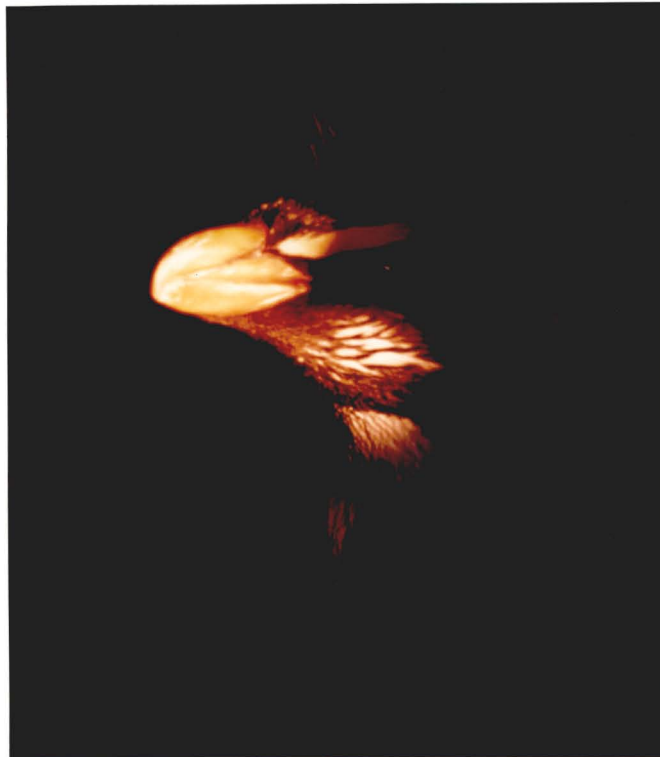# MECHANISMS OF BROOD REDUCTION
IN
FIORDLAND CRESTED PENGUINS (*EUDYPTES PACHYRHYNCHUS*)

A thesis

submitted in fulfilment of the requirements for the Degree

of

Master of Science

by

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The behaviour of animals is, as a rule, not only meaningless to man, but frequently to themselves as well.

(paraphrased from the fictitious Dr. Zaner, 1901)

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ABSTRACT

Mechanisms of brood reduction were studied in Fiordland crested penguins (*Eudyptes pachyrhynchus*) on Open Bay Islands from July through October 1989. I quantified behavioural and environmental causes of egg and chick loss at the time of laying, during incubation, and after hatching to evaluate hypotheses advanced to explain the unique patterns of hatching asynchrony and egg dimorphism in eudyptid penguins.

Although first eggs experienced lower survival than second eggs and most losses occurred during the laying interval, aggression between adult penguins did not appear to contribute to egg loss at any time. Similarly, egg mortality was not influenced by the effects of nest crowding or cover, or by the degree of intra-clutch egg dimorphism.

Egg temperatures were measured throughout the incubation period with thermocouples implanted in preserved eggs. Recorded temperatures increased markedly after the laying of the second natural egg, but did not differ between eggs of different sizes within a nest. First eggs were not consistently incubated in the anterior nest position and that position did not confer a thermal disadvantage. However, first eggs hatched later than second eggs. Retarded brood patch development may contribute to lower egg temperatures during the laying interval.

Chicks from larger, second-laid eggs were larger at hatching, and grew more rapidly than their siblings. Overt aggression between feeding chicks was not observed and begging and feeding rates appeared to be similar. Nonetheless, large chicks experienced higher survival to the creche stage. Intra-clutch egg dimorphism was negatively correlated with the number of days two chicks survived in the same nest, but there was no relationship between survival and hatching asynchrony.

CHAPTER 1:

GENERAL INTRODUCTION

The effects of hatching asynchrony and egg-size dimorphism have been widely studied for many of the avian species in which they are known to occur. Both are most often regarded as mechanisms by which birds can adjust their reproductive effort to match prevailing environmental conditions (Slagsvold et al. 1984), particularly for those species that breed in variable or unpredictable habitats. Hatching asynchrony, the more extensively studied of the two phenomena, was first suggested to be an adaptation for bringing the size of the brood into closer adjustment with the available food supply (Lack 1947; 1954), a hypothesis that forms the basis of the theory of brood reduction (Ricklefs 1965). A fundamental assumption of this theory is that the mortality that results from competitive asymmetries between siblings, commonly termed brood reduction as well, is dependent on both size of the brood (Mock and Parker 1986) and availability of food (Skagen 1988).

From studies in which observed patterns did not fit those predicted by brood reduction theory, several competing and complementary hypotheses have emerged. The most prevalent of these, the nest-failure hypothesis (Hussel 1972; Clark and Wilson 1981; Bancroft 1985) suggests that hatching asynchrony allows some offspring to fledge before others, reducing the length of time that the entire brood is at risk to predation. A gradient of increasing egg-size within clutches, common in the passerine birds to which the model has been applied, is proposed to offset the costs of hatching asynchrony so that all chicks may be reared (Howe 1976). Mortality of last-hatched chicks is therefore a consequence of the benefits gained by hatching asynchrony and not an adaptation *per se*. Richter (1982, but see Clark and Wilson 1985; Hussel 1985a, 1985b) debated the validity of the nest-failure hypothesis, arguing that the loss of younger chicks represents a greater cost than is gained by increased survival for the rest of the brood. Nonetheless, Richter conceded that the hypothesis provides a better explanation for certain biological situations than does traditional brood reduction theory. Others (Bengtsson and Rydén 1983; Magrath 1988) reiterated the suggestion that the two

hypotheses provide complementary explanations for the existence of asynchronous hatching and are not mutually exclusive as had been assumed previously.

In species that exhibit overt aggression among siblings, asynchronous hatching may create natural asymmetries within broods that act to reduce wasteful sibling competition (Hahn 1981). This idea is an extension of the sibling rivalry reduction hypothesis (Hamilton 1964) and differs from Lack's brood reduction explanation in that it could be expected to operate regardless of food supply. Manipulation of hatch asynchrony in cattle egrets (*Bubulcus ibis*) lessened parental efficiency and provided some evidence for the value of eliminating wasteful sibling competition (Mock and Ploger 1987). However, the theory has not been widely tested.

Another explanation of hatching asynchrony is that it functions to reduce the peak load demands of a growing brood (Hussel 1972; Fujioka 1985a). However, this theory does not explain why the pattern should so often result in higher mortality for last-hatched young. Furthermore, the peak load requirements, for even a reduced brood, generally occur long after brood reduction has taken place (Shaw 1985; Anderson 1989).

Finally, asynchronous hatching may be merely a consequence of physiological circumstances. For example, it may result from the necessity of some species to cover the eggs prior to completion of the clutch to protect them from extreme temperatures (Wynne-Edwards 1952; O'Connor 1984; Shaw 1985) or predation (Amundsen and Stokland 1988), although there is little empirical evidence to support these suggestions. Alternatively, Mead and Morton (1985) proposed that birds are constrained to begin incubation before the clutch is complete because the same hormones responsible for the cessation of ovulation also cause incubation behaviour to commence. Because the last egg is still in the oviduct at the start of incubation, eggs are incubated and hatched asynchronously. This hypothesis has not been tested experimentally and does not explain the existence of asynchronous hatching in species that commence incubation before the laying of the penultimate egg, or those in which the male bird is the first to incubate.

The effects of egg-size dimorphism are generally considered to be less important than those of hatching asynchrony (e.g. Stokland and Amundsen 1988), partially because patterns of dimorphism vary considerably among bird groups. For most passerine species, last-laid eggs tend to be somewhat larger than the

clutch mean whereas the opposite pattern exists for many of the non-passerine birds that exhibit consistent intra-clutch egg-size variation. Slagsvold *et al.* (1984) categorized the former group as having adopted a "brood-survival strategy" where the larger size of the final egg compensates for the disadvantage of hatching asynchrony and increases the likelihood that the youngest chick will fledge. The "brood-reduction strategy" adopted by the latter group allows for efficient mortality of the last-hatched chick if conditions are such that the entire brood cannot be raised. Slagsvold *et al.* identified one anomalous group, the crested penguins, which appeared not to fit either pattern.

IMPETUS FOR STUDY

Members of the genus *Eudyptes* differ from other non-passerine birds with regular intra-clutch egg dimorphism in that the second of two eggs laid is also the larger. Other penguin species lay a clutch of either one egg (*Aptenodytes*), or two eggs in which the second is the same size or smaller than the first. Furthermore, despite a laying interval of three to six days, the second egg of eudyptid penguins often hatches first (Gwynn 1953; Williams 1981a; Lamey *in press*), adding hatching asynchrony to the egg-size disadvantage inherent to first eggs. Presumably as a consequence of the size disparities at hatching, first eggs seldom produce fledged chicks and crested penguins do not appear to raise two chicks from a single clutch (Gwynn 1953; Warham 1975). Extreme egg-size dimorphism is a final unusual characteristic of this penguin genus. Second eggs are 20-70% larger than first eggs (Warham 1975; Lamey *in press*); the greatest egg-size dimorphism reported for any bird group (Williams 1981c).

Wynne-Edwards (1962) considered the exceptional pattern of egg dimorphism in crested penguins to have an equivalent purpose to hatching asynchrony in other bird groups. Lack (1968) suggested that the first egg may have insurance value in some species, but is apparently functionless in others. Recently, Johnson *et al.* (1987) reiterated the uncertainty over the function of egg dimorphism in crested penguins and reviewed some of the hypotheses that have been proposed to explain its origin. These authors pointed out that little work has addressed the problem specifically, despite considerable past interest in it, and considered that more quantitative data were needed before competing hypotheses could be evaluated adequately.

Warham (1963; 1971; 1972a; 1972b; 1974a; 1974b; 1975) compiled considerable descriptive information on aspects of the breeding biology and behaviour of five of the six species of crested penguins, building on the previous work of Gywnn (1953), Downes (1955) and Downes *et al.* (1959) all of which was concerned primarily with the sixth species, the macaroni penguin (*Eudyptes chrysolophus*). Published studies directed specifically at patterns of egg dimorphism and hatching asynchrony have focused exclusively on two species - the macaroni and rockhopper (*E. chrysocome*) penguins. The other four species include the royal (*E. schlegeli*), Snares (*E. robustus*), Fiordland (*E. pachyrhynchus*), and erect-crested (*E. sclateri*) penguins, all of which are endemic to New Zealand waters. Of these, only the Fiordland crested penguin breeds on the New Zealand mainland whereas the other three species are breeding residents on the Snares (*robustus*), Macquarie (*schlegeli*), Campbell, Antipodes and Bounty Islands (*sclateri*).

OBJECTIVES OF STUDY

The present study investigated aspects of breeding biology and behaviour of Fiordland crested penguins to evaluate the mechanisms responsible for mortality of eggs and chicks. Although it can be argued that such combined losses are appropriately termed 'offspring reduction' (Williams 1981c), I have followed the convention of terming both types of offspring mortality brood reduction (Lamey *in press*). Specific objectives of the study were, 1) to examine behavioural and environmental factors that could contribute to brood reduction at the time of laying, during incubation, and after hatching and, 2) to determine the effect of these factors on the survival of eggs and chicks. To this end, three aspects of breeding biology and behaviour were assessed and each is the subject of one of the chapters that follow.

1. Incubation behaviour and egg loss

I used periods of continuous behavioural observations to investigate the hypothesis that first-laid eggs are more vulnerable to displacement or predation. Egg loss was quantified and related to the degree of crowding and cover among nests.

2. Egg temperature and brood patch formation

Data on laying intervals, intra-clutch egg dimorphism, temperature and position, brood patch development and hatching intervals were collected and used to evaluate various hypotheses as to why first eggs appear to take longer to develop. I compared my results with those obtained for other species and assessed their relevance to broader patterns of avian brood reduction.

3. Chick growth and competition

Variation in hatchling size and growth was compared among chicks from first and second eggs raised together and raised singly. In addition, I monitored interactions between siblings and the behaviour of parents during feeding, and estimated the effect of these behaviours on chick growth and survival. The reproductive success of breeding adults was compared.

THE STUDY ANIMAL

Fiordland crested penguins are probably the most asocial of the *Eudyptes* genus, nesting in caves and under vegetation along the rugged coast of Fiordland, South Island, New Zealand, and on Stewart and Solander Islands. The breeding habitat, biology, and behaviour have been extensively described by Warham (1974a) who, with Grau (1982, egg formation) and van Heezik (1989, diet), provide the only published studies on this species. Fiordland penguins differ from their congeners in two important ways; they exhibit the least egg dimorphism among the crested penguins, and they often hatch both eggs. These characteristics, combined with the relatively accessible breeding areas, make them ideal subjects for studying the effects of egg dimorphism and hatching asynchrony.

THE STUDY SITE

I conducted field work on Taumaka, the larger of the Open Bay Islands (43° 50'S and 168° 53'E) between 13 July and 19 October 1989. Vegetation on the island is described by Burrows (1972) and consists mostly of kiekie (*Freycinetia banksii*), an epiphytic vine that grows, in the absence of supporting vegetation, in

dense tangles two to three metres high. The north-west side of the island is bordered by gently sloping reefs of limestone on which southern fur seals (*Arctocephalus forsteri*) breed. The south-east side of the island faces the New Zealand mainland and terminates in steep cliffs. Fiordland crested penguins nest primarily under the kiekie or among caves and ledges at the interface of the reefs and vegetation. A few individuals were also seen in caves along the cliff edges. Penguins reached the breeding areas by well-established routes through the seal colonies and, although fur seals are a natural predator of penguins in the water, they appeared to provide no obstacle on land. Little blue penguins (*Eudyptula minor*) nested in caves and crevices behind Fiordland penguin nests, but I did not observe any hostile interactions between the two species.

CHAPTER 2:

INCUBATION BEHAVIOUR AND EGG LOSS

INTRODUCTION

Warham (1975) proposed two hypotheses to explain egg dimorphism in crested penguins and most of the recent work concerning *Eudyptes* has concentrated on these, or variations of these, explanations. The first hypothesis states that egg dimorphism serves to compensate for high frequencies of egg loss prior to hatching. Crested penguins guard, but do not incubate the first egg until the second is laid (Warham 1975; A. Williams 1980a) and it is during the laying interval, when territories are established and aggression rates are high, that first eggs may be most vulnerable to displacement or predation. Warham (1975) suggested that high losses of first eggs are actually a consequence of selection favouring aggressive males. The second explanation of egg dimorphism, that it provides a mechanism to ensure that only one chick is reared when both eggs hatch, is a variation of the brood reduction theory put forth by Lack (1954) and applied to crested penguins by Wynne-Edwards (1962).

The quantitative data available support the existence of some form of brood reduction in eudyptid penguins. Macaroni penguins invariably lose one of the two eggs laid before hatching (Williams 1980a; Mougin 1984; T. Williams 1989). Although twins are common within broods of rockhopper, Snares and Fiordland penguins (Lamey *in press*), it does not appear that any of the eudyptids raise two chicks. Observations on Fiordland penguins (Warham 1974), rockhoppers (Williams 1980a) and Snares penguins (Lamey *in press*) indicate that starvation shortly after hatching is the common fate of the smaller chick. However, an underlying assumption of the brood reduction theory is that offspring number is adjusted to environmental conditions (Lack 1854). Because crested penguins never appear to raise two chicks, brood reduction seems an insufficient explanation of egg dimorphism in this genus.

Johnson *et al.* (1987) reiterated the suggestion that inter-male aggression favours egg dimorphism and proposed that selection for aggression results from competition for centrally located or sheltered nest sites. They reasoned that the first egg is smaller because it represents a smaller investment that is almost invariably lost. Recent work by Williams (1989) on Macaroni penguins does not support this hypothesis. Peak aggression rates did not coincide with maximum loss of first eggs, and neither displacement nor predation of eggs appeared to result from fights. However, macaroni penguins represent an extreme in crested penguins; they exhibit the most marked egg dimorphism of any species (Williams 1981c) and they nest in open, crowded colonies (Williams 1980a) where aggression rates are high (Williams 1989). Johnson and Bednarz (1989) contended that these may not be the conditions under which egg dimorphism evolved and, until similar data are available for other eudyptids, their aggression hypothesis cannot be fairly discarded.

In this chapter, I present information on incubation behaviour, egg loss, and attributes of crowding and cover in a colony of Fiordland penguins. This species provides an ideal contrast to Williams' (1989) study because it represents an opposite extreme within the genus. In Fiordland crested penguins, egg dimorphism is least pronounced, the species is the least social nester, habitually nesting in loose aggregations under dense cover (Warham 1975), and aggression rates are relatively low.

METHODS

I observed incubation behaviour and measured attributes of nest crowding and cover of Fiordland crested penguins on Taumaka, the larger of the Open Bay Islands. Adult birds were captured, measured (weight, flipper length, and bill length, width and depth), marked (Wella hair dye applied with a blunt paintbrush), and banded (standard aluminium flipper bands) between 14-26 July 1989. Birds were sexed by bill measurements (Warham 1975) and sexing was confirmed by observations of nesting behaviour. Late arrivals to the breeding colony, that had not been banded previously, were marked without handling by using a paint brush inserted in the end of a 1.5 m pole. Except to take brood patch measurements (Chapter 3), adult penguins were not handled after egg

laying began. My movement among the birds was always slow and methodical and most birds allowed close approach without leaving their nests.

Egg loss

I continued to visit 46 nests daily throughout the incubation period to determine the timing and causes of egg loss. I ceased visiting several nests that may have been affected by my presence including ten nests for which my disturbance may have caused egg losses through predation by weka (*Gallirallus australis*), five nests occupied by 'flighty' penguins, intolerant of daily checks, and approximately 25 nests located in areas that were particularly vulnerable to weka predation.

