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Effect of body condition on reproductive performance and secondary sex ratios in ring-billed gulls (Larus delawarensis)

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The Effect of Body Condition on Reproductive Performance and Secondary Sex Ratios in Ring-billed Gulls (*Larus delawarensis*)

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science
in the Department of Biology

by

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Lakehead University
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Declaration

The research presented in this thesis was carried out by the author, and has not been previously submitted for credit toward any degree or diploma.

The work of others, where included, has been appropriately cited.

January, 1986

ABSTRACT

Nesting Ring-billed Gulls (Larus delawarensis) were studied on Granite Island, northern Lake Superior, during the breeding seasons of 1983 and 1984 to determine if there was a relationship between food supply and the time of breeding, body condition, and egg characteristics affecting reproductive success.

Eggs laid in 1984 were heavier than those laid in 1983. This may have been related to smaller pre-breeding food abundance in 1983. In each year, Ring-billed Gulls nesting later in the season laid fewer and smaller eggs that had poorer hatching success. Within clutches, third laid eggs were smaller, lighter and produced fewer young than first or second eggs.

Chemical analyses of eggs revealed that eggs laid in 1984 contained more albumen, and proportionately more yolk lipid, than eggs laid in 1983. Eggs laid later in each year contained less albumen and fewer nutrients (lipid and protein) than earlier laid eggs. Within early and late clutches, c-eggs had decreased levels of albumen and nutrients. For all eggs analyzed, an average of 35% of fresh egg weight was yolk, with a fresh yolk to albumen ratio of 0.63. Water accounted for 69% of fresh egg weight. Through the laying sequence, approximately 8% of fresh egg weight was yolk lipid. The energy and nutrient content of eggs remained proportionately constant through the laying sequence each year. Egg weight was strongly correlated with egg volume and water content.

Chick weight at hatching was positively correlated with fresh egg weight, though this correlation was weak. There was no difference in hatch weights within clutches. Male and female eggs did not differ in size or weight. There was no relationship between chick sex and egg sequence in either year. The secondary sex ratio was skewed in favour of female chicks in 1983. The overall secondary sex ratio did not differ from unity, and the ratio of unisexual and bisexual 3-egg clutches laid early in 1984 did not differ from 1:2:1.

In each year, females nesting later in the season had a lower body weight and condition index than earlier nesting females. The indexed body condition of females nesting early in 1983 was smaller than in 1984. Both male and female indexed condition decreased through the breeding season in 1984. The body weight of females was correlated with egg weight but not nutrient content. Egg size and composition were not satisfactory predictors of female body weight and condition. Chemical analyses of post-laying females revealed that late nesters contained proportionately more body water and protein, but less lipid than early nesters. Between years, there were no differences in the body weight or nutrient content of post-laying females. The energy content of the body was most strongly correlated with lipid levels in the body. Both the body weight and indexed condition of early nesting females were correlated with body lipid and energy levels. Females with larger stored nutrient levels (i.e. those nesting earlier each year) laid heavier eggs which contained more nutrients.

Pre-breeding adult males and females tended to weigh more and contain more energy per unit body weight than early nesters. I suggest that reduced body condition, and hence egg quality, for those birds nesting in 1983 and late nesters, were primarily related to differences in food abundance and acquisition efficiency during the pre-breeding period.

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1. INTRODUCTION

Ultimately, genetic fitness is not only a function of the reproductive success in one breeding season, but over a lifetime (Lack 1954, 1968). In any one breeding season, earlier nesting birds usually have greater reproductive success than later nesting conspecifics (Darwin 1871). Greater reproductive success, measured in terms of the success of chick hatching and survival, is partly manifest by intraspecific variations in egg size and weight. The seasonal reduction of clutch size, egg size and hatching success for late nesting birds has been reported in a variety of species (Klomp 1970; Loman 1977, 1982), including waterfowl (Finney and Cooke 1978, Lesser Snow Geese, *Chen caerulescens*; Baillie and Milne 1982, Commom Eider, *Somateria mollissima*) and many larids (Brown 1967b, Lesser Black-backed Gull, *Larus fuscus*; Brown 1967b, Parsons 1970, 1975, Hunt 1972, Herring Gull, *L. argentatus*; Vermeer 1970, California Gull, *L. californicus*; Vermeer 1970, Somppi 1978, D. Boersma 1982, Ring-billed Gull, *L. delawarensis*; Coulson and White 1961, Black-legged Kittiwake, *Rissa tridactyla*). The seasonal decline of clutch and egg size may be explained by several factors, all of which depend somewhat upon the age and experience of the nesting bird (Ryder 1980). The breeding performance of many larids is known to improve with age, including the Red-billed Gull (*L. novaehollandiae*)(Mills 1973, 1979), the Herring Gull (Davis 1975; Chabrzyk and Coulson 1976; Coulson *et al*. 1982), the

Ring-billed Gull (Haymes and Blokpoel 1980) and the California Gull (Pugesek 1983; Pugesek and Diem 1983). Age-related factors which improve breeding performance include the female's selection of older and more experienced males better able to supply more, higher quality courtship feedings (Nisbet 1977; Mills 1979; Taylor 1979; Pugesek 1983), occupation of superior central sites (Patterson 1965; Coulson 1971; Burger 1974, 1984; Somppi 1978; Haymes and Blokpoel 1980; Pugesek and Diem 1983), earlier laying (most studies), larger clutches (most studies) and larger eggs (Richdale 1955; Coulson _et_ _al_. 1969; Thomas 1982). The consequence of these factors is a greater reproductive (hatching and fledging) success (Richdale 1955; Patterson 1965; Parsons 1975; Chardine 1978).

Nisbet _et_ _al_. (1984) reported that within age-classes, both clutch size and egg size were significantly correlated with date of laying. It has also been shown that the timing of nesting may be more strongly correlated with pre-breeding food abundance and availability than with the age-related foraging ability of adults (Lack 1954; Perrins 1970; Hunt and Hunt 1976). Hence, the seasonal decline of clutch and egg size, as well as egg nutrient content (lipid and protein), may be the direct result of the variation in the physiological condition of nesting adults (Coulson 1968; Drent and Daan 1980; Beckerton and Middleton 1982) as affected by changing food availability through the breeding season.

Coulson _et_ _al_. (1982) hypothesized for Herring Gulls that egg quality was related to the body condition of the laying female.

Recently, Houston _et al_. (1983), using chemical testing of adult carcasses, demonstrated that nesting female Lesser Black-backed Gulls in good nutritional state (ie. high levels of body reserves) produced, on average, more eggs and higher quality eggs than females in poorer body condition. Reserves are the lipids and proteins accumulated above baseline starvation levels which may be utilized for egg production and/or adult survival (Young and Boag 1982).

If the body condition of laying females deteriorates through the laying sequence in response to egg-laying stress and food acquisition, as proposed by Ankney (1982) and Ryder (1983), so might egg nutrient levels. Larger eggs, those laid first, ideally should contain more nutrients, and lead to more vigorous and larger chicks - most of which would be males according to the Trivers-Willard (1973) hypothesis.

Stimulated by the relationship between the nutrients found in eggs and adult females by Houston _et al_. (1983), this study attempts to determine whether there were any relationships between the sex, size and nutrient composition of eggs, their position in the laying sequence and the body condition of the attending female Ring-billed Gull.

2. MATERIALS AND METHODS

2.1 Definitions

Clutch size: The number of eggs in a nest laid and attended by a mated pair.

Clutch initiation: The day the first egg is laid in a nest.

Condition index: Body weight (g) / (bill length (mm) + keel length (mm)) (G. Fox, pers. comm.).

Early nesting pairs: Those that initiated their clutches within six days of the start of egg laying on the colony (11 May 1983, 10 May 1984).

Late nesting pairs: Pairs that initiated clutches at least 1 week after the completion of early clutches.

Egg constituents: Yolk, albumen and shell.

Egg nutrient content: Amount of protein and lipid in the yolk and albumen.

Egg quality: The greater the egg weight, constituent weights and the nutrient content of an egg, the better its quality.

Egg size: A measure of egg length and width. Size and volume increase with increasing length and width.

Egg volume: Volume was calculated using the formula klb^2, where $k= 0.489$, l is maximum length (cm) and b is maximum width (cm) (Ryder, 1975).

Energy: energy per gram was calculated utilizing energy equivalents of 9.5 kcal/g lipid and 5.65 kcal/g non-lipid dry weight (Ricklefs 1977b).

2.2 Study Area

This study was conducted on Granite Island, located in Black Bay, northern Lake Superior (48° 43'N, 88°29'W), approximately 80 km northeast of Thunder Bay, Ontario (Figure 1). The island is a 60 ha granite outcrop 402 m by 102 m with steeply inclined slopes rising to about 30 m above water level (Ryder and Carroll 1978). About 50% of the island is covered by vegetation. The forested southern and eastern areas are comprised of White Cedar (*Thuja occidentalis*), Balsam Fir (*Abies balsamea*) and White Birch (*Betula papyrifera*). The more exposed northern and northeastern slopes support stands of Mountain Ash (*Sorbus scopulina*), Pin Cherry (*Prunus pennslyvanica*) and Red Osier Dogwood (*Cornus stolonifera*). The summit and northeastern slopes are mostly bare granite with soil-filled depressions. These depressions consist predominantly of Rough Cinquefoil (*Potentilla norvegica*) and Kentucky Blue-grass (*Poa pratensis*). The north and northwest sides are steep with few soil depressions. Approximately 100 - 150 pairs of Herring Gulls nest on these steep cliffs.

Most Ring-billed Gulls nest in the soil filled depressions on the summit and northeastern slope (Figure 2). The number of nesting

Figure 1. Location of Granite Island and the Wolf River in northern Lake Superior (modified from Ryder 1974).

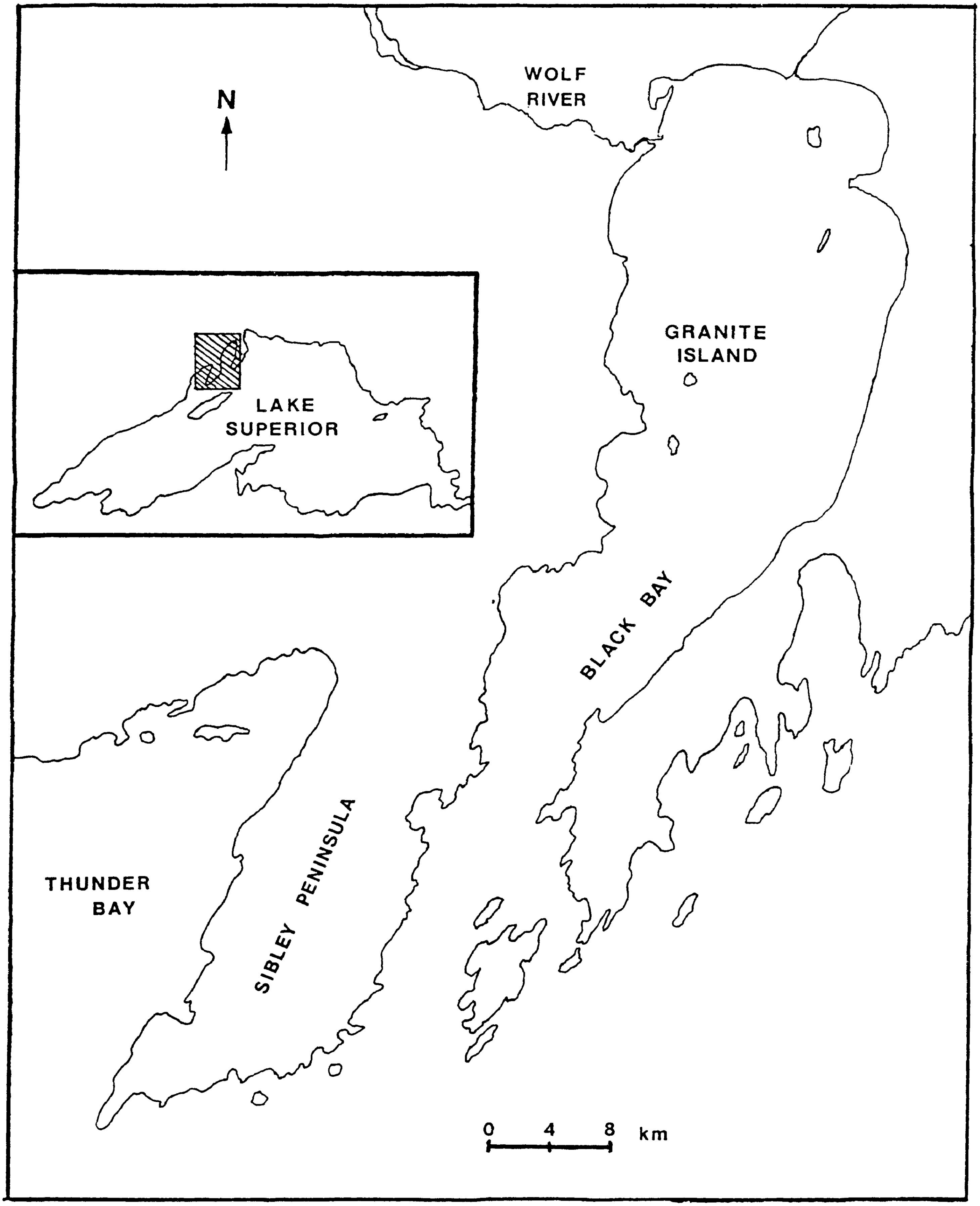

WOLF
RIVER
N
GRANITE
ISLAND
LAKE
SUPERIOR
BLACK BAY
THUNDER
BAY
SIBLEY PENINSULA
0
4
8
km

Figure 2. Bare rock areas occupied by Herring Gulls and Ring-billed Gulls on Granite Island.

Ring-billed Gulls has increased over the last few years. In 1973, Ryder (1975) reported 800 nesting pairs; four years later, Somppi (1978) estimated 1600 pairs. Kovacs-Nunan (1982) counted 2400 and 2600 pairs in 1979 and 1980, respectively, In 1985, there were 4800 nests on Granite Island (B. Termaat, pers. comm.). An additional thirty species of birds have been observed on Granite Island (Chamberlain 1973).

2.3 Statistical Procedures

Statistical analyses followed Nie et al. (1970) and Sokal and Rohlf (1981). Student's t-tests between years and between early and late samples were only used with sample sizes greater than 25. When variances were equal, as determined by F-tests ($p < 0.05$), pooled variance estimates were used rather than separate variance estimates. Variations in egg size and composition within clutches were examined using one-way analysis of variance followed by Scheffé's contrasting. Covariance analyses were used to compare regression lines. Non-parametric testing was performed using Mann-Whitney U and Chi-squared tests, following Zar (1974). Significance was assumed at $p< 0.05$.

2.4 Nest Histories

In 1983, I arrived on Granite Island on 11 May and marked all one-egg clutches on the northeast study area (Figure 3) with numbered wooden blocks. New clutches were marked daily until 17 May to assess the temporal distribution of clutch initiation for early breeding pairs. In 1984, I arrived on the colony on May 5. Snow and ice were abundant, and no early clutches had been initiated. I left the colony until 10 May to avoid disturbing pre-breeding territorial and courtship behaviours. On 10 May, newly initiated nests containing one egg were marked until 14 May. Nest disturbance and potential abandonment were reduced for late nesters in 1983, and early and late nesters in 1984, by including the summit in the areas sampled. Two-hundred and twenty-three and 233 nests were marked in 1983 and 1984, respectively.

In 1983 and 1984, late clutches were marked with numbered wooden blocks at least 1 week after early egg laying was over (as evinced by a marked reduction in new clutches). This ensured an adequate time interval between the early and late samples. In each year, the colony was visited daily to mark new nests for a period of 7 days. In 1983, 137 late nests were marked; 65 in 1984.

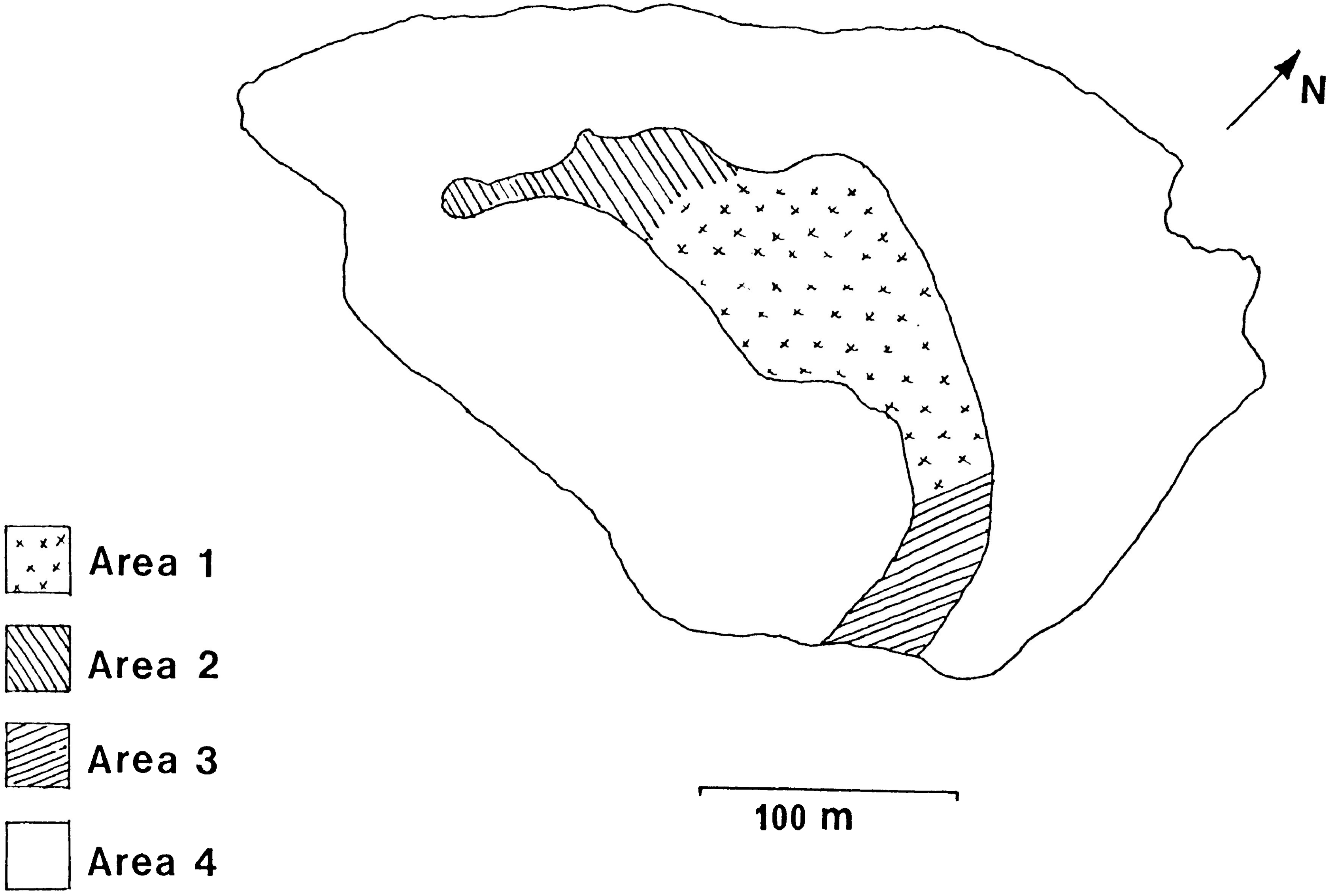
Figure 3. Study areas on Granite Island, 1983 and 1984 (modified from D. Boersma 1982).

Area 1: northeast slope; early and late each year

Area 2: summit; late 1983, early and late 1984

Area 3: lower slope; late 1983, early and late 1984

Area 4: unoccupied by Ring-billed Gulls



N
100 m
Area 1
Area 2
Area 3
Area 4

2.5 Egg Histories

Eggs in all study nests were marked daily in order of laying by placing brown enamel dots on the blunt end of the egg. The a-egg, b-egg and c-egg refer to the first, second and third egg laid in a clutch, respectively. Fresh egg length and width were measured to within 0.01 mm with Vernier calipers to compare the size of early and late eggs. Egg volumes were calculated using the formula given in Section 2.1. A 100 g Pesola spring scale was used to weigh fresh eggs to the nearest 1 g within 12 h of being laid. In 1983 and 1984, 785 and 769 fresh eggs were measured and weighed, respectively.

In each year, clutches marked with an odd numbered wooden block were collected for egg chemical analysis. Even numbered clutches were collected for secondary (at hatch) sex ratio analyses.

2.5.1 Chemical Analyses of Eggs

In 1983, 110 early and 59 late eggs were collected at clutch completion for chemical analyses. In 1984, each egg in a clutch was collected within 12 hours of laying to ensure minimal embryonic development. A total of 370 eggs (318 early, 52 late) were chemically analyzed in 1984. All eggs were weighed to within 0.1 g on an Ohaus digital scale, then boiled for 10 minutes so that yolk, shell and albumen could be easily separated (Jones 1979; Ricklefs 1982). Ricklefs and Montevecchi (1979) reported that this treatment had no effect on the water fraction of the yolk and albumen. Each egg was tightly wrapped in cellophane, sealed in a jar, frozen and returned to the laboratory for chemical analyses.

In the laboratory, eggs were thawed for 24 hours then weighed whole to the nearest 0.0001 g on a Mettler balance in 1983, or on an Oertling balance in 1984. Eggs were then separated into yolk, albumen and shell (with corresponding membranes) and each constituent was weighed again. Any water loss caused by embryonic development or freezing was corrected for by adding the difference between fresh egg weight and thawed weight to wet albumen weight (Williams et al. 1982). Constituents were then dried for 1 week to a constant weight in a Gallenkamp Incubator (56 °C), and weighed again to within 0.0001 g to determine water content. Egg membranes were removed from the shell before measuring shell thickness to within 0.001 mm with a Starret No. 10 dial indicator metric pocket gauge. Thickness was measured at both ends and the middle of the egg shell, then averaged.

Since Romanoff and Romanoff (1949) and Ricklefs (1977a) found that the lipid content of the albumen, and the carbohydrate content of both yolk and albumen, represent less than 1% of fresh egg weight, the levels of these contents were not determined. Ryder et al. (1977) found that carbohydrates averaged 0.6% of yolk weight for Ring-billed Gulls. Nutrient content of dried yolks was determined using Soxhlet-extraction with petroleum ether (BP = 30 - 60°C). Dried post-extraction remains were assumed to consist only of protein. Lipid content was determined by the difference between the dry yolk weights before and after ether-extraction (Ricklefs 1977b).

2.5.2 Artificially Incubated Eggs

Two-hundred and seventy-five eggs were collected to determine the sex ratio of successfully hatching eggs. These were artificially incubated to eliminate egg destruction or parental desertion caused by experimentally induced nest disturbance. In 1983, 18 three-egg clutches and 4 two-egg clutches were collected on 21 May to obtain early hatching chicks. Fifty-four late eggs were collected for incubation on 16 June (12 three-egg clutches and 9 two-egg clutches). Forty-seven early three-egg clutches collected on 17 May were artificially incubated in 1984. Eighteen eggs were collected for late chicks on 5 June 1984 (2 three-egg clutches, 6 two-egg clutches). All eggs were securely wrapped in clothing, placed in a box and transported to the Humidaire egg incubator at Lakehead University within 3 hours of collection. The incubator was regulated to 38 °C at 55% relative humidity, and turned eggs once per hour. Eggs gathered for artificial incubation were replaced from adjacent nests to ensure that adults would not desert.

