Behaviour and Reproductive Success of Female-female Pairs of Ring-billed Gulls (*Larus delawarensis*), Granite Island

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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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.

April, 1982

ABSTRACT

Female-female pairs of Ring-billed Gulls were studied on Granite Island, northern Lake Superior, during the breeding seasons of 1979 and 1980. In 1979 the colony consisted of approximately 2400 pairs with 99 nests (4.1%) containing five to seven eggs. In 1980 the colony had increased in size to 2600 pairs and contained 71 (2.7%) superclutches. Extrapolating from superclutches in my observation areas, where all attendants were known, approximately 85% of the total number of superclutches were attended by female-female pairs. The difficulty distinguishing these nests from those of polygynous groups laying in a single nest-cup or nests receiving dump eggs is discussed. Because of these difficulties, all superclutches were monitored and treated as a single sample.

Eggs laid in superclutches were slightly smaller than those from normal clutches, but did not differ in shape. The incubation period differed significantly for eggs of the two clutch types, with eggs in superclutches taking longer to hatch than those in normal clutches. This may be because the eggs toward the outside edge of nests containing superclutches received significantly less heat. Nests containing superclutches were larger than those containing normal clutches but were of similar quality and were not differentially located by substrate, density or colony location. Nearest neighbour distance was also similar for the two clutch types.

Nest success did not differ significantly between superclutches and normal clutches. Hatching success for superclutches was 33% in 1979 and 29% in 1980, while normal clutches had 77% and 61% in 1979 and 1980, respectively. Significantly more eggs rolled from the nest or were destroyed or abandoned in superclutches compared to those from normal clutches.

Egg fertility rates were 87% and 94% for eggs in superclutches while normal clutches had 100% and 99% fertility in the two years of study. Chicks from normal clutches had a significantly higher fledging success than those of superclutches. Chicks from the latter had a higher rate of mortality due mainly to a higher death rate during the week following hatching. During both years of my study chicks from superclutches hatched at significantly lighter weights than those from normal clutches, but their weights did not differ after the first week post hatch. Tarsal and culmen measurements followed a similar pattern to that of weight. Food types brought to chicks from the two clutch types did not differ. Their diet consisted almost totally of fish and insects.

Females of female-female pairs were of normal size, weight, age and condition compared to heterosexually paired females. Levels of 13 blood chemistry parameters were measured for female-female pair members and heterosexually paired birds. The only consistent differences were low cholesterol and elevated progesterone levels in members of female-female pairs. Intra-pair size differences suggest that the females assortively paired by size. They exhibited mate fidelity and to a lesser extent nest-site tenacity.

Behaviour of female-female pairs is compared to heterosexual pairs during courtship, the incubation period and rearing of the brood. Females involved in female-female pairs cooperated well. Four polygynous groups were monitored, and their behaviour and reproductive success is reported. Existing hypotheses regarding the origin(s) of female-female pairing and their biological significance are discussed.

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1. INTRODUCTION

The study of mating systems in animals was first detailed by Charles Darwin in his 1871 discourse on The Descent of Man and Selection in Relation to Sex. Here Darwin discussed the significance of sexual selection in relation to reproductive fitness and developed concepts of animal courtship and mating that remain valid today.

In birds, the one overriding mating system is monogamy, with over 90 per cent of all species limiting their sexual behaviour to one member of the opposite sex (Lack 1968:149). Other bird species participate in one of three recognized nonmonogamous mating systems collectively known as polygamy, wherein one individual is sexually active with more than one member of the opposite sex. Polygamy is of three types: polygyny, the most common, involves one male mated to two or more females. About two per cent of the world's bird species are involved in such a mating system (Lack 1968:150). Another polygamous form is polyandry, where one female mates with one or more males; the outstanding example being the Jacanidae (Jenni and Collier 1972). Both polygyny and polyandry are characterized by the existence of multiple pair bonds. The third form of polygamy is promiscuity, wherein no pair bonds exist and males and females usually mate with many members of the opposite sex.

Monogamy and polygamy are considered mating system norms in the avian world. They serve to bring males and females together, the outcome of which is generally a high reproductive success. Various natural environmental, and social conditions are known to advance one system or the other (Emlen and Oring 1977, Wilson 1980).

Until recently, abnormal avian mating behaviour was documented only from captive and semi-captive individuals (see Collias and Jahn 1959, Slater, cited in Jefferies 1967, Sauer 1972, Starkey 1972, Dilger, cited in Hunt 1980, Hand 1981). Hunt and Hunt's (1977) discovery of female-female pairs in Western Gulls (Larus occidentalis) added a previously undocumented dimension to avian mating systems in the wild. The subsequent discovery of homosexual pairs in California Gulls (L. californicus)(Conover et al. 1979), Ring-billed Gulls (L. delawarensis)(Conover et al. 1979, Ryder and Somppi 1979) and Herring Gulls (L. argentatus)(Fitch 1979) has lead to speculation about their origin(s) and biological significance and has stimulated interest in the reevaluation of common beliefs regarding mate selection, sex roles, pair bonding, sex ratios and the monogamous breeding stategy.

All published reports dealing with female-female pairs have indicated a significantly lower rate of egg fertility compared to normal heterosexual pairs. In addition, Ryder and Somppi (1979) presented data showing reduced hatching success by female-female pairs. To date, however, there have been no published reports discussing the breeding success or behaviour of such pairs.

The purposes of this study were: to compare the breeding success and characteristics of members of female-female pairs with those of individuals involved in heterosexual bonds; to study the behaviour of homosexual pairs compared to normal pairs; and to attempt to determine the origin(s) and adaptive significance, if any, of female-female pairing. Because this apparently maladaptive behaviour occurs in species considered, until recently, to be classic examples of monogamous, longlived seabirds, this investigation provided an opportunity to consider factors that may influence the development and persistence of a unique mating system.

2. MATERIALS AND METHODS

2.1 DEFINITIONS

Fledging success: the percent of all chicks hatched that survived to 21 days of age (Dexheimer and Southern 1974).

Hatching success: the percent of eggs laid that hatched (Gilman *et al*. 1977).

Nest success: the percent of nests in which at least one egg hatched (Gilman *et al*. 1977).

Condition Index: body weight (g)/ bill length (cm) X keel length (cm)(Harris 1970).

Egg Shape Index: 100 X the breadth of the egg divided by its length (Romanoff and Romanoff 1949, Coulson 1963).

Normal clutch: a nest attended by one male and one female containing 1-4 eggs (Conover et al. 1979, Kovacs and Ryder 1981).

Superclutch: a nest containing 5-8 eggs (Kovacs and Ryder 1981) (Conover *et al*. 1979 and Ryder and Somppi 1979 referred to this clutch type as supernormal, which I felt was a redundant term).

Peak nest: a nest initiated during the week of modal clutch initiation.

Incubation period: the interval between the laying of the last egg in a clutch and the hatching of an individual egg within that clutch.

Homosexual pair: a nesting arrangement in which two individuals of the same sex form a pair-bond. I do not infer any differential sexual desire for those of the same sex.

2.2 STUDY AREA

Granite Island is located in Black Bay, northern Lake Superior, approximately three miles from Sibley Peninsula (Ryder and Somppi 1977) (Figure 1). It is a granite outcrop 402 m by 102 m with steeply inclined slopes that rise to a height of about 30 m above the surrounding water (Ryder and Carroll 1978). Dense forest comprised of White Cedar (Thuja occidentalis), White Birch (Betula papyrifera), Balsam Fir (Abies balsamea), and clumps of Mountain Ash (Sorbus scopulina), Pin Cherry (Prunus pennsylvanica), Red Osier Dogwood (Cornus stolonifera), and Redberried Elder (Sambucus racemosa) cover over 50% of the island (classification according to Britton and Brown 1970).

The ledges and other exposed portions of the sharply inclined north side of the island are occupied by approximately 100-150 pairs of Herring Gulls. There is little overlap between them and the Ring-billed Gull colony.

The Ring-billed Gull colony area is comprised of a small cliff on the northeast, an exposed slope on the northwest tip of the island, and an exposed area at the summit (see Figure 2). The number of birds in this colony has expanded rapidly during the last few years. Ryder (1975) reported the colony's size to be 800 pairs in 1973. Somppi (1978) estimated 1600 pairs of Ring-billed Gulls nesting on Granite Island in 1977. The area was occupied by 2400 and 2600 pairs in 1979 and 1980, respectively.

Ring-billed Gulls nest primarily in soil-filled depressions in the rock. The dominant vegetation in these areas is Rough Cinquefoil (Potentilla norvegica) and Kentucky Bluegrass (Poa pratensis). In addition to the two gull species, 30 other bird species have been ob-

Figure 1. Map showing the location of Granite Island (modified from Ryder 1974).