I removed eggs from nests on the days they were laid, measured them to the nearest 0.1 mm with vernier calipers, weighed them to the nearest 2 g with Pesola spring balances, and marked them with coloured indelible ink for subsequent identification. During daily checks, incubating birds were lifted gently with a stick to determine the presence and position of the eggs. Lost eggs were categorized as:

a) displaced, when they were found intact near the nest,

b) "wekked," when their shells were found empty with a
longitudinal opening characteristic of weka predation or,

c) missing, when the egg remains were not found.

Addled, rotten or abandoned eggs were not considered lost because these fates did not pertain to the hypotheses tested. I compared egg size within nests with the ratio of length x (breadth)^2 for second and first eggs, respectively (Warham 1975).

Incubation behaviour

To determine the effects of incubation behaviour on egg survival, I monitored the behaviour of incubating birds at 17 nests, observing between one and seven nests simultaneously. Observation periods were distributed approximately equally between morning and afternoon sampling and were usually of 30 minute or two hours duration, depending on the number of nests observed. During each period, I remained stationary at one of several vantage points and did not approach the nesting areas. I did not attempt to quantify aggression or

other behaviours before eggs were laid, or after the second week of incubation. There was no indication that my presence influenced the behaviour of the birds.

Focal animal, all occurrance sampling (Altmann 1974) was used to record the position and duration of incubation behaviours. When both members of a pair were present, I recorded only the posture of that bird incubating or protecting the egg. However, aggressive behaviour was recorded for any penguin in the vicinity of the nest areas. Sex of incubating birds was also recorded when possible, but in some cases bird orientation made this impossible to identify. Comfort behaviours (e.g. preening, stretching, etc.) of less than two minutes duration were not recorded as they were unlikely to affect the incubation regime of the egg. Postures were categorized as:

> a) standing off the nest,
> b) standing on the nest with the egg partially exposed,
> c) hunched on the nest with the egg completely covered, and
> d) lying prone on the nest covering the egg.

Incubation intensity (Derksen 1977) was evaluated by comparing the amount of time spent in the latter two positions, which allow effective incubation, with time spent in standing positions, during which eggs were afforded less protection. Time spent in each position was measured in nest-hours, each equivalent to one hour per nest observed. Observation was divided equally between nests containing only the first egg and those containing both eggs. One nest, at which a second natural egg was never laid, was considered to contain two eggs after the mean laying interval of 4 days (Chapter 3). Days of the incubation period were numbered sequentially with the laying of the first egg designated as day 0.

Crowding and cover

Measurements of crowding and cover were taken at 43 nests that occurred in similar surroundings (caves and ledges) and compared with egg survival. I assessed crowding with an index, C, that provides a linear measure of visual and spacial contact and was calculated as:

$$C = \ln[(D1 + D2 + D3)/(v + 1)]$$

where D1, D2, and D3 are the distance in dm to the nearest three nests at which eggs were laid, and v is the number of neighbouring nests within visual contact. For nests with nearest neighbours at distances greater than 10 m, C was calculated using a maximum distance value (D1 + D2 + D3) of 30 m. Thus, indexed values ranged from a minimum of <1 to a maximum of 30 and could be plotted linearly.

Cover was measured categorically with nests described by type; open for those that occurred on ledges or in large caves, and closed for those in small rock cavities. Nests were further designated by position as being peripheral or central within a sub-colony. All nests were divided into two survival categories; those that lost one or both eggs to displacement or predation, and those that lost no eggs.

Statistical tests

Unless otherwise indicated, statistical tests were performed on contigency tables with G-tests of independence or, when expected frequencies were based on hypotheses extrinsic to the sampled data, by G-tests of goodness of fit (Sokal and Rohlf 1981). Interaction effects between parameters of cover were tested by G-tests of goodness of fit after fitting log-linear models (Everitt and Dunn 1983; Wilkinson 1988). Statistical tests in this and the following chapters were performed with SYSTAT. Significance was set at $p \leq 0.05$.

RESULTS

The incubation intensity of both sexes increased through the laying interval, but did not change appreciably after the second egg was laid (Fig. 2.1). Total time spent standing either on or off the nest was much higher, and time spent incubating in a hunched or prone position much lower, before the second egg was laid (Table 2.1; $G = 28.07$, df $= 3, p < 0.001$). Females spent a greater proportion of time in standing positions than did males (Fig. 2.2; $G = 8.92$, df $= 3$, $p = 0.03$) indicating that they were generally less tenacious.

In 85 nest-hours of observation after egg-laying commenced, I saw a single aggressive interaction between nesting birds. This consisted of a sneeze, a common behaviour when the birds were approached by me or by penguins that were not their mates, and did not escalate into a fight. However, high levels of fighting did occur while nest sites were being established early in the season and continued at reduced levels among non-breeding birds throughout incubation and chick rearing periods. Fights among non-breeders seldom involved breeding pairs and it is unlikely that squabbles markedly heightened the risk of displacement or predation of eggs at any time.
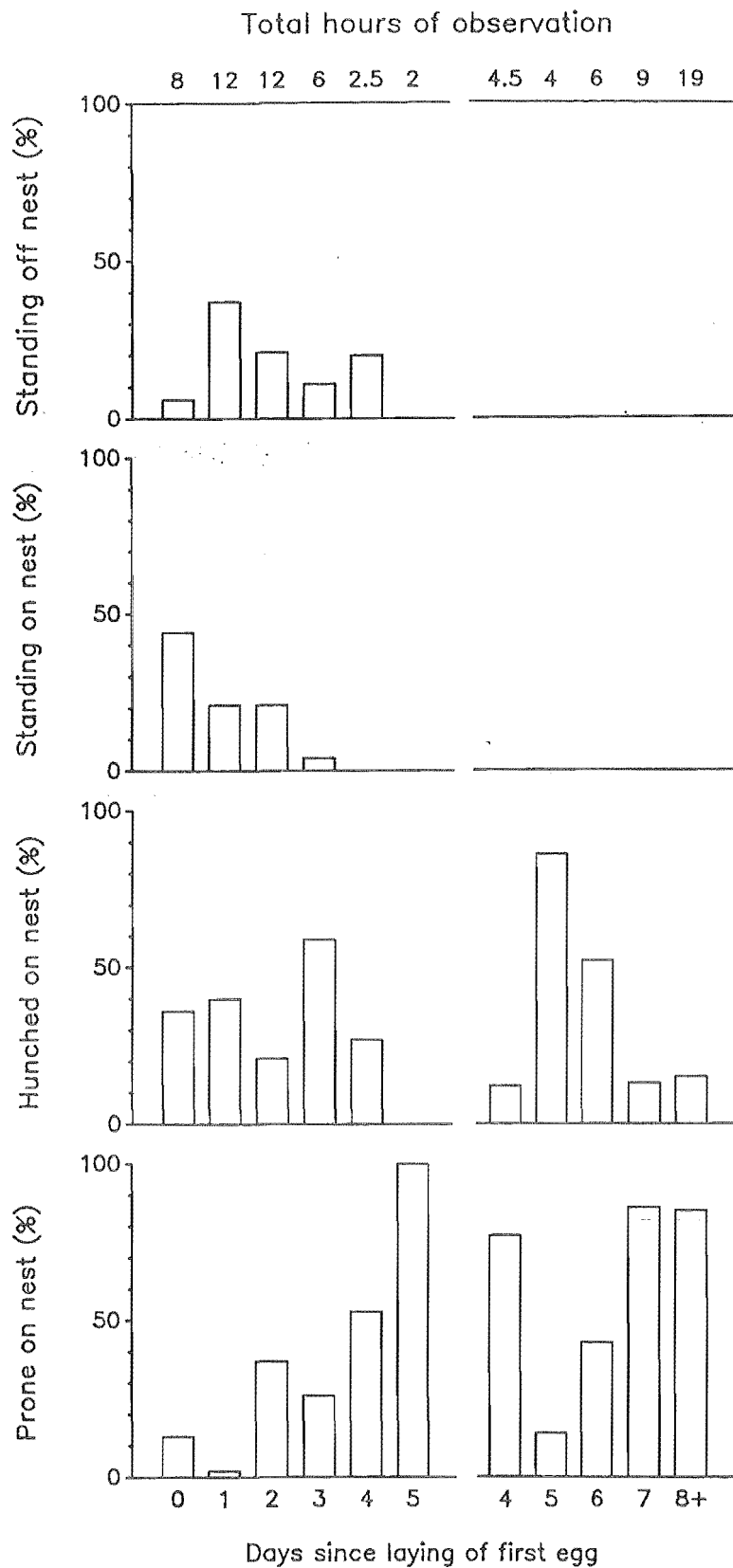
Total hours of observation

Figure 2.1. The percentage of time spent by Fiordland crested penguins in each of four incubation positions on successive days after egg laying. Observations were taken from 17 nests containing only the first egg (left) or both eggs (right).

Table 2.1. Hours spent by penguins in each incubation position on nests containing only the first egg and on nests containing both eggs.

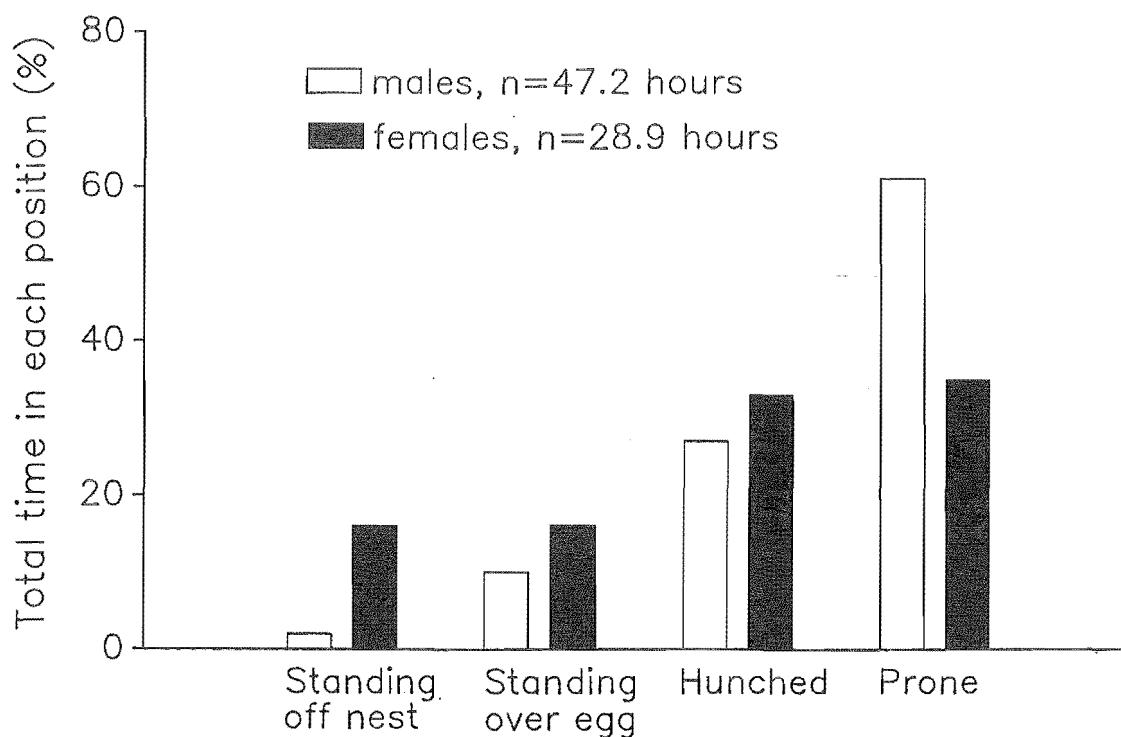| Incubating position	first eggs	both eggs
Standing off nest	8.6	0
Standing on nest	8.8	1
Hunched on nest	14.5	11.1
Prone on nest	10.6	30.4
Total	42.5	42.5

Figure 2.2. The percentage of time spent in each incubation position for male and female penguins from 17 nests during the first 16 days of the incubation period.

A total of 23 eggs was lost from 51 nests monitored, and almost all of these were the first laid (Table 2.2; $G = 10.63$, df $= 1, p < 0.01$). Missing eggs accounted for the greatest loss ($G = 5.024$, df $= 2, p = 0.05$). Most likely, these eggs were taken by weka, although they may have been displaced initially. For the 15 first eggs and one second egg for which dates of loss could be determined, most loss occurred in the first week of the incubation period (Table 2.3; $G = 11.69$, df $= 4, p < 0.005$). The single second egg was lost in the second week. I witnessed the loss of one egg when a two day old first egg was pierced by a weka while both parents stood dozing beside the nest. At the sound of the shell breaking, both birds awoke and drove off the weka but the damaged egg was not recovered from where it had rolled during the struggle.

Table 2.2. Fate and number of first and second eggs lost.

Cause	first eggs	second eggs
"Wekked"	6	0
Displaced	4	0
Missing	9	4
Total	19	4

Table 2.3. Timing of first egg loss in 46 nests of Fiordland crested penguins checked daily until hatching.

Week after laying		Number of eggs
1	(before second egg laid)	5
	(on the day second egg laid)	3
	(after second egg laid)	1
2		1
3		1
4		1
5		3
	Total	15

Egg survival was not influenced by crowding (independent t-test, t = 0.006, df = 41, $p > 0.9$) or nest type (n = 43, G = 0.425, df = 1, $p = 0.51$). However, survival of eggs was higher for peripheral than central nests (n = 43, G = 3.96, df = 1, $p < 0.05$). Sequential elimination of interaction parameters from log-linear models (Table 2.4) indicated that there were no higher-order interactions between egg survival and the two attributes of cover.

Lastly, intra-clutch egg dimorphism was slightly greater for nests of low survival (mean = 1.24, sd = 0.144, range = 1.09-1.63, n = 12) than for those with high survival (mean = 1.18, sd = 0.089, range = 0.88-1.35, n = 24), but these differences were not significant (independent t-test, t = 1.55, $p = 0.13$).

Table 2.4. Significance of interaction effects in log-linear models of cover and survival. A=survival, B=nest position, and C=nest type. Each G statistic is a measure of the variance in the complete model explained by the dropped term.

Model	Parameters included	(dropped)	df	G
1	AB, AC, BC, A, B, C	(ABC)	1	0.79 (ns)
2	AB, AC, A, B, C	(BC)	2	0.82 (ns)
3	AB, A, B, C	(AC)	3	1.24 (ns)
4	A, B, C	(AB)	4	5.20 (ns)

DISCUSSION

Patterns of incubation intensity in Fiordland crested penguins appear to be similar to those recorded for macaroni penguins (Williams 1989) and confirm the qualitative reports by earlier authors that eudyptid penguins do not commence incubation until the second egg is laid (Gywnn 1953; Downes 1955; Warham 1975; Williams 1980a; Mougin 1984). Females tended to incubate with less intensity than males and, in Fiordland penguins, this may reflect the general tendency for males to take the first incubation shift. However, a similar sex bias

was also apparent in the incubation positions of macaroni penguins (Williams 1989), a species in which the first incubation stint is normally undertaken by the female. In general, females tend to be more timid than males, and differences in tenacity between the two sexes may only mean that females take longer to settle into regular incubation patterns.

Neither sex incubated first eggs consistently during the laying interval and, on at least one occasion, lack of attention to the egg resulted in predation. High egg losses early in the incubation period is further evidence that first eggs are at greater risk to diplacement or predation during the laying interval. However, there was no indication that losses were enhanced by aggressive behaviour among nesting birds of either sex. Aggression among breeding birds peaked before egg laying commenced and, although it continued at reduced levels among non-breeders throughout the breeding season, it did not appear to contribute to egg loss. These results are in agreement with those of Williams (1989) and contradict the hypothesis that inter-male aggression and resultant egg loss is a major selective pressure favouring egg dimorphism (Warham 1975; Johnson et al. 1987; Johnson and Bednarz 1989).

Despite the lack of empirical evidence, there remains some intuitive support that aggression rates are somehow linked to egg dimorphism and survival. Egg loss is considerably more severe in macaroni than Fiordland penguins and corresponds to greater egg dimorphism, more crowded colonies and higher rates of aggression. If these differences occur between species, the same gradient may also occur within them. The results of this study do not support such a suggestion. Egg survival was not significantly affected by egg dimorphism or the degree of nest crowding, although it was somewhat higher for peripheral than for central nests. Aggression was not observed at any nest and therefore its potential effects on egg survival cannot be evaluated. Although it appears that variation in aggressive behaviour does not correspond to variation in egg loss, a closer examination of gradients between and within species is needed.

An alternative explanation of high egg loss early in the incubation period is that successful laying of second eggs is causally related to the loss of first eggs (Williams 1989). Thus, first eggs may function as insurance in rare instances when a second egg is not laid or is laid and immediately lost. However, this hypothesis implies that unneeded first eggs are deliberately ejected from the nest when second eggs are laid; a notion that lacks substantiation (Warham 1975; Johnson and Bednarz 1989) despite repeated suggestions of its occurrence (Richdale 1941;

Gwynn 1953; Downes 1955; Downes et al. 1959; Wynne-Edwards 1962; Lack 1968; Mougin 1984).

If egg loss occurs over a greater portion of the incubation period, as is typical of rockhopper, Snares and Fiordland penguins, the hypothesis that first eggs are valuable as insurance seems more plausible. Lack (1968) suggested that first eggs of rockhopper penguins retained until hatching could effectively function as a reserve when second eggs failed to hatch, but could envisage no function for first eggs in the remaining *Eudyptes* species. However, he clearly believed that first eggs did not normally hatch in any of the six eudyptid species except rockhopper penguins. Although it is unclear how long two chicks may survive, both eggs are known to hatch in some broods of Fiordland (Warham 1974a; this study), Snares (Warham 1974b; Lamey *in press*), and royal penguins (Warham 1971) in addition to rockhoppers (Gwynn 1953). Macaroni penguins do not produce two chicks (Gwynn 1953; Downes 1955; Williams 1980a; Mougin 1984; Williams 1989), but similar data are not available for erect-crested penguins. Thus, it appears that the insurance value of first eggs differs among species of *Eudyptes*. First eggs are potentially valuable for at least four species, but without knowing the hatching patterns of the common eudyptid ancestor, it is impossible to determine what is the primitive condition.