When a chick whose position in a clutch was known hatched, its sex was determined by gonadal inspection. In 1984, chick hatch weight was measured to the nearest 0.1 g on a triple beam balance. All chicks were placed in the ornithological holdings of Lakehead University.

2.6 Adult Body Condition

In each year, within 5 days of clutch completion, attending adults were captured using drop traps (Mills and Ryder 1979). The sex of each gull was determined from external measurements (Ryder 1978), and weighed to within 5 g with a 1000 g Pesola spring scale. Bill length, bill depth (gonys), tarsus length, head length (Baldwin _et_ _al_. 1931) and keel length (Harris 1970) were measured to within 0.001 cm using Vernier calipers. In 1983, 96 post-laying females (54 early, 42 late) were trapped. In 1984, 78 females (62 early, 16 late) and 70 males (56 early, 14 late) were trapped, weighed and measured.

2.6.1 Chemical Analyses of Adults

Adults were collected from nests whose eggs had been boiled for chemical analyses. Twenty-five females that had nested early in the season, and 15 later nesting females were chemically analyzed in 1983. Thirty-three (24 early, 9 late) post-laying females were analyzed in 1984. In addition, 10 early and 10 late males were collected for analyses in 1984. Once weighed and measured, adults were sacrificed and quick frozen with dry ice and returned to the laboratory.

In the laboratory, adults were weighed frozen to within 1 g on a Testut Electronique balance, thawed for 24 hours, then reweighed. Next, the digestive tract was excised from the oesophagus to the cloaca. From this, food was removed and the bird, with the cleaned tract, was reweighed to determine actual body weight.

Reproductive tissues were removed and weighed fresh to within 0.0001 g on an Oertling balance. They were then dried in a Gallenkamp incubator (56 °C) for 1 week to a constant weight.

The carcasses were processed by first removing the feet (distally from the patella), bill, outer wings (distally from the wrist), skin and feathers. The processed body was then reweighed to within 1 g on the Testut balance. After removal, the skin and feathers were weighed using the Testut balance.

The processed body was then homogenized for 15 minutes using a Cuisinart food processor until bone fragments were smaller than 0.5 cm. This degree of homogenization ensured that all protein and lipid reserves in the body could be determined. Three subsamples were taken of the homogenate, weighed on the Oertling balance, then dried for 1 week in the Gallenkamp incubator.

Three subsamples were also taken of the fresh skin and feathers. Each subsample was weighed whole to within 0.0001 g on the Oertling balance, plucked, then reweighed to determine skin fresh weight. Skin subsamples were also dried for 1 week to a constant weight. All dry samples (reproductive tissues, skin and body homogenate) were weighed on the Oertling balance to determine water content.

Methodology for determining the levels of nutrient reserves (lipid and protein) in the body, reproductive tissues and skin followed those used to measure nutrients in eggs (see Section 2.5.1). Energy for adult carcasses was calculated in kcal/g dry analyzed weight.

2.6.2 Condition Index of Adults

For all females trapped in 1983 (N=96), and all adults trapped in 1984 (78 females, 70 males), the condition index was calculated (see Definitions). The index is designed to facilitate estimation of body nutrient levels from living birds (Chappell and Titman 1983). Such indices equate body size differences so body weights may be compared (Owen and Cook 1977). Ultimately, this index was used to determine if chick sex ratios changed with adult body condition.

2.6.3 The Body Condition of Pre-breeding Adults

On April 30 and May 4 1984, 5 male and 4 female pre-breeding adult Ring-billed Gulls were collected at the mouth of the Wolf River (Figure 1), ten miles north of Granite Island. These birds were chemically analyzed and an index of body condition calculated (Sections 2.6.1 and 2.6.2). The Wolf River is a spawning ground for Rainbow Smelt (*Osmerus* mordax). Hence, the purpose of Wolf River sampling was to assess the importance of smelt as a food source available to adults before nesting, and to establish to what degree smelt contribute to the acquisition of nutrients stored by adult female gulls before nesting.

3. RESULTS

3.1 Egg Histories of Early And Late Nesting Gulls

3.1.1 Egg Laying

In 1983, egg laying extended from 11 May to 10 June; in 1984 from 10 May to 14 June.

Nests initiated from 11 - 17 May, 1983, and from 10 - 11 May, 1984, were selected to represent early breeding pairs. The modal clutch initiation date for early nesters was 11 May in each year. Nests of late breeding pairs were chosen from those initiated between 1 - 8 June, 1983, and 30 May to 2 June, 1984.

3.1.2 Clutch Size

The overall mean (±S.D.) clutch size in 1983 (2.50 ± 0.76, n= 263) was smaller than the average clutch size in 1984 (2.82 ± 0.55, n= 256) ($F= 30.05$, $p< 0.001$). When early and late clutch sizes were compared between years, the early clutch size in 1983 (2.83 ±0.56, n= 157) was smaller than the early clutch size in 1984 (2.96 ± 0.35, n= 221) ($F= 9.04$, $p< 0.01$). The clutch size of gulls nesting late in 1983 (2.07 ±

0.75, n= 106) was the same as that for gulls nesting late in 1984 (1.86 ± 0.60, n= 35)(F= 1.20).

Clutches initiated early in the breeding season were larger than late initiated clutches in each year (1983: F= 103.09, p< 0.001; 1984: F= 242.58, p< 0.001). The modal clutch size was three eggs for early nests in both 1983 and 1984, but only two eggs for late nests in each year.

3.1.3 Egg Size and Weight

To assess differences in egg size and weight between years, and between early and late eggs within years, only those eggs from three-egg clutches were used since this is considered to be the modal clutch size for Ring-billed Gulls (Ryder 1983).

When all fresh eggs were analyzed together (a-, b- and c-egg data pooled), comparisons of fresh egg size and weight between years revealed that early eggs weighed more in 1984 than in 1983 (t_{679}= -14.54, p< 0.001) (Table 1). Early egg length, width and volume did not differ between years. There was no difference in either egg size or weight for late clutches between years (Mann-Whitney U). The same results were found when a-, b- and c-eggs were examined separately (ie. early 1983 a-egg versus early 1984 a-egg; Table 2).

In each year, when all fresh eggs were analyzed together, eggs from early nests were larger and heavier than eggs from late nests (Table

Table 1. Comparison of egg size and weight of all early and late nesting Ring-billed Gulls, three-egg clutches, Granite Island, 1983 and 1984.

	1983			1984		
	Early	Late	Student's t	Early	Late	Mann-Whitney U
Length (mm)	58.6 ± 2.3 (374)[1]	57.8 ± 1.9 (83)	2.95, $p < 0.01$	58.5 ± 2.3 (590)	57.6 ± 2.0 (13)	NS[4]
Width (mm)	41.8 ± 1.3 (374)	41.0 ± 1.4 (83)	5.09, $p < 0.001$	41.9 ± 1.1 (590)	40.7 ± 1.1 (13)	$p < 0.001$
Volume (mm^3)	50.09 ± 4.79 (374)	47.60 ± 3.89 (83)	5.05, $p < 0.001$	50.37 ± 3.79 (590)	46.65 ± 3.22 (13)	$p < 0.001$
Weight (g)[3]	54.0 ± 4.3 (373)	51.7 ± 5.3 (90)	3.85, $p < 0.001$	58.6 ± 3.8 (308)	54.1 ± 4.6 (7)	$p < 0.05$

[1] Mean ± SD (n)

[2] Non-parametric testing was used to account for the small late sample size.

[3] Pesola spring scale used to measure fresh egg weight (within 12 hr of being laid) each year.

[4] No significant difference

Table 2. Comparison of egg size and weight in three-egg clutches of early and late nesting Ring-billed Gulls, Granite Island, 1983 and 1984.

	1983			1984		
	Early	Late	Student's t	Early	Late	
Length (mm)						
Egg a	58.8 ± 2.4 (125)[1]	57.6 ± 1.8 (28)	2.52, $p < 0.05$	59.0 ± 2.4 (197)	57.7 ± 1.8 (4)	----[5]
b	59.0 ± 2.1 (125)	57.8 ± 2.2 (28)	2.61, $p < 0.01$	58.8 ± 2.2 (197)	57.5 ± 2.2 (5)	
c	58.0 ± 2.2 (124)*[3]	58.0 ± 1.8 (27)	0.00, NS[2]	57.8 ± 2.2 (195)*	57.6 ± 2.6 (4)	
F	6.42, $p < 0.01$	0.31, NS		18.02, $p < 0.001$	0.02, NS	
Width (mm)						
Egg a	42.1 ± 1.2 (125)	41.1 ± 1.3 (28)	4.19, $p < 0.001$	42.4 ± 1.1 (197)	40.1 ± 1.1 (4)	
b	42.1 ± 1.1 (125)	41.3 ± 1.7 (28)	2.28, $p < 0.05$	42.1 ± 1.0 (197)*	41.5 ± 0.9 (5)	
c	41.2 ± 1.4 (124)*	40.6 ± 1.1 (27)	2.24, $p < 0.05$	41.3 ± 1.0 (195)**	40.2 ± 0.7 (4)	
F	23.88, $p < 0.001$	2.24, NS		60.06, $p < 0.001$	3.06, NS	

Table 2 continued ...

Volume (mm³)						
Egg	a	51.16 ± 4.11 (125)	47.57 ± 3.71 (28)	4.26, $p < 0.001$	51.93 ± 3.70 (197)	45.50 ± 3.82 (4)
	b	51.18 ± 3.65 (125)	48.49 ± 4.83 (28)	2.78, $p < 0.01$	50.94 ± 3.43 (197)*	48.44 ± 3.45 (5)
	c	47.91 ± 5.66 (124)*	46.71 ± 2.71 (27)	1.65, NS	48.19 ± 3.21 (195)**	45.58 ± 1.57 (4)
F		21.32, $p < 0.001$	1.46, NS		61.56, $p < 0.001$	1.32, NS
Weight (g)[4]						
Egg	a	55.2 ± 4.3 (125)	52.5 ± 4.3 (30)	3.13, $p < 0.01$	60.2 ± 3.7 (103)	53.0 ± 7.1 (2)
	b	54.9 ± 4.0 (125)	52.9 ± 5.2 (30)	2.02, NS	59.2 ± 3.3 (103)	56.7 ± 4.6 (3)
	c	51.8 ± 3.8 (123)*	49.6 ± 5.9 (30)*	1.93, NS	56.3 ± 3.3 (101)*	51.5 ± 0.7 (2)
F		28.67, $p < 0.001$	3.68, $p < 0.05$		35.90, $p < 0.001$	0.77, NS

---

[1] Mean ± SD (n)

[2] No significant difference

[3] The asterisks denote significant differences from other averages within clutches (Scheffé).

[4] The pesola spring scale was used to measure fresh egg weight (within 12 hr of being laid) in each year.

[5] Comparisons for early versus late in 1984 were not performed because of the small late sample size.

1). The scarcity of late eggs in 1984 renders the Mann-Whitney U statistic questionable. It appears however, that eggs laid later in 1984 were smaller and lighter than earlier laid eggs.

One-way analysis of variance indicated that fresh egg size and weight differed within clutches for early eggs in both 1983 and 1984 (Table 2). The early c-eggs for each year were lighter and smaller than either a- or b-eggs. The early b-eggs in 1984 were narrower and had a smaller average volume than a-eggs. Late 1983 eggs did not differ in size, but did in weight; c-eggs being lighter than late a- or b-eggs.

Generally, late eggs were smaller and lighter than early eggs. Within clutches, c-eggs weighed less than a- or b-eggs, and were smaller.

In both years, fresh egg weight and dimensions were strongly correlated ($p < 0.001$, Table 3). Egg volume was most strongly correlated with egg weight.

3.2 Chemical Analyses of Eggs

Between year comparisons of the wet weight of egg constituents may be inappropriate since eggs were collected at clutch completion in 1983, but were collected fresh (< 12 h) in 1984. Williams _et_ _al_. (1982) have reported that water moves from the albumen to the yolk during embryonic development. For this reason, comparison of early

Table 3. Pearson correlation coefficients for Ring-billed Gull egg [1] dimensions and weight, Granite Island.

	Length(mm)	Width(mm)	Volume(mm³)
Width(mm)			
1983[2]	0.34		
1984[3]	0.28		
Overall[4]	0.32		
Volume(mm³)			
1983	0.66	0.83	
1984	0.73	0.86	
Overall	0.69	0.85	
Weight(g)			
1983	0.67	0.83	0.86
1984	0.65	0.85	0.95
Overall	0.60	0.79	0.83

[1] Early and late eggs were pooled.

[2] n = 456

[3] n = 315

[4] n = 771

eggs between years (Appendix 1), revealed that the eggs laid early in 1984 were heavier ($t_{378} = -2.65$, $p < 0.01$), contained less fresh yolk ($t_{378} = 14.31$, $p < 0.001$) and proportionately less yolk water ($t_{378} = 19.78$, $p < 0.001$), than early 1983 eggs. Eggs laid early in 1984 also contained more fresh albumen ($t_{378} = -14.49$, $p < 0.001$) and proportionately more albumen water ($t_{378} = -12.28$, $p < 0.001$), than early eggs in 1983. These relationships resulted in a lower wet yolk to albumen ratio for eggs laid in 1984. Such relationships, based on wet weights, document the marked alteration of results caused by differing collection procedures used in the 2 years. The between year comparisons of egg nutrient (lipid and protein) levels were valid since these levels were based on dry weights, therefore negating any water evaporation and/or transference from the albumen of developing a- and b-eggs in 1983. The yolks of eggs laid early in 1984 contained proportionately more lipid, expressed as a percentage of wet weight ($t_{378} = -17.21$, $p < 0.001$), but less if expressed as a percentage of yolk dry weight ($t_{378} = 2.49$, $p < 0.05$). Generally, these relationships were found when eggs were examined separately, the only notable difference being that early a-eggs did not differ in the proportion of yolk lipid between years (% dry, $t_{124} = 1.77$).

The comparison of egg composition for late eggs between years (Table 4 & 5) may be questionable since few late clutches of three eggs were laid in 1984. Although late eggs did not differ in weight, eggs laid late in 1983 did contain less fresh yolk ($p < 0.05$), more fresh albumen ($p < 0.05$) and albumen water (as a proportion, $p < 0.05$), and hence a

Table 4. Comparison of early and late egg constituent contents for three-egg clutches, Granite Island, 1983.

		Early	Late	Student's t
		n = 98	n = 47	
Egg weight (g)		52.8 ± 3.7[1]	50.3 ± 4.2	3.64, $p < 0.001$
Yolk:	Weight yolk (g)	23.17 ± 4.71	18.22 ± 3.61 (46)[2]	6.94, $p < 0.001$
	Dry yolk (g)	7.36 ± 0.70	6.83 ± 0.86 (46)	3.89, $p < 0.001$
	% water	67.17 ± 6.04	61.43 ± 0.99 (46)	5.05, $p < 0.001$
	Lipid (g)	4.48 ± 0.47	4.19 ± 0.59 (46)	3.20, $p < 0.01$
	% lipid	20.03 ± 3.92	23.68 ± 4.67 (46)	-4.90, $p < 0.001$
	Lipid (% dry)	60.94 ± 2.61	61.25 ± 2.37 (46)	-0.68, NS[3]
	Non-lipid dry (g)	2.93 ± 0.33	2.67 ± 0.33 (46)	4.57, $p < 0.001$
Albumen:	Wet albumen (g)	23.08 ± 4.58	26.36 ± 3.72	-4.28, $p < 0.001$
	Dry albumen (g)	4.15 ± 0.47	4.07 ± 0.37	0.97, NS
	% water	81.45 ± 3.46	84.31 ± 2.15	-6.08, $p < 0.001$
Shell:	Wet shell (g)	4.67 ± 0.48	4.24 ± 0.39	5.30, $p < 0.001$
	Dry shell (g)	3.53 ± 0.36	3.29 ± 0.27	4.34, $p < 0.001$
	% water	24.40 ± 3.09	22.19 ± 3.48	3.87, $p < 0.001$
Yolk/albumen (wet)		1.08 ± 0.41	0.72 ± 0.24 (46)	6.59, $p < 0.001$
Yolk/albumen (dry)		1.79 ± 0.23	1.69 ± 0.27 (46)	2.33, $p < 0.05$

Table 4 continued ...

Eggshell thickness (mm)	0.235 ± 0.020 (113)	0.234 ± 0.020 (75)	0.38, NS
Energy (Kcal/g fresh weight including shell)	1.55 ± 0.18 (98)	1.52 ± 0.16 (46)	1.06, NS

---

[1] Mean ± SD

[2] Sample size in parentheses. One egg had no yolk.

[3] No significant difference

Table 5. Comparison of early and late egg constituent contents for three-egg clutches, Granite Island, 1984.

		Early n = 282	Late n = 6	Mann-Whitney U
Egg weight (g)		54.0 ± 4.1[1]	51.4 ± 0.9	$p < 0.05$
Yolk:	Wet yolk (g)	16.20 ± 1.72	15.25 ± 0.79	NS[2]
	Dry yolk (g)	7.34 ± 0.68	6.74 ± 0.35	$p < 0.01$
	% water	54.51 ± 3.24	55.78 ± 1.67	NS
	Lipid (g)	4.39 ± 0.45	4.13 ± 0.87	NS
	% lipid	27.23 ± 2.26	28.25 ± 5.63	NS
	Lipid (% dry)	59.97 ± 4.82	63.95 ± 12.79	NS
	Non-lipid dry (g)	2.96 ± 0.32	2.76 ± 0.15	$p < 0.05$
Albumen:	Wet albumen (g)	30.49 ± 3.66	29.52 ± 1.32	NS
	Dry albumen (g)	4.27 ± 0.51	4.05 ± 0.25	NS
	% water	85.94 ± 1.78	86.13 ± 0.42	NS
Shell:	Wet shell (g)	4.59 ± 0.51	4.34 ± 0.41	NS
	Dry shell (g)	3.46 ± 0.33	3.19 ± 0.19	$p < 0.05$
	% water	24.43 ± 4.76	26.12 ± 4.55	NS
Yolk/albumen (wet)		0.54 ± 0.10	0.52 ± 0.05	NS

Table 5 continued ...

Yolk/albumen (dry)	1.74 ± 0.24	1.67 ± 0.18	NS
Eggshell thickness (mm)	0.238 ± 0.016	0.227 ± 0.009	$p < 0.05$
Energy (kcal/g fresh weight including shell)	1.53 ± 0.07	1.55 ± 0.16	NS

---

[1] Mean ± SD

[2] No significant difference

lower wet yolk to albumen ratio ($p < 0.05$), than eggs laid late in 1984. The same results were found when late eggs were examined separately. Any deviations away from the overall results were assumed to have been caused by small sample sizes (see Appendix 2).

Overall comparison of egg composition between early and late samples in 1983 (Table 4) revealed that early eggs were heavier and contained more fresh yolk, dry yolk, yolk water (as a proportion), lipid and protein, than late eggs. Early eggs had less fresh albumen, and proportionately less albumen water, resulting in a higher wet and dry yolk to albumen ratio. Early eggshells were heavier, both fresh and dry, but were not thicker than the shells of late eggs. Relative to eggs laid late in 1983, early eggs had equal amounts of energy.

Mann-Whitney U tests, used to compare early and late eggs separately, revealed variations in the above mentioned relationships. When comparing early and late a-eggs in 1983 (Appendix 3), there were no differences in the proportion of lipid in fresh yolk, for fresh albumen and albumen water amounts, or for kcal content. In 1983, early and late b-eggs contained equal amounts of yolk protein and shell water (as a proportion), but early b-eggs had thicker shells (Appendix 4). Also in 1983, for both b- and c-eggs (Appendices 4 & 5), early and late eggs did not differ in the weights of the fresh egg, dry yolk, and yolk lipid. These eggs did not differ in energy content, or the dry yolk to albumen ratio, when compared between early and late eggs.

Again, the comparison of early versus late eggs in 1984 may be questionable because of the small sample size. This may explain the number of insignificant non-parametric tests (Table 5). However, the data suggested to this researcher that those results obtained in the comparison of early and late eggs in 1983 would also hold for 1984 if in fact a larger late sample had been obtained in 1984.

In summary, late eggs weighed less, and had lighter fresh yolk and albumen weights, than early eggs within each year. Late eggs also contained fewer nutrients than early eggs.

Within early and late clutches each year, c-eggs weighed less and contained fewer nutrients than a- or b-eggs (one-way ANOVA)(Appendices 6 & 7). Within clutches in 1983, c-eggs weighed less (F= 7.22, $p < 0.001$) and contained less fresh yolk (F= 25.02, $p < 0.001$), yolk water (as a proportion, F= 30.45, $p < 0.001$), and had thinner shells (F= 14.39, $p < 0.001$) than a- or b-eggs (Appendix 6). C-eggs also had a lower wet yolk to albumen ratio than a- or b-eggs (F= 19.61, $p < 0.001$) since the freshly collected c-eggs contained more fresh albumen (F= 13.31, $p < 0.001$) with proportionately more water (F= 31.36, $p < 0.001$). The c-eggs also contained less albumen protein than a-eggs (F= 4.96, $p < 0.001$).

In 1983, b-eggs contained more dry yolk (F= 3.16, $p < 0.05$) and yolk protein (F= 3.32, $p < 0.05$) than a- or c-eggs (Appendix 6). The b-eggs contained proportionately less yolk water (F= 30.45, $p < 0.001$) and more albumen water (F= 31.36, $p < 0.001$) than a-eggs. Within 1983 clutches, a-, b- and c-eggs did not differ in the proportion of shell water (F= 0.80), yolk lipid (F= 2.47) energy content (F= 1.29), the dry yolk to albumen ratio (F= 1.64), or the percent lipid content in the dry yolk

($F = 0.30$). However, lipid (as a percent of wet yolk weight) increased through the laying sequence ($F = 26.66$, $p < 0.001$) because of decreased embryonic development.

Other trends were found when within clutch comparisons were made for only those eggs laid early in 1983 (Appendix 6). Dry yolk weight ($F = 2.75$), yolk protein weight ($F = 2.20$) and the energy content of eggs did not differ within early clutches. A- and b-eggs contained proportionately equal amounts of yolk water ($F = 20.18$), albumen water ($F = 27.27$) and lipid (as a proportion of wet weight, $F = 15.79$). Within clutches laid late in 1983, all eggs weighed the same ($F = 0.76$), and contained equal amounts of dry yolk ($F = 3.05$), albumen protein ($F = 1.65$) and kcals ($F = 0.88$)(Appendix 6).

In 1984, egg weight decreased through the laying sequence ($F = 27.51$, $p < 0.001$), as did fresh albumen weight ($F = 43.64$, $p < 0.001$), when early and late eggs were analyzed together (Appendix 7). C-eggs contained less dry yolk ($F = 13.46$, $p < 0.001$), yolk lipid ($F = 8.16$, $p < 0.001$), fresh shell ($F = 23.69$, $p < 0.001$), dry shell ($F = 31.00$, $p < 0.001$), and had thinner shells ($F = 3.88$, $p < 0.05$) than a- or b-eggs. B-eggs had more fresh yolk ($F = 5.72$, $p < 0.01$) and yolk protein ($F = 11.01$, $p < 0.001$) than a- or c-eggs. First laid eggs contained proportionately less yolk water ($F = 3.62$, $p < 0.05$) and more albumen water ($F = 5.40$, $p < 0.01$) than c-eggs. Also, a-eggs contained more albumen protein ($F = 17.60$, $p < 0.001$) and had lower wet ($F = 19.07$, $p < 0.001$) and dry ($F = 10.56$, $p < 0.001$) yolk to albumen ratios than either b- or c-eggs. Although the percent lipid in either wet or dry yolks did not change through the laying sequence (F= 1.69 and 0.72, respectively), a-eggs had less energy than b-eggs (F= 9.57, $p < 0.001$).