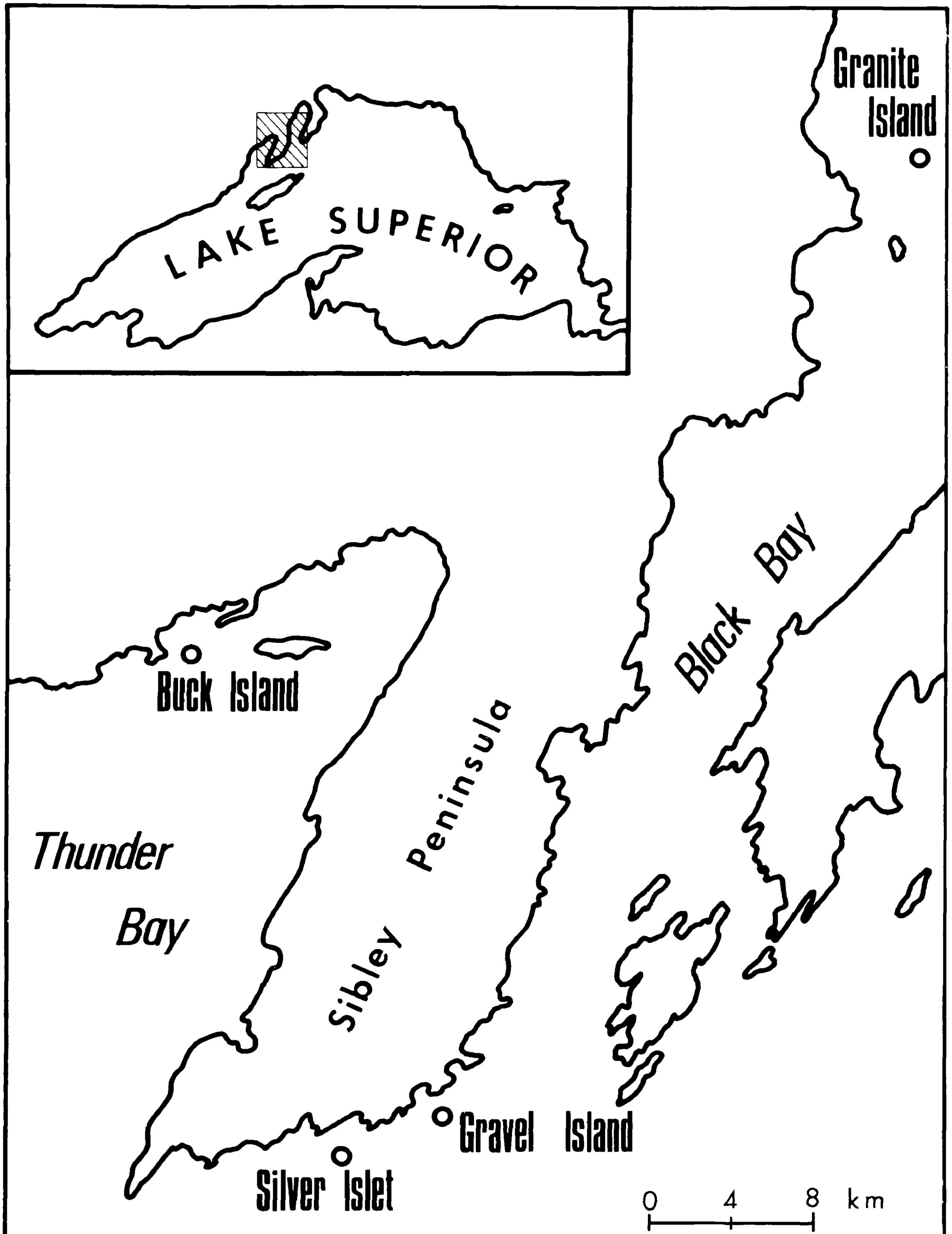
LAKE SUPERIOR
Granite Island
Buck Island
Thunder Bay
Sibley Peninsula
Black Bay
Gravel Island
Silver Islet
0 4 8 km

Figure 2. Aerial photograph of Granite Island. Note the bare rock areas that are occupied by Ring-billed Gulls and Herring Gulls.

served nesting on the island (Chamberlain 1973).

2.3 STATISTICAL PROCEDURES

Statistical analyses followed Nie et al. (1970). T-tests were only used with sample sizes greater than 30. When variances were not homogeneous, as determined by F-tests ($p>.05$), separate variance estimates were used instead of pooled estimates. Nonparametric statistics used included the Mann-Whitney U Test and Chi-squared tests, following Siegal (1956). Significance was assumed at $p<.05$.

2.4 NEST HISTORIES

In 1979, I arrived on Granite Island on 14 May. Snow and ice patches were still abundant and only an estimated 30 clutches had been initiated. None contained more than two eggs. I left the island to avoid disturbance during the early establishment of territories, and returned 20 May. In 1980, my study commenced 6 May. Searches of the colony and marking of clutches did not commence until 11 May, because only scrapes and 1-egg clutches were present upon my arrival and the birds were extremely sensitive to disturbance.

I marked all one egg clutches on the exposed summit area (selected because of its relative accessibility) with numbered wooden blocks. New clutches were marked daily in the same manner so that temporal distribution of clutch initiation could be determined and a sample of clutches of known initiation date could be selected for a base of comparison with superclutches.

Daily searches of the colony were made for superclutches, as they have come to be associated with female-female pairs (Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979, Kovacs and Ryder 1981). This was done to determine their frequency, relative colony location and the temporal distribution of clutch completion. A numbered wooden block was placed beside each superclutch for identification. Their locations n the colony area were mapped so that site tenacity between years could be determined, if it occurred. During searches, nests with a common rim were also noted (see Figure 3). These nests are composed of two individual nest-cups that touch along one edge, resulting in a shape resembling a figure 8. Shugart and Southern (1977) and Shugart (1980) found this arrangement diagnostic of polygynous groupings. Such nests were monitored in the same manner as superclutches, because they too differed from normal clutches, and represented a nesting arrangement involving two females.

During 1979, 70 peak nests, containing normal-sized clutches, were randomly selected from those previously marked to serve as a control group; a basis of comparison with the success of superclutches. In 1980 the control nests were chosen so that early (N=25), peak (n=59) and late (N=26) nests were represented, in order to avoid any bias that may have occurred by restricting my 1979 normal sample to only peak nests.

Eggs in each study nest were marked from 1-N on the blunt end (in sequence laid for eggs in normal clutches), with a non-toxic black felt pen in 1979 and with a number of dots of brown nail enamel representing egg number in 1980. This enabled me to identify eggs after they had rolled out of or were destroyed near the nest. I used nail enamel because it is durable and reduced disturbance caused by remarking eggs with the felt pen. The length and width of each egg was measured with vernier

Figure 3. Double nest-cup, used by a polygynous trio of Ring-billed Gulls, Granite Island, 1979.


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calipers(±0.01 cm) to compare size of eggs between superclutches and normal clutches.

Nest histories were kept by daily visitation until several days after hatching began. After this time nests without signs of pipping eggs were visited once every two days to reduce potential chick mortality resulting from investigator disturbance.

In 1979, four large enclosures in the summit area, and three smaller enclosures in other areas, containing about 12 nests each were constructed of 2.5 cm wire mesh fence for efficiency of locating chicks. Because some chicks were injured by the stiff wire, I switched to soft fiberglass screening in 1980. Only two large enclosures were used in the second year and both were located in the summit area.

Chicks were weighed to the nearest g within 24 hours of hatching using a hand held Pesola 50 g spring scale. They were then individually marked using a numbered aluminum fingerling fish tag placed through one web of the right foot. During 1980 in addition to weight, culmen and tarsus length were measured using vernier calipers (following Baldwin _et al_. 1931) to 0.01 cm. These growth parameters were recorded every few days for as long as was possible for each chick, using appropriately larger Pesola scales as the chicks grew (100±5 g, 300±5 g, 500±5 g). During the third week after hatching each chick was banded with a United States Fish and Wildlife Service aluminum leg band for future identification. Chick fates were recorded up to 21 days of age, at which time they were considered to have successfully fledged. This was done so that I was able to compare growth rates of chicks from the two clutch types and so that their relative success rates could be estimated.

Regurgitation samples were collected from chicks fed by heterosexual and homosexual parents to assess food quality and whether the sex of a parent might influence the type of food brought to chicks. Chicks occassionally regurgitated a single well defined bolus of food when I picked them up to weigh them. I collected them when they occurred and sealed them in bags containing 10% formalin. I combined samples according to date, age of chick, and clutch type. These composite samples were rinsed with water and food items separated. The total number of individual insects of each taxon was recorded for each sample. This was not possible for fish because of the condition of the regurgitated material. Most insects were keyed to family; fish were identified to species.

2.5 NEST-CUP TEMPERATURES, EGG POSITION AND EGG ROTATION

Nest-surface temperatures at the center of the nest-cup and at the outside edge of the outermost egg were recorded daily from a superclutch and a normal clutch while the nests were being incubated, during the last two weeks of incubation, using a Digimite Portable recorder, to 0.1° C, to determine if eggs at the outside of the clutch received less heat than those in the inside of either clutch type. Theremocouples were checked every two days (using my body temperature, by holding them between my thumb and forefinger) to ensure that they were measuring accurately.

The rotation of eggs within the nest-cup is also important to the survival of the embryo (Carey 1980). Twenty nests, 10 superclutches and 10 normal clutches, were monitored daily during the last two weeks of incubation to determine if eggs in superclutches were rotated at different frequencies from those of normal clutches. Eggs within these clutches were marked with felt pen such that the top and bottom of individual eggs were known. A line was drawn longitudinally around each egg so that the degree of turning could be measured (0°-180°). An arrow was painted on the substrate directed out from each nest, to serve as a reference point for the position of eggs within the nest-cup. Each nest was treated as a circle. Egg positions were also recorded in degrees (0°-360°).

2.6 NEST AND NEST-SITE CHARACTERISTICS

In 1980, I measured the distance from the center of the nest-cup to the center of the nearest nest (nearest neighbour distance), the number of neighbours within a two meter radius (density), and the length and width (180° from length), with the widest diameter of the nest representing length, for control clutches and superclutches to determine any differences in nest size or spacing between normal clutches and superclutches. I also evaluated the quality of the nests, subjectively as good, fair, or poor, according to the amount and placement of nesting materials. I noted substrate to determine if actual nest sites differed between the two clutch types. These sets of data were collected three weeks after peak clutch initiation, when very few new clutches were being initiated and initial nest construction had been completed for most nests.

2.7 MORPHOLOGICAL AND PHYSIOLOGICAL CHARACTERISTICS OF FEMALE-FEMALE PAIR MEMBERS

In 1979, 13 gulls incubating normal clutches and 57 incubating superclutches were trapped using the drop trap described by Mills and Ryder

(1979). During 1980, 45 normal clutch attendants and 69 superclutch attendants were trapped, as well as two pairs of females incubating normal clutches.

All trapped birds were weighed using a 500 or 1000 g Pesola hand-held scale (±5 g). Measurements of gonys, gape, tarsus (Baldwin et al. 1931) and keel (Harris 1970) were taken with vernier calipers to the nearest 0.01 cm. This was done so that size comparisons between females of normal pairs and those of female-female pairs could be made, a condition index calculated, and to determine if females of female-female pairs assortatively paired by size. Intrapair size variation was calculated by subtracting the size of the smaller member of a female-female pair from the larger (using the product of Ryder's (1978a) discriminant function to represent size). Sex was determined using the discriminant function described in Ryder (1978a). Five superclutch attendants were collected to confirm their suspected sexes by gonadal inspection. Brood patch condition was subjectively assessed as (1) defeathered and well vascularized (2) full size but lacking vascularization (3) starting to refeather and (4) refeathering (Figure 4). I made comparisons between superclutch and normal clutch attendants according to the stage of incubation. I classified gulls that had not previously been banded as adult or subadult on the basis of plumage. Subadult birds possessed one, or a combination of the following; brownish or brown-edged coverts, lack of white spots in the primaries, a subterminal black band or spots in the rectrices, grayish wing linings, and black-tipped head feathers (Ludwig 1974).

To avoid retrapping birds and to enable identification on the nest,

Figure 4. Four stages of brood patch condition seen in both normal pairs and female-female pairs of Ring-billed Gulls during the breeding seasons of 1979 and 1980, Granite Island; (1) defeathered and well vascularized (2) full size but lacking vascularization (3) starting to refeather and (4) refeathering.


1


2


3


4

I dyed green a patch of breast feathers and a band on the tail, of the first member of a pair captured. If I caught the second member of the pair, I dyed it yellow in the same manner.