Johnson et al. (1987) suggested that the presence of first eggs could serve to signal to other pairs that the nest site is occupied. During my study, many courting pairs were apparently displaced from nest sites by other individuals, but always before eggs were laid. At the same time, breeding females incubating alone on the nest were often courted by nonbreeding males, or pecked and harassed by pairs attempting to establish a nest at the same site. Similar interactions were never observed when the typically more aggressive males were incubating. Warham (1963) reported the same behaviour among rockhopper penguins. He also noted that males were intolerant of any approach by other birds, whereas females were submissive and occasionally receptive to the advances of nonbreeding males. Therefore, it seems likely that birds display greater site tenacity after eggs are laid. Increased territoriality may be associated with a greater investment in the nest site, but it is likely that it is the behaviour of resident birds, rather than the presence of an egg that successfully repels intruders.

In conclusion, the results of this study indicate that incubation tenacity in Fiordland crested penguins increases after second eggs are laid, and that egg loss

consists disproportionately of first eggs early in the incubation period. There was no evidence, however, that egg loss was increased by aggressive behaviour of nesting birds. Suggestions that first eggs function as insurance against immediate loss of second eggs, or to signal occupation of the nest site were not supported.

CHAPTER 3:

EGG TEMPERATURE AND BROOD PATCH FORMATION

INTRODUCTION

Although the selective forces responsible for the origin of egg dimorphism in *Eudyptes* penguins continue to be debated, most authors agree that the proximate effect of differential egg size is a halving of the number of offspring produced. This understanding has generated observation of, and experimentation with, specific mechanisms by which first eggs and chicks are disadvantaged. Differences in survival are directed by the effects of hatching asynchrony and egg dimorphism, but may also be influenced by such factors as the behaviour of incubating parents, surface area to volume ratios of eggs, and inherent differences in metabolism between first and second eggs.

In rockhopper and Snares crested penguins, second eggs hatch slightly before first eggs despite having been laid several days later (Gwynn 1953; Williams 1981a; Brown 1988; Lamey *in press*), indicating that they develop more quickly. Lack (1968) proposed that this occurs because the second egg is incubated immediately after laying whereas the first egg cools down for several days. The observations of Burger and Williams (1979) indicated that first eggs of rockhopper penguins were maintained at lower and more varied temperatures throughout the incubation period and the authors ascribed these differences to the incubating behaviour of the adults. First eggs were found significantly more often in the anterior nest position where the semi-prone posture often adopted by incubating parents afforded the egg less consistent heating and caused it to take longer to develop. Embryonic development in Adélie penguins (*Pygoscelis adeliae*) was retarded by sub-normal incubation temperatures (Weinrich and Baker 1978) and lower temperatues were reported for an artificial egg when it was in the anterior nest position (Derksen 1977).

Burger and Williams (1979) conceded that, because surface area to volume ratios are greater for first eggs, they would be expected to heat and cool more quickly and so could explain the greater variance associated with temperatures taken from them. However, they argued, it could not explain the lower mean temperatures. In addition to the effects caused by differential positioning of eggs within a nest, Williams (1981c) suggested that differences in the time required for first and second eggs to develop could be due to differences in egg content that affect the rate of embryonic development. Second eggs of rockhopper and macaroni penguins contain proportionately more albumen than first eggs (Williams *et al.* 1982) and so do those of Fiordland crested penguins (Grau 1982).

In order to evaluate the suggestions of Williams (1981c) further, Brown (1988) measured temperatures and embryonic metabolism of first and second eggs of macaroni and rockhopper penguins. Second eggs were incubated at slightly, but not significantly, higher temperatures than first eggs and had higher mean embryonic oxygen consumption rates on equivalent days of incubation. Differences in temperatures of the two egg types were insufficient to account for differences in the length of the incubation period, and Brown concluded that second eggs had inherently higher embryonic metabolism that allowed them to hatch sooner.

In both studies concerning egg temperatures of crested penguins (Burger and Williams 1979; Brown 1988) lower incubation temperatures were reported in the first week of the incubation period. In addition to the parental behaviour effects discussed in Chapter 2, a further limiting constraint may be that of brood patch development. In most passerines, defeathering occurs several days before egg laying and effective incubation can commence immediately the eggs are laid (Jones 1971). However, among several non-passerines, patch formation is delayed for several days and results in less effective initial incubation. Little attention has been directed at the timing and stimulation of brood patch formation in crested penguins and its potential implications for the development of first and second eggs.

In this chapter, I present data on egg dimorphism and hatching dates for first and second eggs in a population of Fiordland crested penguins. In addition, patterns of egg position and temperature, and brood patch develpment are shown. Results are compared with those obtained for other species of crested penguins and the relative importance of each attribute is assessed.

METHODS

Egg laying and hatching

Nests were visited daily throughout the laying and incubation period (1-30 August, 1989) to determine the laying and hatching dates of first and second eggs. When possible, I measured and marked eggs on the day they were laid (see Chapter 2). Many nests were discovered after they contained an egg or eggs but, because reversals in the usual egg-size order are possible, I only used data from those nests for which the laying order was known. Laying and hatching intervals and indices of egg dimorphism (Chapter 2) were calculated.

Brood patch formation

Brood patch measurements were taken at intervals corresponding to the first, second and third weeks of the incubation period as measured from the laying of the first egg. I collected 17 observations from 12 individuals; eight from females and nine from males. Brood patch area was estimated as half the product of length and width at the widest point of defeathered skin. Temperature was taken by folding the vascularized skin around an electronic probe thermometer accurate to 0.01 °C in a manner similar to that described by Yom-Tov et al. (1986). Body temperature was measured with a clinical thermometer accurate to 1 °C, inserted 4 cm into the cloaca and held in place for 1 minute before a reading was made. All measurements were taken as quickly as possible but handling appeared to cause increasing stress to incubating birds as the season progressed. For this reason, no data were collected after the third week of the incubation period.

Exertion has considerable effects on penguin body temperature (Farner 1958) and restrained penguins were invariably excited when measurements were taken. They also constricted their stomach muscles which made measurement difficult. Because the errors introduced by these factors seemed to be relatively constant, the data have comparative value, although they almost certainly indicate body and brood patch temperatures that are more variable than normal and estimates of brood patch size are almost certainly underestimated.

Egg position and temperature

Egg position was determined during daily visits whenever it was possible to do so without disturbing the incubating bird. Eggs are generally incubated one in front of the other and were recorded as being either posterior or anterior in the nest, relative to the orientation of the incubating parent. Because it appeared that different birds exhibited different preferences for egg position, these observations were not grouped between nests. Instead, the frequency with which first eggs appeared in the anterior position in each nest was counted from ten observations. The number of nests in each of the resulting categories was then compared to a binomial distribution. To obtain equal sample sizes, nests from which less than ten observations were made were excluded from the analyses and, when more than ten were taken, ten were selected using a random number generator.

Egg temperatures were measured with 36-gauge copper-constantan thermocouple wire, accurate to ± 0.1°C, and attached to a micrologger (21X Campbell Scientific Inc., Logan, Utah, U.S.A.) with 13-gauge extension wire. Transmitters and thermistors have been used extensively to measure incubation temperatures of penguin eggs (Eklund and Charlton 1959; Frost et al. 1976; Derksen 1977; Burger and Williams 1979; Bucher et al. 1986; Haftorn 1986; Yom-Tov et al. 1986; Brown 1988) and, because it would not have been necessary to attach external wires to the eggs, I initially intended to use transmitters to measure egg temperatures in this study. However, electrical difficulties with the transmitters and calibration problems with the plaster eggs in which they were implanted meant that this technique had to be abandoned. Instead, thermocouple eggs were constructed in the field from materials brought in case an alternative method was needed. Although thermocouples do not appear to have been used to measure penguin egg temperatures since the studies of Farner (1958) and Spellerberg (1969), the method has been employed recently to measure egg temperatures of other birds (eg. Barret 1980; Williams and Ricklefs 1984; Bergstrom 1989; Weathers and Sullivan 1989).

I inserted thermocouples into the center of six domestic duck eggs that approximated penguin eggs in size, and injected 1 cc of formalin per egg. A single hole of approximately 1 mm diameter was drilled in the small end of each egg to accommodate the wire and the hole was then sealed with putty (Prestik, Bostick Products NZ Ltd.). To reduce force on the wires that might cause a shift in thermocouple position, I split the wires where they emerged from the egg, taped them with small pieces of electrical tape along either side of the egg and rejoined

them at the opposite pole. A 30 cm long leader enabled the egg to be moved easily within the nest and was connected to 3-4 m of extension wire which was pegged in place at roughly 60 cm intervals. Soon after the trials began, I collected four abandoned penguin eggs and substituted them for the duck eggs. Calibration trials indicated that the penguin and duck eggs gained and lost heat at similar rates so all temperature records were used in subsequent statistical tests. To reduce the likelihood that systematic biases, inherent to individual eggs, were consistently recorded for eggs of a given type, one medium sized penguin egg was used alternately as the first (small) and second (large) natural egg in the majority of the trials.

Nest temperatures were measured with 24-gauge thermocouple wire placed beneath the eggs in the nest. Thermocouples were not anchored in place as this would have neccesitated removing the incubating bird; consequently, wires were sometimes displaced to the top of the eggs or to the periphery of the nest. Nest temperature measurements may, therefore be more variable than natural conditions in the bottom of the nest. Shaded ambient air temperature was measured with thermocouple wire 2 cm above the ground near the cave mouth.

Temperature trials were conducted by rotation of experimental nests in a single cave inhabited by seven pairs of penguins. Natural eggs were replaced with thermocouple eggs in each nest for periods of approximately 24 hours at intervals of five or more days. During these trials, natural eggs were incubated in a styrofoam box with a hot water bottle or, more usually, by a neighbouring bird. Generally, only one nest contained thermocouple eggs at a given time and these were selected to correspond, as closely as possible, to the dimensions of the natural eggs from that nest. Thermocouple eggs were always substitued in the number and position in which they were found, i.e., only one egg was substitued during the laying interval and two eggs were placed in the same anterior-posterior positions that the natural eggs occupied. Second eggs were laid in six nests; the seventh never contained a second egg and was used to monitor the incubation regime in a single-egg nest.

There was no indication that the thermocouple wires restricted movement of the birds or eggs within a nest, and all but one of the 13 eggs from nests involved in the temperature measurement study hatched, indicating that the manipulations had no effect on egg viability. The failed egg had been pierced by a weka and gradually rotted in the nest.

Complete temperature records consisted of shaded ambient, nest and egg temperatures recorded by the data logger every ten minutes for the duration (21-24 hours) of each trial. The first hour was eliminated from the resulting record to allow birds to resettle. Means were calculated from the shortened records and used in subsequent statistical analyses.

The position of thermocouple eggs within nests was recorded twice during each trial that involved two eggs; once in the morning after the trial had started and again before the eggs were removed in the afternoon. Egg position observations were discounted if there was evidence that the penguins changed position or orientation as I approached. The timing of these visits was noted and later compared with the appropriate temperature record.

In addition to the natural nests monitored, two temperature trials were conducted with a single egg at a nest occupied by a non-breeding pair that had courted and established a nest site, but had not laid eggs of their own. I gave them the abandoned egg of another pair as an experiment in cross-fostering. The female penguin developed a full brood patch and incubated the egg continuously for 25 consecutive days. During this time, the mate she had courted previously never returned to the nest site and the egg was finally abandoned. The pair were known to have bred successfully in 1988 and both returned later in the 1989 breeding season and continued to court at a different nest site. Egg abandonment was observed at the nests of several naturally incubating birds whose mates did not return near the end of the incubation period.

Statistical tests

Paired comparison tests of egg size and weight, indices of egg dimorphism and hatching dates were performed using dependent t-tests (Wilkinson 1988). Means, standard deviation, sample size and range are given in the text, or as separate tables. Brood patch measurements were grouped by period - weeks one, two and three - and tested by one-way ANOVAs. For all ANOVAs and independent t-tests, homogeneity of variance was tested with Bartlett's test or, when sample sizes were less than 10, by Box's small sample F-approximation (Sokal and Rohlf 1981; Wilkinson 1988). Heteroscedasticity in brood patch area data was corrected with a square-root transformation before the ANOVA was performed. Subsequent comparisons among means in some ANOVAs were completed with the Tukey-Kramer procedure to allow for unequal sample sizes.

Egg temperature measurements were grouped according to the following schedule determined by the age of the first egg when the trial began:

period 1	= 5-8 days
period 2	= 10-14 days
period 3	= 18-21 days
period 4	= 26-28 days
period 5	= 31-33 days

Three-way ANOVAs were performed on means of data from those trials that involved two eggs using egg status (first or second), nest number (one to six) and period (one to five) as main effects. The design was unbalanced due to some empty cells; hence interaction terms could not be modelled (Wilkinson 1988). Variance within trials was therefore tested separately and reported graphically.

Other statistical tests are described in the results section.

RESULTS

Sixty-three nests were visited daily. Egg laying commenced on 1 August 1989, peaked approximately 12 days later, and was completed on 24 August. The mean interval between the laying of first and second eggs within nests was 4.28 ± 0.71 days (range = 3-6, n = 46). First-laid eggs were smaller (length x breadth) and lighter than second eggs (Table 3.1; dependent t-test, t > 11.0, df = 53, p < 0.00 for each attribute measured). There was a single case where the first egg was larger (by 14%) and heavier (by 11%) than the second. Mean egg dimorphism within nests was 1.19 ± 0.11 (range = 0.88-1.63, n = 54). This values, calculated from linear measures using the formula length x $breadth^2$ (Warham 1975), did not differ from that calculated from weight (mean = 1.18 ± 0.09, range = 0.90-1.38, n = 54; dependent t-test, t = 0.730, p = 0.47).

Hatching occurred between 6 and 30 September. Egg laying to hatching intervals were 37.1 ± 1.57 days (range = 35-41, n = 21) and 32.1 ± 1.12 days (range = 30-35, n = 30) for first and second eggs, respectively. In nests where both eggs hatched, first eggs hatched 0.63 ± 0.90 days later than second eggs (range = 0-3, n = 19; dependent t-test, t = 3.08, p = 0.007).

Table 3.1. Linear dimensions and weights of first and second eggs from 54 Fiordland crested penguin nests on Open Bay Island.

Measurement	mean	SD	range
First eggs:			
length (mm)	67.3	2.81	62.2-73.0
breadth (mm)	51.1	2.08	42.8-54.4
weight (g)	98.9	9.06	75-118
Second eggs:			
length (mm)	70.9	2.53	65.9-78.0
breadth (mm)	54.2	1.63	49.9-58.4
weight (g)	116.6	9.92	93-140

Development of the brood patch appeared to start after the laying of the first egg and continued for several days. Brood patch area increased during the three periods measured (Table 3.2; one-way ANOVA, F = 18.67, df = 2,14, p < 0.01) with significant differences occurring between the first and second, and first and third periods (Tukey-Kramer method, p < 0.01 for each). Similarly, brood patch temperature increased through the incubation period (one-way ANOVA, F = 7.97, df = 2,13, p = 0.005), significantly so between the first and second, and first and third periods measured (Tukey-Kramer method, p = 0.008 and p = 0.012 respectively). However, variation in body temperature was not significant (single-way ANOVA, F = 7.974, df = 2,13, p = 0.09).

Table 3.2. Measurements of brood patch area, brood patch temperature and body temperature taken from 12 Fiordland crested penguins during the first three weeks of the incubation period. Brood patch (bp) area is calculated as 1/2 length x width at the widest point.

Measurement	mean	SD	range	n
Week 1:				
bp area (cm^2)	0.57	0.58	0.0-1.4	5
bp temp.(°C)	34.9	0.42	34.4-35.4	4
body temp.(°C)	36.9	1.12	35.7-38.4	5
Week 2:				
bp area (cm^2)	12.2	7.92	2.8-23.6	9
bp temp.(°C)	37.3	1.38	35.5-38.6	9
body temp.(°C)	38.5	1.32	35.7-40.0	8
Week 3:				
bp area (cm^2)	21.2	7.69	16.0-30.0	3
bp temp.(°C)	37.8	0.44	37.5-38.3	3
body temp.(°C)	38.7	1.16	38.0-40.0	3

The distribution of frequencies with which first eggs were found in the anterior position in 32 nests did not differ from that predicted by a binomial distribution (Fig. 3.1; G test of goodness of fit, G = 13.87, df = 9, $p > 0.10$). Although first eggs occurred anteriorly with much greater frequency in some nests (causing a slight trend to the right), second eggs were more often anterior in others. Parodoxically, the same data tested using the traditional chi-squared method in which all observations were lumped and compared to an expected ratio of 1:1 (Burger and Williams 1979), yielded highly significant results ($x^2 = 11.00$, df = 1, $p < 0.001$).