When intraclutch variation was examined for early and late 1984 clutches separately, all overall results were confirmed in early clutches (Appendix 7). Within late clutches, all constituent content levels did not differ. This was probably related to the small sample size (Appendix 7).

The average composition of Ring-billed Gull eggs was 35% yolk (14% dry matter, 21 % water), 56% albumen (10% protein, 46% water) and 9% shell (7% dry shell, 2% water), with a wet yolk to albumen ratio of 0.63. In total, 69% of the fresh egg was water. Dry yolk consisted of approximately 40% protein and 60% lipid. The average energy content per egg was about 1.55 kcal/g fresh egg weight.

To determine the relationship of fresh egg constituents to fresh egg mass, allometric regressions were calculated for those eggs collected in 1984 (after Ricklefs 1984). Yolk size and nutrient content were poorly correlated with egg mass (Table 6). The constituent most strongly related to egg mass was fresh albumen. Therefore, whole egg mass was strongly correlated with the mass of water in the egg, moderately correlated with caloric content and the mass of egg protein, but was not correlated with the mass of lipid in the egg. Shell weight increased in direct proportion with egg mass. Albumen increased in proportion to the 1.2 power of egg mass, and the yolk in proportion slightly greater than the 2/3 power of egg mass.

In 1983, the constituent weights of early and late eggs, excluding

Table 6. Allometric regressions of egg constituents on fresh egg mass for Ring-billed Gulls nesting in 1984.[1]

Variable		Statistics [2]		
	a	b	s_b	R^2
Yolk: Wet yolk	0.060	0.662	0.070	0.240
Dry yolk	-0.445	0.755	0.062	0.338
Water	-0.134	0.622	0.102	0.116
Lipid	-0.506	0.662	0.070	0.238
Non-lipid dry	-0.762	0.710	0.072	0.254
Albumen: Wet albumen	-0.731	1.278	0.059	0.620
Dry albumen	-1.381	1.160	0.061	0.557
Water	-0.861	1.315	0.069	0.557
Shell: Wet shell	-0.935	0.921	0.066	0.405
Dry shell	-1.128	0.962	0.049	0.579
Water	-1.359	0.808	0.195	0.057
Whole egg: Water	-0.341	1.096	0.029	0.833
Non-lipid dry	-0.640	0.963	0.031	0.772
kcal	0.509	0.813	0.035	0.649

---

[1] Early and late clutches pooled (n = 288).

[2] a and b are the intercept and slope in the equation $\log Y = a + b \log X$; s_b is the standard error of b; R^2 is the coefficient of determination.

fresh albumen weight, were correlated with egg volume and fresh weight (Table 7). The lack of any significant relationship between egg volume and fresh weight with wet albumen weight may have been caused by embryonic development in a- and b-eggs; in which albumen water may have moved into the yolk, or evaporated. Both embryonic development and evaporation in a- and b-eggs would account for the large variability in the overall wet yolk and wet albumen weights (see Table 4, early eggs). Egg weight and volume were most strongly correlated with the total water content of the egg. Although there was generally no relationship between egg volume and weight with energy content, larger, heavier eggs contained more nutrients (lipid and protein). Energy and nutrient content remained proportionately constant between early and late laid eggs in 1983.

In 1984, all the fresh weights of the constituents were correlated with egg volume and weight (Table 8). The strongest correlations were found for the fresh weight of albumen and the total weight of water in the egg. There was a negative correlation of egg size and weight with the yolk to albumen ratios. The negative correlation between egg energy and size and volume may be related to a larger water content in the albumen of these freshly collected eggs.

Within the laying sequence of 1983 eggs, all the wet and dry weights of the egg constituents were correlated with the fresh weight of the egg (Table 9). Although not correlated with the proportion of water in each constituent, egg size and weight were strongly correlated with the total weight of water in the egg through the laying sequence.

Table 7. Relationship between egg weight and volume with egg constituent contents for early and late nesting Ring-billed Gulls, Granite Island, 1983.

		Weight			Volume		
		Overall n=144	Early n=98	Late n=46	Overall n=144	Early n=98	Late n=46
Yolk:	Wet yolk	0.44***[1]	0.39***	0.42**	0.52***	0.43***	0.46***
	Dry yolk	0.66***	0.68***	0.56***	0.67***	0.69***	0.55***
	% water	0.16*	0.07	0.08	0.26***	0.15	0.12
	Lipid	0.61***	0.63***	0.52***	0.61***	0.63***	0.50***
	% lipid	-0.15*	-0.06	-0.06	-0.25***	-0.15	-0.11
	Lipid (% dry)	0.02	0.01	0.09	-0.01	0.00	0.03
	Non-lipid dry	0.62***	0.60***	0.54***	0.65***	0.62***	0.56***
Albumen:							
	Wet albumen	0.10	0.21*	0.25*	0.01	0.12	0.22
	Dry albumen	0.53***	0.52***	0.58***	0.50***	0.49***	0.56***
	% water	-0.18*	-0.06	-0.14	-0.26***	-0.14	-0.16
Shell:	Wet shell	0.62***	0.58***	0.60***	0.65***	0.59***	0.63***
	Dry shell	0.65***	0.61***	0.65***	0.66***	0.61***	0.67***
	% water	0.06	-0.07	0.03	0.10	-0.06	0.06

Table 7 continued ...

Yolk/albumen (wet)	0.19*	0.00	0.35**	0.00	0.02	-0.02
Yolk/albumen (dry)	0.19*	-0.09	0.50***	-0.05	0.00	-0.05
Energy	0.02	-0.09	0.11	0.05	-0.05	0.10
Total water	0.89***	0.70***	0.88***	0.77***	0.69***	0.88***

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[1] Pearson correlation r value

* denotes statistical significance at 0.05 level

* denotes statistical significance at 0.01 level

* denotes statistical significance at 0.001 level

Table 8. Relationship between egg weight and volume with egg constituent contents for early and late nesting Ring-billed Gulls, Granite Island, 1984.

		Weight			Volume		
		Overall	Early	Late	Overall	Early	Late
		n=288	n=282	n=6	n=288	n=282	n=6
Yolk:	Wet yolk	0.47***[1]	0.47***	0.09[2]	0.47***	0.47***	-0.14
	Dry yolk	0.60***	0.60***	-0.37	0.61***	0.61***	-0.43
	% water	-0.06	-0.06	0.89**	-0.07	-0.07	0.60
	Lipid	0.49***	0.51***	-0.54	0.50***	0.52***	-0.03
	% lipid	-0.01	0.01	-0.93**	0.01	0.02	-0.32
	Lipid (% dry)	-0.11*	-0.10*	-0.60	-0.11*	-0.10*	-0.26
	Non-lipid dry	0.50***	0.50***	-0.26	0.52***	0.52***	-0.60
Albumen:							
	Wet albumen	0.80***	0.81***	0.37	0.78***	0.78***	0.37
	Dry albumen	0.72***	0.72***	0.83*	0.69***	0.69***	0.43
	% water	0.12*	0.12*	-0.72*	0.12*	0.12*	-0.03
Shell:	Wet shell	0.61***	0.61***	0.66	0.61***	0.61***	0.20
	Dry shell	0.75***	0.75***	0.20	0.74***	0.74***	-0.09
	% water	-0.05	-0.05	0.58	-0.03	-0.02	0.14

Table 8 continued ...

Yolk/albumen (wet)	-0.28***	-0.28***	-0.03	-0.17***	-0.18***	0.31
Yolk/albumen (dry)	-0.27***	-0.27***	-0.66	-0.16***	-0.17***	0.27
Energy	-0.30***	-0.31***	-0.89**	-0.25***	-0.26***	-0.26
Total water	0.92***	0.92***	0.77*	0.89***	0.90***	0.49

---

[1] Pearson correlation r value

[2] Spearman Rank correlation

*denotes statistical significance at 0.05 level

**denotes statistical significance at 0.01 level

***denotes statistical significance at 0.001 level

Table 9. Relationship between egg weight and volume with egg constituent contents through the laying sequence for Ring-billed Gulls nesting in 1983, Granite Island.

		Weight			Volume		
		Egg			Egg		
		a	b	c	a	b	c
		n=48[1]	n=48	n=48	n=48	n=48	n=48
Yolk:	Wet yolk	0.49***[2]	0.20	0.31*	0.53***	0.28*	0.42**
	Dry yolk	0.73***	0.57***	0.61***	0.76***	0.58***	0.63***
	% water	0.04	-0.07	0.00	0.11	0.00	0.12
	Lipid	0.64***	0.59***	0.58***	0.64***	0.60***	0.60***
	% lipid	-0.08	0.14	0.00	-0.16	0.07	-0.11
	Lipid (% dry)	-0.14	0.34**	0.02	-0.20	0.32*	0.00
	Non-lipid dry	0.73***	0.48***	0.52***	0.79***	0.48***	0.55***
Albumen:							
	Wet albumen	0.34**	0.04	0.42***	0.23	0.00	0.32*
	Dry albumen	0.44***	0.57***	0.53***	0.41**	0.53***	0.48***
	% water	0.07	-0.19	0.08	-0.03	-0.23	-0.01
Shell:	Wet shell	0.66***	0.68***	0.46***	0.65***	0.67***	0.54***
	Dry shell	0.68***	0.69***	0.50***	0.63***	0.69***	0.56***
	% water	0.14	0.10	-0.06	0.07	0.09	0.01

able 9 continued ...

olk/albumen (wet)	-0.04	0.22	-0.01	-0.05	-0.01	-0.06
olk/albumen (dry)	-0.02	0.54***	0.08	-0.06	-0.01	-0.07
nergy	0.10	0.05	-0.02	0.16	0.08	0.02
otal water	0.89***	0.66***	0.80***	0.86***	0.66***	0.81***

---

[1] Early and late eggs were pooled.

[2] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Unlike eggs laid in 1983, egg size and weight in 1984 were negatively correlated with energy content (kcal/g, Table 10). The correlation between both egg size and weight with the total water content in eggs decreased through the laying sequence.

Generally then, the fresh and dry weights of egg constituents were correlated with egg volume and weight; both for early and late eggs, and through the laying sequence.

3.3 Artificially Incubated Eggs

3.3.1 Hatching Failure

Of the 275 eggs collected for artificial incubation, including 2- and 3-egg clutches in each year, 10 were infertile and 46 were rotten. Total hatching failure was 16.7% (15.5% and 17.6% for 1983 and 1984 respectively). In each year, late hatching failure apparently was greater than that for early eggs (1983: 9.7% versus 22.2%; 1984: 16.3% versus 27.8%, for early and late eggs respectively).

3.3.2 Hatchling Weights

For the 110 early chicks that were successfully artificially

Table 10. Relationship between egg weight and volume with egg constituent contents through the laying sequence for Ring-billed Gulls nesting in 1984, Granite Island.

		Weight			Volume		
		Egg			Egg		
		a	b		a	b	
		n=96[1]	n=96	n=96	n=96	n=96	n=96
Yolk:	Wet yolk	0.62***[2]	0.49***	0.46***	0.61***	0.51***	0.45***
	Dry yolk	0.53***	0.63***	0.65***	0.53***	0.66***	0.64***
	% water	0.10	0.06	-0.09	0.08	0.06	-0.11
	Lipid	0.44***	0.44***	0.57***	0.42***	0.48***	0.59***
	% lipid	-0.04	-0.10	0.00	-0.06	-0.08	0.03
	Lipid (% dry)	0.03	-0.09	-0.17*	-0.01	-0.06	-0.16
	Non lipid dry	0.44***	0.53***	0.53***	0.47***	0.53***	0.54***
Albumen:							
	Wet albumen	0.91***	0.81***	0.60***	0.88***	0.76***	0.59***
	Dry albumen	0.81***	0.80***	0.45***	0.79***	0.72***	0.45***
	% water	-0.11	-0.11	0.15	-0.09	-0.06	0.14
Shell:	Wet shell	0.64***	0.59***	0.48***	0.61***	0.57***	0.51***
	Dry shell	0.73***	0.72***	0.66***	0.69***	0.71***	0.66***
	% water	-0.10	-0.02	-0.05	-0.10	-0.02	0.00

Table 10 continued ...

Yolk/albumen (wet)	-0.35***	-0.17	-0.14	-0.12*	-0.19**	-0.18**
Yolk/albumen (dry)	-0.37***	-0.32***	-0.03	-0.12*	-0.20**	-0.16*
Energy	-0.33***	-0.23*	-0.25**	-0.30***	-0.19*	-0.16
Total water	0.97***	0.95***	0.78***	0.94***	0.91***	0.76***

---

[1] Early and late eggs were pooled.

[2] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

incubated in 1984, the average weight at hatch was 34.7 g (± 4.7 g) for chicks from 3-egg clutches (Table 11). No chicks hatched from 3-egg clutches that were laid late in 1984. C-egg chicks from early eggs weighed less than those from a- or b-eggs ($F= 3.82$, $p< 0.05$). There was a weak, positive correlation between chick weight and the fresh weight of the egg ($r= 0.40$, $p< 0.001$), and this correlation increased through the laying sequence (a-egg: $r= 0.08$, NS; b-egg: $r= 0.42$, $p< 0.01$; c-egg: $r= 0.64$, $p< 0.001$).

The average weights of fresh eggs and chicks for male hatchlings did not differ from those for female eggs and chicks (Table 12), either overall, or separately by egg. For both male and female chicks, weight decreased through the laying sequence, but not significantly. However, both male and female c-eggs were lighter than a- or b-eggs.

3.3.3 Secondary (At Hatch) Sex Ratios

Sex ratio data from earlier studies on Granite Island are presented on Table 13 with permission of Ryder (1983). A significant dependance occurred between chick sex and egg sequence in 1978 and 1979 only. The combined secondary sex ratio through the laying sequence shifted from predominantly male a-eggs (56%) to predominantly more female c-eggs (42% males), but the overall male to female ratio did not differ from unity ($X^2= 0.58$). Separately by year, the sex ratios for modal 3-egg clutches did not differ from unity in 1978, 1982 and 1984 ($X^2 = 0.34$,

Table 11. Mean chick weights for early nesting Ring-billed Gulls, Granite Island, 1984.

Egg	n	Mean	S.D.
a	42	35.5	4.4
b	40	35.2	4.9
	28	32.6	4.4
Total	110	34.7	4.7

Table 12. Comparison of early male and female fresh egg and chick weights through the laying sequence, Granite Island, 1984.

			Mann-Whitney U
Egg weight (g)			
overall	59.1 ± 3.7 (52)[1]	58.7 ± 3.6 (58)	t = 0.92, NS[2]
a	60.0 ± 3.9 (23)	60.2 ± 3.6 (19)	NS[3]
b	59.4 ± 2.9 (17)	59.1 ± 3.1 (23)	NS
c	56.9 ± 3.9 (12)	56.4 ± 3.3 (16)	NS
	F = 3.08, $p < 0.05$	F = 5.63, $p < 0.01$	
Chick weight (g)			
overall	35.1 ± 4.4 (52)	34.3 ± 4.9 (58)	t = 0.58, NS
a	35.8 ± 4.1 (23)	35.1 ± 4.9 (19)	NS
b	35.6 ± 4.9 (17)	34.9 ± 4.9 (23)	NS
c	32.9 ± 4.2 (12)	32.4 ± 4.6 (16)	NS
	F = 1.97, NS	F = 1.68, NS	

---

[1] Mean ± SD (n)

[2] Sample size sufficient for Student's t-test.

[3] No significant difference

Table 13. Number of male and female chicks in relation to egg sequence for Ring-billed Gulls, Granite Island, 1978 to 1984.

Year	Sex	Egg[1]			%
		A	B	C	
1978[2]	M	11	4	12	52.9
	F	3	11	10	47.1
	$G = 8.30$,	$p < 0.025$,	$N = 28$ clutches		
1979[2]	M	15	6	6	39.1[4]
	F	11	18	13	60.9
	$G = 6.26$,	$p < 0.05$,	$N = 30$ clutches		
1982[2]	M	18	16	10	54.3
	F	11	12	14	45.7
	$G = 2.40$,	NS,	$N = 31$ clutches		
1983[3]	M	6	5	4	32.6[4]
	F	9	11	11	67.4
	$G = 0.62$,	NS,	$N = 18$ clutches		

Table 13 continued ...

1984[3]	M	21	18	14	47.3
	F	21	22	16	52.7
	G = 0.21,	NS,	N = 47 clutches		
Combined	M	71	49	46	46.2
	F	55	74	64	53.8
	G = 8.08,	$p < 0.025$,	N = 154 clutches 359 chicks		

---

[1] Only 3-egg clutches were used.

[2] Data taken from Ryder (1983).

[3] Only early 3-egg clutches were used.

[4] Sex ratio was significantly different from unity in these years.

0.74, 0.29, respectively), but did in 1979 and 1983 ($X^2 = 4.75, 5.75$, $p < 0.025$). Female chicks accounted for more than 60% of all hatchlings in 1979 and 1983, possibly related to each year being a late breeding season with poor pre-breeding food abundance (J.P. Ryder, pers. comm. for conditions in 1979).

The ratio of unisexual to bisexual clutches did not differ from the 1:2:1 ratio predicted by the random segregation of sex chromosomes ($X^2 = 5.62$, Table 14).

3.4 Adult Body Condition

3.4.1 Body Size, Weight and Condition Index

Comparisons between years revealed that female Ring-billed Gulls nesting early in 1984 had a larger mean condition index than females nesting early in 1983, but did not differ in body weight or size (Table 15). Late nesting females in both years did not differ in size, weight or condition.

Within each year, females nesting later in the season weighed less than earlier nesters (Table 15), but were essentially the same size. Therefore, the average condition index for females laying 3 eggs later in the season was less than that for earlier nesting females in each

Table 14. Number of unisexual and bisexual complete clutches[1] for Ring-billed Gull chicks, Granite Island, 1983 and 1984.

	Proportion		
	1	2	1
	3♀♀	mixed	3♂♂
Year			
1983	2	5	1
1984	2	14	2
Combined	4	19	3

[1] Only 3-egg clutches from which all chicks hatched were used. Those clutches chosen were laid early in the breeding season.

Table 15. Adult female Ring-billed Gull body size and condition index, Granite Island, 1983 and 1984.

	Early	Late	Mann-Whitney U
Body weight (g)			
1983	440.4 ± 28.0 (45)[1]	418.6 ± 22.4 (19)	$p < 0.01$
1984	448.6 ± 30.7 (58)	401.5 ± 19.7 (4)	$p < 0.01$
	$t = -1.39$, NS[2]	NS[3]	
Bill length (mm)			
1983	58.2 ± 1.9 (45)	58.8 ± 2.2 (20)	NS[4]
1984	58.2 ± 1.6 (58)	58.6 ± 2.8 (4)	NS
	$t = -0.02$, NS	NS	
Bill depth (mm)			
1983	12.1 ± 0.6 (45)	12.4 ± 0.3 (20)	$p < 0.05$
1984	12.3 ± 0.4 (58)	12.3 ± 0.6 (4)	NS
	$t = -2.18$, $p < 0.05$	NS	
Keel length (mm)			
1983	65.2 ± 2.8 (45)	62.3 ± 2.2 (19)	$p < 0.01$
1984	64.3 ± 3.5 (58)	61.6 ± 1.5 (4)	NS
	$t = 1.35$, NS	NS	

Table 15 continued ...

Head length (mm)			
1983	89.9 ± 2.3 (45)	90.0 ± 2.2 (19)	NS
1984	89.0 ± 3.4 (58)	89.1 ± 4.6 (4)	NS
	t = 1.58, NS	NS	
Tarsus length (mm)			
1983	62.4 ± 2.1 (24)	62.5 ± 2.8 (10)	NS
1984	62.8 ± 1.7 (22)	62.2 ± 0.4 (2)	NS
	t =-0.74, NS	NS	
Condition Index			
1983	3.57 ± 0.18 (45)	3.47 ± 0.20 (19)	$p < 0.05$
1984	3.66 ± 0.26 (58)	3.34 ± 0.10 (4)	$p < 0.01$
	t =-2.29, $p < 0.05$	NS	

---

[1] Mean ± SD (n)

[2] Student's t-test

[3] Mann-Whitney U used for late comparisons between years.

[4] No significant difference

year.

Table 16 shows that the overall index of body condition was strongly correlated with body weight when all females were considered together (N= 58). Body weight was also correlated with keel length and head length, though very weakly.

3.4.2 Body Condition Index Through the Breeding Season

Figure 4 presents the regressions of mean condition index versus date for post-laying females that laid 3 eggs. Overall, the index of body condition declined through the breeding season ($r= -0.29$, $p< 0.001$; $Y= 3.67- 0.009X$). Indexed body condition was correlated with date in 1983 ($n= 65$, $F= 4.02$, $p< 0.05$), but was not in 1984 ($n= 62$, $F= 3.80$). Analysis of covariance revealed that although the slopes and intercepts of the regression lines of 1983 and 1984 were the same ($F= 1.07$, 0.58, respectively), the variation about the line in 1983 was larger than in 1984 ($F= 2.75$, $p< 0.001$).

3.5 Effect of Body Weight and Condition Index on Egg Size and Composition

One of the objectives of this field study was to test whether egg quality and composition could be used to indicate the body weight (and

Table 16. Relationship between the size, weight and condition index of female[1] Ring-billed Gulls, Granite Island.