F males attending superclutches were double-banded on the left leg using coloured expandable plastic bands. The band numbers for birds trapped on superclutches were recorded with their nest-sites so that instances of mate fidelity and/or nest-site tenacity could be ascertained.

Blood was collected each year from the brachial artery of five birds incubating normal clutches and five birds incubating superclutches during the latter part of the first and again during the latter part of the second week of incubation (N=20), into 5 or 10 ml heparinized vaccum tubes. I took samples at these particular times because I wanted to control for temporal differences occurring through the incubation period. In 1980, blood samples were also taken during the third week of incubation. All samples taken in 1980 were collected between 1700 and 1900 h. The blood was centrifuged for 20 minutes at 2500 rpm within a half our after collection to separate out the blood plasma and to prevent glucose breakdown (Bennett and Bolen 1978). Plasma was extracted, packaged and then transported frozen to the Canadian Wildlife Services Wildlife Toxicology Lab in Ottawa for analyses.

Levels of thyroxine (T_4), corticosterone, progesterone, total androgens and total estrogens were determined by specific radioimmunoassays. Alpha-amino nitrogen (following Mathews et al. 1964), urea nitrogen (Urease-Berthelot reaction, Sigma Kit No. 640), uric acid (Sigma Kit No. 680/American Monitor Colorimetric Uricase Uric Acid reagent system No. 1017), total protein (Biuret method of Henry et al. 1974), glucose (American Monitor's "Trucose" cat. No. 1054), calcium (American Monitor's 60 second calcium cat. No. 1032), and cholesterol (Bio-Rad's Quanta-Zyme Triglycerides Kit) were determined colorimetrically (D. Jefferies pers. comm.). (See Appendix 1 for prolactin levels of heterosexually paired birds). Samples were grouped according to pair type for statistical analyses of metabolite and hormone level differences between birds from normal or female-female pairs because of small sample sizes and the lack of any significant differences between samples from weeks one, two and three during 1980 (determined by Mann-Whitney U Test).

2.8 OBSERVATIONAL SAMPLING OF BEHAVIOUR

I made daily observations from hides (Figure 5) to study pair-formation, courtship activities, territory size and maintenance, incubation activity and care of the brood, for female-female pairs, and polygynous groups. Heterosexual pairs were observed as controls.

Early in the season I conducted _ad libitum_ sampling (Altmann 1974) because it was difficult to keep track of individuals before territories were established. I used a Super-8 Argus movie camera with zoom lens and a 35 mm Pentax with 50, 200, 300, or 600 mm lenses to record behaviour sequences.

Once nest scrapes were established in the observation areas I did Instantaneous Sampling on groups (Scan Sampling, Altmann 1974), during morning, afternoon and evening sessions, weather permitting. I did not enter the colony during heavy precipitation or extreme heat. Every attempt was made to keep time spent per individual brief and even. If exceptional circumstances dictated that my attention remain on one ani-

Figure 5. Locations of observation hides used on Granite Island, 1979, 1980. Insert is a close up of Hide #2.

mal, or if the colony was artificially disturbed, for example by other people, the Scan Sampling was curtailed.

Scanning intervals of 30 seconds, 1 and 2 minutes were used, depending on the number of individuals being scanned. Each scan took approximately half of the allotted time interval. For example, if a scan took 30 seconds to complete, I did them at 60 second intervals.

The termination time for a watch was set apriori in an attempt not to bias the duration of sessions according to the amount and type of activity (i.e. observer interest) during a given session. An average observation session lasted between two and three hours.

Behaviour categories were established (Table 1, Figure 6) according to the posture a bird assumed. The behaviour of the bird attending the nest or young, and the behaviour of its partner were noted during Scan Sampling. The bird incubating or most closely attending the young was designated the Attending Bird, the other bird is referred to as the Partner.

In 1979, I accumulated 90+ h of Scan Sampling between 28 May and 5 July. Unfortunately only two female-female pairs were observable from my hide from the start of the observation period until 26 June, at which time a second hide was located such that eight additional homosexual pairs were in sight. In total, 10 female-female pairs and eight heterosexual pairs were observed during 1979.

Because of small sample sizes early in the season, I examined the behavioural data from 1979 as a single sample for emergent trends. For statistical analyses, the rate of occurrence of each behaviour during each observation session was converted to an average rate per 30 scans (1 hour) using 2 minute intervals, for each session, so that sessions of

Table 1

Behavioral categories observed during behavioral watches on the Ring-billed Gull colony on Granite Island, 1979 and 1980.

Behaviour	Description
Courtship Activities	
Tipping	- a female walks toward her mate, her neck drawn in, body and head pointed horizontally forward - now and then she will make a tossing movement upward with the head, uttering a subadult call at each tossing of the head (Tinbergen 1960).
Begging	- food begging - females's approach to her mate and her insistant peçks at his (usually) chin and bill; usually accompanied by repeated Head-tossing and often performed in a Hunched Posture (Moynihan 1958a, Tinbergen 1959, 1960, Beer 1980).
Courtship Feeding	- regurgitation by a male in response to his mate Begging, usually followed by Copulation (Moynihan 1958a, Tinbergen 1960).
Choking (courtship)	- bird stretches its neck forward and utters the Mew Call, and makes incomplete Nest-Building movements, usually accompanied by its partner (Moynihan 1958a, Tinbergen 1960).

continued.....

Table 1 continued

Mounting/Copulation	- initiated by either sex, but usually the female; both birds toss their heads, each to its own rhythm, female circles male; male stretches his neck upward, still tossing his head, and takes a position obliquely behind the female; he lifts his wings, stops Head-tossing, lowers his tongue bone and begins to utter a hoarse, rhythmic call: male jumps on female's back (Mounting) settles on his tarsi, lowers his tail and wags it from side to side (Tail-wagging); the female still Head-tosses; waving his wings the male brings his cloaca to hers a number of times then jumps down (Copulation)(Tinbergen 1960).
Attending Bird Behaviour	
Incubation	- Sitting Bout, the onshift bird sits on the eggs (Beer 1961); not performing behaviours listed below.
Turning Eggs/ Comfort movements	- Egg Poking, Shifting; the movement of eggs in the nest using the bill and feet; also includes Ruffling, Trampling and Re-settling (Tinbergen 1960, Beer 1961, 1965); includes also comfort movements over the eggs or young that are being brooded.
Nest-Building	- pecking at nesting material lying nearby, or already in the nest, then depositing the material sideways over the bird's shoulder, along the sides of its breast or flanks (Moynihan 1953, Tinbergen 1960, Beer 1965).

continued........

Table 1 continued

	The two categories listed above together constitute Fussing.
Fighting	- aggressive physical contact involving an incubating bird; usually consisting of pulling matches between incubating neighbours.
Brooding	- sitting posture over chicks, somewhat different than incubation; a bird Brooding has its wings slightly lifted (Tinbergen 1960).
Absent	- neither bird on territory
Time on Eggs	- total time spent covering eggs regardless of behaviour category, expressed in minutes.

Behaviour of Partner

Moving Threat	- attack movements toward an intruder, usually preceeded by Anxiety Upright or Aggressive Upright (Moynihan 1958b, Tinbergen 1960).
Fighting	- an attacking bird rushes toward its opponent, tries to jump on top of it, and delivers vigorous downward pecks; this may be accompanied by some beating of the wings; scraping blows are occassionally delivered by downward kicks of the legs and feet (DeUsing 1939, Moynihan 1958b, Tinbergen 1960)
Absent	- second bird not on territory.

Shared activities performed by Attending Bird and / or Partner from their respective positions (ie. Attending Bird sitting on eggs, Partner sitting or Standing).

continued........

Changeover	- Nest Relief (Moynihan 1958a,b, Tinbergen 1960, Beer 1961, 1965); usually follows Greeting Pattern and is followed by Pre-settling Movements and a Settling Sequence.
Feeding	- in response to chicks begging or pecking at the parent's bill a parent regurgitates food; young chicks are fed from the bill while older chicks are more often fed from the ground (Tinbergen 1960).
Standing	- on territory, but not involved in other behaviour categories; includes sitting position.
Choking	- up and down pumping movements of the head and bill synchronized with accompanying notes; some choking postures are accompanied by Aggressive Head-sets or a swollen chin and/or Ruffle of the mantle feathers (Moynihan 1958b, Tinbergen 1960).
Head-tossing	- the bird tosses its head backward each time it utters a note (resuming the Oblique position momentarily between notes (Moynihan 1958b, Tinbergen 1960, Beer 1980).
Threat	- low intensity threat postures including Forward Display, Ground Pecking, Upright Posture, Freeze and Squat, Aggressive Head-set, Gaping Jab Movements; disconnected attack movements, forward and upright jabs of the bill and head combined with occasional traces of downward pecking, without advancing toward, or attempting to make actual

continued..........

Table 1 continued

	contact with an opponent (Moynihan 1955a,b, 1958a, Tinbergen 1952, 1960).
Preening	- ordering the feathers and placing on them the fatty secretion of the tail gland, keeping the barbs of the feathers joined by bringing any protruding feather back into place by nibbling individual feathers between the tips of the bill (Tinbergen 1960).
Sleeping	- eyes remain shut for several seconds or even minutes, the head is often turned to rest on the shoulder with the bill tucked into the scapular feathers (Tinbergen 1960, Beer 1961).

Figure 6. Photographs of some of the behaviour categories observed during behavioral watches on the Ring-billed Gull colony on Granite Island, 1979, 1980: (1) Courtship Feeding (2) Copulation (3) Turning Eggs and (4) Nest-Building.

1

2

3

4

differing length could be directly compared. Note that this is not an actual frequency of occurrence but rather represents the number of times a behaviour was observed upon scanning. Sessions shorter than one hour or those disrupted such that a continuous sample lasted less than one hour were not used because they would bias, in a positive direction, the behaviour categories that had been observed.

The locations of confrontations and the areas used by pairs of birds in the observation areas were recorded so that territory maps could be drawn, and hence territory sizes determined. This was only possible for areas that were in clear view and below the hide.

In 1980, I placed my hides at the same locations that I had used during 1979. I used the same observation and analyses techniques previously described. Because of my earlier arrival date, I was able to observe territory and nest-site establishment and courtship activities. In total, I observed 14 female-female pairs and 15 heterosexual pairs in 1980. The larger sample size allowed statistical analyses of shorter time intervals, so I divided the 120+ h of Scan Sampling into 10 periods. Each period was 5 or 6 days in duration, in an attempt to keep the number of observation sessions per period approximately the same. This was done so that variation in the activities of the birds as they progressed through the breeding season could be accounted for, and so that temporary differences in the behaviour of female-female pairs and normal pairs could be distinguished.