Twenty-three individual temperature trials were carried out on nests containing two eggs. Mean egg temperature did not differ between small and large eggs (32.74 ± 2.59, range = 21.6-35.7 and 32.76 ± 2.42, range = 24.0-36.0, respectively), but differed significantly between intervals in the incubation period, and between nests (Table 3.3). The elimination of a single outlying trial, conducted one day after the second egg was laid in the nest concerned, negated
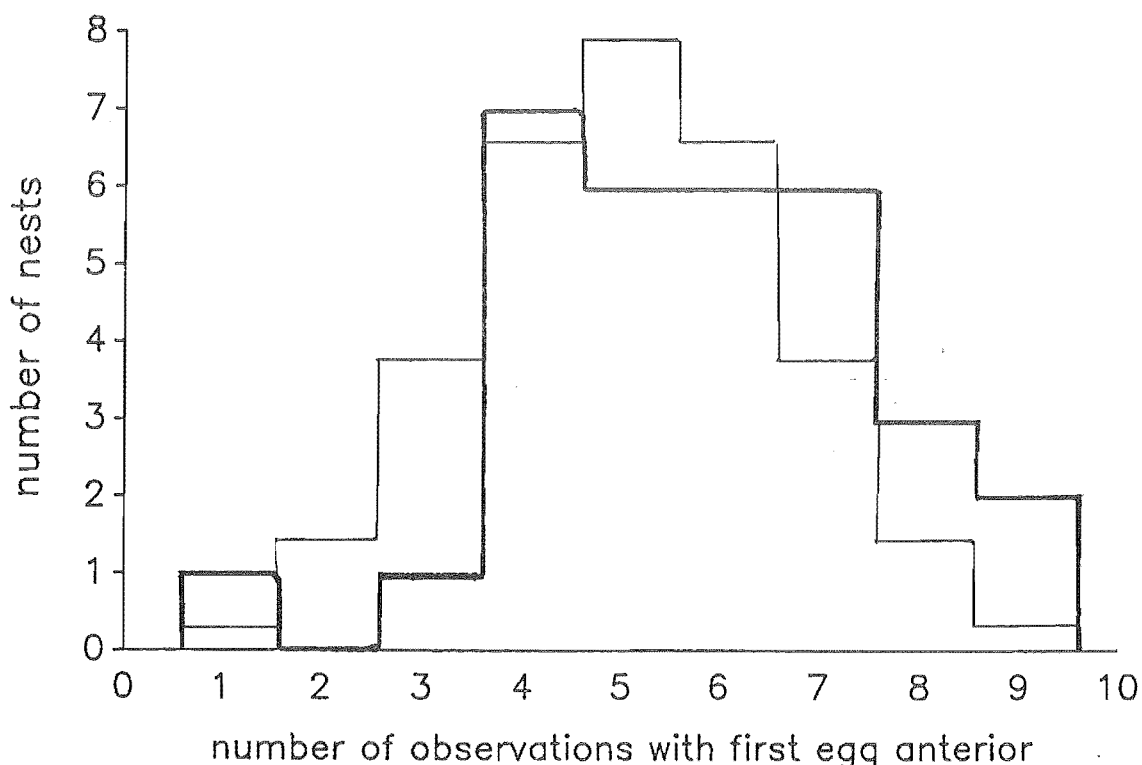
Figure 3.1. The frequency distribution of 32 nests for which egg position was recorded (heavy line) plotted against a binomial distribution (thin line). For each nest, the number of times the first egg was found in the anterior position was determined from 10 observations.

Table 3.3. Three-way analyses of variance of egg temperatures from 23 trials on nests containing two eggs. (a) including the outlier depicted in Figure 2; (b) without the outlier. Interaction effects could not be modeled because of the high proportion of empty cells

(a) ANOVA I

Source	sum of squares	df	mean square	F-ratio	p
Egg	0.026	1	0.026	0.008	0.931
Period	84.795	4	21.199	6.193	0.001
Nest	63.045	5	12.609	3.684	0.009
Error	119.795	3	53.423		

(b) ANOVA II

Source	sum of squares	df	mean square	F-ratio	p
Egg	0.038	1	0.038	0.035	0.854
Period	27.024	4	6.756	6.086	0.001
Nest	4.931	5	0.986	0.888	0.500
Error	36.63	33	1.110		

any significance in differences between nests, but not between periods, and did not affect the lack of significance of differences between the two egg types. Fluctuations in the temperature of both eggs were observed in each of the trials conducted, but there appeared to be no regular pattern to these oscillations (Fig. 3.2). No consistent differences in temperatures between eggs within a nest were recorded. Coefficients of variation indicated that temperature fluctuations were slightly, but not significantly, higher for first eggs (dependent t-test, $t = 1.997$, df $= 22, p = 0.58$).

Mean incubation temperatures increased steadily (Fig. 3.3a) and exhibited less short-term variability (Fig. 3.3b) as the laying interval progressed. In most nests, marked increases in mean temperatures and smaller temperature fluctuations were observed after the second egg was laid. Figure 3.4 depicts results of representative trials, taken from the same nest using the same artificial egg, in the weeks before and after the second natural egg was laid. The nest that
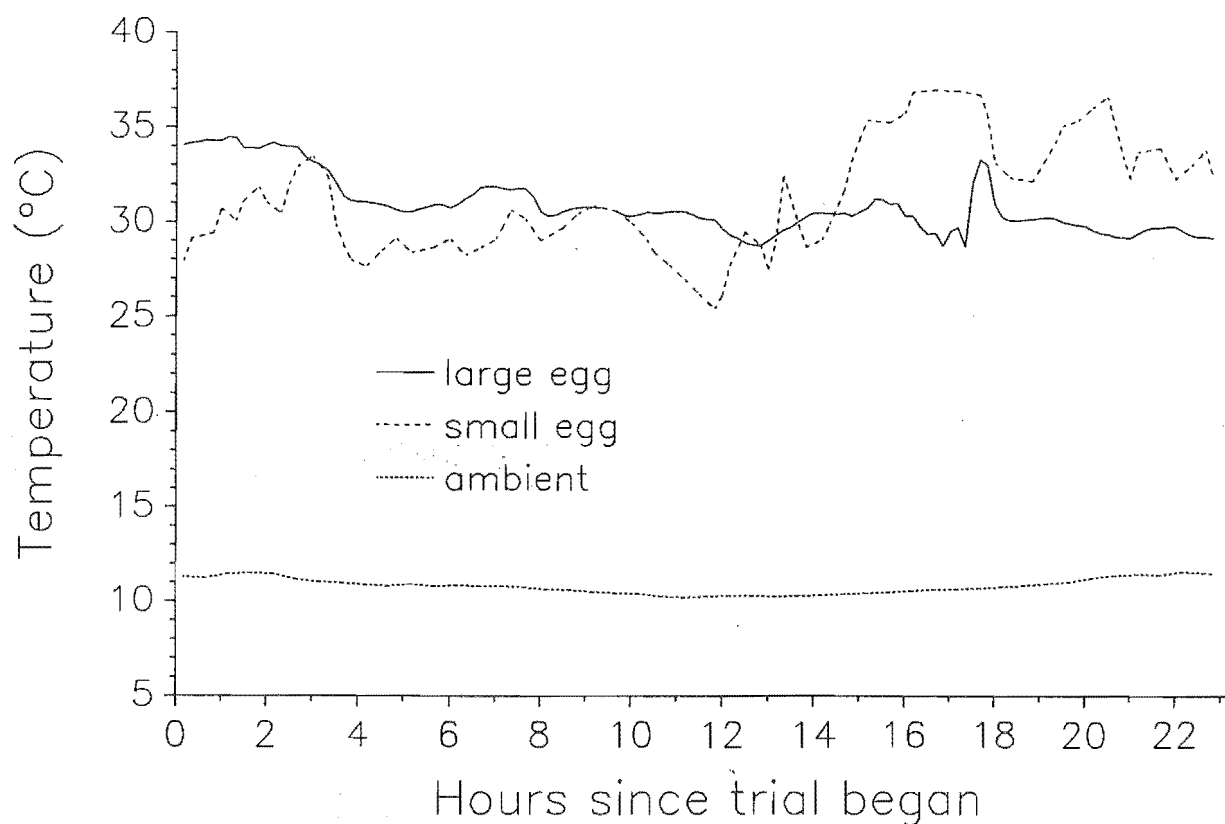
Figure 3.2. Temperature record from a representative trial indicating the fluctuations characteristic of small and large eggs. Means and standard deviations calculated for this trial, made on 28 August 1989 when the natural eggs of the nest were 13 and 9 days old, were 31.3 ± 3.01 °C (small egg), 30.8 ± 1.51 °C (large egg), and 10.8 ± 0.40 °C (ambient air).

contained only a single egg exhibited slightly higher mean temperatures (34.75 ± 1.71, range = 32.2-35.0, n = 4), although this was not tested statistically.

Results from the two trials conducted at the nest occupied by non-breeding penguins indicated that the presence of an egg can induce brood patch formation and incubation behaviour (Plate 3.1). Although the mean egg temperatures recorded in these trials were similar to those in natural nests at the same stage within the incubation period, they were more variable (Fig. 3.5).

Observations of egg position during trials, combined with temperature measurements, indicated that the posterior position did not confer a thermal advantage. The temperature of anterior eggs (mean = 33.52 ± 2.37, range = 26.1-36.9, n = 31) was actually slightly higher than that of posterior eggs (mean = 32.85 ± 2.04, range = 27.9-36.6, n = 31), although differences were not significant
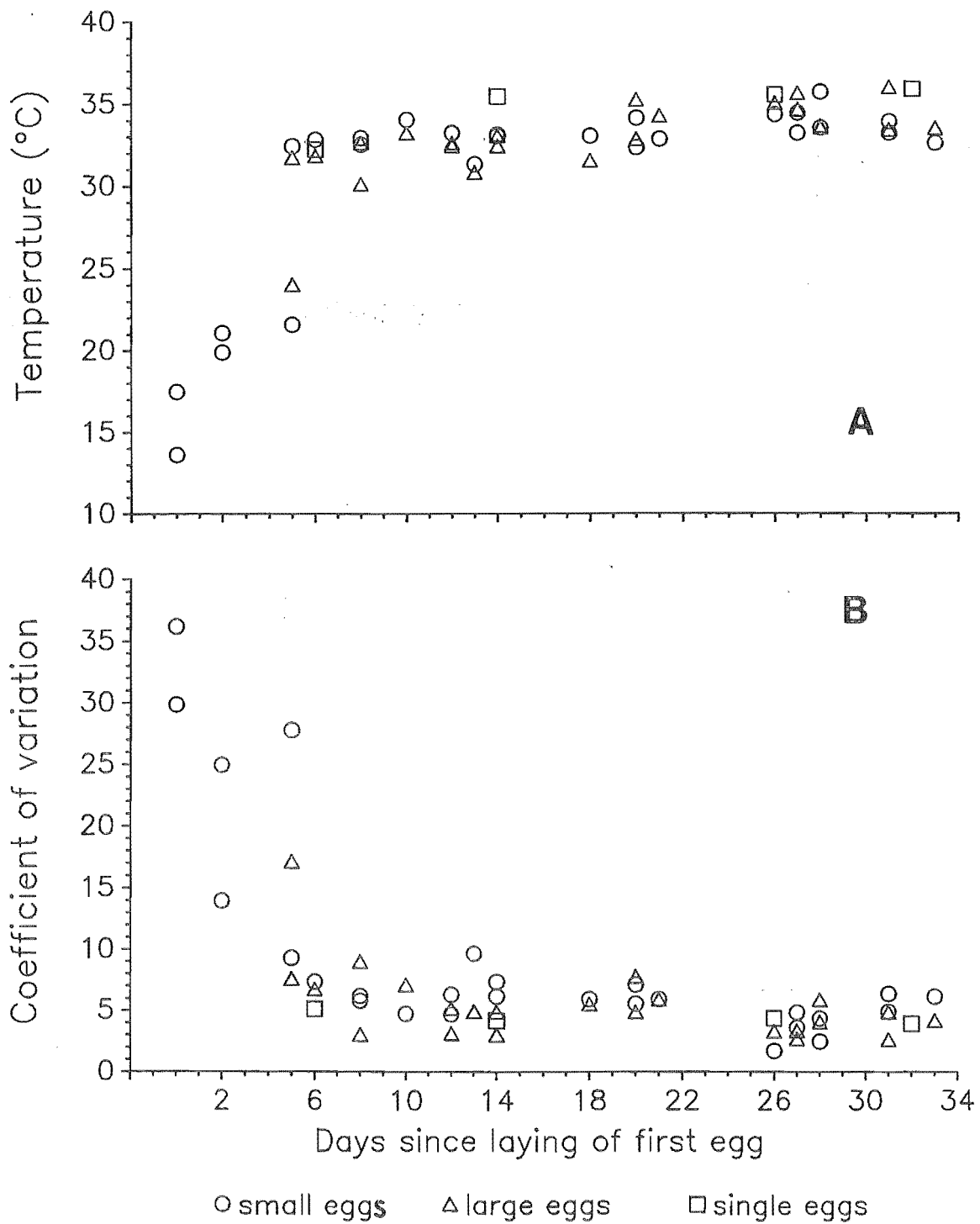
Figure 3.3. Mean temperatures (A) and coefficients of variation (B) obtained in 31 temperature trials conducted on small and large eggs in two-egg nests, and on a single egg in the nest that contained only one natural egg.
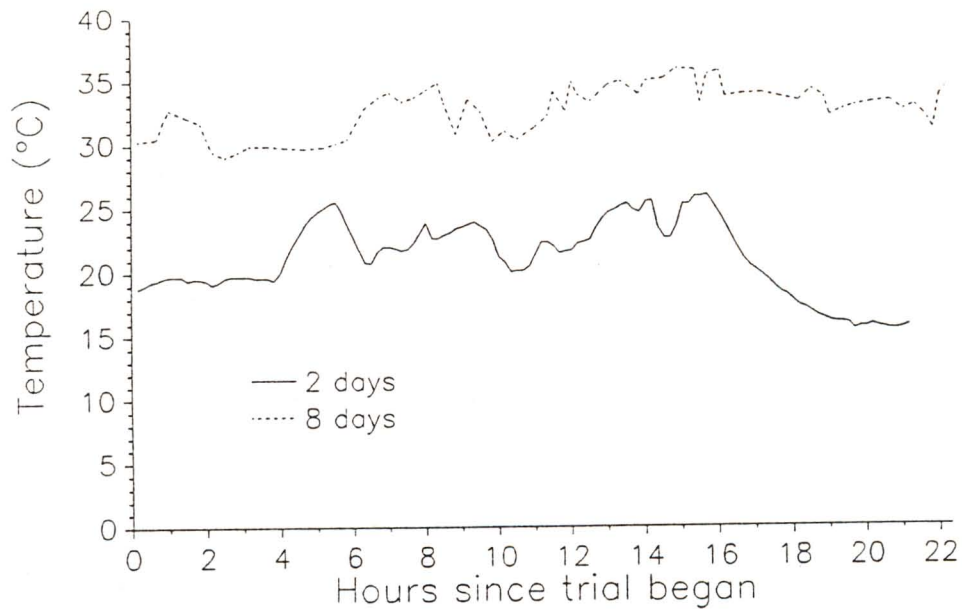
Figure 3.4. Temperatures recorded in representative trials conducted with the same thermocouple egg in the same nest before and after the second natural egg was laid. Means and standard deviation were 21.1 ± 2.93 °C (before) and 32.5 ± 1.88 °C (after). Records were made 2 and 8 days after the first natural egg was laid.

