CLUTCH SIZE IN PIGEON GUILLEMOTS: AN EXPERIMENTAL

MANIPULATION AND REPRODUCTIVE SUCCESS IN

ONE AND TWO EGG CLUTCHES

by

ELIZABETH B. McLAREN

A THESIS

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

March 1991

APPROVED: _____

Dr. Richard W. Castenholz

An Abstract of the Thesis of

Elizabeth B. McLaren   for the degree of   Master of Science

in the Department of Biology   to be taken   March 1991

Title: CLUTCH SIZE IN PIGEON GUILLEMOTS: AN EXPERIMENTAL

         MANIPULATION AND REPRODUCTIVE SUCCESS IN ONE AND TWO

         EGG CLUTCHES

Approved: _____
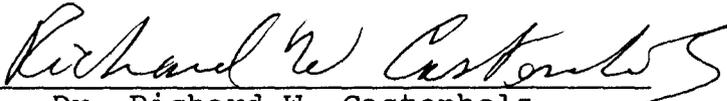
                Dr. Richard W. Castenholz

The ability of the Pigeon Guillemot Cepphus columba to

rear an additional chick was tested by manipulating clutch

sizes. The effect of the manipulations on growth, and

hatching, fledging, and egg success was measured in chicks

from experimental, natural, and control nests. No

significant differences were observed between the nest

types. Data from 1983, 1984, 1985, and 1989 were analyzed

for potential differences in reproductive success of one and

two egg clutches. The ratio of one to two eggs was

significantly higher in 1985 and 1989. Hatching and

fledging success was significantly higher for two egg

clutches in 1985 and 1989. No significant differences were

observed for egg success. Egg volume was significantly

greater in two egg clutches in 1983 and 1984. Egg volume

was correlated with fledging but not with hatching success.

VITA

NAME OF AUTHOR: Elizabeth B. McLaren

PLACE OF BIRTH: Bloomfield Hills, Michigan

DATE OF BIRTH: September 11, 1962

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
University of Colorado

DEGREES AWARDED:

Master of Science, 1991, University of Oregon
Bachelor of Arts, 1985, University of Colorado

AREAS OF SPECIAL INTEREST:

Ecology and Physiology of Seabirds
Physiology of Marine Mammals

PROFESSIONAL EXPERIENCE:

Director, Whitefish Point Bird Observatory, Whitefish
Point, Michigan, 1990

Teaching Assistant, Department of Biology, University
of Oregon, Charleston, 1988

AWARDS AND HONORS:

Sigma Xi Research Grant, 1988

Ethyl and Earl Myers Oceanographic and Marine Biology
Trust, 1987

ACKNOWLEDGMENTS

I would like to express my gratitude to the members of my committee for their support and assistance in the preparation of this manuscript. Special thanks to Dr. Jonathon Geller, whose statistical expertise (which was called upon quite frequently) was invaluable. I am also very grateful to Dr. Ronald Yoshiama and Chad Hewitt for statistical assistance. I am indebted to the many spring and summer term students of O.I.M.B., without whom I could not have conducted this study. I would also like to express my appreciation for the friendship of Dr. Donald Croll, who has provided me with some wonderful opportunities to study and learn about marine birds. Finally, I would like to thank Dr. Jan Hodder for her unending support and good humor throughout the course of my graduate studies.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Numerous studies have focused on the evolution of reproductive strategies in seabirds (for example, Lack, 1954, 1968; Williams, 1966; Ricklefs, 1973, 1977; Hunt, 1980). Patterns of reproduction employed by seabirds vary widely, and are determined both by physical characteristics of the environment, and by biological characteristics of the species. Current hypotheses suggest that favored strategies will balance long-term reproductive potential with current energetic costs of reproduction (Murphy & Haukioja, 1986).

There are several mechanisms which have evolved to maximize reproductive success in birds. The evolution of colonial breeding, a strategy which affords birds increased protection from predation and information regarding food location, is an example of such a mechanism (Gochfeld, 1980). The evolution of an "optimal" clutch size, which balances long-term reproductive potential and current energetic costs of reproduction, is another way in which reproductive success is maximized in birds.

Current hypotheses regarding the evolution of an optimal clutch size in nidiculous birds have centered largely around earlier hypotheses developed by Lack (1947,

1954, 1966). Lack hypothesized that the optimal clutch size in birds is determined by the greatest number of chicks for which the parents can adequately provide, a number which may be smaller than the number of eggs which a female can lay. Thus, environmental quality, or the amount of food available for chick provisioning will determine the largest clutch size that can be supported. This reasoning suggests that any heritable tendency to lay larger than optimal clutch sizes will be eliminated by natural selection.

Further investigations of the selective forces which determine clutch size have expanded Lack's hypotheses to include the costs of reproduction (Perrins, 1965; Williams, 1966; Charnov & Krebs, 1974). This "cost hypothesis" (Bell, 1984) states that a smaller clutch size is favored when the costs of reproduction, in terms of adult mortality, increase with clutch size. In this case, the optimal clutch size may be smaller than the number of chicks which could be successfully reared if costs to the adult, in terms of future reproductive success, increase with clutch size.

An alternative hypothesis put forward by Slagsvold and Lifjeld (1990) states that in species with biparental care, there are three factors which could potentially affect clutch size: (1) environmental quality, or food resources, (2) female quality, and (3) male quality. In a study with three species of tits, they concluded that the optimal

clutch size for these birds is determined by the ability of the female to provision for the chicks, and not on the quality of its mate. These findings support Lack's belief that environmental quality is a key determinant of clutch size, and that of Charnov and Krebs which stresses the importance of female quality and potential costs to future reproductive output.

Lack's hypothesis and those which have followed can be tested most effectively through the use of clutch size manipulations. This technique is accomplished by artificially increasing or decreasing clutch sizes, and subsequently measuring growth rates, hatching success (the number of eggs laid which hatched), fledging success (the number of chicks hatched which fledged) and breeding or egg success (the number of eggs laid which produced fledged chicks) of chicks. Experiments of this type test whether adult birds are able to rear a greater number of chicks than they would normally produce. This addresses the question of the optimal clutch size for an individual, and whether or not it is actually the maximum clutch size supportable. Then, by measuring factors such as adult survival or chick survival to breeding age, actual predictions of hypotheses regarding the evolution of an optimal clutch size in a particular species can be tested.

Most clutch manipulation studies have been conducted on passerines which are, in most cases, easily accessible.

Some studies have been conducted with seabirds. Of these, the majority have focused on members of the order Charadriiformes (e.g. Reid, 1988; Shipley, 1984; Nisbet, 1978; Andersson, 1976), an extremely diverse group of seabirds and shorebirds.

Within the order Charadriiformes is the family Alcidae. This group consists of 22 species which inhabit the colder waters of northern oceans. All are wing-propelled diving birds which spend the majority of their time at sea. During the breeding season, these birds move inshore to nest, with a few exceptions, on cliffs and offshore islands.

Alcids have widely divergent developmental patterns which can be separated into three groups. The precocial species, such as the murrelets, lay two eggs and take their chicks to sea as soon as two days after hatching. The intermediate species, such as the Razorbill, and Common and Thick-billed Murres, lay one egg. Their chicks remain in the nest approximately two weeks, and go to sea at one-quarter of adult weight. The semi-precocial species, such as the auklets and puffins, also lay one egg, and the chick remains in the nest 30-40 days, having obtained 90-95% of adult weight at fledging.

Members of the genus Cepphus, including Pigeon, Black, and Spectacled Guillemots, are the one exception to the reproductive patterns observed for Alcids. The chicks are

semi-precocial, yet unlike the other species with this pattern, they lay two eggs instead of one. This ability to rear two chicks which remain in the nest for an extended period is attributed to their near-shore feeding habits (Birkhead & Harris, 1985).

However, guillemots do not always lay two eggs. Each year a certain percentage of females lay only one egg, for reasons that remain largely unknown. The questions then arise: why do these birds lay just one egg, and are they maximizing their lifetime reproductive output in doing so? These questions pertain to the evolution of clutch size in guillemots, and whether a guillemot which lays only one egg can, in fact, rear two chicks.

To address some of these questions, this study was undertaken with the Pigeon Guillemot, one of Oregon's abundant breeding seabirds. In Coos Bay, there is a large colony where approximately 100 pairs nest annually. These birds provide an excellent opportunity to investigate the evolution of clutch size in Pigeon Guillemots. In an effort to test hypotheses pertaining to maximum and optimal clutch size, I performed clutch size manipulations in an attempt to answer the following questions:

1. Are Pigeon Guillemots which lay only one egg capable of rearing two chicks?

2. Does the addition or removal of an egg affect chick weight, and growth of wing, culmen, and tarsus lengths?

3. Does the addition or removal of an egg affect hatching, fledging, or egg success?

There are also compelling questions to be asked in relation to the potential differences in reproductive success of adults which lay one egg versus those which lay two. In order to partially address these questions, data collected in 1983, 1984, and 1985 by Dr. Janet Hodder and Michael Graybill and data I collected in 1989 were utilized for between year comparisons of reproductive success. The specific questions which I undertook to answer were:

1. Are there annual differences in the proportions of one and two egg clutches?

2. Are there differences in hatching, fledging, and egg success of one and two egg clutches between years?

3. Does the egg volume difference for one and two egg clutches vary between years?

4. Is there a correlation between egg volume and hatching and fledging success?

CHAPTER II

MATERIALS AND METHODS

Study Site

The study site was located in the Coos Bay estuary, Coos County, Oregon at Sitka Dock, an abandoned wooden pier located approximately 4.2 kilometers from the entrance to Coos Bay (Figure 1). Sitka Dock, abandoned in the early seventies, is now an important nesting area for Pigeon Guillemots and is known to be the largest breeding colony in any of Oregon's estuaries (Roy Lowe, personal communication). Coos Bay is the largest natural estuary between San Francisco Bay and Astoria. It is highly productive, supporting at least 66 species of fish, including several species of sculpin, eel blennies, and flatfish (Cummings & Schwartz, 1971) on which the Guillemots feed (Follett & Ainley, 1976).