	Body weight	Condition Index
Body weight	--------	0.84, $p < 0.001$
Bill length	0.72[2], NS[3]	-0.20, NS
Bill depth	0.13, NS	0.00, NS
Keel length	0.54, $p < 0.001$	0.05, NS
Head length	0.26, $p < 0.05$	-0.03, NS
Tarsus length	0.19, NS	-0.01, NS
Condition Index	0.84, $p < 0.001$	-------

---

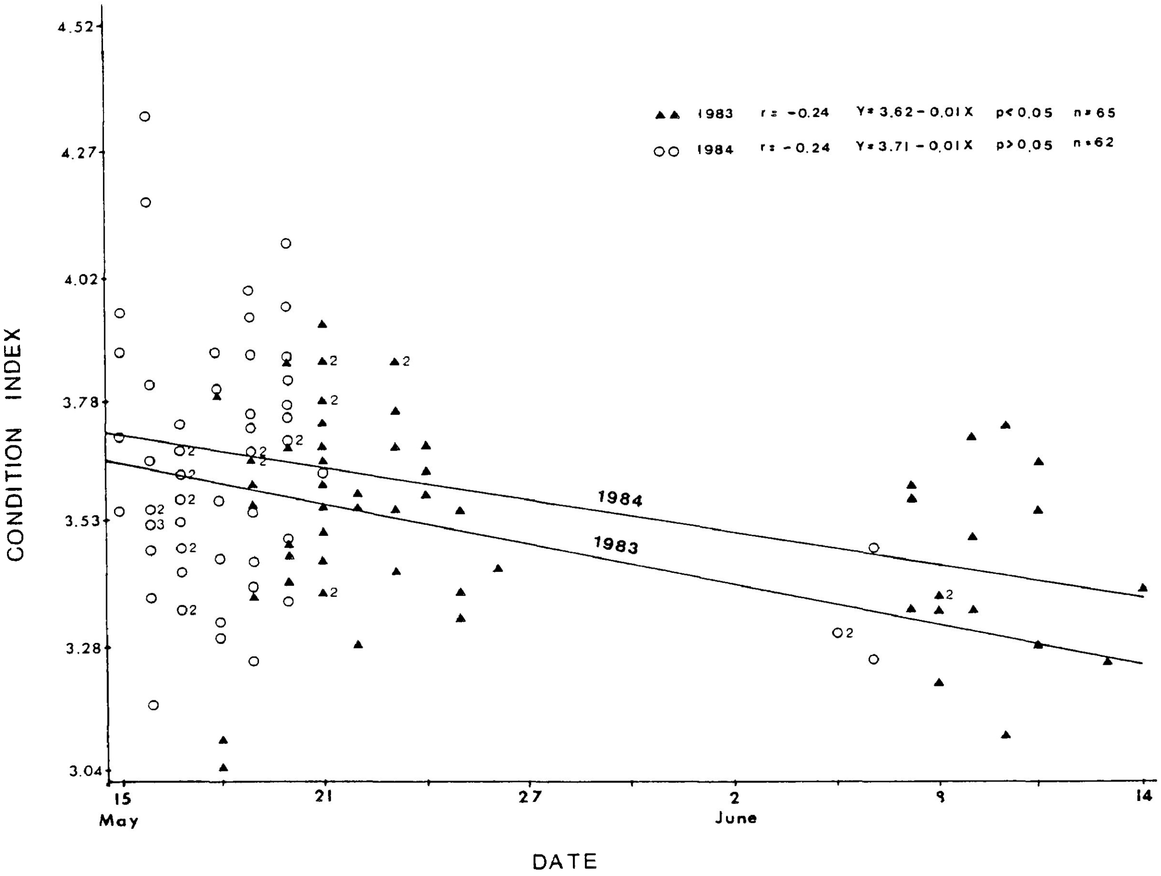
[1] Only 3-egg, post-laying females were used.

[2] Pearson correlation r value

[3] No statistical significance

Note: Data from 1983 and 1984 were pooled (N = 58).

Figure 4. Regression of the condition indices of female Ring-billed Gulls against date trapped, Granite Island, 1983 and 1984. Note: Data for the mean indexed body condition of female Ring-billed Gulls by date are given in Appendix 19. Only 3-egg, post-laying females were used. The number of trap days in 1983 was 16; 9 in 1984.


▲▲ 1983 r = -0.24 Y = 3.62 - 0.01X p< 0.05 n = 65
○○ 1984 r = -0.24 Y = 3.71 - 0.01X p> 0.05 n = 62
CONDITION INDEX
4.52
4.27
4.02
3.78
3.53
3.28
3.04
1984
1983
15
May
21
27
2
June
8
14
DATE

ultimately condition) of the female laying that egg, without ever examining that female. Overall, it appeared that egg size and composition were not satisfactory predictors of female body weight or condition because of the low, but statistically significant correlation values (Tables 17 & 18). The body weight of females nesting early in the season was poorly correlated with fresh egg weight in each year (Table 17). The strong, inverse correlation for the body weight of females nesting late in the season female with egg volume in 1984 may have been the result of limited sample size. The lack of correlation between body weight and egg nutrient reserve levels suggested that larger eggs contained more water in their constituents, as supported by the significant correlations with the total water in the egg for females nesting earlier in the season.

When correlations were repeated using the index of female body condition rather than body weight, egg volume and weight were not correlated with the body condition of early or late nesting females in either year (Table 18).

Stronger, though still statistically weak, correlations were found when a-, b- and c-egg size and composition were correlated separately with the body weight and indexed condition of females. Within 1983 clutches, a-egg weight and volume were more strongly correlated with body weight than b- or c-eggs (Appendix 8). The a-egg correlations between the weights of total water and wet yolk with body weight were better than those for b- or c-eggs. In 1984, b-egg volume, fresh weight, yolk protein weight and total water weight were more strongly

Table 17. Relationship between female[1] Ring-billed Gull body weight with egg volume and composition, Granite Island, 1983 and 1984.

		1983		1984	
		Early n=71[2]	Late n=30	Early n=63	Late n=6
Egg volume		0.15[3]	-0.02	0.24*	-0.88*[4]
Fresh egg weight		0.20*	0.03	0.25*	-0.49
Yolk:	Wet yolk	0.03	0.04	0.25*	-0.10
	Dry yolk	0.04	-0.38*	0.14	0.10
	% water	-0.01	0.34	0.19	-0.68
	Lipid	-0.02	-0.35*	0.14	-0.29
	% lipid	-0.02	-0.31*	-0.13	0.30
	Lipid (% dry)	-0.13	-0.06	0.03	0.29
	Non-lipid dry	0.07	-0.29	0.11	0.29
Albumen:	Wet albumen	0.11	0.06	0.15	0.10
	Dry albumen	0.12	0.22	0.18	-0.10
	% water	0.06	-0.10	-0.02	0.00
Shell:	Wet shell	0.32**	0.26	0.10	-0.29
	Dry shell	0.22*	0.12	0.19	0.29
	% water	0.24*	0.38*	-0.09	-0.40

Table 17 continued ...

Yolk/albumen (wet)	-0.02	-0.03	0.03	-0.10
Yolk/albumen (dry)	-0.04	-0.46**	-0.06	0.10
Energy	-0.19	-0.46*	-0.09	0.10
Total water	0.23*	0.24	0.24*	-0.10

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Sample size not 72 since one a-egg had no yolk.

[3] Pearson correlation r value

[4] Spearman rank correlation (sample size less than 25)

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Table 18. Relationship between female[1] Ring-billed Gull indexed body condition with egg volume and composition, Granite Island, 1983 and 1984.

		1983		1984	
		Early n=71[2]	Late n=30	Early n=63	Late n=6
Egg volume		0.05[3]	0.01	0.13	-0.88 *[4]
Fresh weight egg		0.06	0.01	0.13	-0.49
Yolk:	Wet yolk	-0.01	0.02	0.03	-0.10
	Dry yolk	-0.15	-0.43**	-0.08	0.10
	% water	0.06	0.36*	0.15	-0.68
	Lipid	-0.25*	-0.45**	-0.08	-0.29
	% lipid	-0.13	-0.36*	-0.13	0.29
	Lipid (% dry)	-0.29**	-0.23	-0.04	0.29
	Non-lipid dry	-0.02	-0.30	-0.07	0.29
Albumen:	Wet albumen	0.10	0.02	0.14	0.10
	Dry albumen	0.11	0.14	0.17	-0.10
	% water	0.05	-0.08	-0.02	0.00

Table 18 continued ...

Shell:	Wet shell	0.28***	0.31*	-0.08	-0.29
	Dry shell	0.22*	0.19	-0.01	0.29
	% water	0.14	0.36*	-0.13	-0.40
Yolk/albumen (wet)		-0.04	-0.02	-0.09	-0.10
Yolk/albumen (dry)		-0.18	-0.45**	-0.22*	0.10
Energy		-0.29*	-0.57***	-0.25*	0.10
Total water		0.19	0.20	0.16	-0.10

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Sample size not 72 since one a-egg had no yolk.

[3] Pearson correlation r value

[4] Spearman rank correlation (sample size less than 25)

*denotes statistical significance at 0.05 level

**denotes statistical significance at 0.01 level

***denotes statistical significance at 0.001 level correlated with the body weight of females than a- or c-eggs.

In each year, egg weight, size and composition were not well correlated with the indexed condition of females (Appendix 9). In 1983, the proportion of lipid (as % wet and dry yolk) and energy content of eggs were negatively correlated with body condition.

3.6 Chemical Analyses of Female Adults

Females nesting later in the season contained proportionately more body water and protein, but less lipid than females nesting earlier (Table 19). Late nesting females had less total protein and lipid, and therefore less energy by weight, than earlier nesting females.

Comparisons of the composition of body homogenate for early nesting females between years (Appendix 10) showed that early nesters in each year contained equal amounts of body energy by weight. Between year comparisons for late nesting females revealed no differences in the composition of body homogenate. This may have resulted from the small number of females nesting late in 1984 that laid 3 eggs. Although not statistically significant, late nesters in 1984 appear to have had more body lipid, both by weight and as a proportion, than late 1983 nesters (Appendix 10).

Within 1983, females nesting late in the season weighed less (ie. that part of the carcass homogenized), contained proportionately more body water, and less body lipid, than earlier nesters. The body

Table 19. Comparison of early and late nesting female[1] Ring-billed Gull total body composition, Granite Island.

	Early[2] n=45	Late n=12	Mann-Whitney U
Total analyzed weight (g)[3]	354.3 ± 25.2 [4]	326.5 ± 14.7	$p < 0.001$
Total water (g)	227.2 ± 14.9	221.3 ± 9.2	NS[5]
% water	64.3 ± 3.4	67.8 ± 1.3	$p < 0.001$
Total protein (g)	95.8 ± 12.5	92.2 ± 3.8	$p < 0.01$
% protein	27.2 ± 3.6	28.3 ± 0.9	$p < 0.05$
Total lipid (g)	29.1 ± 13.9	13.1 ± 6.0	$p < 0.001$
% lipid	8.0 ± 3.5	4.0 ± 1.7	$p < 0.001$
Total energy (kcal/g total analyzed weight) [6]	6.40 ± 0.69	6.12 ± 0.19	$p < 0.001$

[1] Only post-laying females that laid 3 eggs were used.

[2] Data from 1983 and 1984 were pooled.

[3] Extrapolated from subsamples of analyzed body homogenate, skin and gonads.

[4] Mean ± SD

[5] No significant difference

[6] Dry weight

homogenate of females nesting late in 1983 contained less protein and lipid by weight, and therefore less energy per gram analyzed (Appendix 10). The composition of the body homogenate did not differ for early and late females in 1984. This again may be a function of limited late sample size. The same results as 1983 would probably have been found if a larger late sample been obtained in 1984.

Appendix 11 presents the chemical composition of skin from post-laying females. For neither early or late nesting females was there a difference in skin composition between years. Within 1983, females nesting earlier in the season had heavier skin containing proportionately more water and lipid, but less protein, than later nesting females. Energy content was greater for females nesting early in 1983, as was lipid weight. As was the case for the composition of body homogenate, skin composition did not differ within 1984. This was probably a result of limited late sample size.

The water and nutrient content of the female reproductive system (ovary plus oviduct) generally did not differ either between or within years (Appendix 12). The reproductive tissues of females nesting early in 1984 contained proportionately less water, more protein and equivalent amounts of lipid when compared to the reproductive tissues of females nesting early in 1983. Hence, there tended to be a higher energy content in the reproductive tissues of females nesting early in 1984 relative to those nesting early in 1983; but this trend is not significant because of the large variation for females nesting early in 1984.

Table 20 summarizes the total body composition for female Ring-billed Gulls that laid 3 eggs. Comparisons between years revealed that females nesting early in 1983 contained proportionately less body water than females nesting early in 1984. There were no compositional differences between the bodies of females nesting late in each year. Within 1983, early nesters weighed more, contained proportionately more body water, less protein and lipid than late nesters. By weight, late nesting females had less protein and lipid, and therefore a lower energy content, than females nesting early in 1983. Again, the small sample size of late nesting birds in 1984 limited the number of significant tests.

Chemical analyses of female carcasses revealed that there were no differences in body weight or nutrient content between years (Table 20). Within years, despite the limited late sample in 1984, it appeared that females nesting earlier were heavier and contained more energy rich lipids than post-laying females nesting later in the season.

Figure 5 presents a correlation matrix designed to assess the importance of the three chemically analyzed nutrient reserves (body, reproductive, skin) to the overall chemical composition of the post-laying female. Although there are a number of correlatiions given, only those that are biologically significant will be mentioned.

Since the levels of water, protein and lipid were expressed as proportions, within the three reserves there was generally a negative correlation between water with lipid and energy content for females

Table 20. Comparison of early and late nesting female[1] Ring-billed Gull total body composition, Granite Island, 1983 and 1984.

	Early	Late	Mann-Whitney U
Total analyzed weight (g)			
1983	358.5 ± 28.2 (24)[2]	326.6 ± 15.6 (10)	$p < 0.01$
1984	349.6 ± 20.8 (21)	325.9 ± 13.1 (2)	NS[3]
	NS	NS	
Total water (g)			
1983	227.8 ± 15.3 (24)	221.9 ± 9.7 (10)	NS
1984	226.6 ± 14.8 (21)	218.0 ± 7.0 (2)	NS
	NS	NS	
% water			
1983	63.7 ± 2.7 (24)	68.0 ± 1.4 (10)	$p < 0.001$
1984	64.9 ± 3.9 (21)	66.9 ± 0.6 (2)	NS
	$p < 0.05$	NS	
Total protein (g)			
1983	95.2 ± 16.0 (24)	92.7 ± 3.8 (10)	$p < 0.05$
1984	96.5 ± 7.2 (21)	89.5 ± 3.2 (2)	NS
	NS	NS	
% protein			
1983	26.7 ± 4.7 (24)	28.4 ± 0.6 (10)	$p < 0.05$
1984	27.7 ± 1.7 (21)	27.5 ± 2.1 (2)	NS
	NS	NS	

Table 20 continued ...

Total lipid (g)			
1983	31.4 ± 14.6 (24)	12.0 ± 5.2 (10)	$p < 0.001$
1984	26.4 ± 13.0 (21)	18.3 ± 9.3 (2)	NS
	NS	NS	
% lipid			
1983	8.6 ± 3.6 (24)	3.6 ± 1.5 (10)	$p < 0.001$
1984	7.4 ± 3.4 (21)	5.6 ± 2.6 (2)	NS
	NS	NS	
Total energy (kcal/g total analyzed weight)[4]			
1983	6.37 ± 0.90 (24)	6.08 ± 0.16 (10)	$p < 0.001$
1984	6.44 ± 0.29 (21)	6.30 ± 0.30 (2)	NS
	NS	NS	

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[1] Only post-laying females that laid 3 eggs were used.

[2] Mean ± SD (n)

[3] No significant difference

[4] Dry weight of tissues.

Figure 5. Spearman rank correlation matrix for the carcass composition (expressed as proportions) of female Ring-billed Gulls, Granite Island, 1983.

	Body homogenate water	Body homogenate protein	Body homogenate lipid	Body homogenate energy	Skin water	Skin protein	Skin lipid	Skin energy	Ovary water	Ovary protein	Ovary lipid	Ovary energy	Total water	Total protein	Total lipid
Body homogenate protein	0.84***[1]														
Body homogenate lipid	-0.84***	-1.00***													
Body homogenate energy	-0.85***	-1.00***	1.00***												
Skin water	0.88***	0.95***	-0.95***	-0.95***											
Skin protein	0.57**	0.71***	-0.71***	-0.71***	0.72***										
Skin lipid	-0.57**	-0.71***	0.71***	0.71***	-0.72***	-1.00***									
Skin energy	-0.57**	-0.71***	0.71***	0.71***	-0.72***	-1.00***	1.00***								
Ovary[2] water	0.18	0.24	-0.24	-0.24	0.27	0.40*	-0.40*	-0.40*							
Ovary protein	-0.09	0.05	-0.05	-0.05	-0.12	0.03	-0.03	-0.03	0.52						
Ovary lipid	0.08	-0.09	0.09	0.09	0.12	0.05	-0.05	-0.05	-0.36	-0.95***					
Ovary energy	0.08	-0.09	0.09	0.09	0.12	0.05	-0.05	-0.05	-0.36	-0.95***	1.00***				
Total water	0.95***	0.93***	-0.93***	-0.93***	0.97***	0.69***	-0.69***	-0.69***	0.25	-0.12	0.11	0.11			
Total protein	0.01	0.39*	-0.39*	-0.39*	0.25	0.54**	-0.54**	-0.54**	0.37*	0.40	-0.40*	-0.40*	0.16		
Total lipid	-0.84***	-0.97***	0.97***	0.97***	-0.96***	-0.82***	0.82***	0.82***	-0.31	-0.01	0.02	0.02	-0.94***	-0.42*	
Total energy	-0.83***	-0.98***	0.98***	0.98***	-0.94***	-0.80***	0.80***	0.80***	-0.29	-0.05	0.08	0.08	-0.93***	-0.46*	0.99***

[1] Only early nesting females were used (n = 21).

[2] Ovary refers to both ovarian and oviducal tissues.

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Note: Only post-laying females that laid 3 eggs were used.

nesting in 1983.

The analyzed reproductive tissues of females did not significantly contribute to the overall chemical composition of post-laying females (Figure 5). The proportion of water in the female was negatively correlated with lipid and energy levels in the body and skin, but positively correlated with the water and protein levels of the body and skin nutrient reserves. Total protein levels in post-laying females were not well correlated with the composition of the three nutrient reserves. Since overall kcal content of tissues is closely linked with energy rich lipid - as exemplified by the near 1.00 correlation between these - both total lipid and total energy levels were negatively correlated with the water and protein levels of the body and skin.

In 1984, only the carcasses of females nesting early in the season were used to examine the interrelationships of carcass composition because of the small late sample size (n=2). Overall, the relationships reported for 1983 carcass composition held true for females nesting in 1984. The total water content of the carcass was negatively correlated with lipid and energy levels (Figure 6). Protein content was negatively correlated to lipid and energy levels. The strongest positive correlation was between total lipid and energy content.

Figure 6. Spearman rank correlation matrix for the carcass composition (expressed as proportions) of female Ring-billed Gulls, Granite Island, 1984.

	Body homogenate water	Body homogenate protein	Body homogenate lipid	Body homogenate energy	Skin water	Skin protein	Skin lipid	Skin energy	Ovary water	Ovary protein	Ovary lipid	Ovary energy	Total water	Total protein	Total lipid
Body homogenate protein	0.56**[1] 0.71*[2]														
Body homogenate lipid	-0.88*** -0.71*	-0.76*** -1.00***													
Body homogenate energy	-0.68*** -0.71*	-0.76*** -1.00***	1.00*** 1.00***												
Skin water	0.78*** 0.76**	0.77*** 0.93***	-0.86*** -0.93***	-0.86*** -0.93***											
Skin protein	0.58** 0.77**	0.86*** 0.87***	-0.85*** -0.87***	-0.85*** -0.87***	0.86*** 0.96***										
Skin lipid	-0.56** -0.77**	-0.83*** -0.87***	0.80*** 0.87***	0.80*** 0.87***	-0.91*** -0.96***	-0.95*** -1.00***									
Skin energy	-0.51** -0.77**	-0.71*** -0.87***	0.68*** 0.87***	0.68*** 0.87***	-0.87*** -0.96***	-0.94*** -0.79**	0.94*** 0.99***								
Ovary [3] water	-0.14 0.67*	0.04 0.54	0.00 -0.54	-0.01 -0.54	0.02 0.70*	0.17 0.83***	-0.19 -0.83***	-0.20 -0.83***							
Ovary protein	-0.10 0.49	0.01 0.55*	-0.13 -0.55*	-0.13 -0.55*	-0.02 0.61*	0.17 0.71*	-0.14 -0.71*	-0.07 -0.71**	0.52** 0.90***						
Ovary lipid	0.10 -0.44	-0.01 -0.48	0.13 0.48	0.13 0.48	0.02 -0.52	-0.17 -0.62*	0.14 0.62*	0.07 0.62*	-0.52** -0.87***	-1.00*** -0.99***					
Ovary energy	0.10 -0.35	-0.01 -0.44	0.13 0.44	0.13 0.44	0.02 -0.47	-0.17 -0.58*	0.14 0.58*	0.07 0.58*	-0.52** -0.82**	-1.00*** -0.96***	1.00*** 0.99***				
Total water	0.92*** 0.92***	0.74*** 0.71*	-0.81*** -0.71*	-0.81*** -0.71*	0.93*** 0.84***	0.80*** 0.89***	-0.81*** -0.89***	-0.74*** -0.89***	-0.06 0.78**	-0.04 0.55*	0.04 -0.47	0.04 -0.37			
Total protein	0.09 -0.19	0.80*** 0.49	-0.56** -0.49	-0.56** -0.49	0.46* 0.35	0.73*** 0.35	-0.68*** -0.35	-0.53** -0.35	0.08 0.15	0.27 0.37	-0.27 -0.36	-0.27 -0.44	0.36* -0.08		
Total lipid	-0.73*** -0.75**	-0.79*** -0.94***	0.97*** 0.94***	0.97*** 0.94***	-0.93*** -0.99***	-0.91*** -0.98***	0.88*** 0.98***	0.76*** 0.98***	0.02 -0.72**	-0.08 -0.64*	0.08 0.55*	0.08 0.52	-0.89*** -0.79**	-0.61** -0.42	
Total energy	-0.69*** -0.75**	-0.71*** -0.94***	0.95*** 0.94***	0.95*** 0.94***	-0.93*** -0.99***	-0.84*** -0.98***	0.87*** 0.98***	0.83*** 0.95***	-0.01 -0.92***	-0.08 -0.64*	0.08 0.55*	0.08 0.52	-0.85*** -0.83***	-0.49** -0.42	0.97*** 1.00***

[1] Early (n = 24)

[2] Late (n = 10)

[3] Ovary refers to both ovarian and oviducal tissues.

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Note: Only post-laying females that laid 3 eggs were used.

3.7 Effect of Female Body Weight and Indexed Condition on Carcass Composition

In each year, neither the nutrient nor water levels in reproductive tissues were correlated to female body weight or indexed condition for both early and late nesting females (Table 21). The body weight of females was negatively correlated with body homogenate and skin protein levels, as well as total carcass protein content. Body weight was also correlated with the lipid level of body homogenate, skin and overall lipid level. In 1984, female body weight was positively correlated with total energy and lipid content.

The positive correlations between total lipid and energy contents with body weight also occurred for the index of female body condition. Condition indices were positively correlated with total carcass lipid content, body homogenate lipid levels and subcutaneous lipid levels for early nesting females (Table 21). Hence, in each year indexed body condition was correlated with total energy content for early nesting females.

3.8 Relationship Between Carcass Composition and Egg Composition

Computation of Pearson correlation coefficients between the chemical content of eggs and that of female carcasses suggested that females

Table 21. Relationship between condition index and body weight with carcass composition[1] for female[2] Ring-billed Gulls, Granite Island, 1983 and 1984.

		Condition Index			Body Weight		
		1983		1984	1983		1984
		Early[3]	Late[4]	Early[5]	Early	Late	Early
Body homogenate:	water	-0.19	-0.30	-0.37*	-0.12	-0.30	-0.44*
	protein	-0.58***	-0.31	-0.32	-0.62***	-0.35	-0.39*
	lipid	0.42*	0.61*	0.56**	0.37*	0.65*	0.59**
	energy	0.45*	0.61*	0.55**	0.40*	0.65*	0.59*
Skin:	water	-0.35*	-0.59*	-0.51**	-0.39*	-0.66*	-0.53**
	protein	-0.60***	-0.03	-0.24	-0.67***	-0.13	-0.17
	lipid	0.48**	0.52	0.47*	0.55**	0.60*	0.42*
	energy	0.42*	0.50	0.48*	0.53**	0.59*	0.36
Ovary:	water	0.01	-0.21	-0.11	-0.02	-0.25	0.01
	protein	-0.26	0.16	0.31	-0.14	0.20	0.09
	lipid	0.25	0.18	-0.06	0.12	0.18	0.06
	energy	0.30	0.08	-0.04	0.15	0.04	0.10
Total carcass:	water	-0.34	-0.37	-0.52**	-0.35*	-0.45	-0.53**
	protein	-0.64***	-0.26	-0.29	-0.74***	-0.32	-0.28
	lipid	0.48**	0.58*	0.56**	0.49*	0.65*	0.55**
	energy	0.42*	0.58*	0.58**	0.42*	0.65*	0.57**

Table 21 continued ...