Plate 3.1. Brood patch development of a non-breeding, female penguin, 21 days after receiving an abandoned egg.
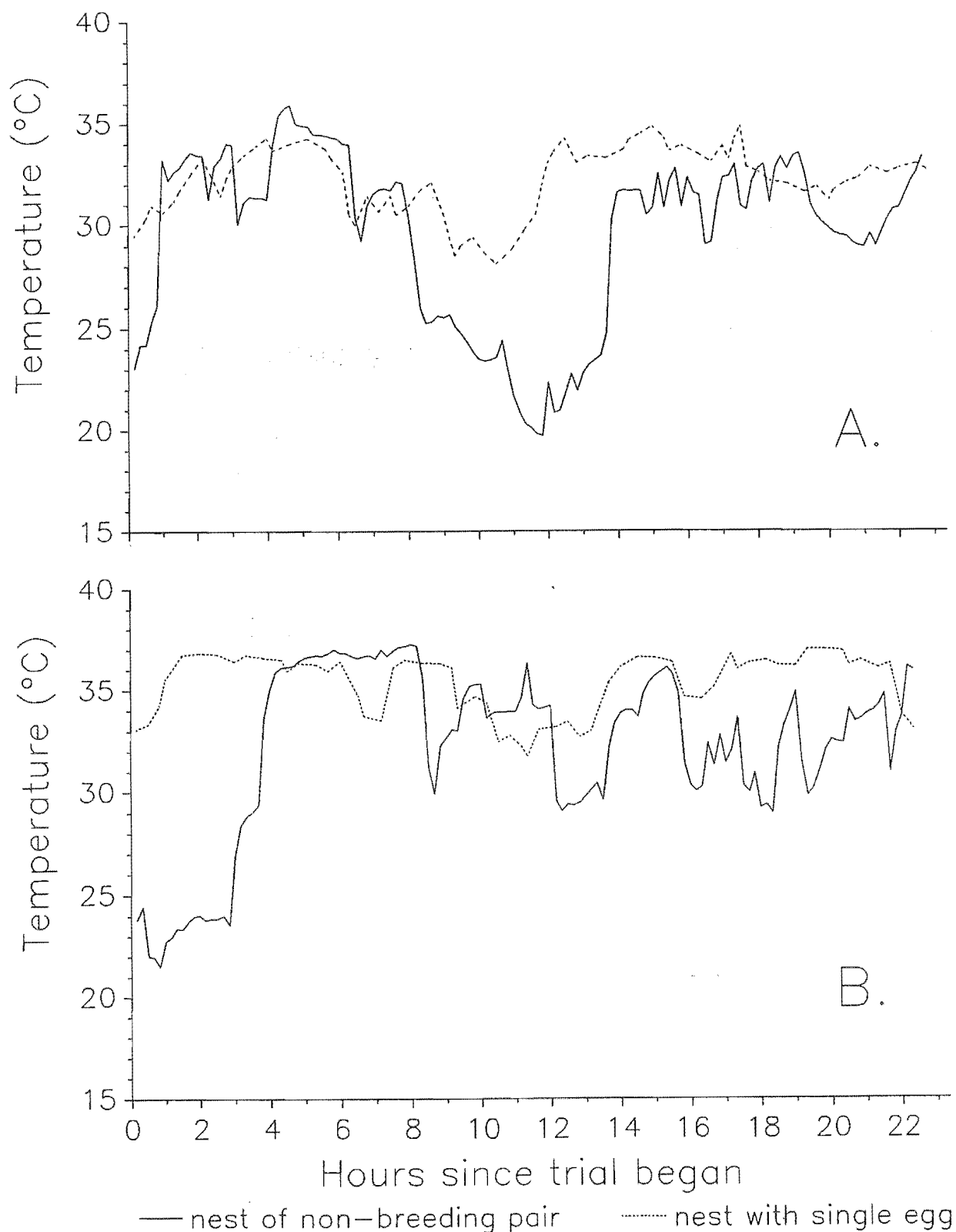
Figure 3.5. Comparisons between incubation temperatures recorded from a non-breeding individual and from a pair that laid a single egg. The same thermocouple egg was used in all four trials conducted on days 9 and 16 after the non-breeding individual received an abandoned egg, and on days 6 and 14 after the laying of the natural egg in the other nest. Mean temperatures and standard deviations are (A.) 29.5 ± 4.22 °C, 32.1 ± 4.16 °C, and (B.) 32.2 ± 3.0 °C, 35.4 ± 1.47 °C for the non-breeding and breeding birds, respectively.
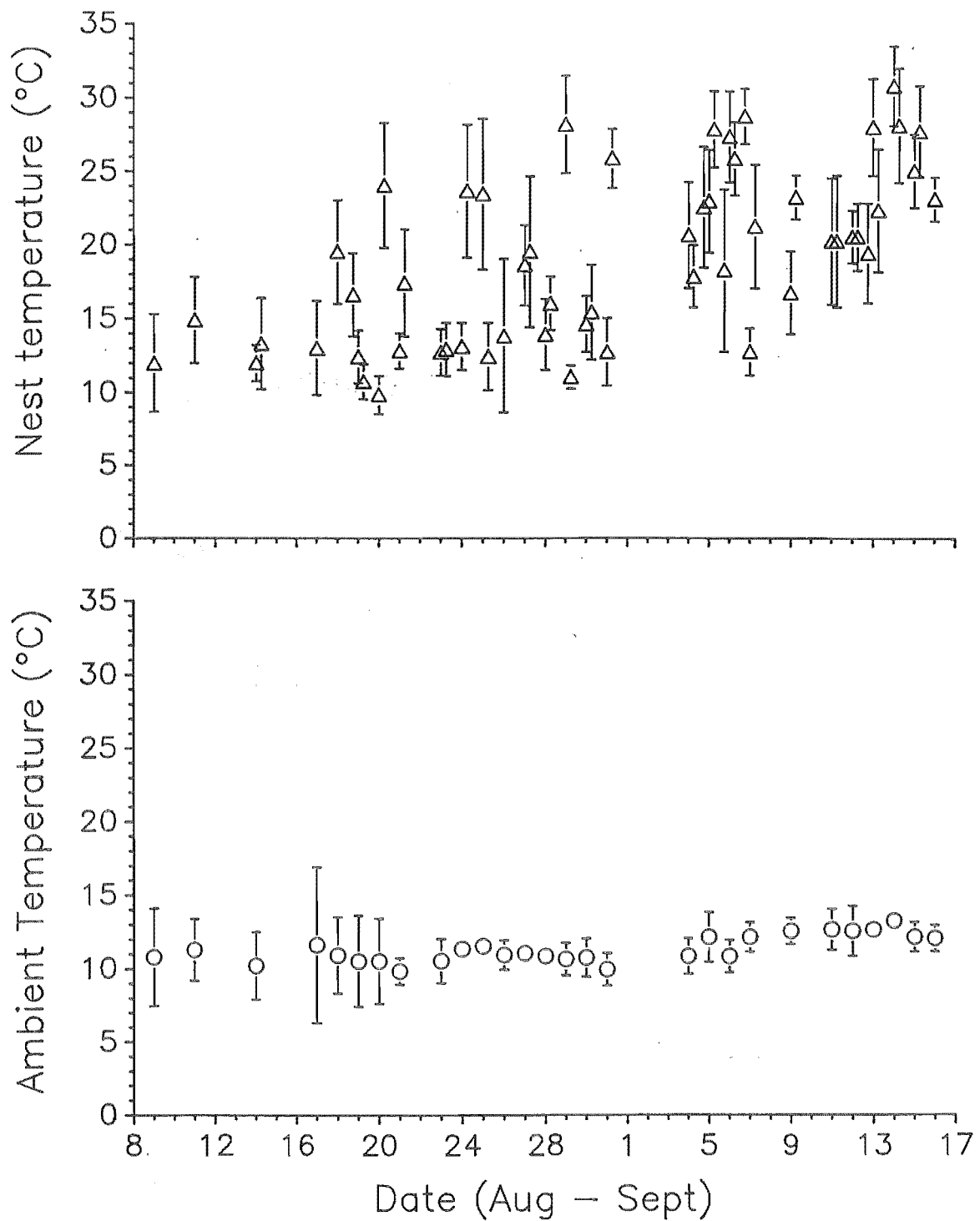
Figure 3.6. Nest and ambient air temperatures (mean ± SD) on the days trials were conducted. Nest temperatures taken on the same day are offset by 0.25 days on the x-axis. The high variability is mostly due to slight changes in thermocouple placement.

(dependent t-test, t = 1.85, p = 0.075). In 18 of these 31 observations, the small egg was in the anterior position.

Mean ambient temperature increased very slightly during the five weeks over which temperature trials were conducted and the observed increase in mean nest temperature appeared to correspond with this (Fig. 3.6). Because thermocouples were sometimes displaced in nests, no effort was made to test these results statistically. Nonetheless, the values recorded give an indication of considerable temperature variation within the immediate environs of the nest.

DISCUSSION

Intra-nest egg dimorphism in the Open Bay Islands population of Fiordland crested penguins was similar to the value of 1.17 reported previously for mainland birds (Warham 1974) and is representative of the lowest degree of dimorphism among the crested penguins. Values for the other five species range from 1.29 for Snares crested to 1.71 for macaroni penguins (Warham 1975). The relatively low dimorphism in Fiordland penguin eggs is important in a consideration of the factors that contribute to, and result from, disparity in egg sizes because the gradient in dimorphism may also reflect a gradient in selective pressures, or the direction of evolutionary processes.

If, as Williams and Burger (1979) suggested, incubating rockhopper penguins treat the second egg preferentially, by placing it more often in the posterior nest position, then eggs must be distinguishable by some external criteria. Because size is the only obvious and consistent difference between first and second eggs, it is most likely to be the criterion used. In general, there is a tendency for larger eggs to elicit more effective incubation behaviour (Drent 1975) but among Fiordland penguins the sizes of first and second eggs overlap considerably and differences within a nest are usually slight. No regular pattern of first eggs occurring in the anterior position emerged in this study and may indicate that the dimorphism exhibited is not sufficient to elicit the behavioural responses necessary. It is possible that preferential treatment of second eggs increases with egg dimorphism and that the behaviour is most advanced in macaroni penguins where first eggs seldom even remain in the nest (Gwynn 1953; Williams 1980a; Mougin 1984; Williams 1989).

An alternative explanation for the disparity between the egg position results of this study and those of Burger and Williams (1979) is that differences in observed patterns can be attributed to differences in the interpretation of the data collected. In Burger and Williams' study, the first egg was observed in the anterior position on 139 (63.2%) of 220 occasions, but the authors do not indicate how many nests were examined nor the number of observations per nest. The value of 63.2% is somewhat higher than the 56.8% (331/582 observations, first egg anterior) obtained in my study, but the proportion of nests exhibiting the same pattern in Burger and Williams' study cannot be assessed. Furthermore, the likelihood of finding a significant difference in egg position preference with the chi-squared statistic increases with sample size. Elsewhere, Williams (1981a) reported that first eggs of macaroni penguins substituted for second eggs, in nests in which natural first eggs were already lost, exhibited a longer incubation period than natural second eggs. These results imply that differences in incubation period were due to inherent characteristics of first and second eggs and not to diffential treatment by incubating parents. Although it is possible that the preferential pattern of incubation depicted by Burger and Williams exists among crested penguins, I suspect it is less universal than they have suggested.

Regardless of the position of eggs within a nest, the results of my study indicate that first and second eggs are exposed to equivalent thermal environments. Although small eggs can be expected to heat and cool more quickly than large eggs - and this may account for the slightly higher coefficients of variation associated with mean temperatures of small eggs throughout the incubation period - they were not consistently incubated at lower temperatures. Results of the egg position data, together with the temperature records, further dispel suggestions that the anterior position subjects eggs to a thermal disadvantage. Nonetheless, there is evidence that the anterior egg can be more exposed to ambient conditions when the incubating penguin adopts an upright or semi-prone posture (Derksen 1977), and the proportion of time spent in different postures may vary among species.

Haftorn (1986) found that macaroni penguins incubate in an upright position considerably more often late in the incubation period (43% of the observed time by weeks four to five) than do Fiordland penguins (approximately 15% of the observed time by the second week; see Chapter 2). Haftorn also noted that chinstrap (*Pygoscelsis antarctica*) and Adélie penguins spend much more time prone than do macaronis and suggested that the discrepancy may be a

consequence of the number of eggs incubated. Late in the incubation period, the nests of most macaroni penguins contain only the second of two eggs laid, whereas chinstrap, Adélie and Fiordland crested penguins usually retain both eggs to hatching. One egg may be incubated adequately in an upright posture, whereas two may not. As the proportion of time spent incubating in an upright posture increases, the thermal advantage of the posterior nest position may also increase. This could be tested by monitoring the incubation behaviour and egg temperatures of species with higher indices of egg dimorphism - the macaroni, royal and erect-crested penguins.

Two additional considerations undoubtedly contributed to lower temperatures recorded from preserved than living eggs used in the present study. The first is the central position of thermocouple placement, used to ensure that subsequent orientation of the egg in the nest would not influence the temperature recorded (e.g. Lill 1979; Evans 1989). In live eggs the embryo is located on the outer surface of the yolk sphere and maintains its position closest to the brood patch by rotation in the shell or, when the extraembryonic membranes have fused, by weight asymmetries (Drent 1975). Hence, the thermal environment of the embryo is somewhat enhanced compared to that of the centre of the egg. Presumably, these differences are less important as development progresses and there is no reason to predict that the effects of thermocouple placement differ between small and large eggs. A second consideration, that of thermogenesis, may affect the temperature of the two egg types differently. After approximately 10 days of development, internal egg temperature rises above that of the surrounding air as a result of embryonic heat production (Drent 1975; Weinrich and Baker 1978). It is possible that larger embryos enhance their own thermal environment more effectively, and hence speed development, through the production of more heat. Because insertion of thermocouples and preservative killed the developing embryos in the eggs used to monitor incubation temperature, the relative effects of thermogenesis could not be assessed.

Brown (1988) found that the daily rate of embryonic oxygen consumption, a measure of embryonic metabolism, was greater for second than first eggs of macaroni and rockhopper penguins and suggested this as evidence that first eggs require a longer period of embryonic development. However, Bucher et al. (1986) advise caution in interpreting rates of metabolism of penguin embryos. In their study, metabolic rates obtained from emperor penguins (Aptenodytes forsteri) were highly variable, even over short periods of time. Bucher et al. attributed much of

this variability, and that reported by previous researchers, to differences in the activity of embyros rather than to differences in the energetic costs of maintenance and growth. Thus, it seems that the role of embryonic metabolism in the development of first and second eggs of *Eudyptes* penguins requires further study.

The nature of egg content may also contribute to differences in the subsequent survival of chicks from large and small eggs (Nisbet 1978; Williams 1981c; Brown 1988). First eggs of macaroni, rockhopper (Williams *et al.* 1982) and Fiordland penguins (Grau 1982) contain proportionately less albumen than second eggs. Similar differences in albumen proportion were reported for large compared to small eggs of many species of petrels (Warham 1983), and for large and small representatives within the normal range of first eggs of common terns (*Sterna hirundo*, Nisbet 1978). However, these differences did not exist between first, second and third-laid eggs of similar size, indicating that differences in albumen proportion are a function of egg size and not laying order. Because approximately two thirds of the protein available to a developing embryo is contained in the albumen (Romanoff and Romanoff 1949; Nisbet 1978), second eggs of eudyptid penguins may have a disproportionate developmental advantage through having more nutrient reserves available.

A final contributor to differences in development between first and second eggs, and one that appeared to have a large effect in this study, was the timing of brood patch formation. Brood patch development did not begin until the first egg was laid and incubation temperatures were low until after the laying of the second. Some of these differences are attributable to changes in behaviour (see Chapter 2); mean incubation temperature increased with increases in time spent in incubating postures. However, maximum egg temperatures, a useful indication of the stage of brood patch development (Haftorn 1981), attained during the laying interval were also lower than they were later and suggest that delayed brood patch vascularization and defeathering inhibits initial incubation. Farner (1958) found maximum incubation temperatures were not reached for up to two weeks in yellow-eyed penguins (*Megadyptes antipodes*) and considered that retarded brood patch formation contributed to the long incubation period of these birds. Nonetheless, defeathering begins several days before egg laying in most other bird species (Drent 1975) and begs an important question. Why is brood patch formation delayed if it causes a lengthening of the incubation period and, presumably, increased costs of reproduction? The question is particularly

relevant to penguins as they are already constrained to temporally limited breeding seasons (Williams 1981c; Mougin 1984) and must fast for the entire time spent ashore.

The development of a full brood patch and maintenance of incubation behaviour by a non-breeding penguin suggests that the stimulus provided by an egg elicits physiological and behavioural changes. The act of incubation in many birds seems to stimulate prolactin release (Jones 1971; Jamieson *et al*. 1987) and prolactin levels are causally linked to the initiation of brood patch formation and incubation behaviour (Etches *et al*. 1979; Lea *et al*. 1981). If brood patch development is dependent on stimuli provided by the act of incubation, it follows that it cannot commence until an egg has been laid. Such a constraint, possibly overcome in other birds by the stimuli provided by the nest cup, presence of a mate, or by hormonal activity induced by changing daylength, may be useful to penguins because of the relative costs of egg production and brood patch formation. In relation to body size, penguin eggs represent a small investment (Lack 1968) and brood patch formation, with the necessary loss of insulative dermal fat and the defeathering of external insulation, may actually be more costly. Thus, it may be energetically prudent to delay brood patch formation until the potential for breeding success has been ensured through the laying of an egg.

Although delayed brood patch formation in penguins might be expected to lengthen the incubation period, there is little evidence to suggest that it differentially affects eggs within a clutch. Except for *Aptenodytes*, all penguins lay two-egg clutches and incubation commences immediately in all but *Eudyptes*. Furthermore, first eggs tend to hatch slightly before second eggs (Lamey *in press* and references therein). Retarded development of first eggs in eudyptid penguins is more likely to be caused by low intensity of incubation behaviour during the laying interval if, as Lack (1968) suggested, they are handicapped by several days of cooling.

CHAPTER 4:

CHICK GROWTH AND COMPETITION

INTRODUCTION

In most bird species that exhibit brood reduction, offspring losses occur after eggs have hatched. The effects of egg dimorphism and hatching asynchrony then operate on chick size and development to produce competitive asymmetries within broods. However, a more proximate cause of brood reduction is the unequal allocation of food resources generated by these asymmetries.

Much of the work concerning patterns of food allocation mediated by differences in chick size has been directed at bird species in which one or more members of the brood invariably perishes - the obligate brood reductionists. In many of these species, chicks from smaller, last hatched eggs grow more slowly than their siblings (e.g. the hen harrier *Circus cyaneus*, Picozzi 1980; cattle egret *Bubulcus ibis*, Fujioka 1984; little egret *Egretta garzetta*, Inoue 1985; American white pelican *Pelecanus erythrorhynchos*, Evans and McMahon 1987). Small chicks are consistently excluded from feeds as a direct result of aggressive interference, or intimidation (Nuechterlein 1981) by a larger sibling, and death may result from the combined effects of starvation and siblicide (see Ingram 1959; O'Connor 1978; Cooper 1980; Edwards and Collopy 1983; Mock 1984a; Fujioka 1985b; Drummond 1987; and Simmons 1988 for reviews of chick aggression and siblicide).

Because both offspring produced in a clutch are seldom, if ever, raised to independence, *Eudyptes* species can be considered obligate brood reductionists. However, unlike many other bird species, sibling aggression does not appear to facilitate brood reduction (Lamey *in press*). When two eggs hatch, the fate of the smaller chick is almost always starvation, although the behaviour of its parents and sibling are likely to influence that process. Nonetheless, disparities in growth

and aggressive interactions between eudyptid siblings have received little attention to date, possibly because both chicks are found in few nests, even a few days after hatching. Some *Eudyptes* species seldom retain both eggs to hatching (see Chapters 2 and 3) and the disappearance or death of the smaller chick in those species where both eggs hatch is rapid. Thus, there is little opportunity to address the role of sibling aggression in brood reduction because there are few nests in which aggression can be observed.

Fiordland crested penguins provide an unusual opportunity to study eudyptid chick interactions because the effects of egg dimorphism and hatching asynchrony are relatively slight (Chapter 2). As a result, the time siblings coexist may be longer than in other species. In this chapter, I present data on the growth of Fiordland penguin chicks raised together and singly, and quantify rates of begging and feeding within nests. In addition, mild forms of aggression are described and their importance assessed. Chick survival from first and second eggs and the reproductive success of pairs that hatched two or one egg are compared.