3. RESULTS

3.1 NEST HISTORIES

3.1.1 FREQUENCY AND SEASONAL DISTRIBUTION OF SUPERCLUTCHES

In 1979 the Ring-billed Gull colony on Granite Island consisted of 2400 breeding pairs on 7 June, with 99 nests (4.1%) containing five to seven eggs over the season (Table 2). In 1980, the colony had increased in size to 2600 pairs on 30-31 May, and contained a total of 71 (2.7%) superclutches (Table 2). Two known female-female pairs laid 3 and 4 eggs respectively in 1980.

Egg laying had commenced before my arrival at Granite Island 14 May 1979, and continued through until 9 July. The peak period of clutch initiation occurred 20-22 May. Nests (N=70) representing peak laying birds were randomly selected from normal nests that were initiated between 20-28 May. Clutch completion dates were used for comparative purposes between normal and superclutches because the latter were not recognizable until a fifth egg was laid in the nest. Nine 5-egg clutches were present on 20 May. The majority (75/99, 76%) of all superclutches that occurred during 1979 were completed within a week of the modal completion date for the sample of normal clutches (Figure 7).

In 1980, egg laying had commenced before I arrived on 6 May, however very few clutches were initiated at this time and none contained more than one egg. The peak period of clutch initiation occurred 11-13 May. The first 5-egg clutch of 1980 was recorded 12 May. Again the majority (57/71, 80%) of all superclutches were completed within a week of the modal completion date for the sample of normal clutches (Figure 7).

Table 2

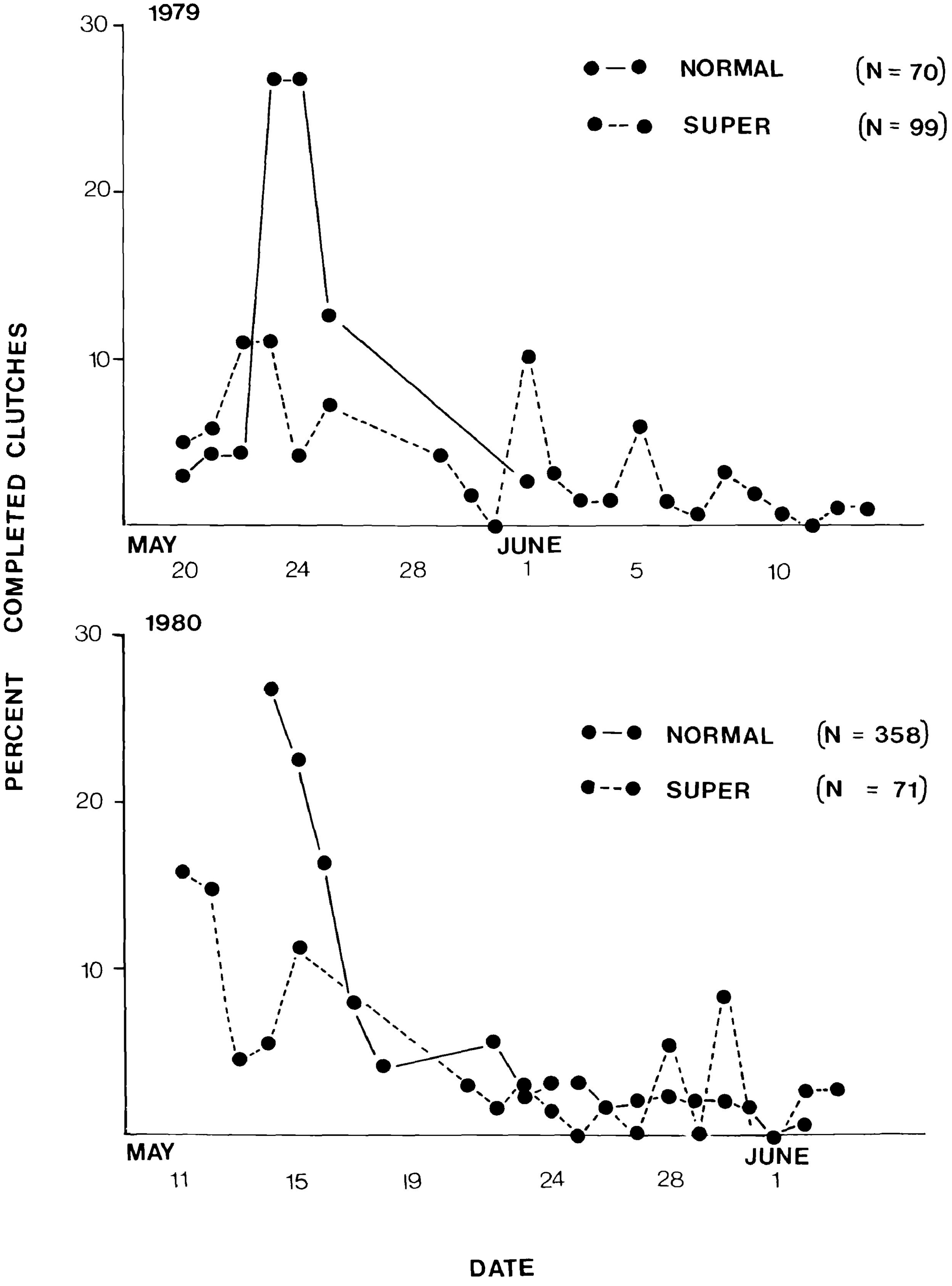
Frequency distribution of clutch sizes
of Ring-billed Gulls, Granite Island, Lake Superior
7 June 1979, 30-31 May 1980.

		Clutch size (Number of eggs)							
		1	2	3	4	5	6	7	Total
Number of nests	1979	141	387	1610	150	59	15	1	2363
		6.0[a]	16.4	68.1	6.3	2.5	0.6	0.0	
	1980	149	434	1832	140	30	5	2	2592
		5.7[a]	16.7	70.7	5.4	1.2	0.2	0.1	

[a] percent of sample

Note: There is an apparent inconsistency in the total number of superclutches. The number of superclutches illustrated in this table differs from the season totals because they represent point samples in time. The size of superclutches can be reduced rapidly.

Figure 7. Clutch completion dates for normal clutches (located in the chosen study area) and superclutches (throughout the colony) of Ring-billed Gulls, Granite Island, 1979,1980. Note: the 1979 normal sample illustrated represents peak nests only.


1979
30
20
10
●—● NORMAL (N = 70)
●--● SUPER (N = 99)
MAY
20
24
28
JUNE
1
5
10
1980
30
20
10
●—● NORMAL (N = 358)
●--● SUPER (N = 71)
MAY
11
15
19
24
28
JUNE
1
PERCENT COMPLETED CLUTCHES
DATE

3.1.2 EGG CHARACTERISTICS AND CLUTCH SIZE

Mean values of length, width and volume of eggs from normal clutches were larger than those from superclutches during both years of my study. Only width and volume during 1979, and length during 1980 differed significantly (Table 3). Average variance in length within clutches was far greater for eggs in superclutches than for those in normal clutches (43.3 mm and 12.8 mm respectively, $t=7.11$m $df=89$, $p<.05$).

The shape of eggs from the two clutch types (as measured by the Egg Shape Index) did not differ (Table 3). No attempts were made to quantitatively measure spot patterning or colouration. In some superclutches, however, two sets of eggs were clearly distinguishable (see Figure 8). Average clutch size per female was smaller for individuals laying in superclutches. The modal clutch size for Ring-billed Gulls is three eggs (see Vermeer 1970, this study normal clutches), but only 32.5% of superclutches in 1979 and 35.2% in 1980 contained six eggs.

3.1.3 INCUBATION PERIOD

Because superclutches were not identifiable until the laying of the fifth egg my definition of incubation period is a measure of the minimum time an egg had been incubated. The incubation period differed significantly for the two clutch types during 1979 ($X2=56.8$, $df=17$, $p<.05$), and 1980 ($X^2=40.7$, $df=11$, $p<.05$). Eggs in superclutches took longer to hatch.

In 1979 and 1980, 14.6% and 29.9% respectively, of eggs that hatched from superclutches had shorter incubation periods than the shortest incubation period of any egg in a normal clutch. These superclutches were probably the result of asynchronous laying of

Table 3

Comparison of length, width, volume and shape index

of eggs from normal and superclutches of Ring-billed Gulls,

Granite Island, 1979, 1980.

	1979			1980		
	Normal	Super	T-value	Normal	Super	T-value
Length (mm)	59.1 ± 2.3[a]	58.9 ± 2.6	0.92 $p > .05$	59.0 ± 2.4	58.6 ± 2.6	1.98 $p < .05$
Width (mm)	42.2 ± 1.3	41.8 ± 1.1	4.41 $p < .05$	42.0 ± 1.3	41.9 ± 1.4	0.98 $p > .05$
Volume (mm^3)	51.6 ± 3.8	50.3 ± 3.8	3.81 $p < .05$	51.0 ± 4.2	50.4 ± 4.3	1.71 $p > .05$
Shape Index	71.5 ± 3.3	71.1 ± 3.4	1.70 $p > .05$	71.3 ± 3.0	71.7 ± 3.5	1.24 $p > .05$
Sample size	193	466		279	355	

[a] Mean ± S.D.

Figure 8. Superclutch of Ring-billed Gulls, Granite Island, 1980. Note the two sets of differently coloured/patterned eggs.


58
58

eggs between members of female-female pairs or dump nesting (Ryder and Somppi 1979 define dump nests). It is not known therefore how long the first clutch was present before the additional eggs occurred. Because of this uncertaintly I did not include eggs from superclutches that hatched after a shorter incubation period than the shortest period for an eggs from a normal clutch in the preceeding analysis.

3.2 NEST-CUP TEMPERATURES, EGG POSITION AND EGG ROTATION DURING INCUBATION

Cup temperature in the center of the nest did not differ between the normal and superclutch ($Z=0.09$, $df=10$, $p>.05$). The temperatures at the edge of the two nests differed significantly ($Z=2.99$, $df=10$, $p<.05$), with the edge of the superclutch being of lower temperature (Figure 10).

The position of eggs in normal clutches changed significantly more than superclutch eggs ($t=2.7$, $df=75$, $p<.05$). Rotation of individual eggs did not differ significantly between clutch types ($t=1.1$, $df=75$, $p>.05$). Average values of total position changes over the 11 days of monitoring superclutches (396 ± 77) and normal clutches (261 ± 28) were greater for superclutches ($t=5.2$, $df=17$, $p<.05$). Average values of total egg rotation for superclutches (436 ± 60) and normal clutches (258 ± 33) per nest over the experimental period were also greater for superclutches ($t=8.2$, $df=17$, $p<.05$)

3.3 NEST AND NEST-SITE CHARACTERISTICS

Nests containing superclutches were significantly longer ($t=3.3$, $df=153$, $p<.05$) and wider ($t=3.1$, $df=153$, $p<.05$) than those with normal clutches (Table 4). Superclutches were of equal or better construction

Figure 9. Frequency distribution of incubation period for normal clutches and superclutches of Ring-billed Gulls, from the time of clutch completion until hatching, Granite Island 1979, 1980. Eggs from clutches that had unknown completion dates and eggs whose exact hatch dates were not known are not included.