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[1] Carcass composition was expressed as a proportion.

[2] Only post-laying females that laid 3 eggs were used.

[3] n = 24

[4] n = 10

[5] n = 21

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

with larger stored nutrient reserves laid eggs of higher quality; but none of the relationships were biologically useful predictors (Table 22). Though weak, there was a statistically significant correlation between total body protein and egg albumen content. Also, lipid rich females laid eggs containing more lipid. When all early laying females from 1983 and 1984 were pooled, carcass protein was correlated with egg albumen content (Table 23). Hence, the yolk to albumen ratios were negatively correlated with carcass protein content. Increased carcass lipid levels were correlated with wet yolk weight.

The carcass contents of late nesting females were not well correlated with egg constituents (Table 24). No carcass parameter was correlated with fresh egg weight, or meaningfully correlated with any parameter of egg composition.

The lipid level in the body homogenate was positively correlated with the yolk wet and dry weights (Appendix 13), but negatively with the proportion of yolk lipid. Protein levels in the homogenate were most strongly correlated with the contents of the albumen.

The composition of fresh skin appeared to be a better predictor of egg quality than the composition of the body homogenate. Subcutaneous lipid content was correlated with yolk weight (wet and dry), lipid and protein content (Appendix 14). Heavier skin was related to greater levels of egg lipid, protein and water content. Egg weight and yolk protein weight were most strongly correlated with the energy level of the skin.

The chemical composition of female reproductive tissues was not well

Table 22. Relationship between female[1] Ring-billed Gull total carcass composition[2] with egg constituent composition, Granite Island.

	Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight[3]	0.27***[4]	0.18**	-0.17*	0.07	-0.09	0.19**	0.18**	0.03
Yolk: Wet yolk	0.23***	0.06	-0.24***	-0.15*	-0.25***	0.22**	0.21**	-0.14*
Dry yolk	0.18*	0.02	-0.23***	0.00	-0.10	0.21**	0.21**	0.02
% water	0.16*	0.06	-0.14*	-0.12	-0.18**	0.13*	0.11	-0.12
Lipid	0.11	0.00	-0.16*	-0.05	-0.10	0.14*	0.13*	-0.04
% lipid	-0.17*	-0.07	0.09	0.09	0.17*	-0.15*	-0.14*	0.08
Lipid (% dry)	-0.09	-0.05	0.16*	-0.09	-0.02	-0.11	-0.12	-0.12
Non-lipid dry	0.19**	0.00	-0.26***	0.05	-0.06	0.25***	0.26***	0.09
Albumen: Wet albumen	-0.03	0.08	0.13*	0.19**	0.17*	-0.08	-0.07	0.16*
Dry albumen	0.14*	0.09	-0.11	0.22**	0.11	0.11	0.11	0.15*

Table 22 continued ...

% water	-0.13*	0.03	0.22**	0.16*	0.21**	-0.16*	-0.15*	0.16*
Shell: Wet shell	0.34***	0.17*	-0.28***	-0.09	-0.27***	0.28***	0.27***	-0.09
Dry shell	0.33***	0.19**	-0.24***	0.02	-0.17*	0.26***	0.25***	0.01
% water	0.11	-0.01	-0.16*	-0.18**	-0.22**	0.12**	0.12	-0.16*
Yolk/albumen (wet)	0.14*	0.00	-0.19**	0.26***	-0.29***	0.14*	0.13*	-0.23***
Yolk/albumen (dry)	-0.01	-0.07	-0.06	-0.18**	-0.14*	0.04	0.04	-0.12
Energy	-0.10	-0.17*	-0.05	-0.02	0.04	0.00	0.00	-0.01
Total water	0.26***	0.23***	-0.11	0.04	-0.11	0.15*	0.14*	0.02

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] The years and nesting times were pooled (N = 171).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical signficiance at 0.01 level

*** denotes statistical significance at 0.001 level

Table 23. Relationship between early nesting female[1] Ring-billed Gull total carcass composition[2] with egg constituent composition, Granite Island.

		Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight[3]		0.18*[4]	0.16*	-0.05	0.05	-0.04	0.06	0.05	-0.02
Yolk:	Wet yolk	0.18*	0.02	-0.21**	-0.20**	-0.26***	0.19*	0.17*	-0.18*
	Dry yolk	0.10	0.00	-0.13	-0.05	-0.09	0.11	0.11	-0.05
	% water	0.17*	0.03	-0.19*	-0.15*	-0.20**	0.17*	0.17*	-0.12
	Lipid	0.07	0.00	-0.10	-0.09	-0.11	0.07	0.07	-0.10
	% lipid	-0.17*	-0.02	0.19*	0.13	0.19*	-0.18*	-0.18*	0.10
	Lipid (% dry)	-0.04	-0.01	0.06	-0.11	-0.07	-0.07	-0.07	-0.12
	Non-lipid dry	0.10	-0.02	-0.16*	0.01	-0.04	0.15*	0.15*	0.02

Table 23 continued ...

Albumen: Wet albumen	-0.04	0.10	0.18*	0.21**	0.20**	-0.12	-0.12	0.16*
Dry albumen	0.09	0.06	-0.05	0.25**	0.18*	0.05	0.04	0.16*
% water	-0.09	0.07	0.21**	0.19*	0.20**	-0.14	-0.14	0.18*
Shell: Wet shell	0.25**	0.13	-0.19*	-0.15*	-0.25**	0.18*	0.17*	-0.15*
Dry shell	0.24**	0.15*	-0.15*	-0.02	-0.13	0.17*	0.17*	-0.03
% water	0.06	-0.04	-0.13	-0.22**	-0.22**	0.08	0.08	-0.21**
Yolk/albumen (wet)	0.09	-0.04	-0.16*	-0.30***	-0.30***	0.11	0.11	-0.26***
Yolk/ablumen (dry)	-0.04	-0.06	-0.03	-0.24**	-0.19*	0.00	0.00	-0.18*
Energy	-0.10	-0.15*	-0.05	-0.03	0.02	0.00	0.01	-0.02
Total water	0.19*	0.22**	0.00	0.02	-0.08	0.05	0.05	-0.02

Table 23 continued ...

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] Data from 1983 and 1984 were pooled (N = 135).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Table 24. Relationship between late nesting female[1] Ring-billed Gull total carcass composition[2] with egg constituent composition, Granite Island.

	Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight[3]	-0.02[4]	-0.03	-0.03	-0.09	-0.08	0.01	0.02	-0.09
Yolk: Wet yolk	0.01	0.11	0.20	0.16	0.15	-0.25	-0.27	-0.14
Dry yolk	-0.36*	-0.32*	0.15	0.02	0.27	-0.24	-0.21	0.04
% water	0.27	0.35*	0.10	0.17	-0.02	-0.09	-0.12	-0.16
Lipid	-0.36*	-0.30*	0.18	-0.02	0.23	-0.29*	-0.27	-0.09
% lipid	-0.29*	-0.33*	-0.04	0.16	0.04	-0.01	0.02	0.04
Lipid (% dry)	-0.16	-0.12	0.11	-0.06	0.05	-0.19	-0.18	-0.19
Non-lipid dry	-0.26	-0.30*	-0.06	0.07	0.26	-0.04	-0.01	0.22
Albumen: Wet albumen	0.02	-0.11	-0.29*	-0.13	-0.15	0.28	0.30	0.14
Dry albumen	0.13	0.08	-0.15	-0.16	-0.26	0.15	0.16	-0.13
% water	-0.07	-0.17	-0.20	0.01	0.06	0.18	0.19	0.24

Table 24 continued ...

Shell: Wet shell	0.17	0.17	-0.05	0.10	-0.03	0.01	0.00	-0.07
Dry shell	0.11	0.19	0.13	0.10	0.01	-0.14	-0.15	-0.15
% water	0.19	0.06	-0.32*	0.06	-0.08	0.25	0.25	0.10
Yolk/albumen (wet)	-0.03	0.09	0.27	0.14	0.16	-0.31*	-0.33*	-0.19
Yolk/albumen (dry)	-0.38**	-0.33*	0.19	0.12	0.40**	-0.28*	-0.27	0.13
Energy	-0.43**	-0.40**	0.15	0.00	0.32*	-0.28*	-0.26	0.01
Total water	0.16	0.08	-0.22	0.04	-0.08	0.16	0.16	0.03

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[1] Only post-laying females that laid 3 eggs were used

[2] Carcass compositions were expressed as proportions.

[3] Data from 1983 and 1984 were pooled (N = 36).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

correlated with the nutrient content of eggs (Appendix 15).

Overall, female Ring-billed Gulls nesting earlier in the season had larger nutritent reserves, and laid eggs with higher nutritional content. Increased levels of carcass protein and lipid were correlated with higher nutrient levels in eggs.

Within the laying sequence of 1984, the fresh weight of eggs was correlated with the total analyzed weight, total water weight and total protein weight of females for a- and b-eggs, but not for c-eggs (Appendices 16, 17 and 18). For a-eggs, yolk weight was positively correlated with the total weight of protein in the carcass (Appendix 16). B-egg albumen and yolk protein weight were positively correlated with total carcass weight and protein (Appendix 17). B-egg weight and dry yolk weight were correlated with the total weight of protein in the carcass. Total b-egg water content was positively correlated with the total analyzed weight and the total water weight of the female carcass. For c-eggs, dry yolk and yolk lipid weight was correlated with total analyzed carcass weight and total protein weight (Appendix 18). The weight of yolk protein in c-eggs was positively correlated with total carcass protein.

Although, through the laying sequence, there were significant correlations between egg and carcass nutrient levels, the strengths of these relationships were statistically weak (ie. no r value greater than 0.65); thereby suggesting that egg composition could not be used to accurately predict the chemical composition of the post-laying female laying that egg.

3.9 The Body Condition of Pre-breeding Adults

The 4 male and 5 female pre-breeding adults collected at the mouth of the Wolf River were assumed to form pairs in which the female would ultimately lay the modal clutch size of 3 eggs. This assumption validated comparisons with the adults that laid 3 eggs and nested on Granite Island in 1984.

The body condition index of pre-breeding males was larger than that for males breeding early in the season, but their body weights did not differ (Table 25). Although numerically larger for pre-breeders, the body weights and conditions of early nesting and pre-breeding females were statistically the same.

When the sexes were combined, indexed body condition was negatively correlated with trap date ($r= -0.36$, $p< 0.001$, $n= 124$). The overall regression of condition with date was expressed by the equation $Y= 4.11- 0.018X$. Figure 7 presents the male and female regressions of condition index against date. Analysis of covariance revealed that the slopes and intercepts of these two regression lines differed ($F= 8.36$, $p< 0.01$; $F= 27.21$, $p<0.001$, respectively), but the variation about each line was the same ($F= 1.19$). Therefore, males were in better condition than females before the breeding season, and body condition declined more rapidly for males. Mean condition indices, by date for each sex, are given in Appendix 19.

The condition index of females nesting early in 1984 (that were

Table 25. Comparison between male and female Ring-billed Gull pre-breeding and breeding condition indices and body weights, 1984.

	Condition Index			Body Weight (g)		
	Pre-breeding [1]	Breeding [2]	Mann-Whitney U	Pre-breeding	Breeding	Mann-Whitney
Male	4.30 ± 0.40 (4)[3]	3.91 ± 0.24 (52)	$p < 0.05$	571.3 ± 51.7 (4)	522.9 ± 39.6 (52)	NS
Female	3.88 ± 0.43 (5)	3.66 ± 0.26 (58)	NS[4]	475.8 ± 48.6 (5)	448.6 ± 30.7 (58)	NS

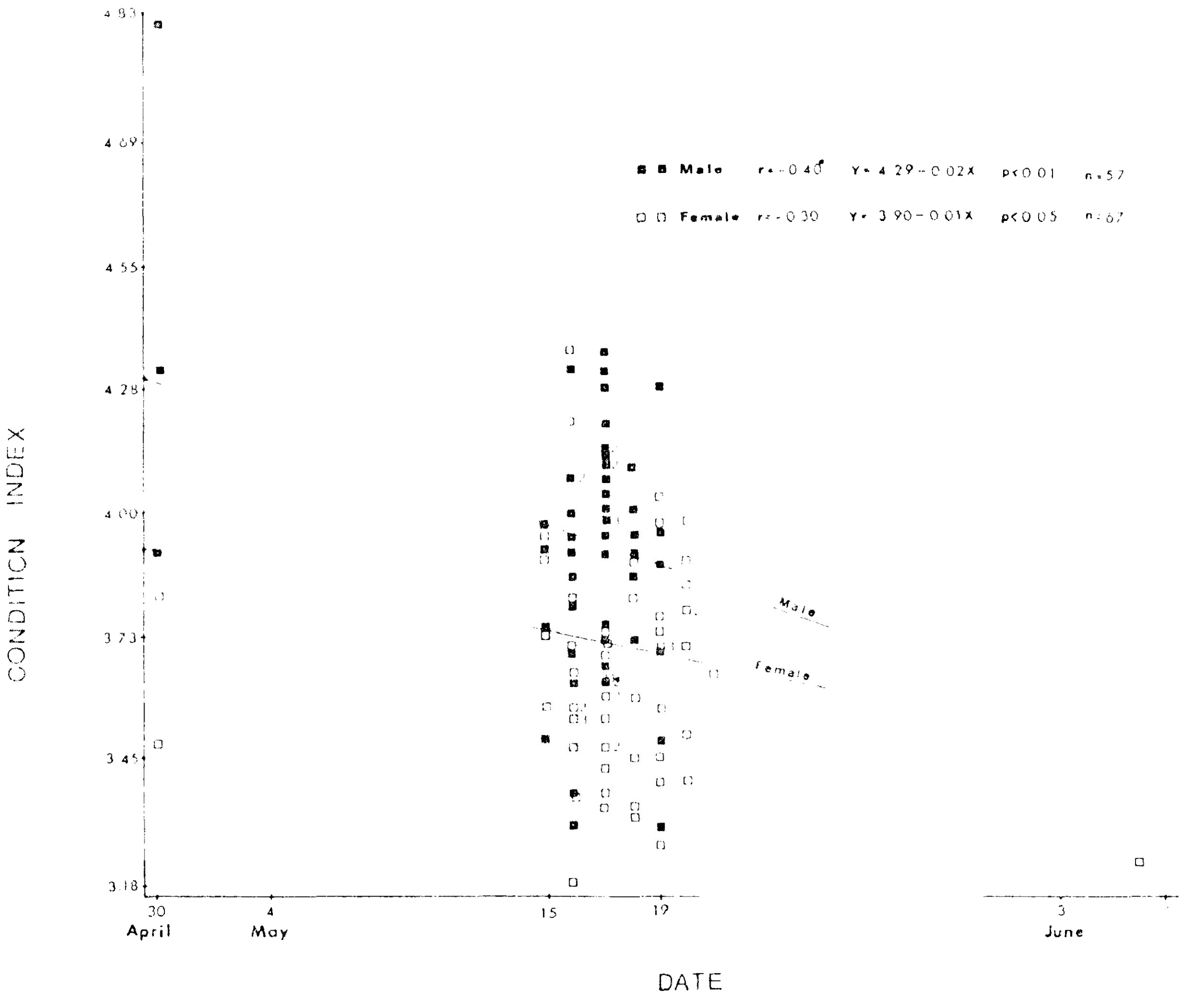
[1] Wolf River sample

[2] Early nesters, Granite Island

[3] Mean ± SD (n)

[4] No significant difference

Figure 7. Regression of the condition indices of pre-breeding, early and late nesting male and female Ring-billed Gulls against date trapped, 1984. (Data for the mean indexed condition of these gulls are given in Appendix 19).


■ Male r = -0.40 Y = 4.29 - 0.02X p<0.01 n = 57
□ Female r = -0.30 Y = 3.90 - 0.01X p<0.05 n = 67
Male
Female
4.83
4.69
4.55
4.28
4.00
3.73
3.45
3.18
CONDITION INDEX
30
April
4
May
15
19
3
June
DATE

chemically analyzed) was smaller than that for pre-breeding females (Table 26). Although not statistically significant, pre-breeding females weighed more, contained more energy per unit body weight and proportionately more total lipid than early nesting females. Subcutaneous and reproductive tissue lipid levels were larger in pre-breeders. Generally, relative to early nesting females, pre-breeding females appeared to have more stored nutrients, but this difference was not significant.

Pre-breeding males had a larger condition index and than males breeding early in the season (Table 27). As was the case in the female comparisons, pre-breeding males apparently weighed more, had heavier testes and skin, contained more energy in the skin, and contained more subcutaneous and total lipid than early nesting males; however, these differences were not significant.

Table 26. Comparison between the body weights, condition indices and chemical composition of Wolf River pre-breeding and Granite Island early nesting female Ring-billed Gulls, 1984.

	Pre-breeding (n = 5)	Early nesting (n = 21)	Mann-Whitney
Body weight (g)	462.4 ± 50.0[1]	424.8 ± 24.8	NS[2]
Condition index	3.88 ± 0.43	3.66 ± 0.26	$p < 0.05$
Homogenized body weight (g)	334.8 ± 44.3	308.3 ± 16.9	NS
Body water (g)	167.0 ± 94.0	205.1 ± 13.4	NS
% body water	63.2 ± 5.8	66.6 ± 3.1	NS
Body protein (g)	74.6 ± 42.7	87.5 ± 6.4	NS
% body protein	27.7 ± 1.3	28.4 ± 2.0	NS
Body lipid (g)	26.2 ± 29.2	15.7 ± 6.8	NS
% body lipid	9.1 ± 6.1	5.0 ± 2.1	NS
Body energy (kcal/g analyzed)[3]	5.22 ± 2.60	6.22 ± 0.20	NS
Wet skin weight (g)	38.8 ± 16.5	33.2 ± 6.2	NS
Skin water (g)	10.2 ± 0.5	15.3 ± 2.4	$p < 0.01$
% skin water	31.9 ± 18.3	47.8 ± 11.5	NS
Skin protein (g)	4.6 ± 0.4	7.5 ± 2.6	$p < 0.001$
% skin protein	14.3 ± 7.5	22.7 ± 6.2	$p < 0.05$
Skin lipid (g)	24.0 ± 16.6	10.4 ± 6.5	NS
% skin lipid	53.8 ± 25.7	29.5 ± 13.8	$p < 0.05$

Table 26 continued ...

Skin energy (kcal/g analyzed)	8.48 ± 1.00	7.74 ± 0.60	$p < 0.05$
Wet ovary weight (g)	3.7 ± 3.6	8.0 ± 2.1	$p < 0.05$
Ovary water (g)	2.8 ± 2.7	6.2 ± 1.6	$p < 0.05$
% ovary water	76.9 ± 3.2	77.5 ± 1.5	NS
Ovary protein (g)	0.8 ± 0.9	1.5 ± 0.4	NS
% ovary protein	16.5 ± 5.1	19.2 ± 1.2	NS
Ovary lipid (g)	0.2 ± 0.1	0.3 ± 0.2	$p < 0.05$
% ovary lipid	6.5 ± 2.6	4.5 ± 5.2	$p < 0.05$
Ovary energy (kcal/g analyzed)	6.78 ± 0.51	6.82 ± 2.81	$p < 0.05$
Total analyzed weight (g)	310.3 ± 156.6	349.6 ± 20.8	NS
Total water (g)	180.0 ± 94.7	226.6 ± 14.8	NS
% water	52.9 ± 17.6	64.9 ± 3.9	NS
Total protein (g)	79.9 ± 43.2	96.5 ± 7.2	NS
% protein	23.0 ± 7.9	27.7 ± 1.7	NS
Total lipid (g)	50.4 ± 42.6	26.4 ± 13.0	NS
% lipid	24.1 ± 25.2	7.4 ± 3.4	NS
Total energy (kcal/g total analyzed weight)	7.28 ± 1.15	6.44 ± 0.29	NS

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[1] Mean ± SD

[2] No significant difference

[3] Dry weight of tissues was used.

Table 27. Comparison between the body weights, condition indices and chemical composition of Wolf River pre-breeding and Granite Island early and late nesting male Ring-billed Gulls, 1984.

	Pre-breeding (n = 4)	Early (n = 9)	Late [1] (n = 1)	Mann-Whitney U [2]
Body weight (g)	571.3 ± 51.7 [3]	512.1 ± 50.3	472.0	NS [4]
Condition index	4.30 ± 0.40	3.75 ± 0.30	3.576	$p < 0.05$
Homogenized body weight (g)	388.3 ± 31.2	361.3 ± 29.0	342.0	NS
Body water (g)	247.0 ± 17.1	231.6 ± 14.9	228.9	NS
% body water	63.7 ± 1.5	64.3 ± 4.1	66.9	NS
Body protein (g)	106.2 ± 5.4	97.8 ± 7.4	100.7	$p < 0.05$
% body protein	27.4 ± 1.0	27.1 ± 1.3	29.4	NS
Body lipid (g)	4.0 ± 1.2	3.9 ± 2.5	1.7	NS
% body lipid	8.9 ± 2.2	8.6 ± 5.0	3.6	NS
Body energy (kcal/g analyzed) [5]	6.59 ± 0.19	6.55 ± 0.37	6.07	NS
Wet skin weight (g)	55.1 ± 13.0	46.4 ± 15.9	31.8	NS
Skin water (g)	14.4 ± 1.1	17.6 ± 3.5	17.0	NS
% skin water	27.2 ± 5.7	41.7 ± 13.9	53.5	NS
Skin protein (g)	8.9 ± 3.3	9.6 ± 2.9	8.2	NS
% skin protein	16.7 ± 6.2	22.2 ± 8.0	25.7	NS
Skin lipid (g)	31.7 ± 12.9	19.2 ± 16.9	6.6	NS
% skin lipid	56.1 ± 10.6	36.1 ± 20.4	20.8	NS

Table 27 continued ...

Skin energy (kcal/g analyzed)	8.60 ± 0.36	7.88 ± 0.85	7.37	NS
Wet testis weight (g)	4.8 ± 2.4	3.9 ± 1.1	3.5	NS
Testis water (g)	4.0 ± 2.1	3.3 ± 0.9	2.9	NS
% testis water	84.0 ± 1.7	82.6 ± 1.2	84.3	NS
Testis protein (g)	0.7 ± 0.4	0.6 ± 0.2	0.5	NS
% testis protein	14.5 ± 1.5	15.2 ± 1.2	13.1	NS
Testis lipid (g)	0.1 ± 0.03	0.1 ± 0.4	0.1	NS
% testis lipid	1.6 ± 0.01	2.2 ± 1.0	2.7	NS
Testis energy (kcal/g analyzed)	6.03 ± 0.20	6.12 ± 0.21	6.30	NS
Total analyzed weight (g)	448.1 ± 41.7	411.7 ± 42.8	377.3	NS
Total water (g)	265.4 ± 18.5	252.4 ± 17.5	248.8	NS
% water	59.4 ± 2.5	61.7 ± 5.8	66.0	NS
Total protein (g)	115.8 ± 6.2	108.1 ± 7.9	109.3	NS
% protein	25.9 ± 1.4	26.4 ± 1.6	29.0	NS
Total lipid (g)	35.8 ± 14.0	23.2 ± 19.2	8.4	NS
% lipid	7.9 ± 2.5	5.4 ± 3.8	2.2	NS
Total energy (kcal/g total analyzed weight)	7.03 ± 0.27	6.79 ± 0.48	6.22	NS

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[1] The late nesting male was not used in the comparison.