METHODS

Chick growth

I measured the body weight, foot length, flipper length and culmen length, depth and width of chicks within 24 hours of hatching. Bill measurements were not used for subsequent comparisons because they were highly variable and difficult to obtain, and because there appeared to be little difference between bill size of small and large chicks (i.e., bill size was not a good indicator of body size). To facilitate individual recognition within nests, chicks from first and second eggs were designated as A and B respectively, and marked on the breast and neck with randomly assigned red or blue indelible marking pen. Initially, newly hatched chicks were also web-tagged to provide permanent identification, but this was found to cause web tearing in some individuals. Later chicks were not web-tagged until they were 10 days old. Between 21-24 November, I returned to the study site to remove tags from fledging chicks and replaced them with standard adult flipper bands.

Chick growth was monitored in two-chick nests by repeating the size measurements taken at hatching approximately every two days until one chick died or disappeared. Chicks raised singly were measured at hatching and on at least one other occasion, usually when about six days old. Initially, measurements were placed into one of four categories, A and B chicks raised together, and A and B chicks raised singly, for comparisons of growth. However, preliminary analyses indicated that the growth rates of A and B chicks raised singly did not differ and so they were lumped together for subsequent analyses. Growth parameters of weight, foot length, and flipper length were regressed separately on chick age.

Sibling interactions

Nests containing two chicks were observed from stationary watch points from late afternoon through dusk (4-6 h) to monitor interactions between siblings. Recorded observations focused on a single nest at a given time and were limited to those taken while a feeding parent was present. Interactions at other times were minimal and I considered them to have had only a peripheral bearing on the distribution of food between chicks. During feeding periods, only two activities were quantified; begging and feeding. Nests were observed continuously at these times, but tallies were made by the one-zero method (Altmann 1974; Martin and Bateson 1986) at 60 second intervals. Thus, for comparative purposes, continuous begging was recorded as having occurred once per minute. To make use of observations from the nest with reversed egg and hatchling dimorphism, begging and feeding rates were compared for chicks from small and large eggs instead of by laying order. Mild forms of aggression were also observed and these are described qualitatively.

Chick survival

Chick survival, defined as survival to the creche stage (the time when chicks are left unguarded by day while both parents forage) was compared for chicks from first and second eggs. For nests within which two chicks hatched, the length of time both chicks survived was compared with intra-nest egg dimorphism and hatching asynchrony (Chapter 3). Reproductive success (defined as the percentage of chicks per nest that entered the creche stage) of pairs that hatched

two chicks was compared with that of pairs that hatched only one. Deserted nests were not included in calcuations of reproductive success or chick survival.

Statistical tests

Hatchling size and rates of begging and feeding were compared within nests by dependent t-tests. Regression coefficients of growth for the three chick types were compared by analyses of covariance with age as the covariate. Survival was compared among nests by G-tests of goodness of fit and by t-tests of correlation coefficients.

RESULTS

Both eggs hatched in 21 of the 63 nests monitored. Only the second egg hatched in an additional 11 nests, only the first egg in one nest, and one egg hatched in a single-egg nest. In nests that hatched two chicks, those from second eggs were heavier and larger at hatching than those from first eggs (Table 4.1; dependent t-tests, df = 19, weight: t = -7.47, p < 0.001, foot: t = -3.96, p = 0.001, flipper: t = -2.874, p = 0.01). However, the nest in which the usual egg-size dimorphism was reversed (Chapter 3) also had chick size reversed.

The slopes of all regression lines of chick growth (weight, foot, flipper),

Table 4.1. Hatch weight, foot length and flipper length of chicks from first eggs (A) and second eggs (B) of 20 Fiordland crested penguin nests on Open Bay Islands.

		mean	SD	range
Weight (g)	(A)	68.55	6.78	57-84
	(B)	87.05	12.10	72-117
Foot (mm)	(A)	32.70	2.45	29-4
	(B)	35.45	2.19	33-41
Flipper (mm)	(A)	30.60	2.76	28-38
	(B)	32.60	1.82	29-35

compared separately for each chick type (A and B chicks raised together and chicks raised singly), differed significantly from 0 ($r^2 > 0.503$, $t > 7.79$, $p < 0.001$ for each). Weight gain was greater for second-egg (B) chicks and those raised singly in a nest than for first-egg (A) chicks (Fig. 4.1; ANCOVA, $F = 4.930$, $p = 0.008$). In some nests, differences were particularly pronounced. For example, many A chicks starved in the nest and weighed less when they died than when they hatched. In other nests, size differences between the chicks remained slight for several days. Foot and flipper length differed slightly, but not significantly, among the three groups and tended to be greatest for chicks raised singly (Fig. 4.2 and 4.3; $F = 3.585$, $p = 0.03$ and $F = 1.206$, $p = 0.302$, respectively). Size measurements of chicks that eventually starved appeared to increase disproportionately with weight.

Although I spent considerable time observing nests (97.6 hours), feeding was seldom seen (22.6 hours with a feeding parent present). Females began to return close to dusk and continued until well after dark when chick behaviour was impossible to observe without artificial light. Most observations involved nests with very young chicks and consequently, size asymmetries were not well developed. Two periods included the nest in which egg dimorphism was reversed.

Begging rates of small chicks, expressed as number of begs per minute (Fig. 4.4; 0.2 ± 0.13, range = 0-0.4) did not differ from those of large chicks (0.2 ± 0.16, range = 0.080-0.64; dependent t-test, $t = -0.508$, $df = 10$, $p = 0.623$). However, feeding rates appeared to be slightly lower for small chicks (0.04 ± 0.04, range = 0-0.12) than for large chicks (0.06 ± 0.043, range = 0-0.13) although these differences were also not significant (dependent t-test, $t = -0.917$, $df = 10$, $p = 0.381$).

I was rarely able to record a complete feeding sequence because observation periods seldom included an entire feeding period i.e., a female returned before the observation period began, or darkness intervened before it concluded. Often, large chicks appeared to dominate early in a feeding session but when they became satiated, the smaller sibling was able to beg and feed freely. Sometimes it appeared that meals became progressively smaller as the feeding period advanced. Thus, the begging and feeding rates observed may not accurately reflect the actual distribution of food between chicks during entire feeds.
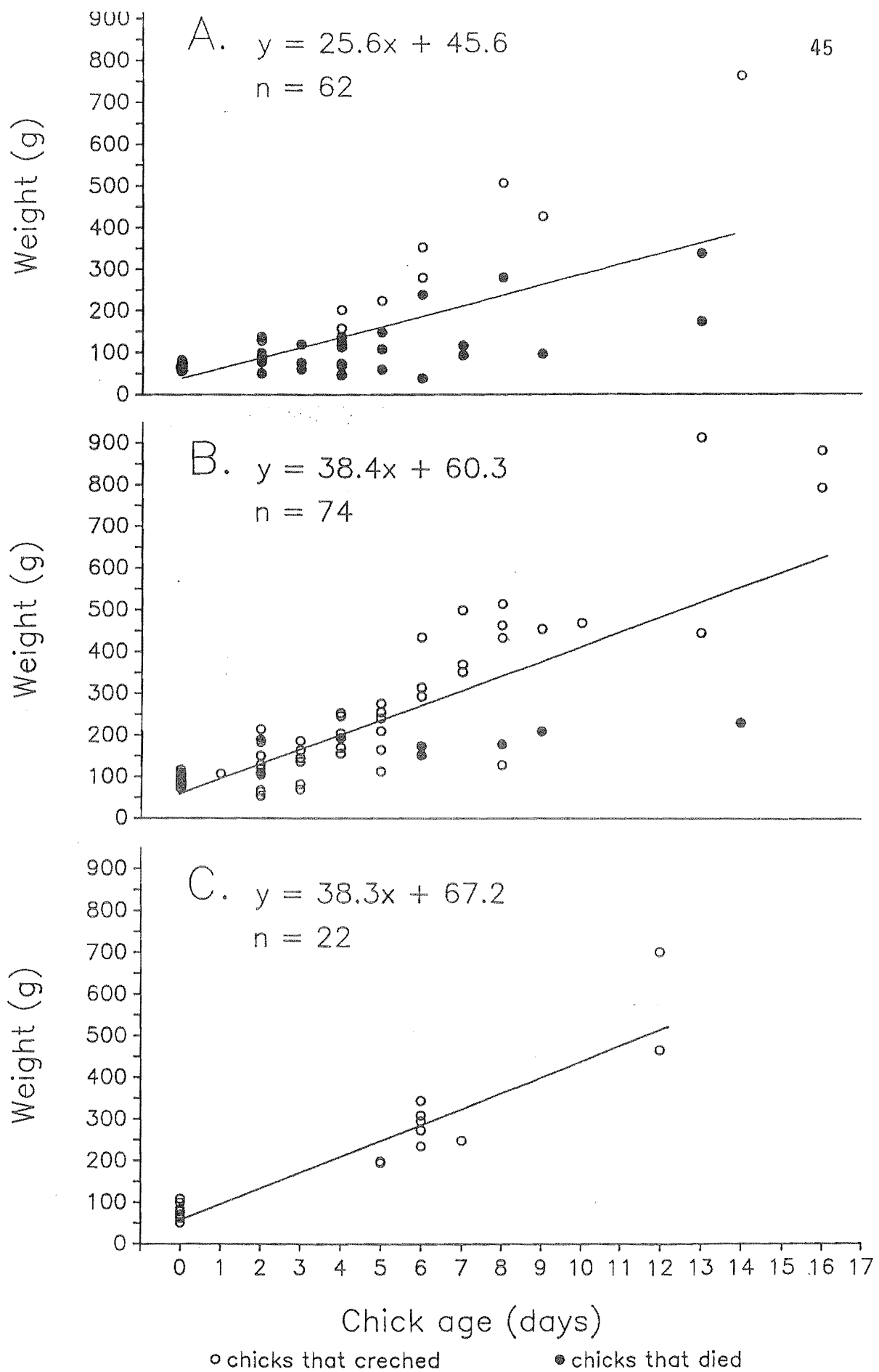
Figure 4.1. Weight of Fiordland crested penguin chicks regressed on age for chicks from first eggs (A), chicks from second eggs (B), and chicks raised singly (C).
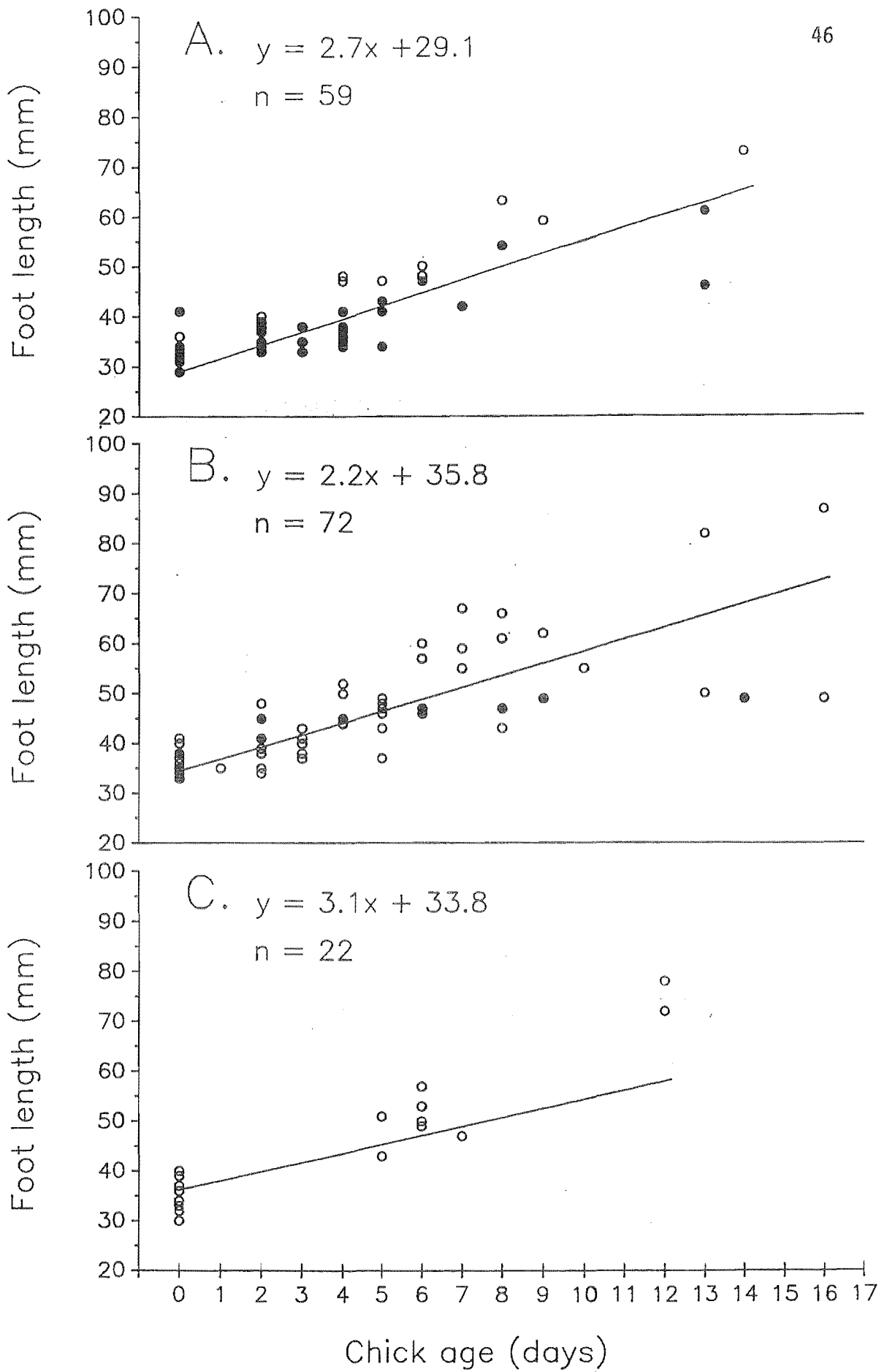
Figure 4.2. Foot length of Fiordland crested penguin chicks regressed on age for chicks from first eggs (A), chicks from second eggs (B), and chicks raised singly (C). Symbols as in Fig. 4.1.
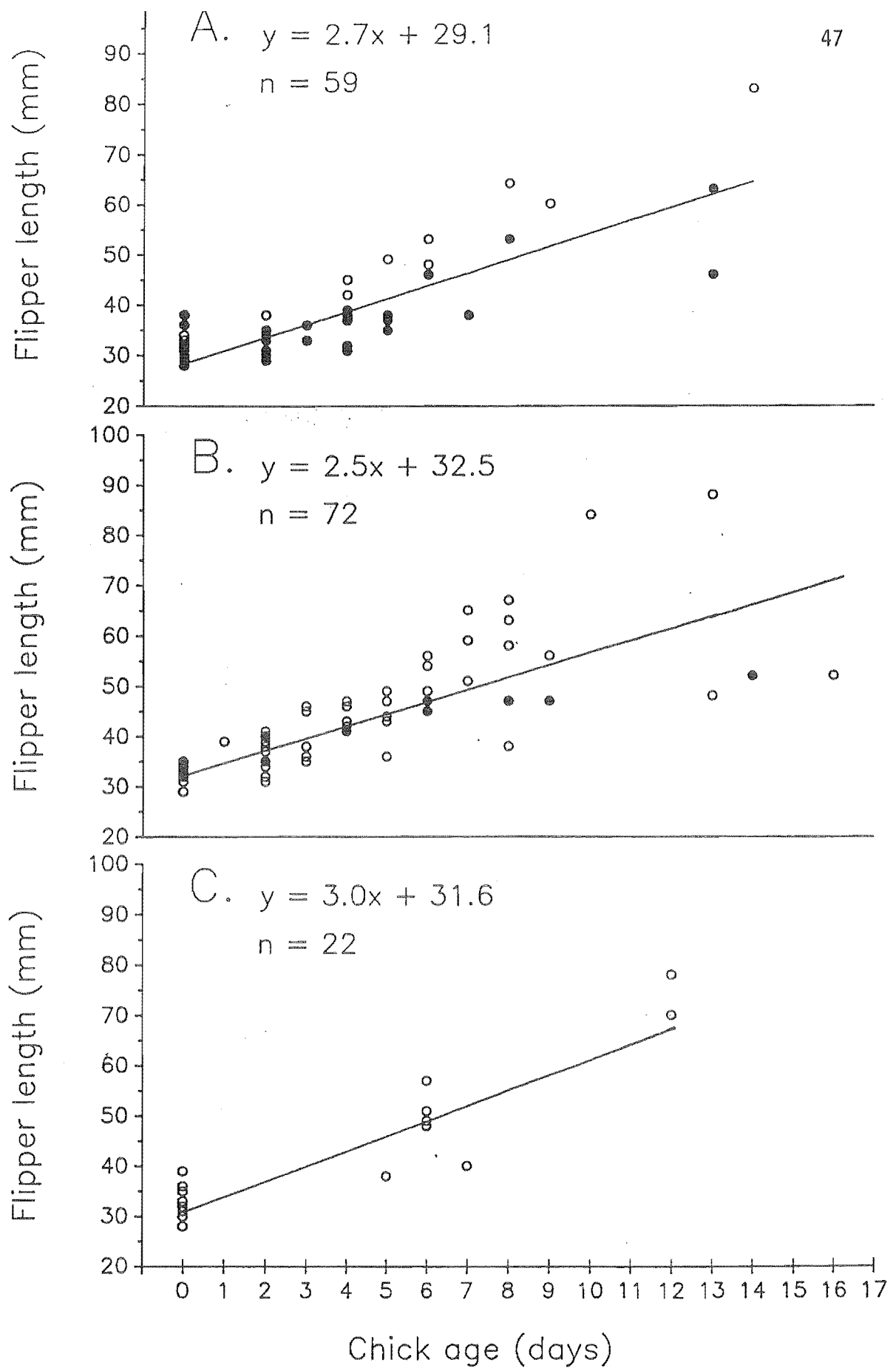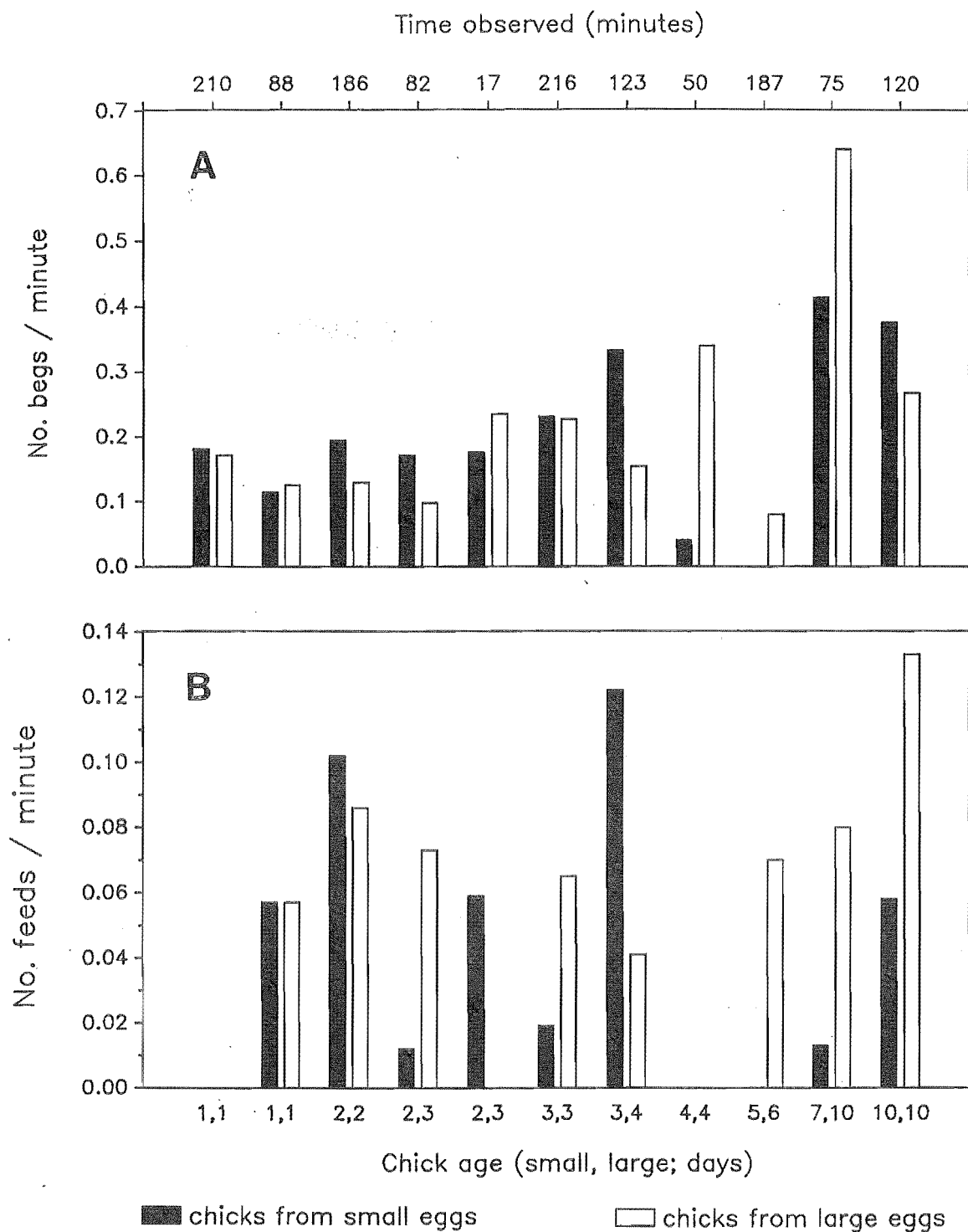
Figure 4.3. Flipper length of Fiordland crested penguin chicks regressed on age for chicks from first eggs (A), chicks from second eggs (B), and chicks raised singly (C). Symbols as in Fig. 4.1.