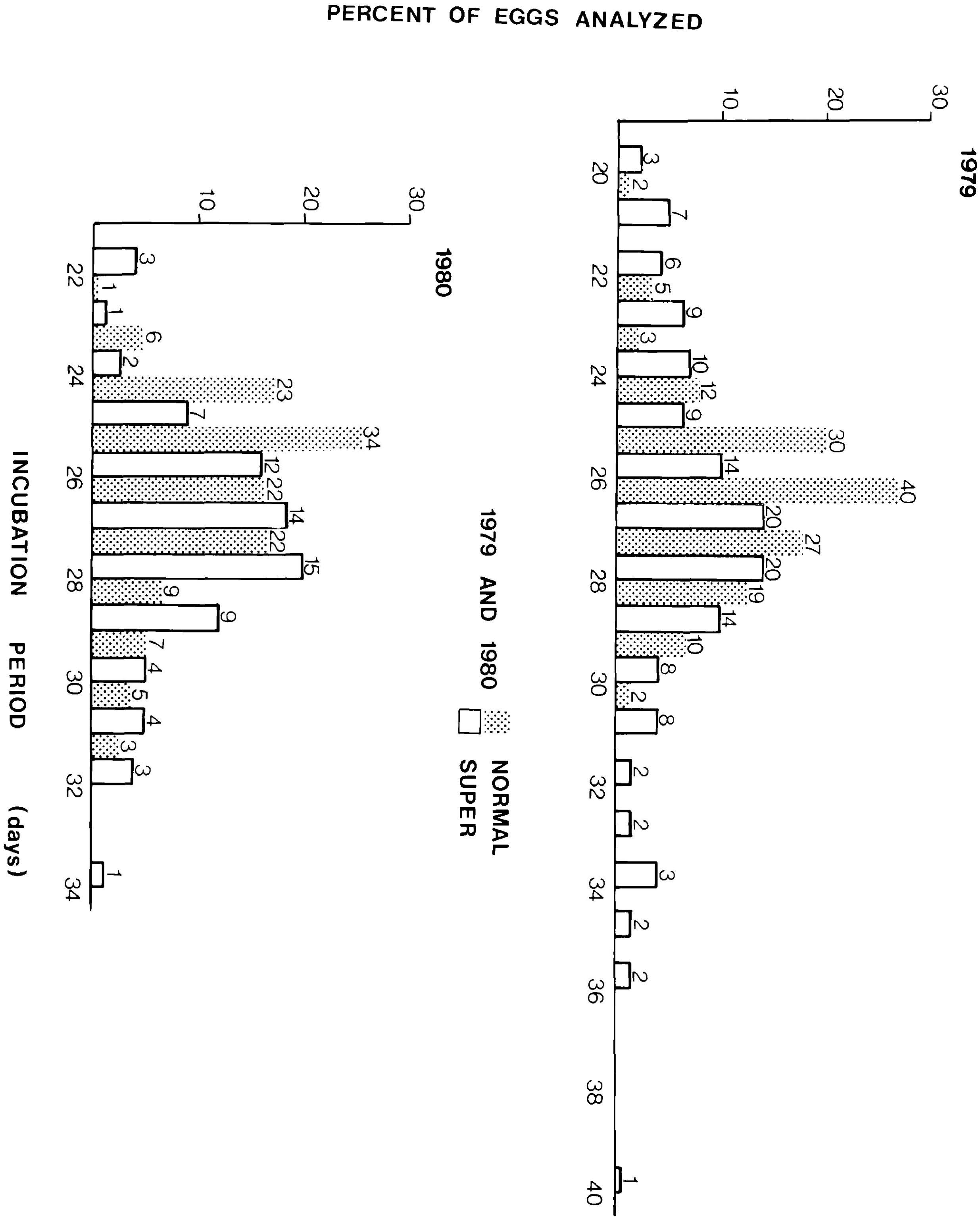
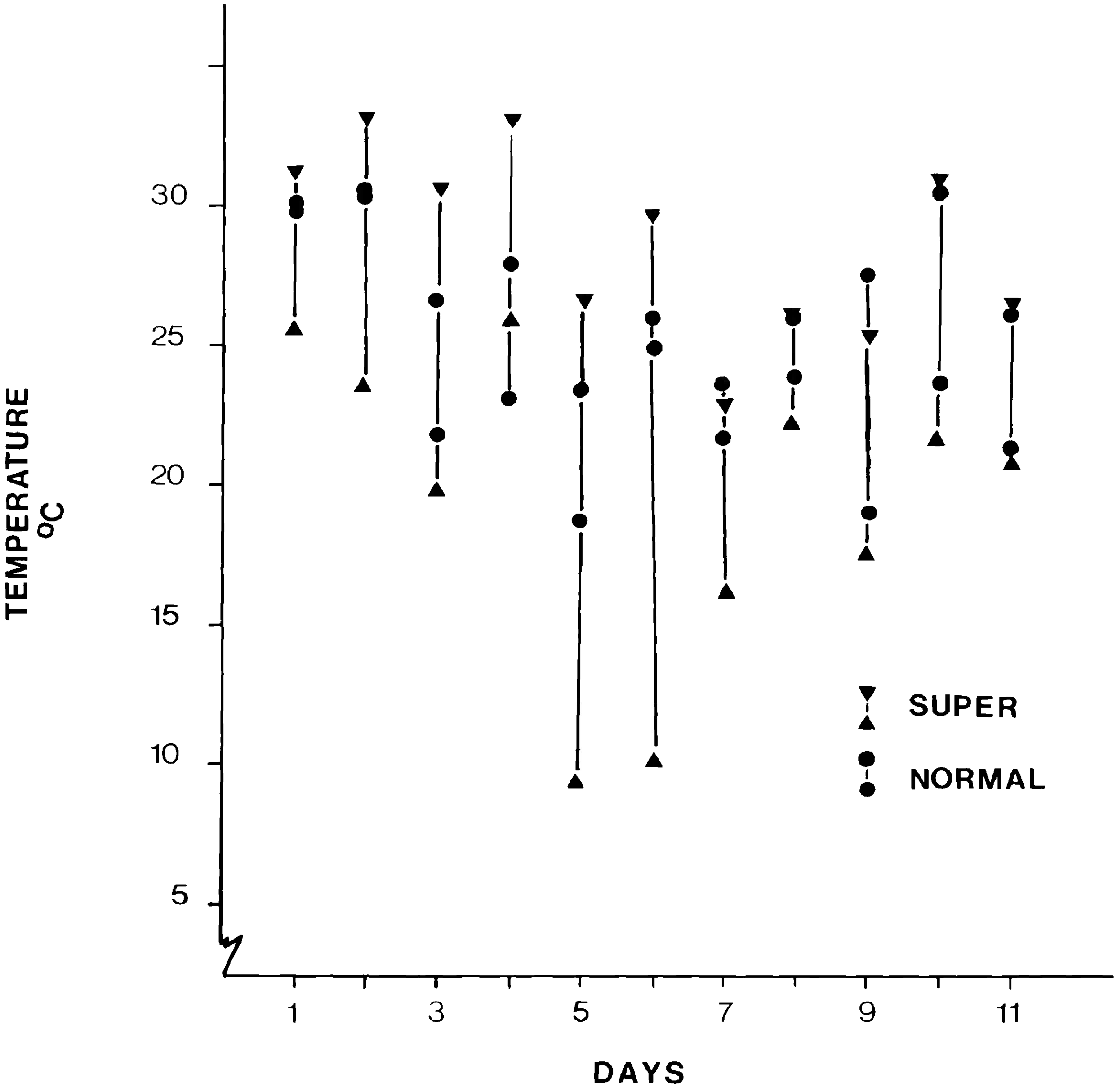

PERCENT OF EGGS ANALYZED
1979
30
20
10
3
2
7
6
5
9
3
10
12
9
30
14
40
20
27
20
19
14
10
8
2
8
2
2
3
2
2
1
20
22
24
26
28
30
32
34
36
38
40
1979 AND 1980
NORMAL
SUPER
1980
30
20
10
3
1
1
6
2
23
7
34
12
22
14
22
15
9
9
7
4
5
4
3
3
1
22
24
26
28
30
32
34
INCUBATION PERIOD (days)

Figure 10. Temperature readings (daily) during the last two weeks of incubation at the center and edge of a superclutch and a normal clutch of Ring-billed Gulls, Granite Island, 1980.


TEMPERATURE
oC
30
25
20
15
10
5
1
3
5
7
9
11
DAYS
SUPER
NORMAL

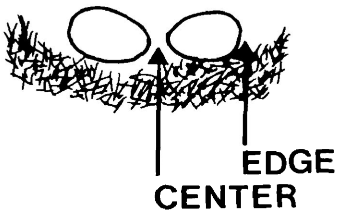

EDGE
CENTER

Table 4

Characteristics of nests containing superclutches and normal clutches of Ring-billed Gulls, Granite Island, 1980.

		Normal	Super
Length (cm)		28.3 ± 7.4 (99)[a]	31.3 ± 13.2 (56)
Width (cm)		25.5 ± 5.0 (99)	28.3 ± 5.0 (56)
Condition	Good	9 (9.6%)	16 (34.8%)
	Fair	77 (81.9%)	25 (54.3%)
	Poor	8 (8.5%)	5 (10.9%)
Substrate	Rock	24 (24.7%)	10 (21.3%)
	Dirt	73 (75.3%)	37 (78.7%)
Nest density per 2 m		4.4 ± 1.9 (98)	4.5 ± 2.5 (46)
Nearest neighbour distance (cm)		83.6 ± 31.8 (97)	79.8 ± 40.0 (46)

[a] Mean ± S.D. (Sample Size)

than were normal clutches with no significant difference in the number of poor nests ($X^2=0.20$, $p>.05$). There was no difference in location by substrate, as the proportion of superclutches and normal clutches on dirt versus rock was the same statistically ($X^2=0.19$, $p>.05$).

Nest density did not differ significantly between normal and superclutches ($t=0.50$, $df=71$, $p>.05$), nor did nearest neighbour distance ($t=0.56$, $df=141$, $p>.05$). Superclutches were distributed throughout the colony, with no apparent pattern of clumping with similar clutches.