Pigeon Guillemots nest on the underside of Sitka Dock on supporting crossbeams. The crossbeams intersect with beams extending the length of the dock. This layout creates partitioned spaces along the crossbeams and it is in these spaces that the guillemots nest. Most of Sitka Dock is intact, but in certain sections the wood is rotting. This

8

Figure 1.   Map of the Coos Bay estuary. ▲ indicates the
             location of Sitka Dock.
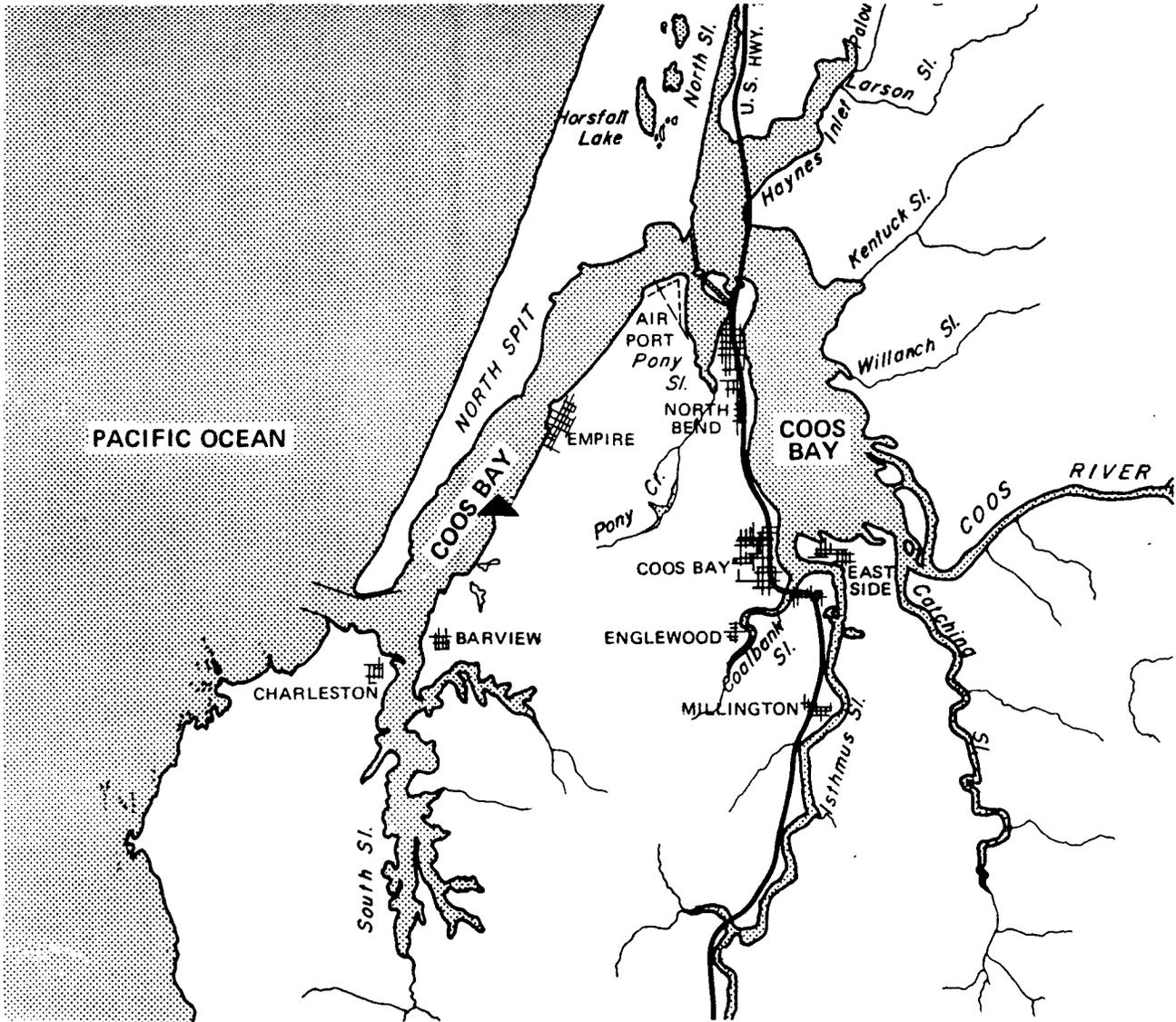
has created ideal nesting habitat for the Guillemots because they are able to dig shallow depressions in the wood to contain their eggs. Although birds utilize the entire dock, it is in these rotted areas that the majority of nests are found. Sitka dock is an excellent colony site because it allows Pigeon Guillemots easy access to intertidal and subtidal fishes. In addition, the dock provides the birds with protection from both aerial and terrestrial predation.

The underside of Sitka dock is easily accessible by small boat during a high tide within a +4 to +6 foot range. Nests utilized in previous years have been marked and all potential sites at the dock have an "address" designated by Dr. Jan Hodder and Michael Graybill in 1983. The address system divides the dock into two sections, the first being PA, which includes the portion of the dock which runs parallel to the bay. The second section, PE, includes the portion which is perpendicular to the bay. Within each section, pylon rows are numbered (1 to 70 in PA, 1 to 45 in PE), as are the individual pylons within each row. The spaces on the crossbeam between each pylon in a row are lettered A, B, C, etc. Therefore, a nest which has the address PA68.3E would be located in the parallel section of the dock on the crossbeam extending over the 68th row of pylons. To find the nest, one would then look between the third and fourth pylons, at the fifth space along the beam.

Clutch Size Manipulations

To test for the effects of altered clutch size on growth rates, hatching, fledging, and egg success of Pigeon Guillemots, the following methods were employed. At the end of May 1989, I began checking all potential nest sites at Sitka Dock for freshly laid eggs. My intention was to visit the colony daily, however I was constrained by weather and tides. As a result, I censused the entire colony every three to four days. When eggs were first found, the date, nest site and number of eggs present was recorded. The site was then marked with yellow spray paint to denote its status as an active nest. Egg length and breadth were measured to the nearest 0.1 mm using stainless steel calipers. An index of egg volume was subsequently calculated by taking the length x breadth^2 (Hoyt, 1979).

Clutch size manipulations were undertaken in the following manner: an egg from a bird which had laid only one egg was moved to the nest of a bird which had laid two eggs. The two eggs from this second bird were then placed back into the nest of the first bird. By performing the manipulations in this way, eggs from two egg clutches were not split up into different nests. To maintain the proper timing of hatch for the adults, care was taken to ensure that all eggs utilized in a particular manipulation were layed within 2-3 days of each other.

The end result of these manipulations was that 11 artificial one egg clutches and 10 artificial two egg clutches were created. These were compared with 9 natural one and 20 natural two egg clutches. To control for possible effects resulting from the mechanics of transplanting eggs, movement controls were performed on 12 two egg clutches. At these nests, eggs were not switched, but were instead taken out of the nest, and placed into the boat for the approximate time in which a manipulation would take place. They were then replaced into their original nest.

When chicks began to hatch, I marked the first chick to appear in a two egg nest by clipping its toenail (St. Louis et al., 1989). This enabled me to distinguish between them for subsequent collection of the data. Approximately one week after hatching, chicks were banded with USFW Munnell stainless steel bands or with USFW aluminum bands.

Chick weight was measured to the nearest gram using first a 100g and later a 1000g Pesola spring balance. Wing chord measurements were taken from the right wing using the maximum chord method. Measurements were made to the nearest 1mm with a ruler. Tarsal length was measured on the right leg from the inter-tarsal joint to the tarso-phalangial joint of the middle toe. The culmen was measured from the tip of the bill to the end of the upper mandible. Tarsal and culmen measurements were made to the nearest 0.1 mm with

stainless steel calipers.

All measurements were conducted until the chicks
fledged. Chicks were considered to be fledged once they had
departed the nest, unless I had reason to believe that I
directly induced the departure. In the few instances where
this occurred, those nests were excluded from the analysis.
Occasionally, I was not able to determine the date of
departure for a chick. In these instances, I considered the
chick to have successfully fledged only if it had obtained a
weight of at least 400 grams or if it had been in the nest
at least 31 days at the time I last measured it. Nests were
checked until all chicks had departed.

Between Year Comparisons

Data were collected using similar procedures by Dr.
Janet Hodder and Michael Graybill during the years of 1983,
1984, and 1985. These data, and data I collected were
compared to observe potential annual differences in clutch
size. In addition, data from 1983, 1984, and 1989 were
analyzed to determine whether differences existed in
hatching, fledging and egg success between one and two egg
clutches. Egg morphometric data from these years were also
compared to test for differences in egg size between one and
two egg clutches.

Analysis of Results

To avoid pseudoreplication (Hurlburt, 1984), means of measurements of chicks from two egg nests were utilized in all analyses. Non-parametric statistical tests were used when the data were not normally distributed or they did not meet the requirement of homoscadasticity, as determined by the Bartlett test for homogeneity of variances.

Clutch Manipulation Data

For purposes of analysis, growth data from hatching to fledging for chicks in experimental, natural, and control nests were divided into twelve time intervals, with each interval consisting of at least three days. By pooling the data in this manner, differences between groups within each time interval could be analyzed separately, over time. The analyses were conducted with one-way analysis of variance (ANOVA).

An index of growth rate was calculated using the logistic equation (Ricklefs, 1967) from weights of birds which had attained an age of at least 21 days. The logistic equation transforms growth curves into straight lines which are proportional to the overall growth rate. This particular equation was chosen because, by eye, it appeared to best fit the observed growth curve of Pigeon Guillemot chicks. Growth rate indices calculated from the

experimental, natural and control nests were then analyzed with a one-way ANOVA. Subsequent analyses of hatching, fledging and egg success for all nests were conducted with a chi-squared test.

Comparative Data

Data analyses of differences in clutch size were conducted using a row x column G-test of independence (see Sokal & Rohlf, 1981) to establish if the proportion of one and two egg clutches differed among the four years compared. Subsequently, pairwise standard G-tests of independence were performed to determine which among the four years was responsible for the differences observed.

Hatching, fledging and egg success were analyzed with the Mann-Whitney U Test as were the egg morphometric data. To test the significance of correlations between egg volume and hatching and fledging success, a Kendall rank correlation test was performed.

CHAPTER III

RESULTS

Clutch Size Manipulations

Growth of Chicks

Growth curves derived from measurements of weight, and from wing, culmen and tarsus lengths of chicks from experimental, natural and control nests are shown in Figures 2 and 3. F-ratios from the one-way analyses of variance for growth data performed on each of the twelve time periods are presented in Table 1. Because of the number of analyses performed on the data set, I adjusted the P value to $\alpha = 0.0025$. There were no significant differences observed in weight, nor in growth of wing, culmen, and tarsus lengths for chicks from the five nest groups. Mean values for these parameters at fledging for each group are presented in Table 2.