[2] Non-parametric comparison was made between the pre-breeding and early samples.

[3] Mean ± SD

[4] No significant difference

[5] Dry weight of the tissues was used.

4. DISCUSSION

4.1 Egg Quality

4.1.1 Clutch Size and Egg Size

The breeding performance of Ring-billed Gulls on Granite Island was poor in 1983 relative to 1984 as evinced by the smaller average clutch size, egg weight and hatching success. Clutches laid later in the season were smaller than those laid earlier in each year. Other studies of larids have reported the seasonal reduction in clutch size, egg size and hatching success (Coulson 1963; Coulson and White 1961; Coulson *et al*. 1969; Parsons 1970, 1972, 1975; Ryder 1975; Chardine 1978; Somppi 1978; D. Boersma 1982).

In each year, there was no evidence of the relationship of decreasing egg size with egg sequence in late clutches, but there was for early clutches. Coulson (1963), Parsons (1972, 1976), Davis (1975), Coulter (1977, 1980) and Schreiber *et al*. (1979) have shown for larids that the third egg in a clutch generally is smaller than a- or b-eggs. There appears to be a trade-off between the size and number of eggs produced by a laying female. In studies of egg and clutch size in Red-billed Gulls, Mills (1979) found that extremely early or late nesters laid either fewer eggs or smaller eggs, and that this was caused by poor food availability at these nesting times. Smaller eggs will be at a selective disadvantage since chick survival is directly related to egg size (Parsons 1970; Nisbet 1973; Davis 1975; Ryder 1975; Lundberg and Vaisanen 1979). There may be a minimum size at which an ovarian follicle may rupture (Parsons 1975). I suggest that the egg-laying tactic of Ring-billed Gulls when nutrients are in short supply might be to produce fewer eggs (approaching average size) as a trade-off, rather than producing the usual 3 smaller, poorer-hatching eggs. This was supported by the larger average clutch size in 1984 relative to 1983, and the smaller clutch size of late nesters in each year. Hence, the production of fewer, larger eggs may maximize a female's seasonal reproductive success. This tactic may vary yearly so as to maximize her total lifetime fitness.

The production of eggs induces a physiological stress on the laying female (King 1972). Various researchers have emphasized the effect of food availability on the nutritional status of females at the time of laying, as it may determine egg size and weight (Scott 1973; Murton _et al_. 1974; Schreiber and Lawrence 1976; Mills 1979; Schreiber _et al_. 1979; Thomas 1982; Kovacs and Ryder 1983; Murphy _et al_. 1984). Courtship feeding in gulls is likely an important source of energy for the female during egg formation. Annual egg size may be influenced directly by a male's ability to supply sufficient food of high quality during the period of courtship feeding (Lack 1966, 1968; Brown 1967a; Nisbet 1973; Mills 1973, 1979; Davis 1975). Perrins (1970) documented that an abundant available food supply before the breeding season resulted in an advance of the laying date, whereas limited food supply at this time postponed the onset of laying. In the White-crowned Sparrow (*Zonotrichia leucophrys*), King (1972) found that the nutritional state of the female affects the levels of endocrine stimuli necessary for gonadal growth and productivity. A male's courtship feeding apparently accelerates the final growth phase of the ovary and the mobilization of nutrients into developing follicles (Lehrman 1959; Brown 1967b). Therefore, the pairing of a female with an inefficient or inexperienced foraging male would mean that her ovarian stimulation would be delayed, and thus, she would take longer to initiate a clutch.

4.1.2 Egg Composition

Since gulls typically begin effective incubation after laying the first egg (Parsons 1972), some a-eggs collected in this study for chemical analyses in 1983 contained 5-day old embryos (aged by the methodology of Ryder and Somppi 1977). This was manifest in the higher proportion of albumen and less yolk in later laid b- and c-eggs, and was related to the movement of water from the albumen to the yolk during embryonic development in a-eggs (Williams *et al*. 1982). This chemical alteration problem was eliminated by the collection of eggs within 12 hours of laying in 1984.

The lower fresh weight of albumen in the late eggs of this study suggested that females were not obtaining enough food at the time of laying, possibly related to the quality of their mate's resource acquisition abilities. This was evinced also in the reduced yolk size of late eggs. Nutrient deprivation during egg production may effect the nutrient composition of eggs, as well as egg size. Nisbet (1977, 1978) found for Common Terns (Sterna hirundo) that the quality as well as quantity of food acquired by the nesting female was reflected in her eggs. There are two main nutrient reserves in the egg vital to chick growth and development (Romanoff and Romanoff 1949). About two-thirds of the albumen's protein is available to the embryo for growth (P. Boersma 1982). Therefore, more albumen results in a larger chick. Yolk reserves (protein and lipid) are for maintenance and development rather than growth (P. Boersma 1982), so that more yolk yields a more precocial hatchling. Donaldson (1981) noted that avian embryos derive over 90% of their caloric requirements from the yolk lipid via fatty acid oxidation. The derived metabolites (triglycerides) are vital to chick post-hatching survival. Intraspecific and intraclutch variation in egg size is attributable to the amount of albumen laid down around the yolk in larids, such as the Herring Gull (Parsons 1976) and Western Gull (Larus occidentalis)(Coulter 1977), as well as other species (ie. Ricklefs 1977a, European Starling, Sturnus vulgaris; Jones 1979, Great White Pelecan, Pelecanus onocrotalus; and numerous Procellariiformes, Warham 1983).

In 1984, c-eggs weighed less and had a smaller yolk which contained fewer nutrients than a- or b-eggs. This indicated that the female's stored nutrient reserves, important to the production of eggs (Houston et al. 1983), were being depleted as subsequent eggs were laid. This observation contradicted P. Boersma's (1982) suggestion that yolk size is proportionately constant with varying egg size. In this study, small eggs may have had small yolks that were proportionately the same size as the yolks of larger eggs. However, allometric regressions of egg components on the weight of fresh eggs demonstrated that this was not the case. Yolk size was very poorly correlated with egg weight, and did not increase in direct proportion with increasing egg size. Large eggs apparently provided more albumen and more water to the developing embryo, but egg size was a poor predictor of yolk size. Rather than laying three smaller eggs of poorer quality relative to earlier laid eggs, late nesting females typically laid 2 eggs, and may have done so because their nutrient stores were exhausted.

The fresh yolk to albumen ratios of 1984 agreed with the 0.58 value reported by Ricklefs (1977b) for Laughing Gulls (Larus atricilla). Carey et al. (1980) stated that the mean relative yolk content of semiprecocial eggs is 33%, very close to the results of this study (35%).

This study's results of Ring-billed Gull egg lipid (8%) and energy (about 1.6 kcal/g) content agreed well with other studies on the energetics of eggs. Ricklefs (1977b) reported that yolks are large and contain 9 - 12% total lipids in precocial and semiprecocial species relative to altricial species (6%). The chemical energy of fresh eggs increases directly with yolk size since the yolk contains high energy lipid (9.5 kcal/g) relative to protein (5.65 kcal/g). The energy content of eggs increased with increasing egg size since larger eggs contained more albumen and yolk. Carey _et_ _al_. (1980) stated that, for semiprecocial species such as the Ring-billed Gull, yolk lipid accounted for 9.5% of fresh egg weight, and that larid eggs averaged 1.67 kcal/g. In this study, dry yolk consisted of 60% lipid and 40% protein. This agreed with Ricklefs' (1977b) results for the Laughing Gull, wherein yolk lipid accounted for 64% of yolk dry matter.

Egg weight and volume were most strongly correlated with the water content of the egg, as was reported by Ricklefs and Montevecchi (1979). The major source of water in the egg is the albumen. Ricklefs (1977b) found that Laughing Gull eggs consisted of 75.4% water. Generally for semiprecocial species, water accounts for 76.5% of fresh egg weight (Carey _et_ _al_. 1980). Ring-billed Gull eggs in this study averaged 69% water, falling just below the range given by Ricklefs (1977b) for semiprecocial species (70 - 75%).

Because egg weight and volume were most strongly correlated with total water content, one cannot assume a larger egg contains more energy per gram. Allometric regressions revealed that increasing egg size was a function of increasing albumen content. More albumen meant proportionately more water, and proportionately less yolk and energy, in larger eggs. Obviously, larger eggs with more albumen have absolutely more energy because they have more albumen protein than do smaller eggs. But lower energy by weight does not infer lower egg quality (Sibbald 1979). Nisbet (1978) concluded that the albumen protein level may be the critical factor involved in chick hatching and survival; not lipid content, as suggested by Parsons (1970).

4.2 Condition of Adults

The larger condition indices of females nesting early in the season, and those nesting in 1984, support the hypothesis that females in better nutritional condition lay higher quality eggs (Ankney and MacInnes 1978; Houston *et al*. 1983).

4.2.1 Comparison of Body Condition Indices Between Years

The smaller condition index of nesting females in 1983 relative to 1984, evinced by poorer egg quality, suggested that pre-breeding food supply is important to the reproductive success of gulls. Poor weather conditions at the start of laying have been shown to depress egg quality in a number of species (cf. Case 1972, Dabney and Dimmick 1977, Bobwhite Quail, *Colinus virginianus*; Wooller and Dunlop 1981, Silver Gulls, *Larus novaehollandiae*; Iverson and Vohs 1982, Sandhill Cranes, *Grus canadensis*; Joyner *et al*. 1984, Canada Geese, *Branta canadensis*). The spring of 1983 was very cold and wet, and ice breakup in Black Bay did not occur until the second week of May. This late disappearance of ice caused a postponement of the Rainbow Smelt spawning run in Lake Superior (P. Colby, Ministry of Natural Resources, Thunder Bay, Ont., pers. comm.). Spawning smelt, available at the mouth of the Wolf River, are a major food source for Granite Island gulls before breeding. In 1984 (a much warmer, dry spring), the abundance of forage was unlimited. Breakup occurred the third week of April, and smelt were spawning the last week of that month. So in 1984, Ring-billed Gulls had three weeks before nesting to accumulate nutrients for egg laying and maintenance during incubation.

Despite the possible differences in food abundance between years, the date of clutch initiation differed only by one day, contradicting the predictions of Loman (1982) and Wingfield et al. (1983) that limited pre-breeding food abundance would delay the onset of laying. Therefore, female Ring-billed Gulls entered the 1983 breeding season before the peak of the smelt run, and were in poorer physiological condition than those females entering the breeding season of 1984.

4.2.2 Body Condition of Early Versus Late Nesting Females

On average, late nesting females had significantly lower condition indices than early nesters in each year. This implied that late nesters had lower levels of body reserves, possibly caused by lower food intake and/or stress caused by competition with early nesters for breeding territories. The supposed lower nutrient levels in late nesting females resulted in the production of fewer, smaller and poorer quality eggs. There were few late nesting gulls in 1984. It appeared that large resource abundance early in the season facilitated earlier breeding for the majority of gulls.

4.2.3 Relationship of Body Composition, Indexed Condition and Egg Quality

The extrapolation of body water, lipid and protein amounts from subsampling may be inaccurate, as evidenced by over-estimates of compositional weights (see Table 19). Proportions may be more indicative of body nutrient reserve levels, although their use is not recommended (C.D. Ankney, pers. comm.). However, like condition indices, the use of proportions equates body weight differences.

Levels of water, protein and lipid for chemically analyzed females did not differ between years. Firstly, this may have been the result of limited sample size necessitating non-parametric testing. Secondly, although larger nutrient levels were expected for females laying in 1984 relative to 1983, the lack of compositional differences may be the result of analyzing post-laying females. I have assumed that body reserve levels at the end of laying were proportional to those of the female prior to laying, so that a female initially in better condition would be in equally better condition after laying. There may be a physiological minimum state attained after laying to ensure survival of the female so that she may incubate efficiently. To go below this limit may jeopardize not only the female's survival, but also her future genetic fitness (McGillivray 1983). The main function of the extra body reserve then is probably to buffer the female against temporary food shortages during incubation (Newton *et al*. 1983). Morris (1984) has documented the desertion of both eggs and chicks in seabirds because of poor food availability. As expected, the females laying in 1984 put their nutrient reserves into the production of higher quality eggs. This further attests the importance of pre-breeding food resources to reproductive performance.

Generally, female Ring-billed Gulls nesting late in the season had significantly smaller body fat reserves, but had equivalent protein levels, when compared to early nesters. Since post-laying females were used, it was not surprising that the chemical composition of the reproductive tissues did not differ between early and late nesters. The condition of the reproductive tissues is a function of how long it has been since the female laid her last egg - in this case, within 4 days. The most visible nutrient reserve in females was subcutaneous fat, which was markedly larger in early nesters. The abdominal fat stores, visible only on pre- and early nesting females, suggested that lipid reserves in the ovary are allocated to the production of ova, and those lipids in the mesenteries of the oviduct are likely allocated to female sustanence. Body reserves (abdominal, visceral and muscular (intercellular)), and subcutaneous lipids are probably the more important endogenous nutrient reserves for egg production and/or female sustanence. Figure 5 and 6 suggested that both these reserves are important indicators of carcass composition, not just the major muscles used by most researchers (see Ankney 1977; Young and Boag 1982). Since total protein levels did not differ between early and late nesters, it appeared that the most important nutrient reserve in breeding birds is fat, and that this is reflected in higher lipid levels in earlier eggs.

Fat levels drop off throughout the period of egg formation, notably in the Anseriformes (Ankney 1977, 1984; Ankney and MacInnes 1978; Drobney 1982, 1984). This is also true for protein reserves in a variety of species (Jones and Ward 1976; Raveling 1979; Houston et al. 1983; Tome 1984), as reflected in the decreasing size of digestive organs and atrophied muscles during egg production. Condition indices used in this study acted as satisfactory predictors of female weight, nutrient reserves (especially lipid) and the corresponding quality of eggs. However, care should be used in using the condition index to accurately predict the chemical composition of post-laying females. The above mentioned correlations, given on Table 21, were statistically significant, but not statistically strong (i.e. $r > 0.80$). Ideally, a female's body condition index should be determined before, and through, the entire breeding cycle. In this way, the correlations between egg and body nutrient reserves could be accurately assessed. This was unfeasable in this study because Ring-billed Gulls, especially the late nesters, which were exposed to disturbance quickly become trap shy and often deserted their eggs (Somppi 1978; D. Boersma 1982; this study). On the basis of statistically significant correlations among the body condition index, body reserves and egg nutrient levels, and the decline of indexed condition versus date through the breeding season, it appeared that female nutrient reserves did decrease through the laying sequence. This would explain the inverse correlation between the body weight of late nesting females and egg constituents. It appeared that females sacrificed their own tissue reserves to put into eggs. This was supported by the decrease of egg quality through the laying sequence.

The body condition of males and females declined unequally through the breeding season in 1984. This was not as expected because both sexes incubate with equal frequency and duration (Somppi 1978). Perhaps the faster decline of the body condition of males reflects the physical demands of securing and maintaining a nesting territory. However, this is solely speculation, since information about territorial defense was not gathered. Unlike breeding Lesser Snow Geese (Ankney 1977; Ankney and MacInnes 1978), female Ring-billed Gulls are not wholly dependent on reserves acquired before laying for sustanence during incubation because their mates aid in incubation, thus allowing females to feed while off the nest. Males remained in better condition than females, and may reflect a physiological stress incurred upon the female during egg formation and laying.

4.3 Egg Size, Sequence and Secondary (At Hatch) Sex Ratios

Late eggs were smaller, of poorer quality and had greater hatching failure than earlier laid eggs in each year. This agreed with Nisbet's

(1978) hypothesis that chick hatching and survival is directly related to egg size. Within clutches, the smaller c-eggs hatched fewer young relative to a- and b-eggs. Nisbet (1978) and P. Boersma (1982) predicted that increased albumen content results in larger hatchlings, demonstrated in this study by the positive correlation between egg weight and chick weight. C-egg chicks, and late chicks weighed less than those laid earlier in the season or in the clutch.

The body condition of laying female Ring-billed Gulls did deteriorate through the laying sequence, as did egg quality. This has been reported to have implications to within clutch sex ratios (Ankney 1982; Ryder 1983). First laid, larger eggs contained proportionately more nutrients, and lead to larger chicks - but not males, contrary to the Trivers and Willard (1973) prediction. Trivers and Willard (1973) postulated that, according to the theory of natural selection, females should be expected to produce a higher proportion of males when they are healthiest, and shift progressively to the production of daughters as her body condition deteriorates. Ideally, large, first eggs should produce males since these sons will be larger and more vigorous, and eventually secure a higher proportion of fertilizations relative to males from later laid eggs (Trivers and Willard 1973). In accordance with the Trivers and Willard (1973) theory, the superior reproductive conditions in 1984 resulted in more male representation in the secondary sex ratio (47% versus 35% in 1983). But, the 1984 secondary sex ratio did not differ from unity, either overall, or by egg through the laying sequence. These results suggested that the allocation of sex chromosomes by the heterogametic female may be random.

Ankney (1982) supported the hypothesis of nonrandom segregation of sex chromosomes for Lesser Snow Geese, as did Ryder (1983) for Ring-billed Gulls. Ankney (1982) found that in 4-egg clutches more males (64%) than females hatched from the first 2 eggs, and more females (72%) than males from the last 2 eggs. The combined sex-sequence data over 5 years for Ring-billed Gulls presented in this study also document the male to female shift through the egg sequence. The reverse trend was found for Common Grackles (*Quiscalus quiscula*)(Howe 1977) and Red-winged Blackbirds (*Agelaius phoeniceus*)(Weatherhead 1985). As more data are collected on the secondary sex ratio of Granite Island gull chicks, the sex-sequence relationship appears to become less robust (ie. the value of the G-statistic is decreasing with increasing sample size). For this reason, I believe sex determination in Ring-billed Gulls is randon. Also, the clutch sex ratio (ie. all male chicks, mixed male and female, all female) did not differ from the 1:2:1 ratio predicted by the Mendelian random segregation of sex chromosomes during meiosis. Unfortunately, most sex-sequence data (Ankney 1982; Ryder 1983; this study) result from incomplete clutches. Failure of eggs to hatch, or the loss of eggs, makes questionable the biological inferences made on the basis of incomplete ratios.

If in fact it exists, the mechanisms of secondary sex ratio determination are enigmatic. Other than nonrandom segregation of sex chromosomes, Ankney (1982) has proposed that lower levels of follicle stimulation hormone and/or luteinizing hormone may cause that earlier and/or faster growth of ovarian follicles which may subsequently produce males. Ankney (1982) also proposed that cold shock of first laid eggs, caused by interrupted incubation, may produce males, since this has been documented in reptilian species (reviewed by Bull 1980). Both hormonal levels and the interruption of incubation by the parent to forage may be linked to the physiological condition of females, and ultimately to food supply and acquisition during egg laying.

To date, empirical support of the Trivers and Willard (1973) theory for avian species is wanting. Although skewed avian sex ratios are common, these ratios are tertiary - the post-fledging (immature) and adult ratios in birds (for a review of these dealing with gulls see Burger and Gochfeld 1981). Parental manipulation of offspring sex ratios by infanticide is widely documented (McClure 1981, Burley 1982). Differential mortality between the sexes after hatch (Cronmiller 1981), infanticide, and asynchronous hatching leading to siblicide by the first-hatched chick often act to skew population sex ratios (Charnov 1982; Edwards and Collopy 1983; Mock 1984). Most researchers recognize that both the primary (at fertilization) and secondary sex ratios are 1:1, and that parental manipulation of offspring sex may be an adaptive mechanism that can maximize an adult's reproductive success in years of limited food supply (Myers 1978).

Sex ratio results in this study agree with the logic of Charnov (1982). Contrary to Trivers and Willard (1973), Charnov (1982) stated that the avian secondary sex ratio is typically very near equality, and that alterations in the sex ratio away from 50:50 may be of short term adaptive significance (Werren and Charnov 1978; Clutton-Brock 1982). Charnov (1982) believes that, over the long term, the secondary sex ratio does not differ from unity. The production of the rarer sex in the tertiary ratio will be favoured until that sex becomes the most common, then favouring the production of the other sex (Fisher 1930; Maynard Smith 1978; Fiala 1981). The data presented here show a female chick bias in poor breeding seasons (1979 and 1983), and may over time, be masked by good food abundance seasons producing a 50:50 secondary sex ratio.

5. CONCLUSIONS

The primary objective of this study was to determine the relationship between pre-laying food reserves and the subsequent reproductive performance in Ring-billed Gulls. I propose that the abundance and availability of food resources, primarily Rainbow Smelt at the mouth of the Wolf River, may be important factors governing the reproductive performance of gulls nesting on Granite Island.

In the spring of 1984 when smelt were more abundant than in 1983, female gulls stored more nutrients. These reserves resulted in the production of heavier eggs, which contained more nutrients and had a higher hatching success, than those laid in 1983.

Within each year, females nesting earlier had more stored reserves at the time of laying, and were more reproductively successful, than late nesting females. The late birds started their clutches after the smelt population had peaked at the mouth of the Wolf River, and likely entered the nesting season in a less than optimal breeding condition. This was manifest in smaller clutches and eggs, which hatched proportionately fewer young, than earlier nesting conspecifics.

Although body condition deteriorated through the laying sequence, there was no relationship between egg number and chick sex. With the relatively sparse food supply and consequent poorer body conditions observed in 1983 females, there were significantly more females hatched that year. A shift away from the expected 1:1 secondary sex ratio occurred in the year of limited food supply, possibly related to differential mortality of the sexes *in situ*.

In summary, this study has shown that food supply at the time of laying appeared to be an important factor in the reproductive performance of Ring-billed Gulls. Food supply also appeared to influence the secondary sex ratio, especially in years of pre-laying food shortage. Future research should be designed to determine the condition of gulls upon arrival at the breeding grounds and quantify actual food abundance and availability. Ultimately, social, environmental, genetic, behavioural and age-related factors all interact to govern the annual reproductive success of a nesting pair. The individual importance of these factors requires long term study.

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Appendix 1. Comparison of early egg constituent contents between years, Granite Island.

