the first five days after the chicks had hatched, females would preferentially feed one of the chicks. In a majority of cases the recipient of the directed feeding was the larger of the two chicks. When this was the case the smaller chicks would usually starve to death after exhausting their yolk reserves i.e. within five to seven days of hatching. Because the chicks lacked coordination and motor skills before they were five days old the larger chick had little involvement in the demise of the smaller chick.

In the reverse situation i.e. when the smaller of the two chicks was the recipient of the preferential feeding, the smaller chick began to grow at a similar rate to its larger sib. However, as the chicks grew older, the larger chick was better able to dominate access to food (simply as a consequence of its greater mass), and consequently the smaller chick would stop growing and starve to death. The brood reduction process in these nests involved active competition between chicks to decide the eventual survivor. Data on the periods that twins of rockhopper and Snares crested penguins coexist suggest that similar variations in the brood reduction process of these two

species may occur. From my observations, it appears that the brood reduction process of tawaki closely resembles that seen in other, more typical, brood reductionist species. However, two features of it stand out as being unusual.

The tawaki habit of preferentially feeding one of the chicks after they both hatch rarely has been observed among other brood reductionists. I feel, however, that once the brood reduction process of other species are studied more thoroughly it is likely that preferential feeding of some offspring will be found to be a more common occurrence than it presently appears.

The second unusual feature of the tawaki brood reduction process is the lack of aggression between the two sibs. In the majority of other obligate brood reductionist species, an aggression based dominance hierarchy is established between the chicks. In a number of species the dominant chick kills its sib outright i.e. brood reduction is by siblicide. This form of brood reduction is especially prevalent in the raptors that display a similar degree of egg and chick dimorphism as that shown by tawaki.

### **5.3 Implications for a Tawaki Conservation Strategy**

The obligate brood reduction breeding strategy shown by tawaki would have major implications in formulating a recovery plan for the species, should this ever become necessary.

Traditionally, increasing the reproductive output of a species, in conjunction with other techniques such as habitat protection, is often employed to help arrest the decline of a threatened or endangered population. Because tawaki parents will only raise one offspring in a breeding season, this seriously limits the magnitude of any increase in reproductive output we could achieve. In fact, the only obvious way to raise the overall reproductive output from a colony of tawaki would be to ensure that all breeding pairs incubated and hatched at least one viable egg in a season (details in chapter four). This implies that any conservation or management strategy we may adopt should concentrate on improving other aspects of the population dynamics, or habitat, to improve the chances of the animals' survival.

#### **5.4 Afterword**

Tawaki are a little recognised, unique, part of our native fauna. They are one of only three species of penguin that nest on the main islands of New Zealand. Despite the birds being quite conspicuous in appearance they are little known and little studied, probably as a result of their breeding colonies largely being remote from human habitation and activities.

Biologically tawaki are of interest because of their unusual breeding biology, most of the features of which they hold in common with the other crested penguin species. Contained within the tawaki breeding pattern are clues that may one day help us to better understand the evolution of the avian breeding strategies that we currently observe.



From a conservation point of view I believe that tawaki have been neglected. I believe that tawaki, and the other species of mainland nesting seabirds, should receive more attention than they currently attract. After all, they are an integral component of the marine ecosystem on which much of our country's economic and environmental well being revolves and are part of the great diversity of seabird species that is a unique feature of this nation's biota.

Lastly, I believe that the coastal forest and islands of South Westland and Fiordland would be a poorer and more lonely place with out them.

## ACKNOWLEDGEMENTS

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