An index of growth rate was calculated for chicks from the five nest groups. Figure 4 shows a plot of the weight curves transformed into straight lines using the logistic equation (Ricklefs, 1967). Chick growth rates are proportional to the slope of the lines (Table 3). Results from the one-way analysis of variance testing differences in

Figure 2.   Growth curves for weights of chicks from
              experimental, natural, and control nests.
              Differences were not significant for the five
              nest groups.   Error bars represent 95%
              confidence intervals.
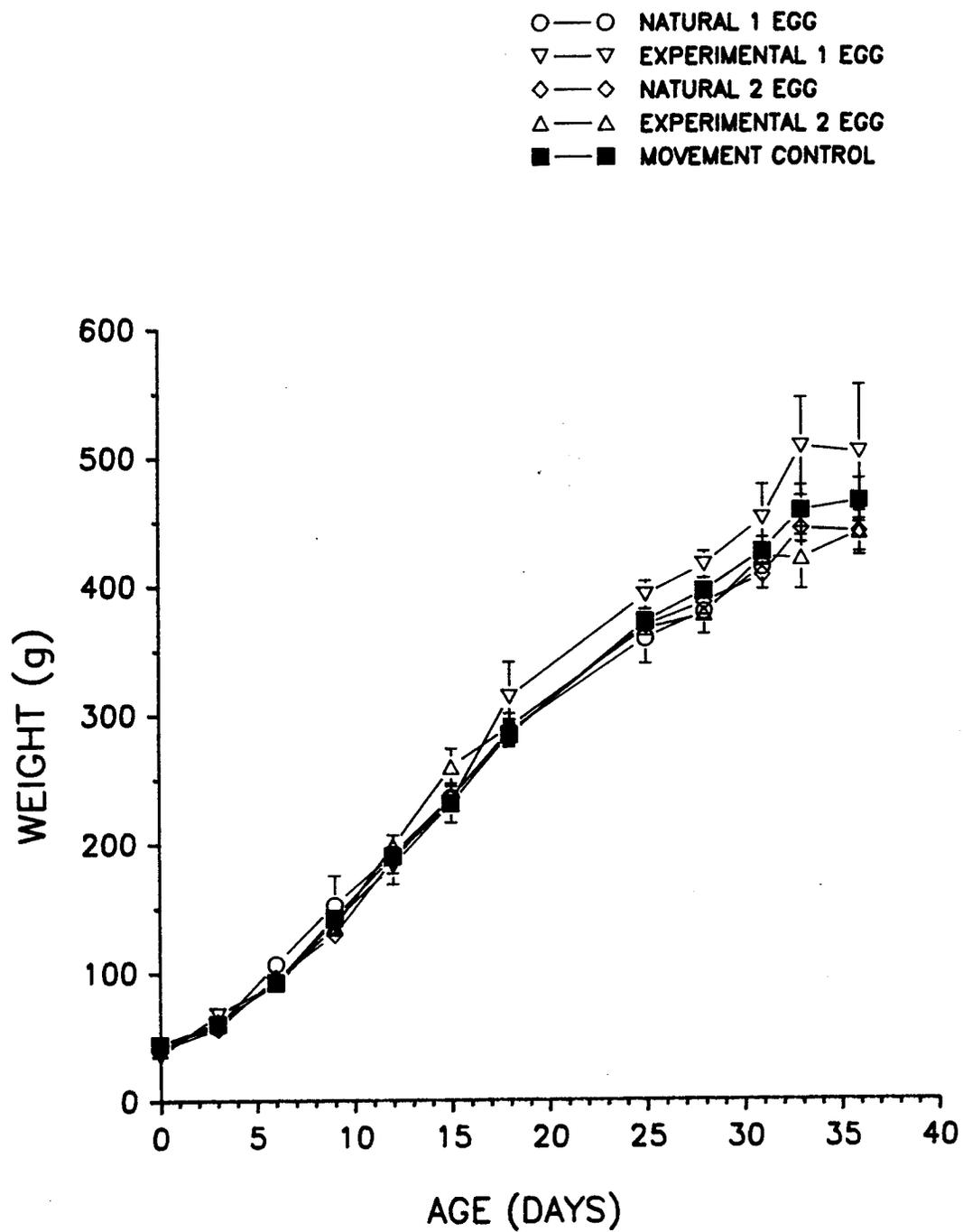
Figure 3.   Growth curves for wing, culmen, and tarsus
             lengths of chicks from experimental, natural,
             and control nests. Differences were not
             significant.
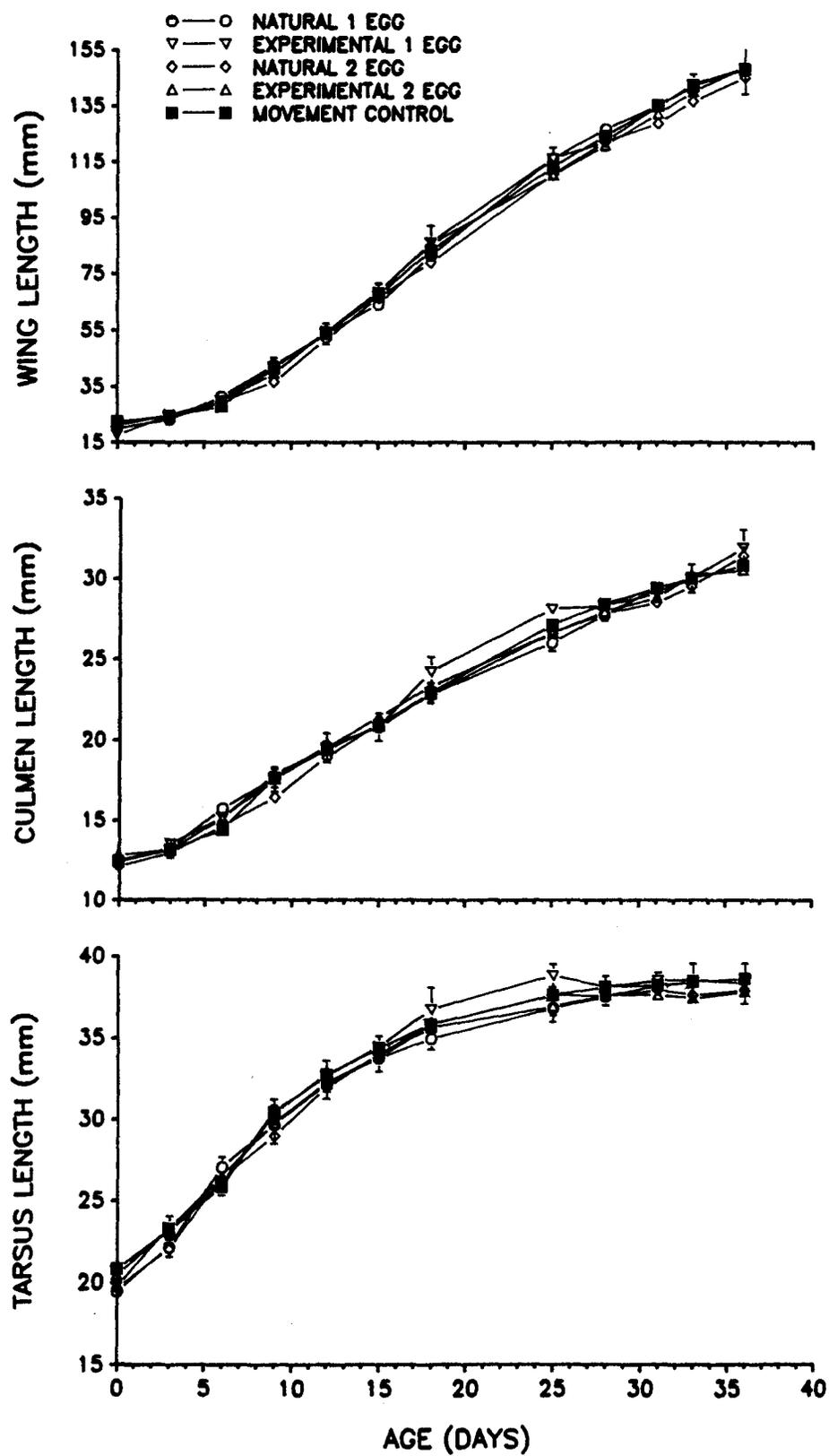
Table 1. F-ratios of ANOVAs performed on growth data for
chicks from experimental, natural, and control nests

Age (df)	Weight	Wing	Culmen	Tarsus
0-2 $_{(4,24)}$	1.82	2.19	4.34	–
3-5 $_{(4,56)}$	1.48	1.08	0.57	2.67
6-8 $_{(4,53)}$	0.94	1.95	1.94	0.73
9-11 $_{(4,51)}$	1.31	3.35	2.90	3.20
12-14 $_{(4,46)}$	0.31	0.30	0.51	0.65
15-17 $_{(4,42)}$	1.18	0.33	0.24	0.49
18-20 $_{(4,34)}$	0.47	0.98	0.61	0.60
21-23 $_{(4,31)}$	0.67	1.25	2.32	2.01
24-26 $_{(4,39)}$	1.25	0.76	0.77	0.92
27-29 $_{(4,36)}$	1.50	2.21	1.43	1.07
30-33 $_{(3,24)}$	1.97	1.64	0.60	1.82
34-36 $_{(3,33)}$	0.89	0.98	0.66	1.27

Note. Degrees of freedom are in parentheses.
Differences were not significant.

Table 2. Means for weight, wing, culmen, and tarsus length
of chicks at fledging from experimental,
natural and control nests

Nest Group	N	Weight (g)	Wing (mm)	Culmen (mm)	Tarsus (mm)
Natural 1 Egg	3	410 (30)	135.0 (4.36)	29.4 (0.75)	38.2 (0.32)
Exper. 1 Egg	6	490 (55)	145.3 (10.7)	30.7 (1.84)	38.4 (1.36)
Natural 2 Egg	15	437 (46)	145.3 (10.2)	30.3 (1.32)	38.2 (0.88)
Exper. 2 Egg	7	436 (57)	149.8 (4.60)	30.7 (1.10)	37.6 (1.17)
Movmnt. Control	10	448 (46)	144.9 (7.66)	30.4 (0.90)	38.5 (0.92)

Note. Standard deviations are in parentheses.

23

Figure 4.   Growth rates calculated from weights of chicks
            from experimental, natural, and control nests.
            Growth rates (slopes) for each group were not
            significantly different.