		Overall	Egg		
		98,282^1	a	b	c
			32,94	33,94	33,94
Egg weight (g)		-2.65, $p < 0.001$ ^{2}	-2.52, $p < 0.05$	-0.83, NS	-1.56, NS
Yolk:	Wet yolk (g)	14.31, $p < 0.001$	13.14, $p < 0.001$	9.79, $p < 0.001$	6.32, $p < 0.001$
	Dry yolk (g)	0.20, NS	0.69, NS	-0.67, NS	0.35, NS
	% water	19.78, $p < 0.001$	18.55, $p < 0.001$	14.72, $p < 0.001$	8.28, $p < 0.001$
	Lipid (g)	1.69, NS	1.37, NS	0.80, NS	0.83, NS
	% lipid	-17.21, $p < 0.001$	-14.29, $p < 0.001$	-12.18, $p < 0.001$	-6.92, $p < 0.001$
	Lipid (% dry)	2.49, $p < 0.05$	1.77, NS	2.97, $p < 0.01$	0.23, NS
	Non-lipid dry (g)	-0.73, NS	0.38, NS	-1.50, NS	-0.25, NS
Albumen:	Wet albumen (g)	-14.49, $p < 0.001$	-14.58, $p < 0.001$	-9.33, $p < 0.001$	-3.74, $p < 0.001$
	Dry albumen (g)	-1.95, NS	-1.96, NS	-0.50, NS	-0.91, NS
	% water	-12.28, $p < 0.001$	-11.80, $p < 0.001$	-9.75, $p < 0.001$	-2.96, $p < 0.01$

Appendix 1 continued ...

Shell: Wet shell (g)	1.28, NS	1.92, NS	-0.50, NS	1.09, NS
Dry shell (g)	1.71, NS	1.39, NS	0.99, NS	0.82, NS
% water	-0.06, NS	1.28, NS	-2.80, $p < 0.01$	0.94, NS
Yolk/albumen (wet)	12.73, $p < 0.001$	11.77, $p < 0.001$	7.97, $p < 0.001$	5.17, $p < 0.001$
Yolk/albumen (dry)	1.65, NS	2.36, $p < 0.05$	-0.16, NS	0.76, NS
Eggshell thickness (mm)	-1.56, NS	0.66, NS	-1.19, NS	-2.42, $p < 0.05$
Energy (kcal/g fresh weight and shell)	1.18, NS	0.32, NS	1.11, NS	2.03, $p < 0.05$

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[1] Number of eggs in 1983, number in 1984

[2] Student's t-test, probability

Note: The results are based on the means found on Tables 4 and 5, and in Appendices 3 through 5.

Appendix 2. Comparison of late egg constituent contents between years, Granite Island.

	Overall	Egg		
		a	b	c
	46,6[1]	16,2	15,2	15,2
Egg weight (g)	NS[2]	NS	NS	NS
Yolk: Wet yolk (g)	$p< 0.05$	$p < 0.05$	NS	NS
Dry yolk (g)	NS	NS	NS	NS
% water	NS	NS	NS	NS
Lipid (g)	NS	NS	NS	NS
% lipid	NS	NS	$p< 0.05$	NS
Lipid (% dry)	NS	NS	NS	NS
Non-lipid dry (g)	NS	NS	NS	NS
Albumen: Wet albumen (g)	$p< 0.05$	NS	NS	NS
Dry albumen (g)	NS	NS	NS	NS
% water	$p< 0.05$	$p < 0.05$	$p< 0.05$	NS
Shell: Wet shell (g)	NS	NS	NS	$p < 0.05$
Dry shell (g)	NS	NS	$p <0.05$	NS
% water	$p< 0.05$	NS	NS	$p < 0.05$
Yolk/albumen (wet)	$p < 0.05$	$p <0.05$	NS	NS
Yolk/albumen (dry)	NS	NS	NS	NS

Appendix 2 continued ...

Eggshell thickness (mm)	NS	NS	NS	NS
Energy (kcal/g fresh weight and shell)	NS	NS	NS	NS

[1] Number of eggs in 1983, number in 1984

[2] Mann-Whitney U probability

Note: The results are based on means found on Tables 4 and 5, and in Appendices 3 through 5.

Appendix 3. Comparison of early and late a-egg constituent contents from three-egg clutches, Granite Island, 1983 and 1984.

	1983			1984		
	Early n = 32	Late n = 16	Mann-Whitney U	Early n = 94	Late n = 2	Mann-Whitney U
Egg weight (g)[1]	53.8 ± 3.7 [4]	50.5 ± 3.5	$p < 0.05$	55.9 ± 4.1	51.9 ± 1.1	NS
Yolk: Wet yolk (g)	26.01 ± 4.24	20.20 ± 3.80	$p < 0.001$	16.02 ± 1.28	14.68 ± 0.67	NS
Dry yolk (g)	7.45 ± 0.61	6.51 ± 1.01	$p < 0.01$	7.37 ± 0.61	6.49 ± 0.53	NS
% water	70.64 ± 4.90	67.07 ± 6.60	$p < 0.05$	53.95 ± 2.30	55.80 ± 1.60	NS
Lipid (g)	4.54 ± 0.37	3.97 ± 0.72	$p < 0.01$	4.41 ± 0.45	3.80 ± 0.38	NS
% lipid	17.94 ± 3.60	20.07 ± 4.32	NS [6]	27.59 ± 2.18	25.80 ± 1.41	NS
Lipid (% dry)	60.93 ± 2.97	60.76 ± 1.99	NS	59.87 ± 2.89	58.40 ± 1.13	NS
Non-lipid dry (g)[2]	2.99 ± 0.35	2.56 ± 0.31	$p < 0.001$	2.96 ± 0.31	2.70 ± 0.15	NS
Albumen:						
Wet albumen (g)	21.18 ± 4.12	23.87 ± 4.09	NS	32.74 ± 3.06	30.90 ± 0.84	NS
Dry albumen (g)[3]	4.28 ± 0.59	4.15 ± 0.37	NS	4.49 ± 0.50	4.28 ± 0.27	NS

Appendix 3 continued ...

% water	79.33 ± 3.30	82.31 ± 2.30	$p < 0.01$	86.30 ± 0.60	86.15 ± 0.50	NS
Shell: Wet shell (g)	4.87 ± 0.42	4.49 ± 0.30	$p < 0.01$	4.70 ± 0.43	4.45 ± 0.54	NS
Dry shell (g)	3.67 ± 0.29	3.44 ± 0.20	$p < 0.01$	3.58 ± 0.31	3.36 ± 0.28	NS
% water	24.61 ± 2.80	23.28 ± 3.60	NS	23.73 ± 3.50	24.45 ± 2.90	NS
Yolk/albumen (wet)	1.30 ± 0.38	0.88 ± 0.28	$p < 0.001$	0.49 ± 0.05	0.48 ± 0.03	NS
Yolk/albumen (dry)	1.77 ± 0.23	1.58 ± 0.29	$p < 0.05$	1.66 ± 0.22	1.52 ± 0.22	NS
Eggshell thickness (mm)	0.241 ± 0.020 (38)[5]	0.243 ± 0.020 (26)	$t = -0.53$, NS[7]	0.238 ± 0.020	0.233 ± 0.010	NS
Energy (kcal/g fresh weight including shell)	1.52 ± 0.28	1.50 ± 0.11	NS	1.51 ± 0.07	1.46 ± 0.09	NS

---

[1] The digital scale was used to weigh thawed eggs.

[2] Yolk protein

[3] Albumen protein

[4] Mean ± SD

[5] The sample sizes are given in parentheses.

[6] No significant difference

[7] The sample size was adequate for the Student's t-test.

Appendix 4. Comparison of early and late b-egg constituent contents from three-egg clutches, Granite Island, 1983 and 1984.

	1983			1984		
	Early n = 33	Late n = 15	Mann-Whitney U	Early n = 94	Late n = 2	Mann-Whit U
Egg weight (g)[1]	53.8 ± 3.2[4]	51.1 ± 5.8	NS[6]	54.4 ± 3.8	50.5 ± 0.4	NS
Yolk: Wet yolk (g)	24.08 ± 4.20	19.22 ± 2.80	$p < 0.001$	16.69 ± 1.88	15.06 ± 0.31	NS
Dry yolk (g)	7.49 ± 0.71	7.24 ± 0.76	NS	7.57 ± 0.61	6.84 ± 0.20	NS
% water	68.19 ± 5.10	61.85 ± 4.90	$p < 0.001$	54.41 ± 2.80	54.55 ± 2.30	NS
Lipid (g)	4.58 ± 0.55	4.39 ± 0.49	NS	4.51 ± 0.45	5.07 ± 1.35	NS
% lipid	19.46 ± 3.36	23.19 ± 3.20	$p < 0.001$	27.12 ± 2.26	33.60 ± 8.34	NS
Lipid (% dry)	61.11 ± 2.64	60.73 ± 1.48	NS	59.45 ± 2.80	74.50 ± 21.92	NS
Non-lipid dry (g)[2]	2.98 ± 0.29	2.86 ± 0.30	NS	3.07 ± 0.30	2.77 ± 0.14	NS
Albumen:						
Wet albumen (g)	22.33 ± 4.57	26.99 ± 2.92	$p < 0.001$	30.30 ± 3.02	29.15 ± 0.16	NS

ppendix 4 continued ...

Dry albumen (g)[3]	4.19 ± 0.36	4.13 ± 0.37	NS	4.23 ± 0.46	3.83 ± 0.03	NS
% water	80.68 ± 3.10	84.63 ± 1.10	p< 0.001	86.03 ± 0.80	86.40 ± 0.60	NS
hell: Wet shell(g)	4.72 ± 0.38	4.33 ± 0.39	p< 0.01	4.77 ± 0.49	4.06 ± 0.32	p< 0.
Dry shell(g)	3.60 ± 0.30	3.36 ± 0.26	p< 0.05	3.54 ± 0.29	3.07 ± 0.13	p< 0.
% water	23.79 ± 2.60	22.33 ± 2.60	NS	25.57 ± 4.40	24.20 ± 2.50	NS
olk/albumen (wet)	1.16 ± 0.43	0.73 ± 0.15	p< 0.001	0.56 ± 0.09	0.52 ± 0.01	NS
olk/albumen (dry)	1.80 ± 0.23	1.75 ± 0.26	NS	1.81 ± 0.22	1.79 ± 0.07	NS
ggshell thickness (mm)	0.238 ± 0.020 (38)[5]	0.236 ± 0.020 (26)	t = 0.42, NS[7]	0.242 ± 0.010	0.223 ± 0.010	NS
nergy (kcal/g fresh weight including shell)	1.57 ± 0.08	1.50 ± 0.24	NS	1.55 ± 0.07	1.69 ± 0.23	NS

---

[1] The digital scale was used to weigh thawed eggs.

[2] Yolk protein

[3] Albumen protein

[4] Mean ± SD

[5] The sample sizes are given in parentheses.

[6] No significant difference

[7] The sample size was adequate for the Student's t-test.

Appendix 5. Comparison of early and late c-egg constituent contents from three-egg clutches, Granite Island.

	1983			1984		
	Early n = 33	Late n = 15	Mann-Whitney U	Early n = 94	Late n = 2	Mann-Whitne U
Egg weight (g)[1]	50.7 ± 3.3[4]	49.1 ± 2.6	NS[6]	51.8 ± 3.5	51.9 ± 0.1	NS
Yolk: Wet yolk (g)	19.50 ± 3.08	15.09 ± 1.61	$p< 0.001$	15.90 ± 1.85	16.01 ± 0.86	NS
Dry yolk (g)	7.13 ± 0.72	6.78 ± 0.65	NS	7.08 ± 0.72	6.88 ± 0.32	NS
% water	62.78 ± 5.30	55.01 ± 2.50	$p< 0.001$	55.17 ± 4.30	57.00 ± 0.30	NS
Lipid (g)	4.33 ± 0.44	4.22 ± 0.48	NS	4.26 ± 0.40	4.05 ± 0.09	NS
% lipid	22.62 ± 3.34	28.04 ± 2.10	$p< 0.001$	26.96 ± 2.31	25.35 ± 0.78	NS
Lipid (% dry)	60.79 ± 2.26	62.30 ± 3.15	NS	60.60 ± 7.30	58.95 ± 1.34	NS
Non-lipid dry(g)[2]	2.84 ± 0.33	2.59 ± 0.30	$p< 0.05$	2.85 ± 0.31	2.83 ± 0.23	NS
Albumen:						
Wet albumen(g)	25.66 ± 3.90	28.33 ± 2.57	$p< 0.05$	28.42 ± 3.54	28.50 ± 1.33	NS

Dry albumen (g) [3]	3.99 ± 0.39	3.93 ± 0.35	NS	4.08 ± 0.50	4.03 ± 0.20	NS
% water	84.26 ± 1.70	86.10 ± 0.50	$p < 0.001$	85.48 ± 2.80	85.85 ± 0.10	NS
Shell: Wet shell (g)	4.43 ± 0.53	3.88 ± 0.18	$p < 0.001$	4.31 ± 0.50	4.50 ± 0.45	NS
Dry shell (g)	3.32 ± 0.39	3.07 ± 0.22	$p < 0.05$	3.26 ± 0.29	3.15 ± 0.03	NS
% water	24.82 ± 3.80	20.89 ± 3.90	$p < 0.01$	23.98 ± 5.90	29.70 ± 7.10	NS
Yolk/albumen (wet)	0.79 ± 0.23	0.54 ± 0.08	$p < 0.001$	0.57 ± 0.13	0.56 ± 0.06	NS
Yolk/albumen (dry)	1.80 ± 0.23	1.74 ± 0.25	NS	1.76 ± 0.26	1.71 ± 0.16	NS
Eggshell thickness (mm)	0.226 ± 0.020 (37)[5]	0.221 ± 0.020 (23)	t = 0.98, NS[7]	0.235 ± 0.020	0.224 ± 0.010	NS
Energy (kcal/g fresh weight including shell)	1.57 ± 0.08	1.56 ± 0.09	NS	1.54 ± 0.08	1.49 ± 0.02	NS

---

[1] The digital scale was used to weigh thawed eggs.

[2] Yolk protein

[3] Albumen protein

[4] Mean ± SD

[5] The sample sizes are given in parentheses.

[6] No significant difference

[7] The sample size was adequate for the Student's t-test.

Appendix 6. Within clutch comparison of 1983 egg constituent contents, Granite Island.

		Early + Late	Early	Late
Egg weight (g)		7.22, $p < 0.001$, $a=b>c$[1]	9.17, $p < 0.001$, $a=b>c$	0.76, NS, $a=b=c$
Yolk:	Wet yolk (g)	25.02, $p < 0.001$, $a=b>c$	24.38, $p < 0.001$, $a=b>c$	13.33, $p < 0.001$, $a=b>c$
	Dry yolk (g)	3.16, $p < 0.05$, $a=c>b$	2.75, NS, $a=b=c$	3.05, NS, $a=b=c$
	% water	30.45, $p < 0.001$, $a>b>c$	20.18, $p < 0.001$, $a=b>c$	22.79, $p < 0.001$, $a>b>c$
	Lipid (g)	2.47, NS, $a=b=c$	2.74 , NS $a=b=c$	2.16, NS, $a=b=c$
	% lipid	26.66, $p < 0.001$, $a<b<c$	15.79, $p < 0.001$, $a=b<c$	22.06, $p < 0.001$, $a<b<c$
	Lipid (% dry)	0.30, NS, $a=b=c$	0.12, NS, $a=b=c$	2.29, NS, $a=b=c$
	Non-lipid dry (g)	3.32, $p < 0.05$, $a=c<b$	2.20, NS, $a=b=c$	4.55, $p < 0.05$, $a=c<b$
Albumen:	Wet albumen (g)	13.31, $p < 0.001$, $a=b<c$	10.02, $p < 0.001$, $a=b<c$	7.65, $p < 0.01$, $a<b=c$
	Dry albumen (g)	4.96, $p < 0.01$, $a>c$	3.44, $p < 0.05$, $a>c$	1.65, NS, $a=b=c$
	% water	31.36, $p < 0.001$, $a<b<c$	27.27, $p < 0.001$, $a=b<c$	25.32, $p < 0.01$, $a<b<c$
Shell:	Wet shell (g)	14.38, $p < 0.001$, $a=b>c$	8.19, $p < 0.001$, $a=b>c$	16.79, $p < 0.001$, $a=b>c$
	Dry shell (g)	15.80, $p < 0.001$, $a=b>c$	9.88, $p < 0.001$, $a=b>c$	11.21, $p < 0.001$, $a=b>c$
	% water	0.80, NS, $a=b=c$	1.01, NS, $a=b=c$	1.90, NS, $a=b=c$

Appendix 6 continued ...

Yolk/albumen (wet)	19.61, $p < 0.001$, $a=b>c$	17.41, $p < 0.001$, $a=b>c$	12.48, $p < 0.001$, $a=b>c$
Yolk/albumen (dry)	1.64, NS, $a=b=c$	0.24, NS, $a=b=c$	2.01, NS, $a=b=c$
Eggshell thickness (mm)	14.39, $p < 0.001$, $a=b>c$	6.17, $p < 0.01$, $a=b>c$	8.87, $p < 0.001$, $a=b>c$
Energy (kcal/g fresh weight + shell)	1.29 , NS, $a=b=c$	0.73 , NS, $a=b=c$	0.88, NS, $a=b=c$

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[1] ANOVA F ratio, probability, Scheffé's contrasting

Note: The results are based on the means found in Appendices 3 through 5.

Appendix 7. Within clutch comparison of 1984 egg constituent contents, Granite Island.

		Early + Late	Early	Late
Egg weight (g)		27.51, $p < 0.001$, $a>b>c$ [1]	28.01, $p < 0.001$, $a>b>c$	2.95, NS, $a=b=c$
Yolk:	Wet yolk (g)	5.72, $p < 0.01$, $a=c<b$	5.94, $p < 0.01$, $a=c<b$	2.21, NS, $a=b=c$
	Dry yolk (g)	13.46, $p < 0.001$, $a=b>c$	13.90, $p < 0.001$, $a=b>c$	0.66, NS, $a=b=c$
	% water	3.63, $p < 0.05$, $a<c$	3.47, $p < 0.05$, $a<c$	1.13, NS, $a=b=c$
	Lipid (g)	8.16, $p < 0.001$, $b>c$	7.45, $p < 0.001$, $b>c$	1.38, NS, $a=b=c$
	% lipid	1.69, NS, $a=b=c$	1.99, NS, $a=b=c$	1.79, NS, $a=b=c$
	Lipid (% dry)	0.72, NS, $a=b=c$	1.37, NS, $a=b=c$	1.04, NS, $a=b=c$
	Non-lipid dry (g)	11.01, $p < 0.001$, $b>c$	11.32, $p < 0.001$, $b>c$	0.29, NS, $a=b=c$
Albumen:	Wet albumen (g)	43.64, $p < 0.001$, $a>b>c$	42.78, $p < 0.001$, $a>b>c$	3.72, NS, $a=b=c$
	Dry albumen (g)	17.60, $p < 0.001$, $a>b=c$	17.18, $p < 0.001$, $a>b=c$	2.66, NS, $a=b=c$
	% water	5.40, $p < 0.01$, $a>c$	5.29, $p < 0.01$, $a>c$	0.80, NS, $a=b=c$
Shell:	Wet shell (g)	23.69, $p < 0.001$, $a=b>c$	25.07, $p < 0.001$, $a=b>c$	0.58, NS, $a=b=c$
	Dry shell (g)	31.00, $p < 0.001$, $a=b>c$	31.35, $p < 0.001$, $a=b>c$	1.33, NS, $a=b=c$
	% water	3.93, $p < 0.05$, $a<b$	4.23, $p < 0.05$, $a<b$	0.89, NS, $a=b=c$

Appendix 7 continued ...

Yolk/albumen (wet)	19.07, $p < 0.001$, $a<b=c$	18.37, $p < 0.001$, $a<b=c$	2.60, NS, $a=b=c$
Yolk / albumen (dry)	10.56, $p < 0.001$, $a<b=c$	9.87, $p < 0.001$, $a<b=c$	1.39, NS, $a=b=c$
Eggshell thickness (mm)	3.88, $p < 0.05$, $b>c$	3.98, $p < 0.05$, $b>c$	0.71, NS, $a=b=c$
Energy (kcal/g fresh weight + shell)	9.57, $p < 0.001$, $a<b$	8.61, $p < 0.001$, $a<b$	1.65, NS, $a=b=c$

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[1] ANOVA F ratio, probability, Scheffé's contrasting

Note: The results are based on the means found in Appendices 3 through 5.

Appendix 8. Relationship between female[1] Ring-billed Gull body weight with egg volume and composition through the laying sequence, Granite Island, 1983 and 1984.

		1983			1984[2]		
		a	b	c	a	b	c
		n=33 [3]	n=34	n=34	n=24	n=24	n=24
Egg volume		0.44** [4]	0.17	0.30*	0.29	0.41*	0.29
Fresh weight egg		0.43**	0.19	0.32*	0.38*	0.43*	0.36*
Yolk:	Wet yolk	0.33*	0.31*	0.33*	0.37*	0.39*	0.16
	Dry yolk	0.24	0.02	0.19	0.19	0.37	0.36*
	% water	0.20	0.34*	0.30*	0.10	0.13	-0.17
	Lipid	0.21	0.03	0.06	0.23	0.09	0.35*
	% lipid	-0.18	-0.32*	-0.35**	0.01	-0.30	0.10
	Lipid (% dry)	-0.05	0.03	-0.25	0.06	-0.08	-0.09
	Non-lipid dry	0.23	0.02	0.32*	0.02	0.47**	0.35*
Albumen:	Wet albumen	0.02	-0.19	-0.03	0.09	0.21	0.22
	Dry albumen	0.19	0.12	0.10	0.10	0.31	0.16
	% water	-0.10	-0.35*	-0.11	-0.14	-0.15	0.16
Shell:	Wet shell	0.53***	0.41**	0.51***	0.17	0.14	0.31
	Dry shell	0.42**	0.39*	0.34*	0.28	0.31	0.37*
	% water	0.34*	0.10	0.48**	-0.05	-0.19	0.00

Appendix 8 continued ...

Yolk/albumen (wet)	0.19	0.30*	0.19	0.09	0.11	-0.05
Yolk/albumen (dry)	0.09	-0.06	0.07	0.11	0.07	0.06
Energy	-0.13	-0.09	-0.07	0.08	-0.06	0.00
Total water	0.45**	0.13	0.39*	0.27	0.46*	0.25

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[1] Only post-laying females that laid 3 eggs were used.

[2] Spearman rank correlation (sample size less than 25)

[3] The total was not 34 since one a-egg had no yolk.

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 9. Relationship between female[1] Ring-billed Gull condition index with egg volume and composition through the laying sequence, Granite Island, 1983 and 1984.

		1983			1984[2]		
		a n=33 [3]	b n=34	c n=34	a n=24	b n=24	c n=24
Egg volume		0.28 [4]	0.03	0.21	0.27	0.27	0.11
Fresh weight egg		0.22	0.02	0.21	0.29	0.26	0.16
Yolk:	Wet yolk	0.19	0.13	0.31*	0.07	0.15	-0.17
	Dry yolk	-0.02	-0.25	0.00	0.03	0.13	-0.01
	% water	0.27	0.32*	0.38*	-0.17	-0.01	-0.11
	Lipid	-0.08	-0.28	-0.15	0.03	-0.12	-0.04
	% lipid	-0.27	-0.37*	-0.44**	0.04	-0.25	-0.02
	Lipid (% dry)	-0.20	-0.22	-0.33*	-0.09	-0.17	-0.25
	Non-lipid dry	0.07	-0.17	0.20	-0.09	0.27	0.07
Albumen:	Wet albumen	-0.01	-0.05	-0.05	0.25	0.11	0.22
	Dry albumen	0.14	0.12	0.12	0.21	0.13	0.18
	% water	-0.09	-0.16	-0.18	0.04	-0.02	0.04
Shell:	Wet shell	0.46**	0.30*	0.46**	-0.03	-0.08	0.07
	Dry shell	0.35*	0.30*	0.36*	0.04	0.10	0.15
	% water	0.37*	0.03	0.33*	-0.11	-0.23	-0.10

Appendix 9 continued ...