3.4 REPRODUCTIVE SUCCESS

3.4.1 NEST SUCCESS

The number of successful nests did not differ between superclutches and normal clutches ((1979; $X^2=3.08$,$p>.05$)(1980; $X^2=0.01$, $p>.05$)). Nest success by clutch size is shown in Table 5.

3.4.2 HATCHING SUCCESS

Hatching success differed significantly between normal clutches and superclutches ((1979; $X^2=110.0$, $p<.05$)(1980; $X^2=69.8$, $p<.o5$)). Normal clutches had a consistantly higher average hatching success rate than superclutches (Figure 11). Superclutch success dropped with increasing clutch size.

In 1979 superclutches hatched an average of 1.8 ± 1.6 chicks per nest while normal clutches hatched an average of 2.2 ± 1.1 chicks per nest ($t=1.82$, $df=172$, $p<.05$). In 1980 superclutches hatched 1.6 ± 1.3 chicks per nest as opposed to 1.7 ± 1.3 in normal clutches ($t=0.04$, $df= 177$, $p>.05$).

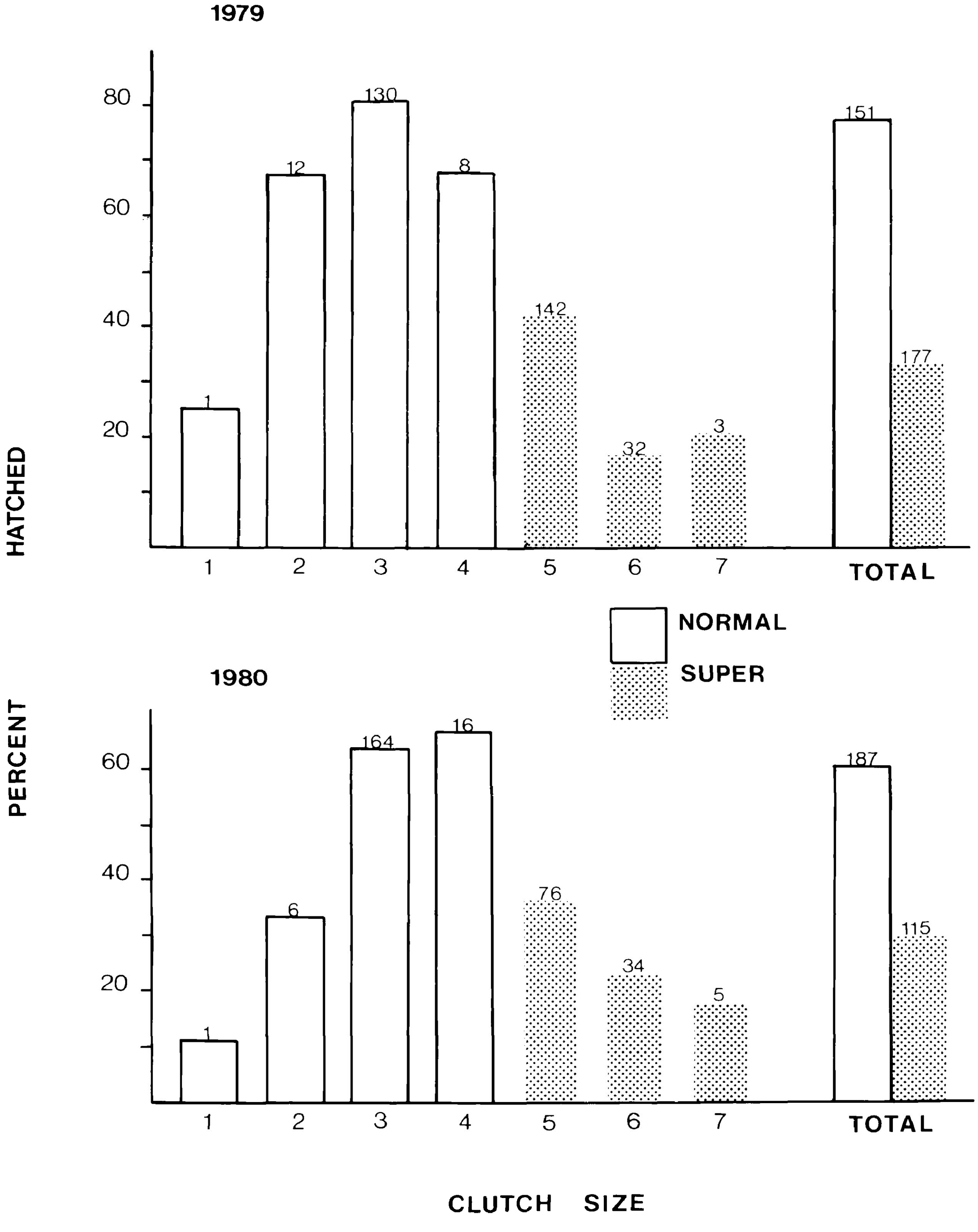
Table 5

Nest success by clutch size

for Ring-billed Gulls, Granite Island, 1979, 1980.

	Normal					Super			
Clutch size	1	2	3	4	Total	5	6	7	Total
No. successful nests 1979	$\frac{1}{4}$	$\frac{8}{9}$	$\frac{49}{54}$	$\frac{3}{3}$	$\frac{61}{70}$	$\frac{54}{65}$	$\frac{13}{32}$	$\frac{2}{2}$	$\frac{69}{99}$
Percent	25.0	88.9	90.7	100%	87.1	83.0	40.6	100	69.7
No. successful nests 1980	$\frac{1}{9}$	$\frac{3}{9}$	$\frac{65}{86}$	$\frac{5}{6}$	$\frac{74}{110}$	$\frac{31}{42}$	$\frac{16}{25}$	$\frac{3}{4}$	$\frac{50}{71}$
Percent	11.1	33.3	75.6	83.3	67.3	73.8	66.7	75	69.4

Figure 11. Hatching success by clutch size of Ring-billed Gulls, Granite Island, 1979, 1980.



1979
80
60
40
20
130
12
8
142
1
32
3
151
177
1
2
3
4
5
6
7
TOTAL
NORMAL
SUPER
1980
60
40
20
164
16
6
76
34
5
1
187
115
1
2
3
4
5
6
7
TOTAL
PERCENT HATCHED
CLUTCH SIZE

3.4.3 FATE OF EGGS

The fates of eggs are illustrated in Figure 12. There was a significant difference in the frequency of occurrence of fate categories between normal and superclutches ((1979; $X^2=48.2$, df=11, $p<.05$)(1980; $X^2=33.4$, df=11, $p<.05$)). The differences in the frequency of rolled, destroyed and abandoned account for most of the variation. In addition to higher frequencies of these shared causes of egg loss, superclutches suffered from eggs being buried in the nest cup and fracture pips (included in dead pip, Figure 12), which may be the result of pipping chicks drying out while attempting to hatch, or may be stress fractures from eggs bumping in the crowded nests (P.L. Ryder pers. comm.).

3.4.4 FERTILITY OF EGGS

Due to egg losses and the uncertainty involved in distinguishing infertile eggs from those in which the embryo died at a very young age there is a large undetermined fertility category (Table 6). Fertility rates of superclutches were significantly lower than those of normal clutches ($X^2=19.2$, $p<.05$).

3.4.5 FLEDGING SUCCESS

Because not all chicks were recaptured or found dead I calculated fledging success based on the proportions of chicks found dead before and after 10 days of age being extended to missing chicks following the method of Ryder and Carroll (1978). Separate estimates were made each year for each clutch type. The actual number of chicks known to have fledged as well as the calculated proportion are illustrated in Figure 13.

Chicks from normal clutches had a significantly higher fledging

Figure 12. Egg fates of eggs from normal clutches and superclutches of Ring-billed Gulls, Granite Island, 1979, 1980. Numbers to the right of histogram bars are the number of eggs per fate category.

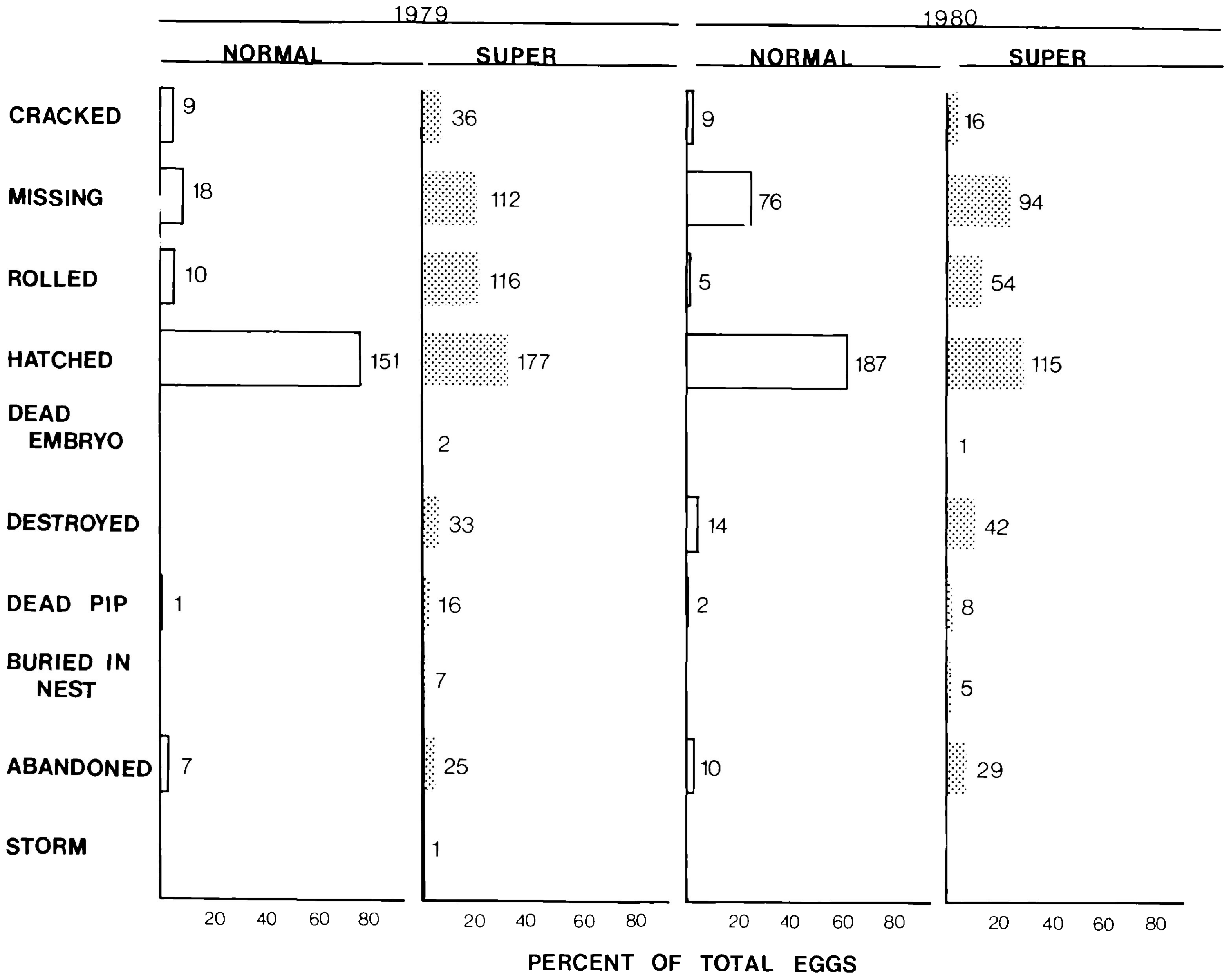

1979
1980
NORMAL
SUPER
NORMAL
SUPER
CRACKED
MISSING
ROLLED
HATCHED
DEAD EMBRYO
DESTROYED
DEAD PIP
BURIED IN NEST
ABANDONED
STORM
9
18
10
151
1
7
36
112
116
177
2
33
16
7
25
1
9
76
5
187
14
2
10
16
94
54
115
1
42
8
5
29
20
40
60
80
PERCENT OF TOTAL EGGS