——	NATURAL 1 EGG = 0.181
· · · ·	EXPERIMENTAL 1 EGG = 0.162
— · —	NATURAL 2 EGG = 0.158
— — —	EXPERIMENTAL 2 EGG = 0.155
— · ·	MOVEMENT CONTROL = 0.154
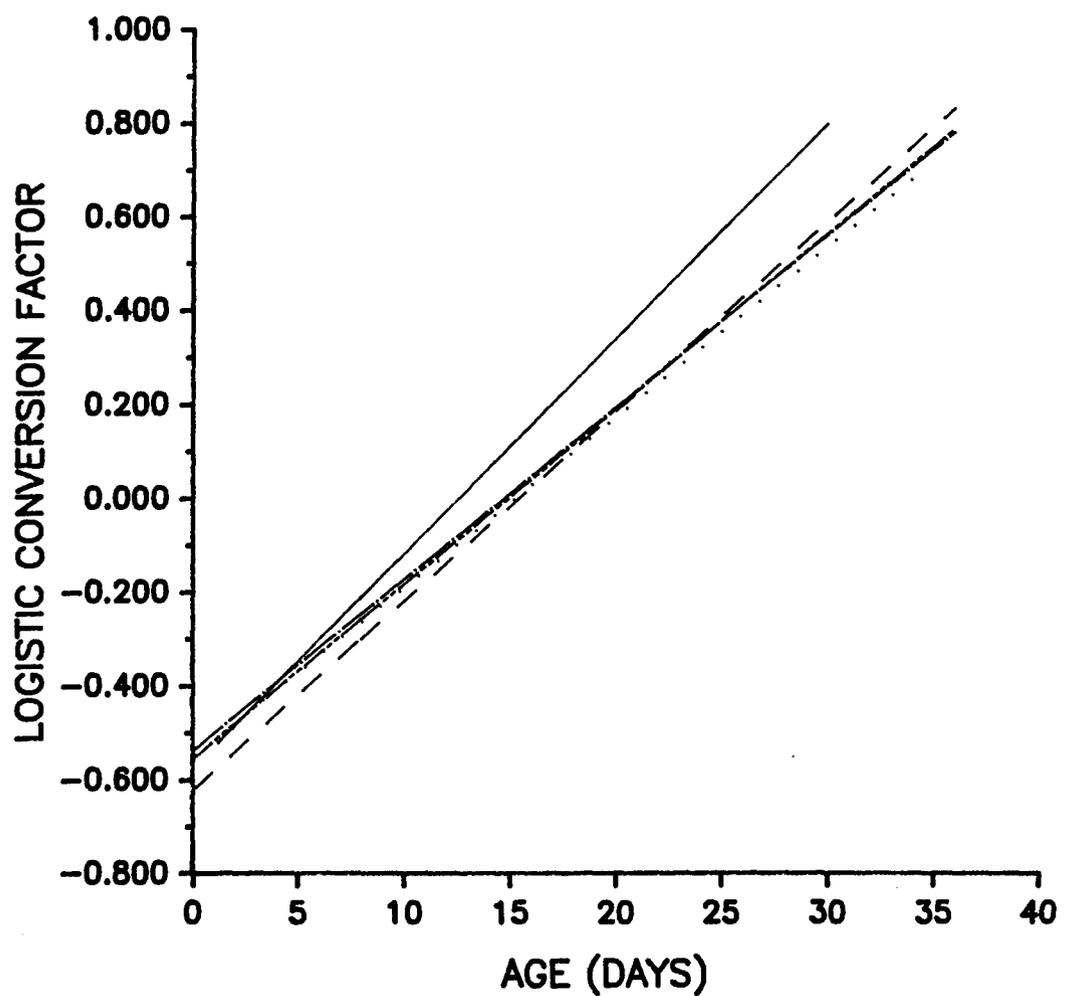
Table 3. Growth rate constants for chicks from
experimental, natural, and control nests

Nest Group	N	Growth Rate Constant (K)
Natural 1 Egg	3	0.181(0.023)
Experimental 1 Egg	6	0.162(0.022)
Natural 2 Egg	15	0.158(0.017)
Experimental 2 Egg	8	0.155(0.011)
Movement Control	10	0.154(0.017)

Note. Standard deviations are in parentheses.
Differences were not significant.

these slopes indicate that differences in growth for Pigeon Guillemot chicks from experimental, natural, and control nests were not significant ($F_{(4,37)}=1.68$, $P=.176$).

Hatching, Fledging, and Egg Success

The percentages of chicks which hatched successfully were not significantly different for the five nest groups ($X^2=8.38$, $p>.05$, $df=4$). This was also true of fledging success ($X^2=0.17$, $p>.05$, $df=4$) and egg success ($X^2=2.96$, $p>.05$, $df=4$) (Table 4).

Between Year Comparisons

Clutch Size

The row x column G-test of independence indicates that there were significant differences in the proportions of one and two egg clutches among the four years analyzed ($G=7.93$, $P<.025$, $df=3$) (Figure 5). Standard G-tests of independence were subsequently performed to determine how the four years differed from each other (Table 5). A comparison of the proportions of one and two egg clutches in 1983 and 1984 indicate that there were no significant differences between these two years ($G=0.813$, $P>.05$, $df=1$). However, a comparison between 1984 and 1985 showed that the proportion of two egg clutches was significantly higher in 1984 ($G=5.74$, $P<.025$, $df=1$). No significant differences were

Table 4. Comparison of hatching, fledging and egg success
for chicks from experimental, natural, and control nests

Nest Group	No. of Eggs	% Hatch	% Fledge	% Egg
Natural 1 Egg	9	56	60	33
Experimental 1 Egg	11	81	74	56
Natural 2 Egg	40	87	68	60
Experimental 2 Egg	20	65	69	45
Movement Control	24	87	67	58

Note. Differences were not significant.

Figure 5.   Comparison of one and two egg clutches for
             four years. There was a significant
             difference in the proportion of one and two
             egg clutches in 1984 and 1985 (G=7.93, P<.025,
             df=3).
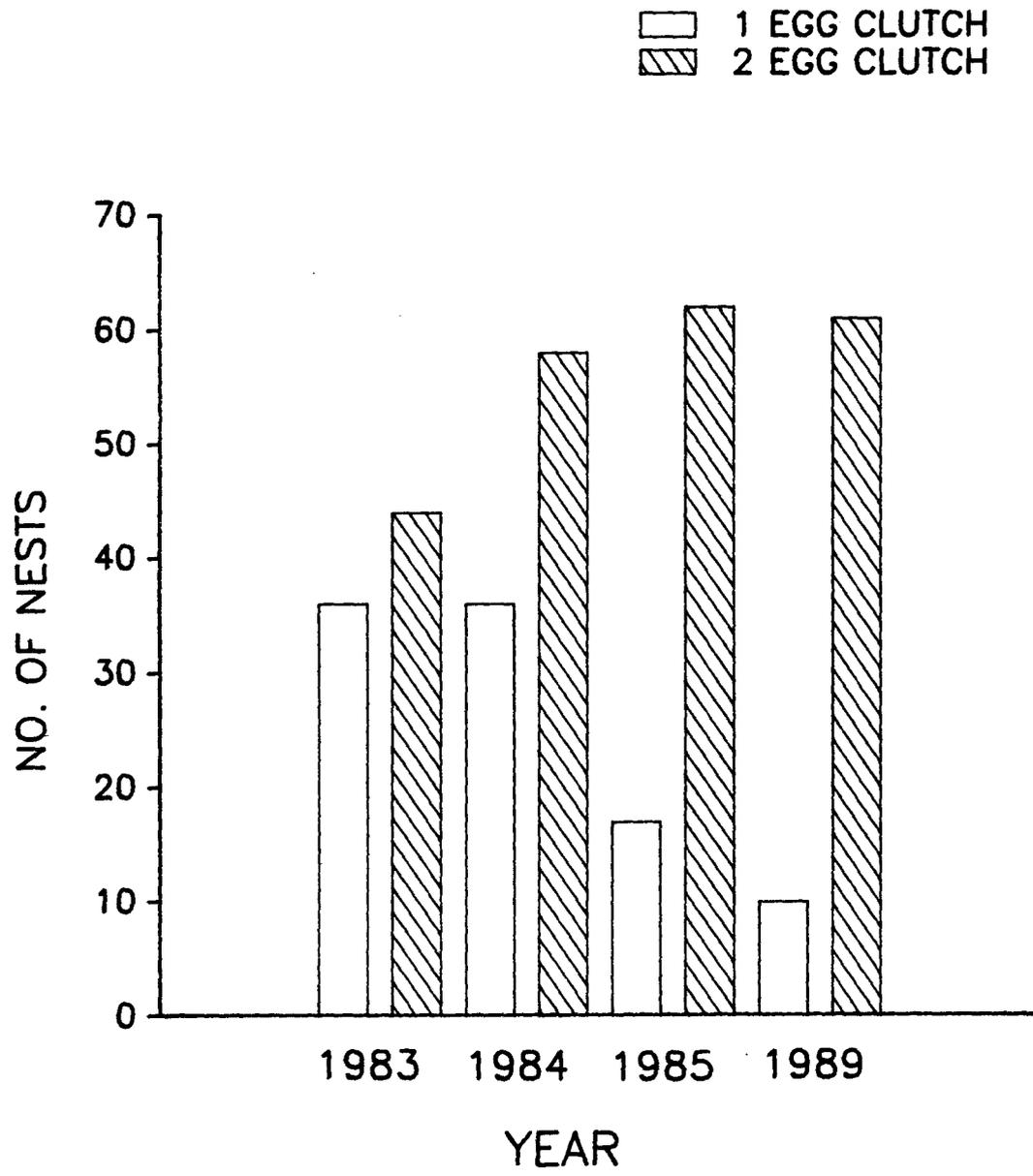
Table 5.   Comparison of proportions of one and two egg
clutches

Year	1 Egg	2 Egg	G	P.
1983	36	44	0.813	NS
1984	36	58		
1984	36	58	5.735	P<.025
1985	17	62		
1985	17	62	1.390	NS
1989	10	61		

Note.   NS - nonsignificant.

observed when 1985 and 1989 were compared (G=1.39, P>.05, df=1).

Hatching, Fledging, and Egg Success

Hatching success for one and two egg clutches in 1983, 1984, 1985, and 1989 are presented in Table 6. Significant differences in hatching success were observed between one and two egg clutches in 1985 (U=368.0, P=.035, df=1) and in 1989 (U=207.5, P=.045, df=1), with two egg clutches being more successful in both cases. However, the differences in hatching success between one and two egg clutches were not significant in 1983 (U=714.0, P=.395, df=1) nor in 1984 (U=995.0, P=.662, df=1) (Figure 6).

Fledging success was analyzed for one and two egg clutches in 1983, 1984, and 1989 (Table 7). For all years, mean fledging success was higher for chicks from two egg clutches, although the differences were not significant. (Figure 7).

Egg success was analyzed in 1983, 1984, and 1989 (Table 8). As with fledging success, mean egg success was higher for two egg clutches, however the differences were not significant (Figure 8).

Egg Morphometrics

Differences in egg volume for one and two egg clutches

Table 6. Comparison of mean hatching success
for one and two egg clutches

Year	Clutch Size	N	% Hatched	U
1983	1	36	58(25)	714.0
	2	44	71(14)	
1984	1	36	64(24)	995.0
	2	58	72(13)	
1985	1	17	30(11)	368.0*
	2	62	57(06)	
1989	1	10	50(17)	207.5*
	2	61	82(04)	

Note. Standard deviations are in parentheses.

* Significant at $\alpha = 0.05$.