Figure 4.4. Rates of begging (A) and feeding (B) for pairs of chicks from small and large eggs during 11 observation periods on five nests.

Overt aggression between siblings, such as has been described for many brood reductionist species (see Simmons 1988 for a recent review), was not observed during feeding periods or at any other time. Nonetheless, considerable shoving, "flopping" and jockeying for advantageous nest positions accompanied most activity while a feeding parent was present. Flopping, the most common of these behaviours, was characterized by one chick dropping its head and neck over that of its sibling. Often this act was carried out by very young chicks with poor motor coordination and before their eyes were open. Although it did not constitute overt aggression, flopping by one chick often resulted in the bill of the other chick being pushed out of line with that of the feeding parent. Older chicks often prevented a smaller sibling from feeding by occupying a central position between the feet of the parent and by extending each flipper so as to inhibit close approach by the sibling (Plate 4.1). At other times, large chicks held a posterior position relative to their sibling, and from there were able to intercept food that otherwise would have gone to the sibling. Although it sometimes appeared that parents selectively fed the smaller chick, and at other times selectively ignored its begging, no regular pattern of feeding preference was observed. Asymmetries in chick growth seemed to result primarily from differential feeding rates facilitated by consistent exclusion of the smaller chick.

Plate 4.1. Exclusion of the smaller chick by its sibling during a feeding period when the chicks were 10 days old. The weights of the chicks, taken two days previous to the photo, were 505 g (large chick) and 179 g (small chick).

Chicks from second eggs experienced greater survival (Fig. 4.5; G = 9.765, df = 1, p < 0.01). Of 17 chicks that successfully creched from nests that initially contained two chicks, 14 were the larger chicks from second eggs. The three A chicks that creched successfully, included the one in the nest with reversed egg dimorphism, one in which the B chick appeared to suffer from some degenerative condition, and one in which the B chick disappeared when it was three days old.
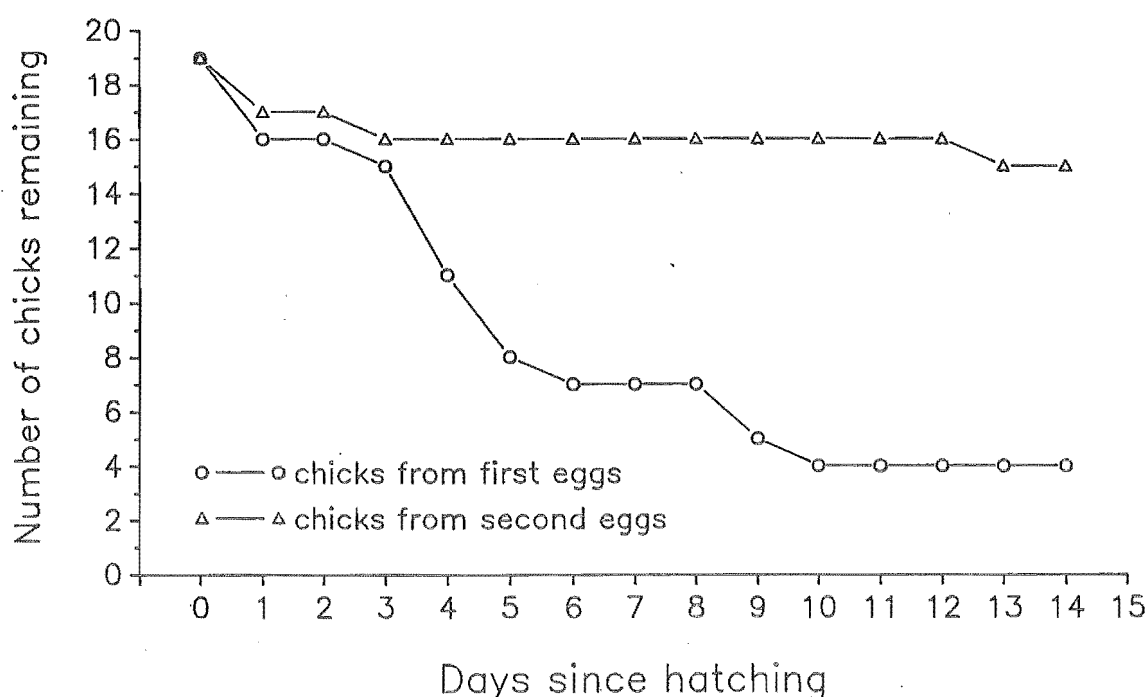

Figure 4.5. Survival of Fiordland crested penguin chicks from first and second eggs on Open Bay Islands.

Egg dimorphism was negatively correlated with the number of days two chicks survived in the same nest (r^2 = 0.294; t = -2.50, df = 16, p = 0.025). However, no relationship was found between hatching asynchrony (measured in days) and the number of days two chicks survived (r^2 = 0.001; t = -0.109, df = 16, p = 0.915). The reproductive success of pairs that hatched two chicks (17 chicks from 21 nests or 81.0%) was greater than that for pairs that hatched a single chick (5 chicks from 12 nests or 41.7%; G = -7.706, df = 1, p < 0.01).

DISCUSSION

On Open Bay Islands, the larger eggs within clutches of Fiordland crested penguins produced larger hatchlings than small eggs. The same relationship has been reported for a wide range of bird species (Schifferli 1973; Nolan and Thompson 1978; Ricklefs et al. 1978; Ankney 1980; Furness 1983; Richter 1984; Ricklefs 1984a; Quinn and Morris 1986), although it has not been clear whether observed differences were due primarily to larger body size at hatching or to greater yolk reserves imparted to the chicks from large eggs (Ricklefs et al. 1978; Bancroft 1984). In my study, measurements of body size at hatching exhibited a greater overlap between chicks from first and second eggs than did hatchling weight, and may indicate that yolk reserves accounted for some of the weight differences recorded. Extra apportionment of yolk is valuable in providing increased resistance to starvation (Ankney 1980) and could be particularly important in the period immediately after hatching. Considerable chick loss in Adélie penguins (*Pygoscelis adeliae*) resulted from starvation after one member of a pair was late in relieving its brooding mate (Davis 1982a). In one nest observed in this study, the female of the pair returned to provide the first feed three days after her eggs hatched. The chick from the smaller egg died after the first day but that from the larger survived for the three days without food, possibly indicating that chicks from second eggs are less likely to starve.

Differences in chick growth were more pronounced when considered in terms of weight rather than foot and flipper length. In addition, heterogeneity of slopes for regression equations of weight and age were increased by the tendency of starving chicks to lose weight before they died, whereas there was no corresponding decrease in linear measurements. Although large or first-hatched chicks do not necessarily grow more rapidly than their siblings (Ricklefs 1984b; O'Connor 1975; Haydock and Ligon 1986), such a relationship has been found in many bird species (see introduction in addition to Schifferli 1973; Ricklefs et al. 1978; Williams 1980c; Hérbert and Barclay 1986).

Ultimately, chicks from larger eggs were more likely to survive. This pattern has been reported repeatedly (Parsons 1970; Davis 1975; Gochfield 1977; Lundberg and Väisänen 1979; Quinn and Morris 1986), although some authors reported that hatchling size and growth do not necessarily affect post-fledgling survival (O'Connor 1975; Ankney 1980). Among obligate brood reductionist species, it is rarely likely that the competitive disadvantages of smaller hatchling

size and slower initial growth will be overcome subsequently to result in successful fledging. Nevertheless, two such cases occurred in this study, once when the larger sibling disappeared, possibly through predation, and once when it appeared to suffer from some degenerative condition. Both times, the smaller sibling grew rapidly only after the demise of the larger one. Preferential feeding, such as that reported by Ferguson and Sealy (1983) for disadvantaged offspring of horned grebes (*Podiceps auritus*), is a means by which smaller siblings could be compensated for disparities in size, but was not observed in this study. Conversely, others have reported that preferential feeding favours larger offspring (Bengtsson and Rydén 1983; Braun and Hunt 1983; Horsfall 1984; Inoue 1985; Skagen 1987) and this may be true of eudyptid penguins (Williams 1981d).

Differences in growth of chicks within nests undoubtedly relate to the competitive advantage generated by the larger size of one hatchling which is, in turn, a result of egg dimorphism and hatching asynchrony. In my study, egg dimorphism was more causally linked to the death of the smaller chick than was the degree of hatching asynchrony, although manipulation of hatching can exaggerate asymmetries between Adelie penguin chicks (Davis and McCaffrey 1989). Anecdotal evidence of the importance of egg dimorphism was provided by the nest with reversed egg dimorphism in which the chick from the first-laid egg dominated its sibling. Although hatching asynchrony has been considered to be the most important proximate factor influencing hatchling size in many species (see for example, Howe 1976; Stokland and Amundsen 1988), I believe egg-size dimorphism accounts for the greatest part of the variation in crested penguins.

Food allocation, as opposed to the absolute amount of food delivered, results in differential chick growth (Werschkul 1979), and begging behaviour is a means by which chicks may regulate parental feeding efforts (Henderson 1975; Harper 1986). Despite differences in size and growth, chicks from small and large eggs appeared to beg and feed at similar rates. However, my results need to be interpreted cautiously as they may have been confounded by the effects of satiation and the timing of the observations. In most nests, chicks from large eggs clearly received most of the food as indicated by the increasing differences in weight and size of siblings. Although overt aggression was not observed, large chicks used various displacement behaviours to exclude their smaller sibling from feeding. Groves (1984) reported similar results for American black oystercatchers (*Haematopus bachmani*) where dominance hierarchies were based on weight and heavier chicks controlled access to parental feeding. The ability to secure and

maintain advantageous nest positions is a non-aggressive means of dominance (Rydén and Bengtsson 1980; Greig-Smith 1985) that was often observed on Open Bay Islands.

Because sibling aggression is so widespread among the obligate brood reductionists, one may ask why aggression is not exhibited by crested penguins. Two explanations may be found in the semi-altricial nature of penguin hatchlings (Nice 1962; Williams 1980d) and their inherent inability to injure one another, and the type of food and the method of its delivery used by parents. Mock (1984b; 1985) described how sibling aggression was much more pronounced in great egrets (*Casmerodius albus*) than great blue herons (*Ardea herodias*), and hypothesized that this was related to the smaller and more easily monopolized food delivered to the egret chicks. In general, aggression rates were higher in both species when it was possible to monopolize and defend the prey. Prey delivery in crested penguins is by regurgitation directly into the mouth of a recipient chick (Warham 1975) and, except by interception, there is little opportunity to redirect food once feeding of an individual has begun. Particularly if fighting is energetically costly (Ploger and Mock 1986), aggressive behaviour between siblings may have no advantage beyond that necessary to obtain the most favourable nest position.

Another potential explanation for the lack of aggression among crested penguins siblings may relate to other aspects of their social structure. Following the guard stage, young chicks are left alone by day while both parents forage to meet the increasing food demands of their offspring. At these times, chicks gather in large groups or creches, a behaviour that reduces vulnerability to the predation that is common in colonies of most penguin species (Spurr 1975; Davis 1982b). On Open Bay Islands, I repeatedly observed chicks of various sizes huddling together to form small creches in the vicinity of weka (*Gallirallus australis*) - a flightless rail that occasionally preyed upon creched chicks. Often small chicks, crouching against cave walls where creches tended to be formed, were protected by larger chicks that could successfully ward off weka attacks. Rather than ascribe an altruistic function to this arrangement, I suspect the positioning resulted from the smaller chicks' ability to crawl into the smaller spaces available against the rocks. Nonetheless, creche formation undoubtedly resulted in reduced risk of predation, particularly for smaller chicks. The tendency to form creches appeared to be well developed in the population and chicks travelled several metres from relatively isolated nests to join creches in more populated areas. Creche-forming

may result in a behavioural paradox for obligate brood reductionist species: if creche behaviour is beneficial to individuals, and if selection for this trait requires some degree of cooperation between chicks, then it is possible that concomitant selection for aggressive behaviour between siblings cannot occur.

The extreme infrequency with which first eggs of crested penguins result in successfully creched chicks begs the question as to why two eggs are produced at all. For avian species that exhibit brood reduction, O'Connor (1978, but see Howe 1978) described conditions under which senior siblings, parents, and even junior siblings could benefit from the death of the smallest (junior) sibling. O'Connor's theory drew on the concepts of kin selection and inclusive fitness (Hamilton 1964) and supports the notion that brood reduction is an adaptive response to limited or unpredictable food resources. In extreme situations, the youngest sibling, ultimately doomed to starvation, may maximise its fitness by dying relatively early so that the energy invested in it can be channelled into siblings more likely to survive. In so doing, a measure of inclusive fitness is conferred on it. Conversely, if conditions are more favourable and all offspring can be raised, then older siblings maximise their inclusive fitness by allowing the younger one to survive (Mock and Parker 1986). In obligate brood reductionist species, such as crested penguins, environmental conditions may be regarded as being perpetually severe, favouring the loss of the smaller sibling. However, premature death of the larger chick removes selection for loss of the smaller one. The results of this study indicate that loss of the large chick is frequent enough that parents retaining both eggs to hatching experience significantly higher reproductive success than do those which retain only one. Therefore, the 'insurance' value (Lack 1968; Warham 1975) of eudyptid penguins' second egg may be substantial enough to warrant its retention even if two chicks are never raised from a single brood.