Table 6

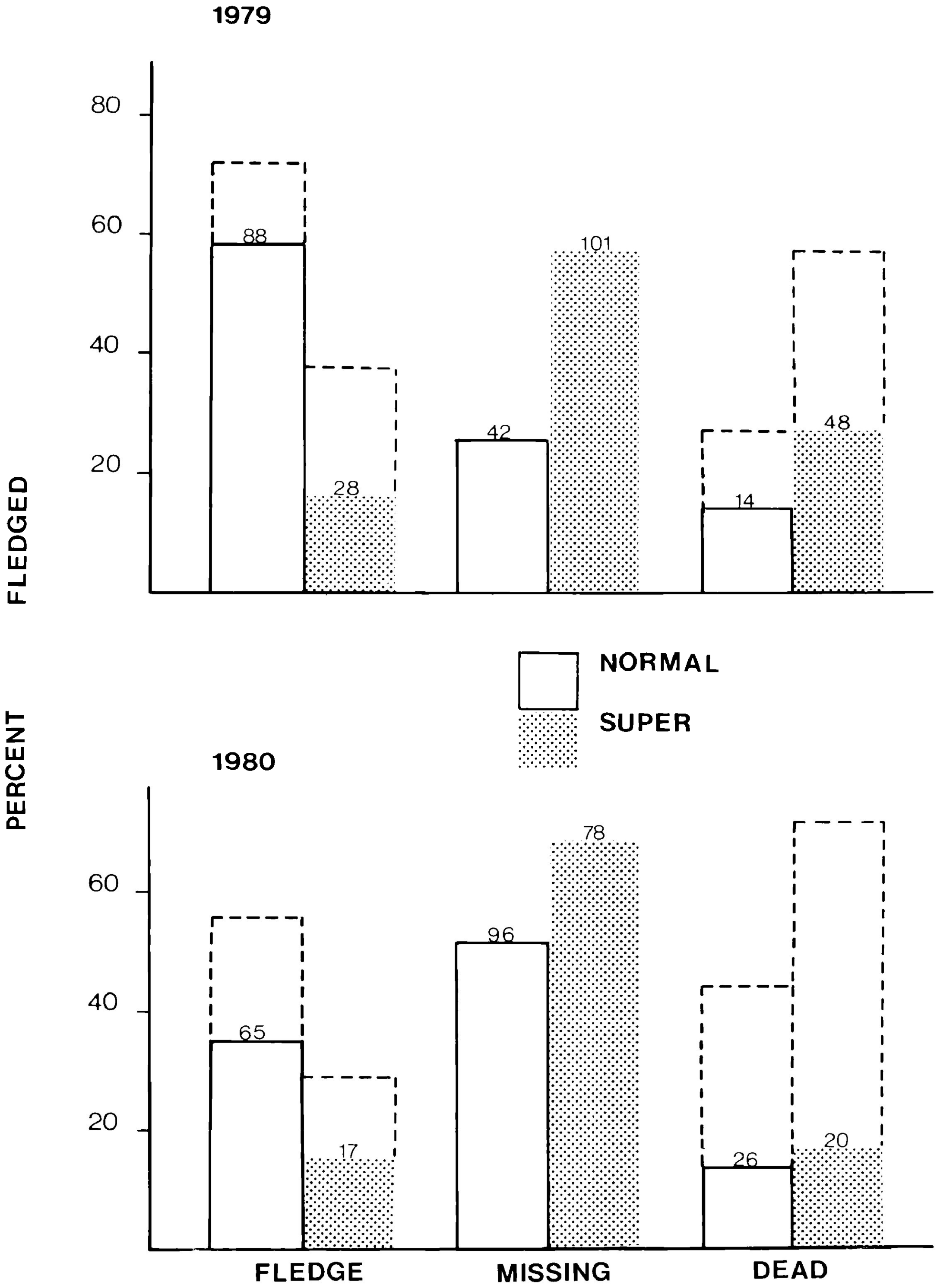
Fertility of eggs from normal clutches and superclutches of Ring-billed Gulls on Granite Island, 1979, 1980.

	1979		1980	
	Normal	Super	Normal	Super
Fertile	197 (99.5)	182 (86.7)	152 (99.3)	228 (94.2)
Infertile	1 (0.5)	28 (13.3)	1 (0.7)	14 (5.8)
Undetermined	111	185	43	289
Total number of eggs	309	395	196	531[a]

[a] Includes one 3-egg and one 4-egg clutch attended by female-female pairs

[b] Number in parenthesis is percent of total

Figure 13. Fledging success of chicks hatching from normal clutches and superclutches of Ring-billed Gulls on Granite Island, 1979, 1980. Dotted lines illustrate calculated estimates, according to the method of Ryder and Carroll (1978).


1979
80
60
40
20
88
28
42
101
14
48
NORMAL
SUPER
1980
60
40
20
65
17
96
78
26
20
FLEDGE
MISSING
DEAD
PERCENT FLEDGED

success ((1979; $X^2=37.0$, $p<.05$)(1980; $X^2=20.9$, $p<.05$)), than those from superclutches.

3.4.6 MORTALITY OF CHICKS

The majority of chick deaths occurred during the week following hatching. This trend was most pronounced for superclutches (Figure 14). The cause of death in most cases was pecking on the head by adult gulls (chicks from normal clutches 69%, superclutches 50%). Exposure and crushing in the nest were more prevalent in superclutches than in normal clutches (12% vs 35%). In 20% of normal clutch chick deaths and 15% of superclutch chick deaths the cause of death could not be determined.

3.4.7 CHICK GROWTH

During both years of my study chicks from superclutches hatched at significantly lighter weights than those from normal clutches (Figure 15 and 16)(see Appendix 2 and 3 for sample sizes and t or Z values comparing chicks from the two clutch types). In 1979 this dichotomy was not present for two day old chicks but was again seen for those three days old. During 1980 chicks from superclutches remained significantly lighter than chicks from normal clutches until four days of age. From this time on their weights did not differ significantly with any consistent pattern.

Regression lines of the $\log_e$ transformed weight data (Figure 15 and 16 inserts) illustrate the lower hatching weight (y-intercept) and faster growth rate (slope) of chicks from superclutches. This transformation produced linear relationships, as shown by the correlation between the transformed weight data and age which was .96 in all cases except the normal sample from 1979, when it was .95.

Figure 14. Age at death by weeks, from hatch until fledging for Ring-billed Gull chicks from normal clutches and superclutches, Granite Island, 1979, 1980.

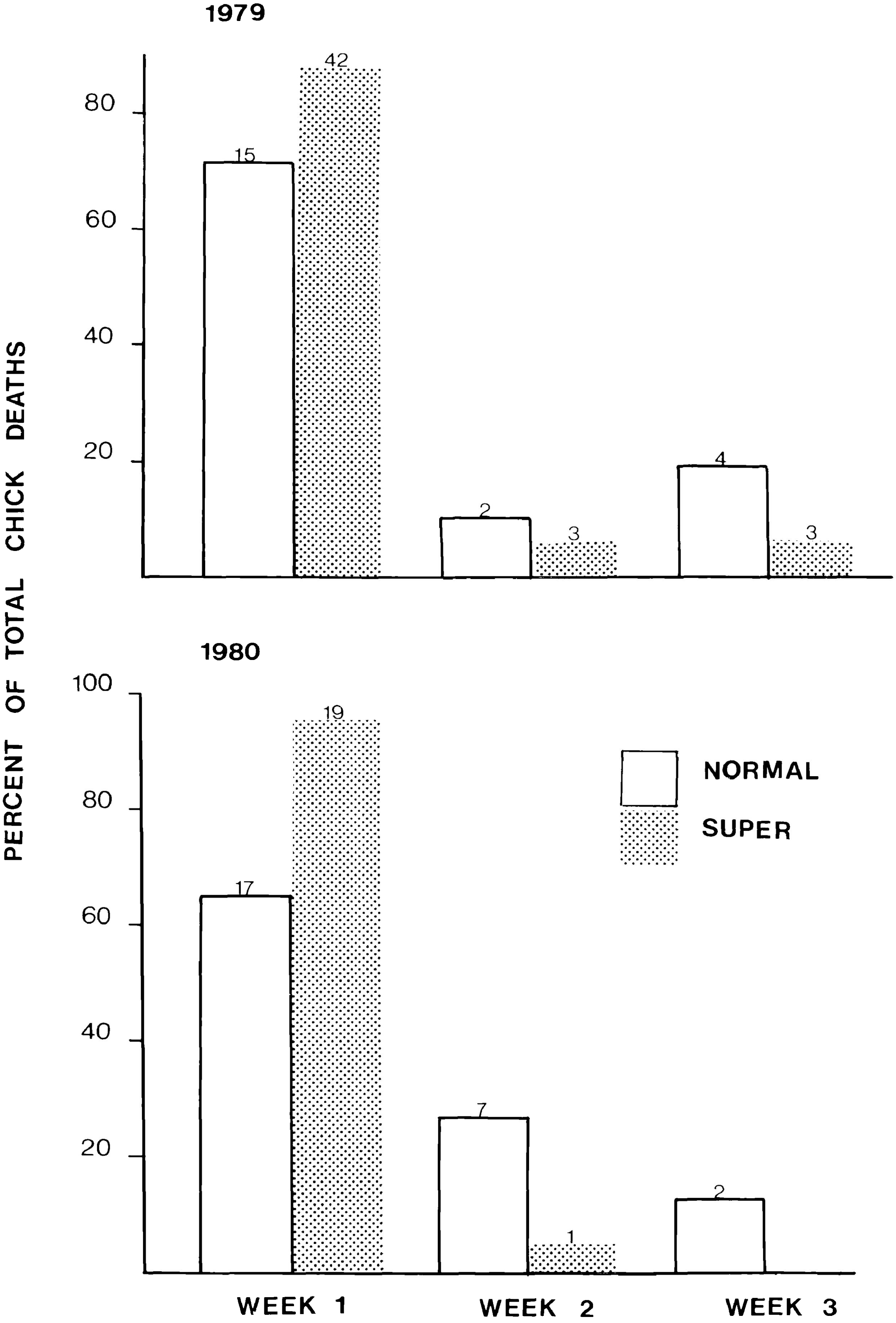

1979
PERCENT OF TOTAL CHICK DEATHS
80
60
40
20
15
42
2
3
4
3
1980
100
80
60
40
20
17
19
7
1
2
NORMAL
SUPER
WEEK 1
WEEK 2
WEEK 3

Figure 15. Mean weight (g) of chicks hatching from normal clutches and superclutches of Ring-billed Gulls from the day of hatch until 22 days of age, Granite Island, 1979. The inserted graph is the plot of the $\log_e$ transformed weight data against age. See Appendix 2 for sample sizes and t or Z values comparing chicks from the two clutch types.