33

Figure 6. Comparison of mean hatching success for one and two egg clutches. Differences were significant in 1985 (U=368.0, P=.035, df=1) and 1989 (U=207.5, P=.045, df=1). Error bars represent 95% confidence intervals.
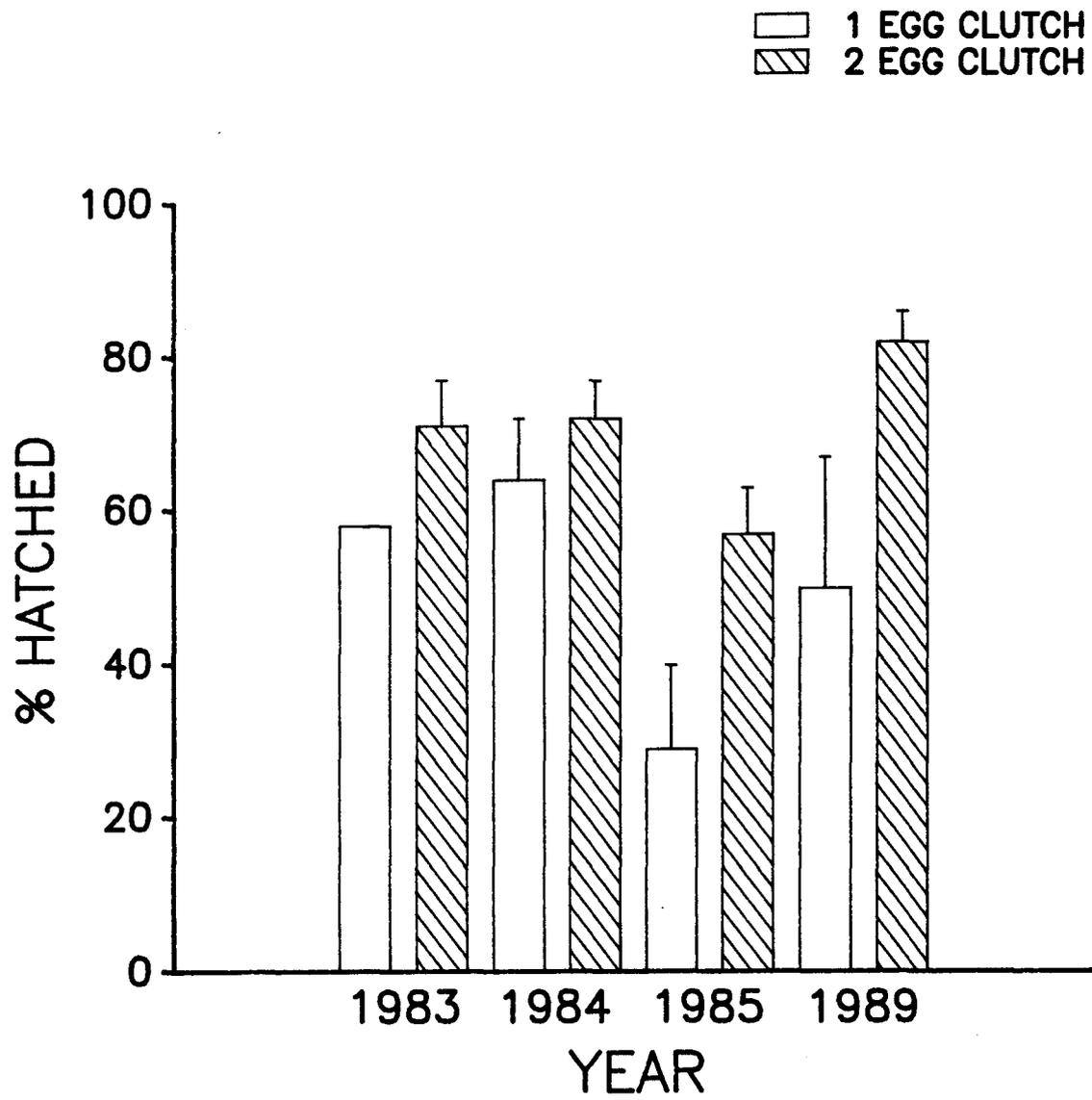
Table 7. Comparison of mean fledging success for chicks
from one and two egg clutches

Year	Clutch Size	N	% Fledged	U
1983	1	35	43(25)	620.0
	2	43	58(17)	
1984	1	36	39(24)	855.0
	2	58	53(15)	
1989	1	15	40(26)	271.5
	2	49	63(16)	

Note. Standard deviations are in parentheses.
Differences were not significant.

Figure 7.   Comparison of mean fledging success for chicks
             from one and two egg clutches. Differences
             were not significant.
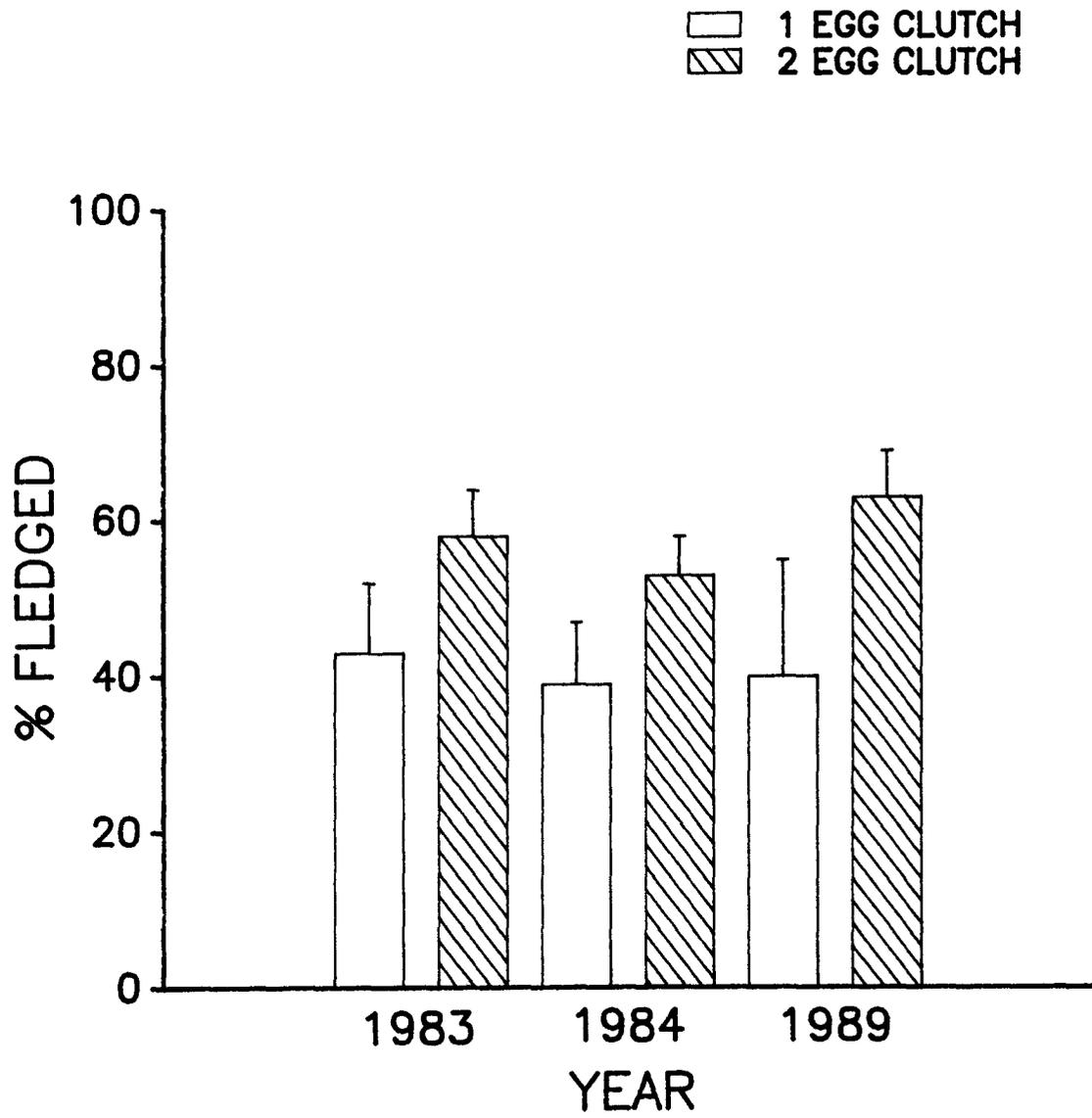
Table 8. Comparison of mean egg success for chicks from
one and two egg clutches

Year	Clutch Size	N	% Egg	U
1983	1	35	43(25)	680.0
	2	43	49(13)	
1984	1	36	39(24)	918.0
	2	58	45(11)	
1989	1	10	30(23)	155.5
	2	49	59(15)	

Note. Standard deviations are in parentheses.
Differences were not significant.

Figure 8.   Comparison of mean egg success for one and two
             egg clutches.   Differences were not
   significant.
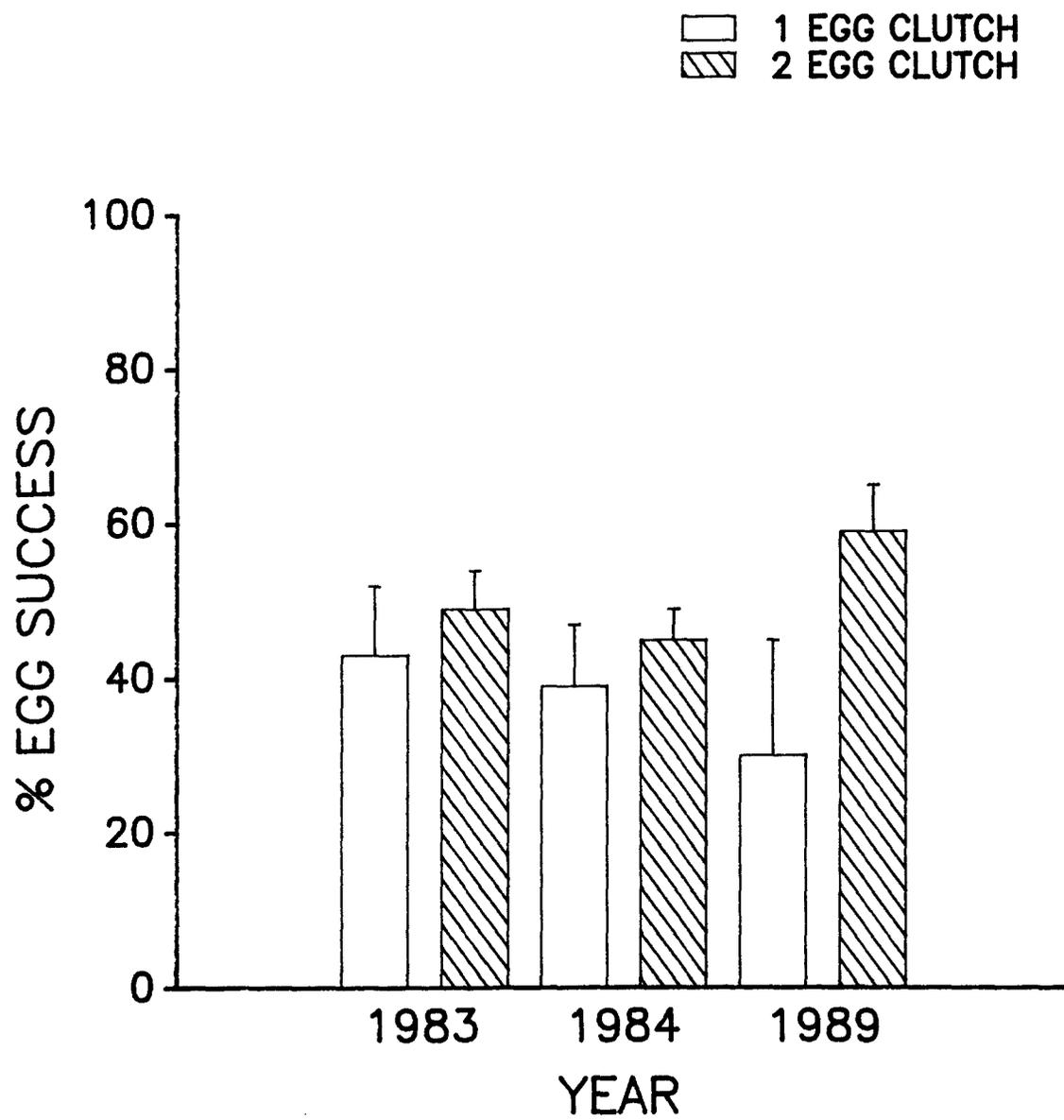
were tested in 1983, 1984 and 1989 with a Mann-Whitney U test (Figure 9). Eggs from two egg clutches were significantly greater in volume than those from one egg clutches in 1983 (U=585.5, P=.046, df=1) and in 1984 (U=606.0, P=.002, df=1). In 1989, however, the difference was not significant (U=549.5, P=.321, df=1) (Table 9).