Yolk/albumen (wet)	0.11	0.13	0.22	-0.19	-0.01	-0.22
Yolk/albumen (dry)	-0.12	-0.26	-0.08	-0.05	-0.01	-0.26
Energy	-0.33*	-0.35*	-0.20	0.05	-0.20	-0.33
Total water	0.29	0.18	0.36*	0.30	0.27	0.07

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Spearman rank correlation (sample size less than 25)

[3] The total was not 34 since one a-egg had no yolk.

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

ppendix 10. Comparison of the body homogenate composition of female[1] Ring-billed Gulls, Granite Island, 1983 and 1984.

	Early	Late	Mann-Whitney U
ody weight (g)			
1983	432.9 ± 27.5 (24)[2]	403.0 ± 17.9 (10)	$p < 0.01$
1984	424.8 ± 24.8 (21)	402.5 ± 7.8 (2)	NS[3]
	NS	NS	
rocessed body weight (g)			
1983	317.2 ± 20.5 (24)	295.6 ± 14.2 (10)	$p < 0.01$
1984	308.3 ± 16.9 (21)	292.0 ± 9.9 (2)	NS
	NS	NS	
ody water (g)			
1983	207.4 ± 12.9 (24)	202.3 ± 9.7 (10)	NS
1984	205.1 ± 13.4 (21)	198.6 ± 8.2 (2)	NS
	NS	NS	
body water			
1983	65.4 ± 1.8 (24)	68.4 ± 1.0 (10)	$p < 0.001$
1984	66.6 ± 3.1 (21)	68.0 ± 0.5 (2)	NS
	$p < 0.01$	NS	
ody protein (g)			
1983	87.1 ± 16.3 (24)	84.8 ± 3.5 (10)	$p < 0.01$
1984	87.5 ± 6.4 (21)	82.2 ± 2.5 (2)	NS
	$p < 0.05$	NS	

pendix 10 continued ...

ody protein			
1983	27.6 ± 5.2 (24)	28.7 ± 0.7 (10)	NS
1984	28.4 ± 2.0 (21)	28.2 ± 1.8 (2)	NS
	NS	NS	
dy lipid (g)			
1983	18.8 ± 7.7 (24)	8.5 ± 2.9 (10)	$p < 0.001$
1984	15.7 ± 6.8 (21)	11.2 ± 4.2 (2)	NS
	NS	NS	
ody lipid			
1983	5.9 ± 2.2 (24)	2.9 ± 0.9 (10)	$p < 0.001$
1984	5.0 ± 2.1 (21)	3.8 ± 1.3 (2)	NS
	NS	NS	
dy energy (kcal/g body weight) [4]			
1983	6.10 ± 1.05 (24)	6.00 ± 0.10 (10)	$p < 0.001$
1984	6.21 ± 0.20 (21)	6.11 ± 0.17 (2)	NS
	NS	NS	

Only post-laying females that laid 3 eggs were used.

Mean ± SD (n)

No significant difference

Dry weight of the tissues was used.

Appendix 11. Comparison for the skin composition of female[1] Ring-billed Gulls, Granite Island, 1983 and 1984.

	Early	Late	Mann-Whitney U
Wet skin weight (g)			
1983	33.2 ± 9.5 (24)[2]	23.7 ± 3.2 (10)	$p < 0.01$
1984	33.2 ± 6.2 (21)	27.6 ± 2.8 (2)	NS[3]
	NS	NS	
Skin water (g)			
1983	14.1 ± 2.9 (24)	14.0 ± 1.1 (10)	NS
1984	15.3 ± 2.4 (21)	14.7 ± 1.6 (2)	NS
	$p < 0.05$	NS	
% skin water			
1983	44.5 ± 9.6 (24)	59.6 ± 6.4 (10)	$p < 0.001$
1984	47.8 ± 11.5 (21)	53.5 ± 11.1 (2)	NS
	NS	NS	
Skin protein (g)			
1983	6.6 ± 1.4 (24)	6.5 ± 0.8 (10)	NS
1984	7.5 ± 2.6 (21)	6.1 ± 0.8 (2)	NS
	NS	NS	
skin protein			
1983	21.1 ± 5.7 (24)	27.5 ± 2.4 (10)	$p < 0.01$
1984	22.7 ± 6.2 (21)	22.3 ± 5.1 (2)	NS
	NS	NS	

ppendix 11 continued ...

kin lipid (g)			
1983	12.3 ± 7.7 (24)	3.2 ± 2.4 (10)	$p < 0.001$
1984	10.4 ± 6.5 (21)	7.0 ± 5.2 (2)	NS
	NS	NS	
skin lipid			
1983	33.8 ± 14.2 (24)	12.9 ± 8.2 (10)	$p < 0.001$
1984	29.5 ± 13.8 (21)	24.2 ± 16.2 (2)	NS
	NS	NS	
kin energy (kcal/g body weight)[4]			
1983	7.83 ± 0.72 (24)	6.80 ± 0.58 (10)	$p < 0.01$
1984	7.74 ± 0.60 (21)	7.55 ± 0.89 (2)	NS
	NS	NS	

Only post-laying females that laid 3 eggs were used.

Mean ± SD (n)

No significant difference

Dry weight of the tissues was used.

ppendix 12. Comparison of the ovary (with oviduct) composition of female[1] Ring-billed Gulls, Granite Island, 1983 and 1984.

	Early	Late	Mann-Whitney U
et ovary weight (g)			
1983	8.2 ± 3.9 (24) [2]	7.3 ± 1.2 (10)	NS [3]
1984	8.0 ± 2.1 (21)	6.1 ± 0.4 (2)	NS
	NS	NS	
vary water (g)			
1983	6.3 ± 2.8 (24)	5.7 ± 0.9 (10)	NS
1984	6.2 ± 1.6 (21)	4.7 ± 0.4 (2)	NS
	NS	NS	
ovary water			
1983	78.0 ± 1.9 (24)	77.7 ± 2.3 (10)	NS
1984	77.5 ± 1.5 (21)	77.2 ± 1.0 (2)	NS
	$p < 0.05$	NS	
vary protein (g)			
1983	1.5 ± 0.7 (24)	1.4 ± 0.2 (10)	NS
1984	1.5 ± 0.4 (21)	1.2 ± 0.1 (2)	NS
	NS	NS	
ovary protein			
1983	18.6 ± 1.2 (24)	19.2 ± 0.6 (10)	NS
1984	19.2 ± 1.2 (21)	19.2 ± 0.0 (2)	NS
	$p < 0.05$	NS	

ppendix 12 continued ...

ary lipid (g)			
1983	0.3 ± 0.4 (24)	0.2 ± 0.2 (10)	NS
1984	0.3 ± 0.2 (21)	0.2 ± 0.0 (2)	NS
	NS	NS	
ovary lipid			
1983	3.5 ± 1.7 (24)	3.2 ± 2.4 (10)	NS
1984	4.5 ± 5.2 (21)	3.7 ± 1.0 (2)	NS
	NS	NS	
ary energy (kcal/g body weight)[4]			
1983	6.24 ± 0.27 (24)	6.17 ± 0.34 (10)	NS
1984	6.82 ± 2.81 (21)	6.27 ± 0.14 (2)	NS
	NS	NS	

Only post-laying females that laid 3 eggs were used.

Mean ± SD (n)

No significant difference

Dry weight of the tissues was used.

Appendix 13. Relationship between female[1] Ring-billed Gull body homogenate composition[2] with egg constituent composition, Granite Island.

		Processed body weight	Body water	% body water	Body protein	% body protein	Body lipid	% body lipid	Body energy
Fresh egg weight [3]		0.24*** [4]	0.16*	-0.15*	0.04	-0.07	0.18**	0.17*	-0.01
Yolk:	Wet yolk	0.26***	0.11	-0.26***	-0.13*	-0.22***	0.22**	0.21**	-0.19**
	Dry yolk	0.14*	0.01	-0.22**	-0.01	-0.07	0.21**	0.21***	-0.02
	% water	0.21**	0.12	-0.16*	-0.08	-0.17*	0.14*	0.12	-0.14*
	Lipid	0.08	-0.02	-0.17*	-0.05	-0.08	0.12	0.12	-0.07
	% lipid	-0.23**	-0.13*	0.17*	0.06	0.16*	-0.17*	-0.15*	0.11
	Lipid (% dry)	-0.10	-0.07	0.07	-0.08	-0.03	-0.13*	-0.14*	-0.11
	Non-lipid dry	0.16*	0.01	-0.25***	0.03	-0.03	0.27***	0.27***	0.04
Albumen:	Wet albumen	-0.07	0.03	0.15*	0.15*	0.16*	-0.07	-0.06	0.18**
	Dry albumen	0.12	0.06	-0.10	0.19**	0.12	0.13*	0.12	0.14*
	% water	-0.16*	-0.02	0.23***	0.14*	0.19**	-0.15*	-0.14*	0.20**

Appendix 13 continued ...

Shell:	Wet shell	0.30***	0.15*	-0.26***	-0.12	-0.23***	0.28***	0.27***	-0.15*
	Dry shell	0.29***	0.17*	-0.23**	-0.01	-0.13*	0.27***	0.26***	-0.03
	% water	0.09	0.00	-0.15*	-0.20**	-0.21**	0.09	0.09	-0.21**
Yolk/albumen (wet)		0.17*	0.05	-0.20**	-0.23***	-0.28***	0.13*	0.12	-0.28***
Yolk/albumen (dry)		-0.02	-0.07	-0.07	-0.17*	-0.14*	0.03	0.03	-0.14*
Energy		-0.12	-0.18**	-0.08	-0.02	0.00	0.01	0.00	0.00
Total water		0.25***	0.21**	-0.09	0.02	-0.10	0.17*	0.16*	-0.01

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] Data from 1983 and 1984 were pooled (N = 171).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 14. Relationship between female[1] Ring-billed Gull skin composition [2] with egg constituent composition, Granite Island.

	Wet skin weight	Skin water	% skin water	Skin protein	% skin protein	Skin lipid	% skin lipid	Skin energy
Fresh egg weight [3]	0.31*** [4]	0.27***	-0.16*	0.20**	-0.10	0.19**	0.15*	0.14*
Yolk: Wet yolk	0.16*	-0.07	-0.21**	-0.10	-0.16**	0.21**	0.20**	0.11
Dry yolk	0.25***	0.10	-0.18**	0.08	-0.14*	0.21**	0.17*	0.11
% water	0.03	-0.14*	-0.12	-0.16*	-0.11	0.12	0.12	0.05
Lipid	0.19**	0.09	-0.10	0.04	-0.11	0.15*	0.10	0.04
% lipid	-0.06	0.13*	0.16*	0.12	0.12	-0.13*	-0.14*	-0.08
Lipid (% dry)	-0.09	0.00	0.14*	-0.09	0.04	-0.08	-0.12	-0.13*
Non-lipid dry	0.27***	0.09	-0.24***	0.12	-0.15*	0.22**	0.21**	0.16*
Albumen: Wet albumen	0.01	0.19**	0.10	0.18**	0.11	-0.09	-0.10	-0.03
Dry albumen	0.14*	0.09	-0.09	0.16*	0.02	0.09	0.06	0.08
% water	-0.08	0.16*	0.18**	0.13*	0.15*	-0.17*	-0.17*	-0.10

Appendix 14 continued ...

Shell:	Wet shell	0.38***	0.26***	-0.26***	0.18**	-0.18*	0.27***	0.24***	0.20**
	Dry shell	0.33***	0.24***	-0.23***	0.14*	-0.17*	0.24***	0.21**	0.17*
	% water	0.18**	0.07	-0.15*	0.12	-0.06	0.14*	0.13*	0.11
Yolk/albumen (wet)		0.08	-0.11	-0.16*	-0.13*	-0.16*	0.15*	0.16*	0.08
Yolk/albumen (dry)		0.05	0.02	-0.03	-0.03	-0.08	0.05	0.04	-0.02
Energy		-0.05	-0.11	0.01	-0.03	0.05	-0.02	-0.07	-0.09
Total water		0.21**	0.19**	-0.11	0.13*	-0.07	0.13*	0.10	0.09

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] Data from 1983 and 1984 were pooled (N = 171).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significnace at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 15. Relationship between female[1] Ring-billed Gull ovary (with oviduct) composition[2] with egg constituent composition, Granite Island.

	Wet ovary weight	Ovary water	% ovary water	Ovary protein	% ovary protein	Ovary lipid	% ovary lipid	Ovary energy
Fresh egg weight [3]	-0.04 [4]	-0.03	0.25***	-0.04	-0.02	-0.11	0.02	0.12
Yolk: Wet yolk	-0.15*	-0.14*	0.19**	-0.17*	-0.19**	-0.16*	-0.09	-0.07
Dry yolk	-0.08	-0.07	0.26***	-0.10	-0.14*	-0.11	0.03	0.11
% water	-0.13*	-0.13*	0.09	-0.16*	-0.16*	-0.12	-0.11	-0.12
Lipid	-0.05	-0.03	0.24***	-0.06	-0.10	-0.10	-0.01	0.07
% lipid	0.14*	0.14*	-0.09	0.17*	0.17*	0.12	0.09	0.10
Lipid (% dry)	0.07	0.07	-0.01	0.08	0.05	0.02	-0.06	-0.06
Non-lipid dry	-0.16*	-0.14*	0.24***	-0.18**	-0.17*	-0.13*	0.06	0.13
Albumen: Wet albumen	0.17*	0.17*	-0.04	0.20**	0.12	0.14*	0.11	0.14*
Dry albumen	0.10	0.11	0.10	0.13*	0.10	-0.02	-0.04	0.02
% water	0.15*	0.15*	-0.08	0.16*	0.06	0.18*	0.13*	0.13*

Appendix 15 continued ...

Shell:	Wet shell	-0.02	-0.02	0.08	-0.02	-0.01	-0.03	0.04	0.08
	Dry shell	0.03	0.04	0.09	0.03	0.00	-0.02	-0.01	0.03
	% water	-0.12	-0.13	0.00	-0.13*	-0.03	-0.03	0.10	0.10
Yolk/albumen (wet)		-0.14*	-0.14*	0.08	-0.16*	-0.12	-0.14*	-0.08	-0.09
Yolk/albumen (dry)		-0.10	-0.10	0.11	-0.13*	-0.15*	-0.05	0.05	0.06
Energy		0.04	0.05	0.02	0.03	-0.02	0.01	0.00	0.00
Total water		0.07	0.08	0.15*	0.07	-0.06	0.03	0.06	0.11

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[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] Data from 1983 and 1984 were pooled (N = 171).

[4] Pearson correlation r value

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 16. Relationship between female[1] Ring-billed Gull total carcass composition[2] with a-egg constituent composition, Granite Island, 1984.

	Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight[3]	0.36*[4]	0.49**	0.02	0.46*	0.05	0.03	-0.03	0.00
Yolk: Wet yolk	0.32	0.39*	0.01	0.42*	0.14	0.00	-0.05	-0.02
Dry yolk	0.21	0.27	0.08	0.32	0.20	-0.05	-0.12	-0.09
% water	0.03	0.03	-0.02	-0.13	-0.22	0.01	0.05	0.04
Lipid	0.22	0.31	0.06	0.38*	0.28	-0.09	-0.17	-0.14
% lipid	0.04	0.09	0.04	0.12	0.19	-0.07	-0.11	-0.11
Lipid (% dry)	-0.03	0.19	0.19	-0.04	0.03	-0.21	-0.24	-0.24
Non-lipid dry	0.08	0.06	0.07	0.23	0.17	-0.03	-0.08	-0.04
Albumen: Wet albumen	0.09	0.27	0.17	0.15	-0.07	-0.09	-0.11	-0.11
Dry albumen	0.03	0.23	0.22	0.18	0.00	-0.14	-0.14	-0.15
% water	0.03	0.09	-0.10	-0.29	-0.36*	0.12	0.09	0.13

Appendix 16 continued ...

Shell:	Wet shell	0.22	0.04	-0.24	0.63***	0.55**	0.07	0.02	0.00
	Dry shell	0.27	0.36*	-0.02	0.57**	0.34	-0.07	-0.15	-0.13
	% water	-0.01	-0.28	-0.20	0.28	0.52**	0.03	0.05	-0.02
Yolk/albumen (wet)		0.00	-0.06	-0.01	0.05	0.13	-0.04	-0.05	-0.02
Yolk/albumen (dry)		0.12	0.06	-0.11	0.06	0.06	0.07	0.02	0.06
Energy		0.00	0.00	0.03	0.05	0.12	-0.01	-0.04	-0.03
Total water		0.26	0.45*	0.08	0.30	-0.07	-0.01	-0.04	-0.03

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[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] N = 23

[4] Spearman rank correlation coefficient

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 17. Relationship between female[1] Ring-billed Gull total carcass composition[2] with b-egg constituent composition, Granite Island, 1984.

	Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight [3]	0.48**[4]	0.37*	-0.17	0.60***	0.16	0.24	0.19	0.18
Yolk: Wet yolk	0.34	0.23	-0.20	0.50**	0.20	0.18	0.15	0.15
Dry yolk	0.30	0.20	-0.10	0.51**	0.24	0.12	0.08	0.08
% water	0.17	0.31	-0.06	0.11	-0.07	0.00	-0.01	-0.01
Lipid	0.06	-0.09	-0.03	0.32	0.39*	-0.03	-0.03	-0.02
% lipid	-0.26	-0.43*	0.14	-0.15	0.21	-0.13	-0.12	-0.09
Lipid (% dry)	-0.04	-0.24	-0.05	0.08	0.20	0.04	0.04	0.08
Non-lipid dry	0.37*	0.30	-0.17	0.58**	0.25	0.14	0.11	0.07
Albumen: Wet albumen	0.27	0.31	0.09	0.34	0.01	0.01	-0.03	-0.04
Dry albumen	0.42*	0.24	-0.23	0.59***	0.16	0.27	0.24	0.20
% water	-0.25	0.05	0.51**	-0.34	-0.13	-0.40*	-0.43*	-0.40*

Appendix 17 continued ...

Shell:	Wet shell	0.18	-0.05	-0.17	0.41*	0.33	0.10	0.06	0.03
	Dry shell	0.36*	0.18	-0.27	0.70***	0.36*	0.21	0.15	0.12
	% water	-0.11	-0.34	-0.02	-0.18	0.07	0.01	0.01	0.00
Yolk/albumen (wet)		0.02	-0.08	-0.11	0.21	0.27	0.02	0.03	0.03
Yolk/albumen (dry)		-0.09	-0.10	0.09	0.00	0.20	-0.13	-0.13	-0.11
Energy		-0.10	-0.28	-0.08	0.13	0.38*	-0.04	-0.01	0.00
Total water		0.50**	0.47*	-0.15	0.59***	0.05	0.21	0.16	0.15

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] N = 23

[4] Spearman rank correlation coefficient

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 18. Relationship between female[1] Ring-billed Gull total carcass composition[2] with c-egg constituent composition, Granite Island, 1984.

	Total analyzed weight	Total water	% water	Total protein	% protein	Total lipid	% lipid	Total energy
Fresh egg weight [3]	0.35*[4]	0.31	-0.04	0.46*	0.02	0.16	0.10	0.10
Yolk: Wet yolk	0.14	0.09	0.01	0.22	0.00	0.04	-0.01	-0.01
Dry yolk	0.39*	0.21	-0.19	0.57**	0.19	0.22	0.15	0.16
% water	-0.26	-0.17	0.14	-0.47*	-0.36*	-0.09	-0.06	-0.07
Lipid	0.41*	0.24	-0.23	0.54**	0.10	0.27	0.21	0.20
% lipid	0.24	0.10	-0.17	0.36*	0.29	0.12	0.10	0.10
Lipid (% dry)	0.04	-0.06	-0.14	-0.08	-0.10	0.14	0.16	0.12
Non-lipid dry	0.26	0.15	-0.07	0.49**	0.21	0.10	0.04	0.05
Albumen: Wet albumen	0.36*	0.47*	0.01	0.26	-0.16	0.09	0.04	0.06
Dry albumen	0.17	0.16	0.02	0.29	0.05	0.08	0.06	0.04
% water	0.30	0.42*	0.08	0.02	-0.25	0.02	-0.03	0.02

Appendix 18 continued ...

Shell:	Wet shell	0.24	0.14	-0.11	0.35	0.13	0.10	0.05	0.04
	Dry shell	0.27	0.20	-0.14	0.50**	0.11	0.16	0.10	0.08
	% water	0.01	-0.03	0.00	-0.13	0.01	-0.02	-0.03	-0.03
Yolk/albumen (wet)		-0.09	0.12	-0.25	-0.11	-0.05	-0.01	0.09	0.08
Yolk/albumen (dry)		0.13	0.10	-0.06	0.12	-0.01	0.04	0.00	0.02
Energy		0.08	-0.18	-0.22	0.19	0.23	0.14	0.13	0.11
Total water		0.32	0.37*	0.05	0.14	-0.25	0.10	0.05	0.06

---

[1] Only post-laying females that laid 3 eggs were used.

[2] Carcass compositions were expressed as proportions.

[3] N = 23

[4] Spearman rank correlation coefficient

* denotes statistical significance at 0.05 level

** denotes statistical significance at 0.01 level

*** denotes statistical significance at 0.001 level

Appendix 19. Mean condition index of male and female Ring-billed Gulls, Wolf River and Granite Island, 1983 and 1984.

Date[1]	1983 ♀ n = 65	1984 ♀ n = 62	1984 ♂ n = 57
April 30[2]		3.64 ± 0.24 (2)	4.33 ± 0.48 (3)
May 4		4.04 ± 0.49 (3)	4.20 ± 0.00 (1)
15[3]		3.78 ± 0.18 (4)	3.79 ± 0.21 (4)
16		3.64 ± 0.33 (12)	3.85 ± 0.27 (13)
17		3.55 ± 0.13 (13)	3.97 ± 0.22 (22)
18	3.30 ± 0.41 (3)[5]	3.56 ± 0.24 (6)	3.98 ± 0.17 (6)
19	3.61 ± 0.11 (7)	3.74 ± 0.32 (12)	3.85 ± 0.27 (7)
20	3.68 ± 0.34 (6)	3.77 ± 0.21 (10)	
21	3.63 ± 0.18 (14)	3.64 ± 0.00 (1)	
22	3.45 ± 0.16 (3)		
23	3.66 ± 0.16 (6)		
24	3.61 ± 0.04 (3)		
25	3.40 ± 0.13 (3)		
26	3.41 ± 0.00 (1)		
June 5[4]		3.32 ± 0.00 (2)	
6		3.36 ± 0.16 (2)	
7	3.60 ± 0.22 (4)		3.58 ± 0.00 (1)
8	3.33 ± 0.08 (4)		

Appendix 19 continued ...

June 9	3.52 ± 0.17 (3)
10	3.42 ± 0.45 (2)
11	3.50 ± 0.19 (3)
13	3.44 ± 0.26 (2)
14	3.40 ± 0.00 (1)

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[1] Date indexed

[2] Pre-breeding, Wolf River sample (April 30 and May 4)

[3] Early nesters (May 15 to May 26)

[4] Late nesters (June 5 to June 14)

[5] Mean ± SD (n)