CHAPTER 5:

GENERAL DISCUSSION

The exceptional patterns of egg dimorphism and hatching asynchrony among crested penguins most likely result from several of the behavioural, morphological and physiological factors on which selection pressures may act. Some of these factors were evaluated in Fiordland crested penguins on Open Bay Islands. Here, I will review the major conclusions of each of the preceding chapters and assess their importance to an understanding of the phenomenon of brood reduction in birds, especially eudyptid penguins. Lastly, I will propose an evolutionary scenario by which current patterns of egg and chick loss in *Eudyptes* may have come about and ways in which these patterns may continue to change.

In Chapter 2, the behaviour of incubating penguins was quantified and related to egg loss prior to hatching. Previous authors (Warham 1975; Johnson *et al.* 1987; Johnson and Bednarz 1989) have suggested that aggressive behaviour between nesting male penguins is responsible for a substantial portion of early egg loss that consists disproportionately of first-laid eggs. My data do not support this hypothesis. Aggression between breeding penguins was almost entirely limited to the period before egg laying commenced and I did not observe aggression contributing to displacement or predation of eggs on any occasion. Nonetheless, the behaviour of incubating birds changed markedly after the second egg was laid and provided some evidence that first eggs were more vulnerable during the laying interval than either egg was afterwards. Significantly more first eggs were lost than second eggs and most losses occurred in the first week of the incubation period. Egg survival did not appear to be influenced by the effects of nest crowding or cover, or by the degree of intra-clutch egg dimorphism.

In Chapter 3, I examined the incubation regimes of first and second eggs to determine why first eggs require a longer period to develop. Temperature trials, conducted throughout the incubation period, indicated that egg temperatures increased after the second egg was laid, but subsequently did not differ between small and large eggs. Contrary to the findings of Burger and Williams (1979), first

eggs were not incubated more often in the anterior nest position and eggs in that position did not have lower temperatures. Incubation temperatures during the laying interval were likely to be limited by brood patch development which did not commence until the second egg was laid. A non-breeding penguin developed a full brood patch after receiving an abandoned egg, suggesting that the act of incubation is an important stimulant for the initiation of brood patch development. I proposed that foregoing brood patch formation with the production of the first egg may be beneficial to penguins as it would enable them to avoid costly defeathering and vascularization when successful breeding could not be realized, i.e., for young, inexperienced birds that court and establish a nest site, but do not produce any offspring.

Although first and second eggs appeared to be exposed to equivalent thermal environments after the completion of the laying interval, first eggs hatched significantly later than second eggs. Factors additional to those measured that would affect the length of embryonic development were discussed and evaluated qualitatively.

In Chapter 4, I addressed the role of sibling competition in chick growth and survival. Chicks from second eggs (except for one nest with reversed egg dimorphism) were larger and heavier at hatching than their siblings. Weight gain of singly raised chicks and chicks from second eggs was greater than for chicks from first eggs, but growth rates of feet and flippers did not differ significantly. Interestingly, observed begging and feeding rates of small and large chicks were similar, although large chicks clearly received more food overall. Overt aggression was not observed although large chicks dominated their siblings by non-aggressive means. Chicks from second eggs experienced considerably higher survival to the creche stage, and no siblings coexisted longer than 16 days. Intra-clutch egg dimorphism was negatively correlated with the number of days two chicks survived, but there was no relationship between suvival and hatching asynchrony. On Open Bay Islands, penguin pairs that hatched both eggs raised proportionately more chicks than pairs that hatched only one egg, a finding that suggests first eggs provide valuable insurance against failure of the larger egg or chick to develop.

The results of this study provide some empirical evidence with which to assess several of the hypotheses advanced to explain the origin and adaptive

values of the brood reduction phenomenon in avian species. The brood reduction hypothesis (Lack 1947; 1954) has been the most prevalent of these explanations, but because initial brood size and the number of offspring reared by crested penguins do not vary, Lack's theory of brood reduction is unlikely to apply to species of *Eudyptes*. In this study, as in the reports of others, there was no indication that the number of chicks that could be raised from each clutch was limited by temporary food shortages. Artificially twinned rockhopper penguin chicks of equal size survived for longer periods than siblings in natural nests, but did not receive enough food for both chicks to fledge (Williams 1981d). Therefore, it is probable that limited food delivery, rather than competition between siblings, constrains members of the genus to the production of a single chick per brood. For crested penguins, as for all obligate brood reductionist species, Lack's explanation of brood reduction may have applied historically, but changing food type or availability has removed plasticity in the number of offspring that may be raised. In species for which offspring loss is mediated by chick aggression, the effects of temporary food abundance may be overridden by selection for siblicide that has operated during years of more typical food availability (Mock *et al.* 1987). In sum, traditional brood reduction theory does not appear to apply to eudyptid penguins at present, but may well have had some historic influence.

The nest-failure hypothesis of hatching asynchrony and chick loss (Hussel 1972; Clark and Wilson 1981) is also unlikely to apply to crested penguins because of the low predation rates and very long nestling periods common to all penguins. Eudyptid penguin chicks do not fledge until they are approximately 75 days old (Warham 1975) and the shortening of this period for the older sibling through one or more days of hatching asynchrony does not provide a plausible explanation for the existence of the trait. Furthermore, young penguin chicks are considerably more vulnerable to land predators than older chicks (Spurr 1975; Davis 1982b; this study).

An extension of the nest-failure hypothesis predicts that hatching asynchrony may also increase parental survival (Magrath 1988). If egg dimorphism and hatching asynchrony operate to create asymmetries within *Eudyptes* broods to ensure that only one chick can be reared, parents may benefit from the reduced costs of providing enough food for a single chick. However, an hypothesis that predicts increased survival for parents that raise one chick, implies that other pairs are capable of raising two chicks, a condition that does not occur

in eudyptid penguins. For the same reason, hypotheses that asynchronous hatching serves to eliminate wasteful sibling rivalry (Hamilton 1964; Hahn 1981; Ploger and Mock 1986) or reduce peak load requirements of the brood (Hussel 1972) cannot currently apply to crested penguins.

Suggestions that asynchronous hatching can be a consequence of physiological characteristics (Mead and Morton 1985) were anecdotally supported by this study. The development of a full brood patch by a non-breeding penguin provided with an abandoned egg, combined with observations that brood patch development did not commence until the second egg was laid, may indicate that patch formation is contingent upon successful breeding. Because needless defeathering and vascularization would be particularly costly to penguins in their cold-water environment, it is conceivable that the disadvantages of asynchronous hatching are offset by the benefits of delaying brood patch formation until the potential for raising young is ensured. However, this explanation does not account for the reduction in clutch or brood that invariably occurs subsequently in all the eudyptid species.

Hypotheses put forth as specific explanations for the unique pattern of egg dimorphism in *Eudyptes* were also evaluated. In general, these were not supported. From the results of this study, and that of Williams (1989), it does not appear that egg dimorphism is driven by compensation for high egg loss resulting from the aggressive behaviour of incubating adults (Warham 1975; Johnson *et al.* 1987). Similarly, there is no evidence that first eggs function to signal nest site occupation, or enhance laying synchrony (Johnson *et al.* 1987; Johnson and Bednarz 1989).

The hypothesis that egg loss, and compensatory egg dimorphism, results from the inability of crested penguins to adequately cover two eggs, is suggested by the semi-prone incubating posture characteristic of macaroni penguins (Haftorn 1986). However, both eggs are known to hatch in several species of eudyptid penguins (Gywnn 1953; Warham 1971; 1974a; 1974b; Lamey *in press*; this study), negating the possibility that members of the genus are unable to incubate two eggs effectively.

Warham (1975) attempted to determine if crested penguin egg dimorphism was a precursor to the slight sexual dimorphism characteristic of adult penguins of the genus. Although the results were inconclusive, it seems extremely unlikely that small eggs produce females and large eggs males. Neither an abundance of

male birds, nor exceptional mortality of males has been reported from natural populations (Warham 1975), and the extreme infrequency with which first eggs result in fledged chicks in some eudyptid species points to the impossibility of a link between laying order and sex of the embryo.

The most plausible hypotheses concerning *Eudyptes* egg dimorphism and hatching asynchrony, are those that promote insurance as a function of the first egg. Lack (1968) suggested that the first egg functioned as a reserve in eudyptid species that hatched both eggs, in case the second egg failed to hatch. Interestingly, he did not predict that the unusual pattern of hatching asynchrony and egg dimorphism in crested penguins provided a mechanism for efficient chick mortality equivalent to the function of asynchronous hatching described for other bird species (Lack 1947; 1954; 1968). Nonetheless, variations of the brood reduction hypothesis have been referred to repeatedly as explanations of hatching asynchrony and egg dimorphism in *Eudyptes* (Wynne-Edwards 1962; Warham 1975; Slagsvold *et al.* 1984; Johnson *et al.* 1987; Johnson and Bednarz 1989).

Warham (1975) discounted the insurance function of eudyptid first eggs because egg loss in many species occurred before the insurance value of a replacement chick could be realized. Conversely, Williams (1989) suggested that first eggs were valuable as insurance only against immediate losses of second eggs, or in cases in which second eggs were not laid. Williams also proposed that the laying of the second egg was causally linked to the loss of the first. This suggestion implies deliberate ejection of first eggs; a behaviour not supported by empirical evidence (Chapter 2).

In this study, the heightened reproductive success of pairs that hatched both eggs underlines the considerable insurance value of first eggs. For Fiordland crested penguins on Open Bay Islands, it was clearly advantageous to lay and hatch two eggs even though no pairs succeeded in raising both chicks. However, an equivalent insurance value is unlikely to exist among macaroni penguins in which the first egg rarely survives the first week of the incubation period. To date, there is not a single report of a fledged chick arising from the first egg of a macaroni penguin (Williams 1989), belying any insurance value whatsoever of first eggs in that species. Thus, insurance hypotheses also do not account for the full variation in patterns of egg and chick loss in crested penguins.

Eudyptid penguins are a closely related bird group (Livezey 1989) and the principle of parsimony dictates that the unique characteristics of egg dimorphism and hatching asynchrony common to the genus have evolved only once. Therefore, inter-specific variation in those characteristics, and in the nature of egg and chick loss, probably represent evolutionary processes that are still taking place. Ancestral penguins of the Eocene through Miocene epochs inhabited waters of comparatively high temperatures (Simpson 1975) more typical of those found at present-day tropical latitudes. Most likely, these differences in habitat were accompanied by associated differences in breeding ecology and physiology, and current patterns of egg dimorphism and hatching asynchrony may have evolved to track changes in the environment of ancestral penguins.

Willliams (1981c) speculated that ancestral *Eudyptes* were inshore-foraging species, faced with an unpredictable and variable food supply comparable to that of extant penguins that forage close to shore (Boersma 1976; Croxall and Prince 1980). He further predicted that historic patterns of egg dimorphism and hatching asynchrony in eudyptid penguins were the reverse of current patterns which allowed for adjustment of brood size to the available food resources by the usual brood reduction means (*sensu* Lack 1954; Ricklefs 1965; O'Connor 1978). As ancestral eudyptid stock moved from inshore to offshore foraging areas, food predictability increased, but with a commmmensurate decrease in the frequency with which chicks could be fed and, following changes to a more seasonal climate, in the duration of the chick rearing period. Williams hypothesized that a gradual reversal in egg dimorphism and hatching asynchrony allowed eudyptid penguins to halve the number of offspring produced to better match the changing conditions. In short, his theory predicted that *Eudyptes* ancestors were initially adapted to an unstable and unpredictable food source, but experienced a transitional period of relative food abundance in which the mechanisms that allowed for efficient brood reduction were eliminated. Continued changes in habitat and climate forced the evolution of a mechanism by which reproductive output could be realigned with the available resources; hence a halving in the number of chicks produced.

Mougin (1984) independently advanced an hypothesis similar to that of Williams (1981c) to explain the current pattern of egg dimorphism and hatching asynchrony in crested penguins. His theory differed in that it did not invoke a reversal in egg dimorphism from the eudyptid ancestral stock, but instead suggested that the warm-water ancestor laid two eggs of equal size, similar to the pattern of the extant yellow-eyed penguin (*Megadyptes antipodes*). *Megadyptes* is

the closest living relative of *Eudyptes* (Zusi 1975; Livezy 1989) and its breeding areas overlap with those of Fiordland and erect-crested penguins. In addition to an increase in food availability and a reduction in the chick rearing period, Mougin suggested that adaptation to cold waters by ancestral penguins included an increase in body size. Thus, the penguins currently adapted to the coldest environments could be expected to exhibit the greatest egg dimorphism and largest body size. Some evidence supports such a relationship. Clutches of *Aptenodytes*, the largest of the extant penguins, consist of a single egg and *A. forsteri* breeds under the coldest conditions of any penguin species. Furthermore, macaroni and erect-crested penguins exhibit the greatest egg dimorphism and are among the largest of the eudyptid penguins. Although Warham (1975) stated that there was no regular increase in egg dimorphism with body size within the genus, current patterns may have been modified by other selective pressures and a slight trend to increasing egg dimorphism among the larger *Eudyptes* seems evident (Fig. 5.1).
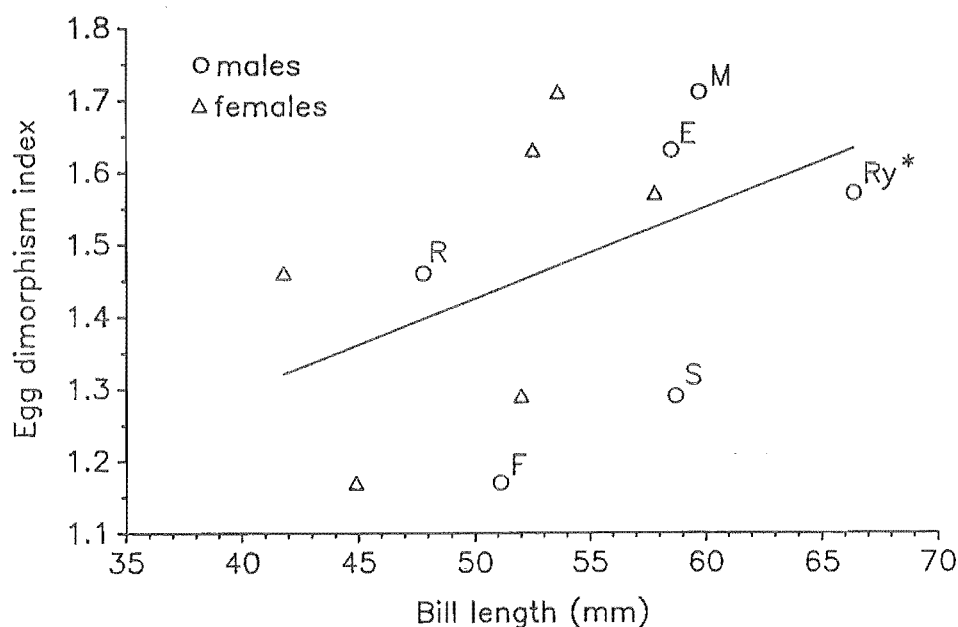
Figure 5.1. Egg dimorphism regressed on bill length (as an indication of body size) of male and female eudyptid penguins. All bill lengths and indices of egg dimorphism (lb^2 large / lb^2 small, chapter 2) for rockhopper (R), Fiordland (F), Snares (S), erect-crested (E), and macaroni (M) penguins are by Warham (1975). Species labels are given for males only. Horizontally adjacent symbols represent females of the same species. The regression line is indicative of a trend only and does not statistically differ from 0 ($r^2 = 0.204$, t = 1.601, $p = 0.14$)

* The index of egg dimorphism for the royal penguin (Ry) was estimated from the mean egg weights given by Soucek (in Gywnn 1953; Warham 1971), and is comparable to indices calculated with Warham's (1975) method (Chapter 3).

An explanation as to why brood reduction has evolved in *Eudyptes* answers only one of two pertinent questions (Johnson *et al.* 1987); it does not explain why it is the first egg that is smaller. I suspect brood reduction involves the first egg, rather than the second, because of the physiological constraints of brood patch development and a long laying interval. If brood patch development and, possibly, incubation behaviour, is stimulated by the presence of an egg, first eggs cannot be incubated effectively, immediately after laying. The longer incubation period of first eggs may reflect, among other things, the effects of cooling during the laying interval. Furthermore, the reduced protection of non-incubating postures adopted during the laying interval (Chapter 2) may heighten the vulnerability of first eggs to predation.

The long laying interval, characteristic of all penguins that lay two eggs (Williams 1981e), may also disadvantage first eggs. Although egg losses do not appear to be caused by the aggressive behaviour of adults (Williams 1989; this study), first eggs were lost at much greater frequencies than second eggs in both studies, and most occurred during the 3-6 day laying interval. Williams (1981d) speculated that penguins have long laying intervals because they have relatively heavy eggshells consisting of disproportionately large amounts of phosphorus, and because of the extra time required for the mobilization and deposition of calcium. Astheimer (1985) discounted these hypotheses and argued that neither shell weight nor calcium demand in penguins could be considered extraordinary. Instead, she proposed that long laying intervals in penguins and other seabirds were a result of delayed initiation of yolk deposition. By extending the period of yolk formation, more time is provided for the synthesis and storage of albumen and shell membrane material (Grau 1984), possibly reducing the depletion of lipid and protein reserves (Astheimer 1985). A long period of yolk formation could be valuable to penguins or, as there is some evidence that lags between the yolk formation of successive eggs was characteristic of ancient birds (Grau 1984), may be a remnant of phylogeny. Nonetheless, eudyptid penguins are constrained by a long laying interval which appears to affect the survival of first-laid eggs.

If, as Mougin (1984) suggested, *Eudyptes* ancestors laid a clutch of two equal-sized eggs, it seems likely that selection for brood reduction would favour a decrease in the size of the first, rather than the second, egg. Patterns of egg dimorphism and hatching asynchrony in crested penguins can therefore be seen as an example of convergent evolution, having an equivalent function to other brood reductionist species, but arising through separate evolutionary processes.

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photo: C. Mason

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