Egg Volume Vs. Hatching and Fledging Success

The Kendall rank correlation test for 218 observations of egg volume and hatching success indicate no significant correlation (tau=0.75, P=0.46). However, there is a significant correlation between egg volume and fledging success (tau=2.52, P=0.043).

Figure 9.   Comparison of mean egg volume for eggs from
            one and two egg clutches. Egg volume was
            significantly greater in two egg clutches in
            1983 (U=585.5, P=.046, df=1) and 1984
            (U=606.0, P=.002, df=1).
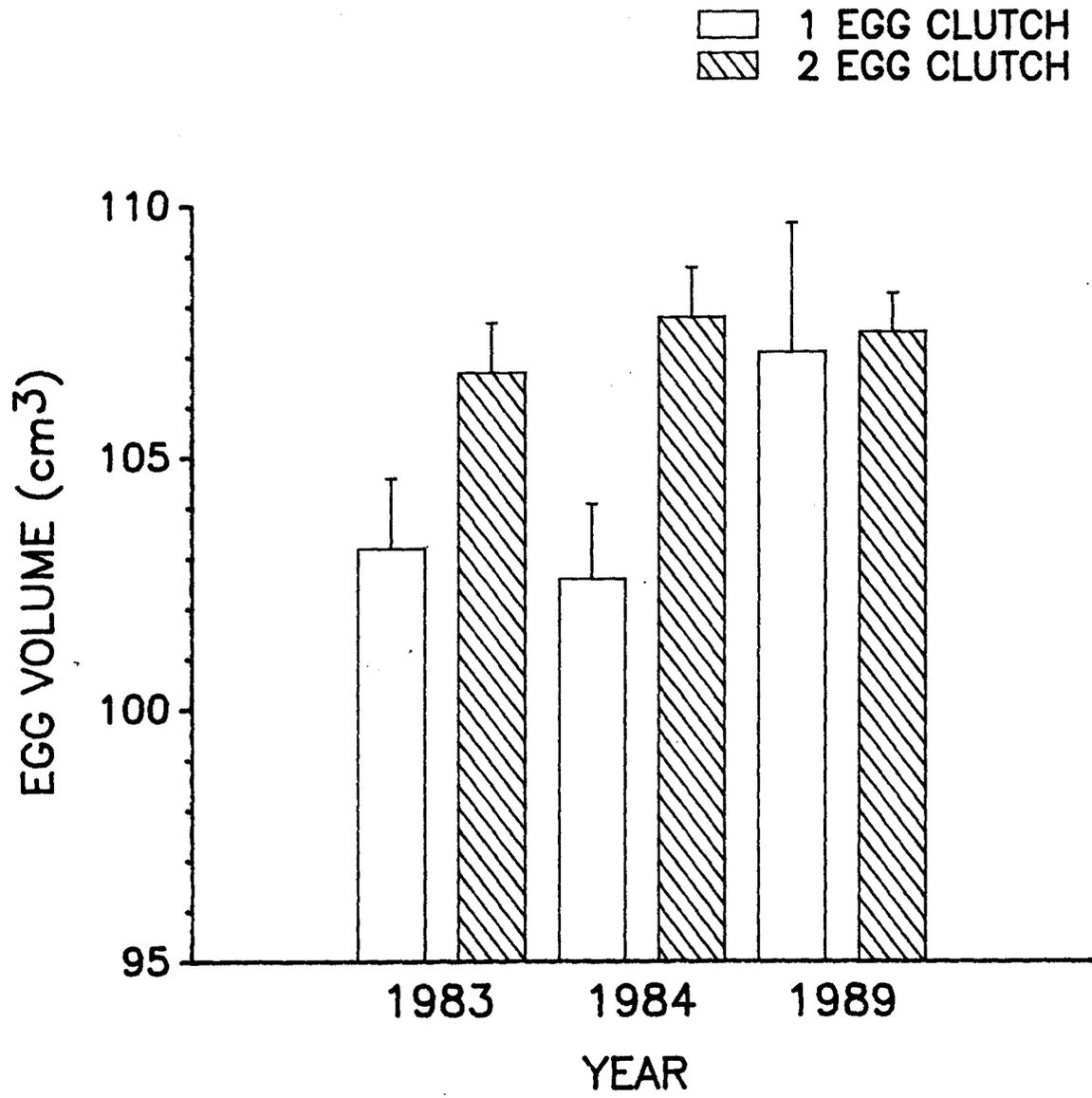
Table 9.   Comparison of mean egg volume for one and two egg
clutches

Year	Clutch Size	N	Egg Volume	U
1983	1	36	103.2 (69.5)	585.5*
	2	44	106.7 (43.5)	
1984	1	33	102.6 (73.6)	606.0*
	2	60	107.8 (58.3)	
1989	1	19	107.1 (125.6)	549.5
	2	68	107.5 (39.8)	

Note.   Standard deviations are in parentheses.

* Significant at $\alpha = 0.05$.

CHAPTER IV

DISCUSSION

Clutch Size Manipulations

Growth

The results of this study have shown that there were no significant differences in weight, nor in growth of wing, culmen, and tarsus lengths for Pigeon Guillemot chicks from experimental, natural, and control nests at Sitka Dock. These findings show unequivocally that adult Pigeon Guillemots which lay only one egg are capable of rearing two chicks equal in quality to chicks from natural two egg clutches.

Past clutch manipulation experiments in which chick growth was measured have produced varying results. For example, Shifferli (1978) conducted experiments with the House Sparrow Passer domesticus in which brood sizes were manipulated within the naturally occurring range. For this passerine, broods that were experimentally increased experienced higher mortality and chicks weighed less at fledging than control broods. Comparable results were found in an experiment with the Tree Swallow Iridoprocne bicolor (DeSteven, 1980).

Similar findings have been observed for seabirds. In a study of the Kittiwake Rissa tridactyla (Lack, 1966) in which brood sizes were manipulated within and above the normal range, more young were fledged in augmented broods, but they experienced retarded growth which may have reduced post-fledging survival. Clutch size manipulation studies conducted with four species of gulls (Harris & Plumb, 1965; Coulter, 1973; Haymes & Morris, 1977; Reid, 1988) have shown that adults are capable of fledging more chicks than they normally produce. However, as with Kittiwakes, the gull chicks experienced reduced growth rates, and were lighter at fledging than those of natural broods. Experiments conducted with the Black Guillemot, Cepphus grylle, (Asbirk, 1979; Peterson, 1981), an alcid closely related to the Pigeon Guillemot, showed that chicks hatched from experimental three egg clutches also experienced reduced growth rates.

The experiments mentioned above present results which contrast my findings with Pigeon Guillemots. However, there have also been clutch manipulation studies which have yielded results similar to mine. For example, in a study with the Red-winged Blackbird Agelaius phoeniceus in which brood sizes were enlarged above the naturally occurring range, no significance differences in weight nor in skeletal growth for chicks from natural and experimental nests were reported (Cronmiller & Thompson, 1980). A study with

House Wrens <u>Troglodytes</u> <u>aedon</u> (Finke et al., 1987)
determined that weights of chicks at fledging from
experimental broods enlarged above the natural range, were
not significantly different from weights of chicks from
control nests. Thus, the authors concluded that the wrens
were withholding reproductive effort, for reasons which they
could not determine.

There are also similar data for seabirds. Studies of
Northern Gannets <u>Sula</u> <u>bassana</u> (Nelson, 1964) and Lesser
Black-backed Gulls <u>Larus</u> <u>fuscus</u> (Harris & Plumb, 1965) have
shown that chicks from broods which were experimentally
enlarged above the natural range reared more young which
fledged at weights not significantly different from chicks
in natural broods.

Hatching, Fledging, and Egg Success

Results of the analyses of hatching, fledging, and egg
success indicate that experimentally altered clutch sizes of
Pigeon Guillemots were not significantly different from
natural and control nests. Past studies which have examined
these parameters for manipulated clutches show no consistent
patterns. For example, in a study of the Little Penguin
<u>Eudyptula</u> <u>minor</u>, for which the natural clutch size is two,
clutches of one, two, and three eggs were established (Dann,
1988). There were no significant differences reported for
hatching, fledging, or egg success between any clutch size.

Conversely, a study with the Long-tailed Jaegar *Stercorarius longicaudus* (Andersson, 1976) found that hatching, fledging, and egg success were dramatically reduced for clutches larger than two. The results in this instance were attributed in part to the inability of the adults to incubate more than two eggs.

Variations in results of clutch size manipulations indicate that there are several processes operating in the ultimate determination of clutch size in birds. Thus, Lack's food limitation hypothesis (1947) may explain the clutch sizes observed in certain species under certain conditions, but it can not be generalized for the evolution of clutch size in all species.

At this juncture, a note of caution regarding the interpretation of these studies with respect to my own must be made. In most of the above cases, clutches or broods were manipulated to sizes greater than the naturally occurring range. It is possible that this confers a disadvantage upon the overall reproductive success observed because the adults are not normally confronted with an energy demand of this degree. This may explain why the clutch size manipulation experiments with Black Guillemots (Asbirk, 1979; Peterson, 1981) reported reduced growth rates and decreased hatching, fledging, and egg success, while my own study did not. It is also possible that while adults may be capable of rearing additional

chicks, they may be physically incapable of laying additional eggs. This might explain why some species maintain constant or show increased reproductive success from augmented clutch sizes.

The appropriate question to answer here is why some Pigeon Guillemots lay only one egg. Lack's food limitation hypothesis (1947) is not supported by the results of this study and thus does not provide a plausible explanation. It is clear that in 1989, when my experimental manipulations were performed, the environmental food supply was adequate and that adults of experimental two egg clutches were able to respond to the increased food demands of another chick. This type of behavior has been documented in earlier studies with Pigeon Guillemots in which parents were shown to respond to increased hunger needs of chicks by increasing foraging efforts (Drent et al., 1964; Aitchison, 1972).

There are other hypotheses which may expain the findings of this study. The first of these, the parental mortality hypothesis (Williams, 1966; Charnov & Krebs, 1974), states that there may be some adverse effect on the future reproductive potential of the adults in rearing larger clutches. This has been shown for Blue Tits (Nur 1984) and for Rooks (Roskaft, 1985). In this case, the threshold at which egg formation stops is determined by a trade-off between current reproductive effort and future expectations of reproduction (Winkler, 1985). I do not have

data to support or reject this hypothesis for the Pigeon Guillemot, however, the increased energy demands of rearing an additional chick could result in adults being unable to reach a satisfactory physical condition for the oncoming winter, a time of extreme physiological stress for alcids. Selection then, would favor a smaller clutch size for guillemots which are in poorer overall condition.

It is also possible that female Pigeon Guillemots are unable to lay two eggs in years when food availability is low (Perrins, 1970). It has been demonstrated that clutch size for several species of seabirds and geese is affected by female condition at the time of egg formation (Nisbet, 1977; Ankney & MacInnes, 1978; Drent & Dann, 1980; Houston et al., 1983).

Another possible hypothesis is that those Pigeon Guillemots which lay one egg are, in fact, younger than the birds which lay two. The observation that young birds lay smaller clutches has been documented in several species (Coulson & White, 1958; Pugesek, 1981; Curio, 1983) although this has not been reported for Pigeon Guillemots. Young birds may have a lower foraging efficiency and may suffer from poorer access to nest sites due to competition with older, more experienced birds (Curio, 1983). This hypothesis seems quite reasonable for the Pigeon Guillemot which is a long-lived seabird. Members of the genus <u>Cepphus</u>

are thought to attain breeding age at three years, and to
continue to rear chicks until scenescence occurs (Peterson,
1981). Thus, it may take several years for guillemots to
reach a level of breeding competence to where two eggs can
be laid.

Although the majority of the population at Sitka Dock
is banded, I could not determine ages of the adults in my
study because I was unable to capture them. This
information would be extremely useful in determining the
importance of the age hypothesis for the evolution of clutch
size in Pigeon Guillemots.

The final hypothesis I will address here is the
possibility that clutch size in Pigeon Guillemots is
determined by territory or nest site quality (Hogstedt,
1980). This hypothesis, developed for territorial birds,
states that the optimal strategy for birds is to be highly
flexible in the choice of clutch size, such that it is
possible to adapt to available resources. Territory quality
will be the most important factor in determining the optimal
clutch size. Although Pigeon Guillemots are not highly
territorial birds, I believe this hypothesis merits
discussion because of the nature of the nest sites at Sitka
Dock.

While I did not measure nest quality, it was apparent
to me during the course of my study that certain portions of
Sitka Dock are better suited for nests than others. Areas

where the wood is rotten and holes could be excavated were heavily utilized by the guillemots, and these areas produced high numbers of successful two egg clutches. In contrast, portions of the dock which were in better condition (i.e., the wood was not rotten) did not contain as many nests. Eggs laid in these areas often disappeared or were abandoned shortly thereafter. Presumably, the birds responsible for these eggs experienced lower reproductive success, but may have been forced to lay eggs there due to strong competition for the better nest sites.

Ewins (1986) has shown that hatching and fledging success for Black Guillemots in Shetland was correlated to various physical parameters of the nest cavities. This is probably also true for Pigeon Guillemots. However, it seems less plausible to postulate that the initial clutch size is determined by nest site quality, as Hogstedt (1980) maintains. More likely, it is the younger birds which lay eggs in poor quality nests, and this, combined with their breeding inexperience, reduces breeding success for these birds.

An ancillary result of the clutch size manipulations I performed is that Pigeon Guillemots do not appear to recognize their own eggs. Egg recognition has been documented in Common Murres *Uria aalge* (Tschanz, 1959) and in Thick-billed Murres *Uria lomvia* (de Forest & Gaston, 1990), both alcids. Until now, this question had never been

addressed for the Pigeon Guillemot.

Between Year Comparisons

Clutch Size

The data derived from four years of monitoring clutch sizes for Pigeon Guillemots at Sitka Dock have shown that there were significant differences in the proportion of one and two egg clutches between these years. The recorded frequency of one egg clutches in Pigeon Guillemots is 7-21% (Thoresen & Booth, 1958; Drent et al., 1964) however in 1983 and 1984, the proportion of one egg clutches at Sitka Dock was 36%. This may be attributable to the occurrence of the 1982-1983 El Niño, which increased sea surface temperatures during these two years and was associated with a markedly adverse effect on seabird reproduction and mortality in Oregon (Hodder & Graybill, 1985). This is further substantiated by the fact that the highest number of dead Pigeon Guillemot chicks in five years was recorded during 1983 (Hodder & Graybill, 1985). In addition, reproductive success, as determined by the number of nests and the mean clutch size, at Sitka Dock during 1983 was significantly lower than in 1982 (Hodder & Graybill, 1985).

Coulson and Porter (1985) have stated that for the Kittiwake, clutch size is an indicator of parental quality. This may also be true for the Pigeon Guillemot. The fact

that my results show the proportion of one egg clutches to be significantly higher in 1983 and 1984 than in 1985 and 1989 suggests that the El Niño had an effect on parental quality, which subsequently affected reproductive success and lowered the mean clutch size. In 1985, reproductive output began to rebound which suggests that environmental quality, and thus, parental quality, began to improve.

One last hypothesis with respect to the differences I observed in clutch size should be discussed. That is that these differences were in fact due to the age structure of the population at each time. It has been shown for several species that young birds produce smaller clutch sizes and breed later in the season than older, more experienced birds (Coulson & White, 1958; Pugesek, 1981; Curio, 1983). If there were a large number of first or second time breeders at Sitka Dock in 1983 and 1984, this could account for the increased number of one egg clutches in these years, and the subsequent increase in two egg clutches as that cohort of breeders matured.

Hatching, Fledging, and Egg Success

Hatching success for Pigeon Guillemots at Sitka Dock was measured in 1983, 1984, 1985 and 1989. Contrary to my expectations, hatching success for one egg clutches in 1983 and 1984 was significantly higher than in 1985 and 1989. The mean hatching success for one and two egg clutches for

the four years was 50.5% and 70.5% respectively. These results are surprising, for given the El Niño event of 1982-1983, the opposite might have been expected.

A possible explanation of these results could be that, due to a low availability of food caused by the El Niño, experienced birds, which under normal circumstances would lay two eggs, were in fact laying only one. Given that these birds would be experienced breeders, it is likely that their chances of successfully incubating the egg until it hatched would be higher than for inexperienced birds. Thus, the hatching successes reported for one and two egg clutches in 1985 and in 1989 may be representative of a more normal situation.

Peterson (1981) reported a mean hatching success of 59% for one egg clutches and 82.5% for two egg clutches of Black Guillemots on Flatey Island in Iceland. These figures are considerably higher than those reported here for Pigeon Guillemots. Cairns (1981) however, reported hatching success of 32% and 58% for one and two egg clutches of Black Guillemots in Quebec, figures which more closely match my own.

Fledging success for Pigeon Guillemots at Sitka Dock was not significantly different in the three years analyzed. In all cases, two egg clutches were more successful. The mean fledging success for the three years studied was 37.3% for one egg clutches and 58% for two egg

clutches. Peterson (1981) reported fledging successes of
84.7% for one egg and 86.7% for two egg clutches of Black
Guillemots, values which seem extraordinarily high. Cairns
(1981) however, reported fledging successes of 38% for one
egg and 65% for two egg clutches of Black Guillemots in
Quebec. Again, these values are similar to mine.

While none of the data for fledging success are
significant, certain trends seem to be apparent. For
example, fledging success in 1989 was elevated above 1983
and 1984. The increased success of two egg clutches in 1989
may have been due to abundant prey resources, as evidenced
by the high number of two egg clutches laid. Fledging
success for one egg clutches decreased slightly in 1984 and
1989. As discussed for hatching success, this trend could
be a result of the El Niño, which may have caused
experienced birds to lay only one egg.

The patterns described above in hatching and fledging
success were also apparent in egg success. Egg success for
two egg clutches in 1989 was elevated above levels observed
in 1983 and 1984, which I attribute to environmental
quality. As with hatching success, egg success for one egg
clutches in 1983 and 1984, was higher than in 1989, which I
attribute to the El Niño. While fledging success for one
egg clutches was fairly constant, egg success, which
incorporates both hatching and fledging success, appeared to
show the effects of the El Niño more readily. Annual

differences in the breeding or egg success of alcids have been shown to be due, in large part, to the availability of food (Harris, 1980; Harris & Hislop, 1978). A plausible consequence of the El Niño event would have been a reduction in prey items within the Coos Bay estuary. This then, could explain the seemingly anomalous patterns for hatching, fledging, and egg success observed in this study for Pigeon Guillemots.

Egg Volume

Egg volume for one and two egg clutches was analyzed in 1983, 1984 and 1989. Egg volume for one egg clutches was significantly lower than for two egg clutches in 1983 and 1984. In 1989, however, egg volumes overall were considerably greater, and there was only a slight, non-significant difference between the two clutch sizes.

The physiological condition of the female at the time of egg formation has been shown to have an effect on egg volume in several species (Price et al., 1988; Pettifor et al., 1988; Reid & Boersma, 1990). It is possible that female Pigeon Guillemots, in poor condition in 1983 and 1984 due to the El Niño, might have laid smaller eggs and a higher percentage of one egg clutches in those years. A correlation between age and egg volume has been observed for the Herring Gull *Larus argentatus* (Davis, 1975) and for the Kittiwake (Thomas, 1983). It may therefore be reasonable to

suggest that it was not only experienced yet physically taxed birds, but also younger birds which were responsible for the lower egg volumes observed in 1983 and 1984.

The fact that egg volume for one egg clutches increased so dramatically in 1989 lends further support to the suggestion that prey were abundant either during the breeding season or in the winter prior to laying. As mentioned previously, there was a high number of two egg clutches in 1989, which may be an indicator of enviromental. quality. If this were the case, then even younger or "poor quality" adults would have experienced less difficulty foraging and may have also had sufficient reserves to form larger eggs.

Egg Volume vs. Hatching and Fledging Success

Egg volume was not shown to have an effect on hatching success for Pigeon Guillemots at Sitka Dock in 1983, 1984, and 1989. This finding is in agreement with other studies (Schifferli, 1973; Ollason & Dunnet, 1986; Reid & Boersma, 1990) and seems to make sense. The ability of a chick to hatch is not likely to be influenced by the volume of the egg it originated from. The act of hatching is probably relatively easy when compared to survival in the nest and on the open ocean. It is in these later stages of the chick's life-cycle where egg volume might be expected to have an effect.

In accordance with the above hypothesis, a correlation test was performed on egg volume and fledging success and there was a significant positive correlation between the two parameters. Several studies have documented this relationship (Schifferli, 1973; Davis, 1975; Hogstedt, 1981), however a controversy exists as to whether it can be attributed to the actual volume of the egg or to the quality of the parent which laid it (Nisbet, 1978; Reid & Boersma, 1990).

In a recent study of the role of egg size in hatching and fledging success in the Magellanic Penguin <u>Spheniscus</u> <u>magellanicus</u> (Reid & Boersma, 1990), this problem was addressed by manipulating eggs among nests. This served to reduce the covariation between egg volume and parental quality. The results indicated that egg size was not correlated to overall fledging success, but instead influenced chick mass and size for the first ten days after hatching. After that time, effects of egg size were not detected.

My data on egg volume and fledging success for Pigeon Guillemots do not test whether the positive correlation is determined by maternal quality or by the actual size of the egg itself. This information could easily be gathered for Pigeon Guillemots at Sitka Dock and would provide valuable insight into the question of egg size and breeding success.

Conclusions

Clutch Size Manipulations

The clutch size manipulation experiments performed with Pigeon Guillemots have shown that birds which lay only one egg can successfully rear two chicks. This finding disproves Lack's food limitation hypothesis (1948) for this species. Other hypotheses have been presented which may explain the observed results. My data, however, are not sufficient at this time to discern which of these best interprets the findings of this study.

The factors which determine clutch size in Pigeon Guillemots would be elucidated by future studies focusing on reproductive success in adults of known age. As mentioned previously, much of the population at Sitka Dock is banded. If a means of capturing adults on the nest could be developed, the age of those birds which were banded could be determined. This would enable us to know if young birds experience lower reproductive success. Then, if reproductive success was monitored in future years, the annual clutch size for an individual could be documented. This information, in conjunction with data regarding environmental quality would provide insight as to whether birds adjust clutch size to balance future reproductive success with current reproductive output.

Between Year Comparisons

The between year comparisons of reproductive success have provided an opportunity to observe these parameters in years when environmental quality was known to be poor, versus years in which food was probably more abundant. Based on the results presented in this study, an hypothesis regarding the reproductive performance of Pigeon Guillemots can be formulated. When environmental quality is poor, we would expect to observe an increase in the number of one egg clutches, and a concurrent decrease in egg volume. Because experienced birds may not have sufficient energetic reserves to lay two eggs, hatching success for one egg clutches would increase, due to the experience level of the adults. Fledging and egg success for one egg clutches would remain constant or increase only slightly, as these parameters are more dependant upon prey abundance. Reproductive success for two egg clutches would be lower overall.

Conversely, when environmental quality is high, we would expect to observe a high number of two egg clutches, yielding eggs of large volume. Hatching, fledging, and egg success for two egg clutches would increase over levels observed in poor quality years, due to abundant prey resources. Hatching, fledging, and egg success for one egg clutches would remain constant, or decrease slightly, as

only young or poor quality birds would lay only one egg.
Egg volume, however, would increase for one egg clutches due
to the availability of prey for these young birds.
Presumably, adults in poor physiological condition during
times when environmental quality is high would nonetheless,
lay single eggs of small volume.

BIBLIOGRAPHY

Aitchison, N. W. 1972. The Pigeon Guillemot, Cepphus columba: breeding biology and brood size. B.Sc. thesis, Univ. of British Columbia.

Andersson, A. 1976. Clutch size in the Long-tailed Skua Stercorarius longicaudus: some field experiments. Ibis 118: 586-588.

Ankney, C. D., & C. D. MacInnes. 1978. Nutrient Reserves and reproductive performance of Lesser Snow Geese. Auk 95: 459-471.

Asbirk, S. 1979. The adaptive significance of the reproductive pattern in the Black Guillemot Cepphus grylle. Vidensk. Meddr. Dansk Naturh. Foren. 141: 29-80.

Bell, G. 1984. Measuring the cost of reproduction. I. The correlation structure of the life table of a plankton rotifer. Evolution 38: 300-313.

Birkhead, T. R., & M. P. Harris. 1985. Ecological adaptations for breeding. Pp. 205-231 in The Atlantic Alcidae (D.N. Nettleship and T.R. Birkhead, Eds.). London, Academic Press.

Cairns, D. K. 1981. Breeding, feeding and chick growth of the Black Guillemot Cepphus grylle in Southern Quebec. Can. Field Nat. 95: 312-318.

Charnov, E. L., & J. R. Krebs. 1974. On clutch size and fitness. Ibis 116: 217-219.

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

Coulson, J. C., & E. White. 1958. Observations on the breeding of the Kittiwake. Bird Study 5: 74-83.

Coulter, M. C. 1973. Breeding biology of the Western Gull, Larus occidentalis. M.S. thesis, Oxford Univ., England.

Cronmiller, J. R., & C. F. Thompson. 1980. Experimental manipulation of brood size in Red-winged Blackbirds. Auk 97: 559-565.

Cummings, E., & E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Report 70-11, Oregon Fish Commission Research Division, Oregon Dept. Fish & Wildlife.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

Dann, P. 1988. An experimental manipulation of clutch size in the Little Penguin *Eudyptula minor*. Emu 88: 101-103.

Davis, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. Ibis 117: 460-473.

de Forest, L. N., & A. J. Gaston. 1990. Egg recognition in Thick-billed Murres. Pacific Seabird Group Bull. 17: 15-16.

DeSteven, D. 1980. Clutch size, breeding success, and parental survival in the Tree Swallow (*Iridoprocne bicolor*). Evolution 34: 278-291.

Drent, R. H., & S. Dann. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Drent, R. H., G. F. van Tets, F. Tompa, & K. Vermeer. 1964. The breeding birds of Mandarte Island, British Columbia. Canad. Field-Nat. 78: 208-263.

Ewins, P. 1986. The ecology of the Black Guillemot *Cepphus grylle* in Shetland. Ph.D. dissertation, Oxford Univ., England.

Finke, M. A., D. J. Milinkovich, & C. F. Thompson. 1987. Evolution of clutch size: An experimental test in the House Wren (*Troglodytes aedon*). J. Anim. Ecol. 56: 99-114.

Follett, W. I., & D. G. Ainley. 1976. Fishes collected by Pigeon Guillemots, *Cepphus columba* (Pallas), nesting on southeast Farallon Island, California. Calif. Fish and Game 62: 28-31.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pp. 207-270 in Behavior of Marine Animals, Vol. 4: Marine Birds (J. Burger, B. Olla, and H. Winn, Eds.). New York, Plenum Press.

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

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

Harris, M. P., & W. J. Plumb. 1965. Experiments on the ability of Herring Gulls and Lesser Black-backed Gulls to raise larger than normal broods. Ibis 107: 256-257.

Haymes, G. T., & R. D. Morris. 1977. Brood size manipulations in Herring Gulls. Can. J. Zool. 55: 1762-1766.

Hodder, J., & M. R. Graybill. 1985. Reproduction and survival of seabirds in Oregon during the 1982-1983 El Nino. Condor 87: 535-541.

Hogstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. Science 210: 1148-1150.

Hogstedt, G. 1981. Should there be a positive or negative correlation between survival of adults in a bird population and clutch size? Amer. Nat. 118: 568-571.

Houston, D. C., P. J. Jones, & R. M. Sibley. 1983. The effect of female body condition on egg laying in Lesser Black-backed Gulls Larus fuscus. J. Zool. Lond. 200: 509-520.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96: 73-77.

Hunt, G. L. 1980. Mate selection and mating systems in seabirds. Pp. 113-153 in Behavior of Marine Animals, Vol. 4: Marine Birds (J. Burger, B. Olla, and H. Winn, Eds.). New York, Plenum Press.

Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302-352.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon, Oxford.

Lack, D. 1966. Population Studies of Birds. Clarendon, Oxford.

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

Murphy, E. C., & E. Haukioja. 1986. Clutch size in nidicolous birds. Current Ornithology 4: 141-180.

Nelson, J. B. 1964. Factors influencing clutch size and chick growth in the North Atlantic Gannet Sula bassana. Ibis 106: 63-77.

Nisbet, I. C. T. 1977. Courtship-feeding and clutch size in Common Terns Sterna hirundo. Pp. 101-109 in Evolutionary Ecology (B. Stonehouse and C. Perrins, Eds.). London, Macmillan.

Nisbet, I. C. T. 1978. Dependance of fledging success on egg-size, parental performance and egg composition among Common and Roseate Terns, Sterna hirundo and S. dougallii. Ibis 120: 207-215.

Nur, N. 1984. The consequences of brood size for breeding Blue Tits. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. 53: 497-517.

Ollason, J. C., & G. M. Dunnet. 1986. Relative effects of parental performance and egg quality on breeding success of Fulmars Fulmarus glacialis. Ibis 128: 290-296.

Perrins, C. M. 1965. Population fluctuations and clutch size in the Great Tit, Parus major. J. Animal Ecology 34: 601-647.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Peterson, A. 1981. Breeding biology and feeding ecology of Black Guillemots. Ph.D. dissertation, Oxford Univ., England.

Pettifor, R. A., C. M. Perrins, & R. H. McCleery. 1988. Individual optimization of clutch size in Great Tits. Nature 336: 160-162.

Price, T., M. Kirkpatrick, & S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science 240: 798-799.

Pugesek, B. H. 1981. Increased reproductive effort with age in the California Gull (Larus californicus). Science 212: 822-823.

Reid, W. V. 1988. Fledging success of experimentally enlarged broods of the Glaucous-winged Gull. Wilson Bull. 100: 476-482.

Reid, W. V., & P. D. Boersma. 1990. Parental quality and selection on egg size in the Magellanic Penguin. Evolution 44: 1780-1786.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983.

Ricklefs, R. E. 1973. Fecundity, mortality, and avian demography. Pp. 366-435 in Breeding Biology of Birds (D. S. Farner, Ed.). Washington D.C., Nat. Acad. Sci.

Ricklefs, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. Am. Nat. 111: 453-478.

Roskaft, E. 1985. The effect of enlarged brood size on the future reproductive potential of the Rook. J. Anim. Ecol. 54: 255-260.

Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling Great Tits Parus major. Ibis 115: 549-558.

Schifferli, L. 1978. Experimental modification of brood size among House Sparrows Passer domesticus. Ibis 120: 365-369.

Shipley, F. S. 1984. The 4-egg experiment in the Charadrii: an experiment with American Avocets. Southwestern Naturalist 29: 143-147.

Slagsvold, T., & T. J. Lifjeld. 1990. Influence of male and female quality on clutch size in Tits (Parus spp.). Ecology 71: 1258-1266.

Sokal, R. R., & F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York.

St. Louis, V. L., J. C. Barlow, & J. R. A. Sweerts. 1989. Toenail-clipping: a simple technique for marking individual nidioulous chicks. J. Field Ornithol. 60: 211-215.

Thomas, C. S. 1983. The relationships between breeding experience, egg volume and reproductive success of the Kittiwake *Rissa tridactyla*. Ibis 125: 567-574.

Thoresen, A. C., & E. S. Booth. 1958. Breeding activities of the Pigeon Guillemot *Cepphus columba* (Pallas). Walla Walla Coll. Publ. Biol. Sci. 23: 1-36.

Tschanz, B. 1959. Zur brutbiologie der Trottellumme (*Uria aalge*). Behavior 14: 1-100.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Amer. Nat. 100: 687-690.

Winkler, D. W. 1985. Factors determining a clutch size reduction in California Gulls (*Larus californicus*): A multi-hypothesis approach. Evolution 39: 667-677.