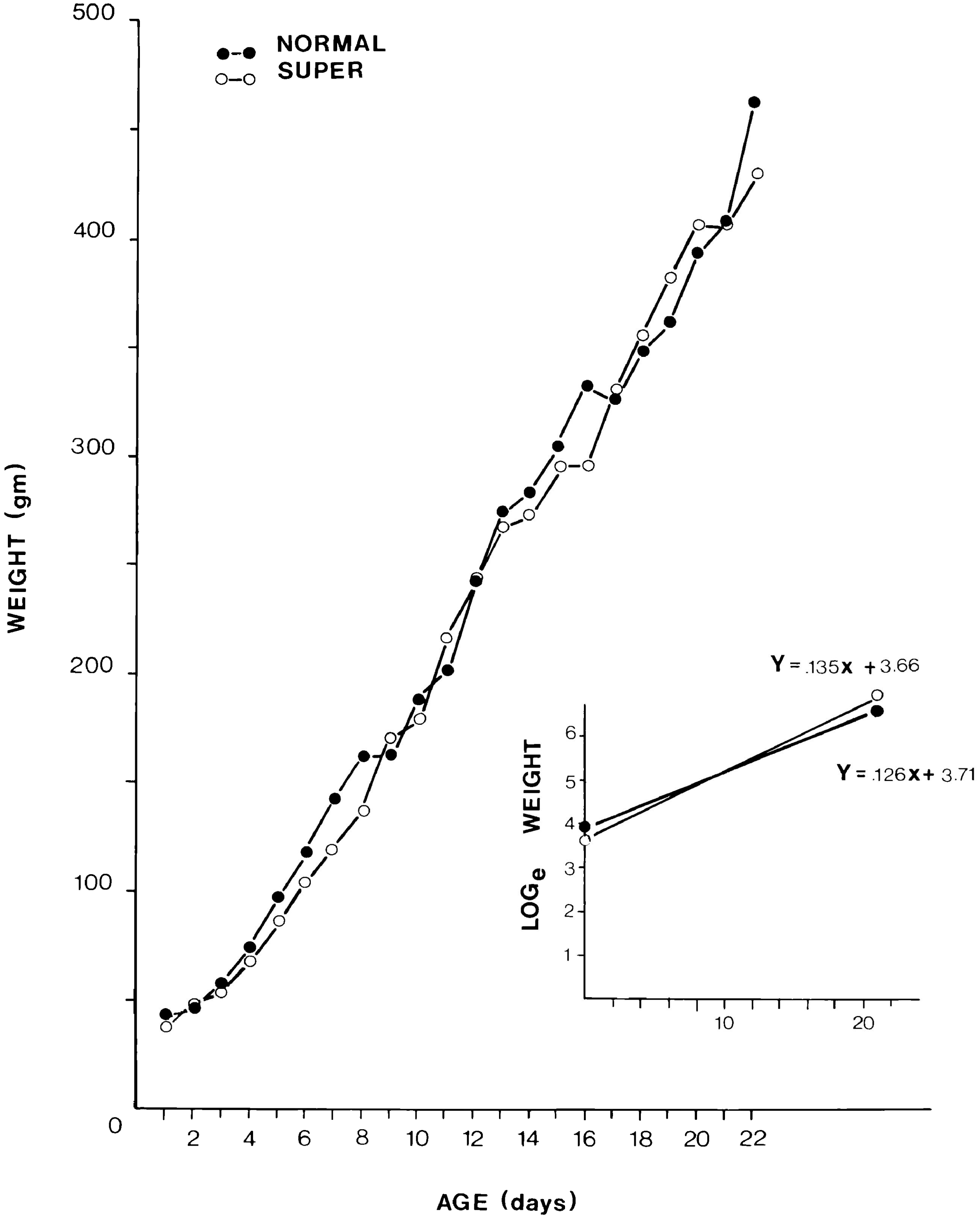
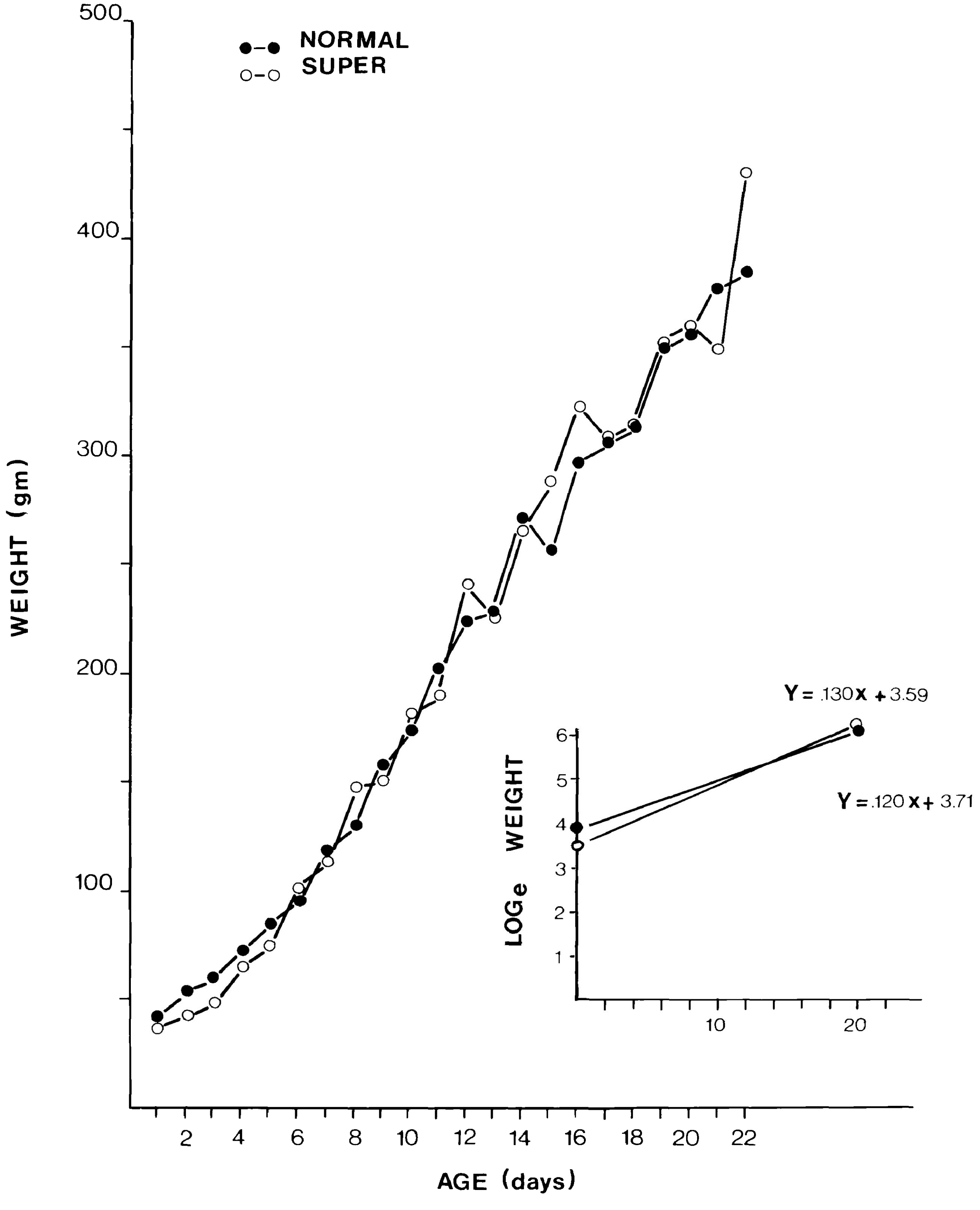

500
400
300
200
100
0
WEIGHT (gm)
●–● NORMAL
○–○ SUPER
2
4
6
8
10
12
14
16
18
20
22
AGE (days)
Y = .135X + 3.66
Y = .126X + 3.71
LOGe WEIGHT
6
5
4
3
2
1
10
20

Figure 16. Mean weight (g) of chicks hatching from normal clutches and superclutches of Ring-billed Gulls from the day of hatch until 22 days of age, Granite Island, 1980. The inserted graph is the plot of the $\log_e$ transformed weight data against age. See Appendix 3 for sample sizes and t or Z values comparing chicks from the two clutch types.



500
400
300
200
100
WEIGHT (gm)
●–● NORMAL
○–○ SUPER
2
4
6
8
10
12
14
16
18
20
22
AGE (days)
Y = .130X + 3.59
Y = .120X + 3.71
LOGe WEIGHT
6
5
4
3
2
1
10
20

Tarsal measurements followed the same pattern as did weight with normal chicks being larger until day 3 (see Appendix 4). Measurements of culmen did not differ significantly between chicks from the two clutch types even at the time of hatching. However, mean values were consistently smaller for chicks from superclutches during the first seven days following hatching (see Appendix 5).

3.5 REGURGITATION ANALYSES

Insects found in the regurgitation samples included members of 12 orders and more than 44 families. (see Appendix 6). The major orders (by total number of individuals/order, Appendix 6) were represented in samples from normal and superclutch chicks. Insects were found in 25 of 40 (63%) samples in the collection period (2 June - 2 July), with mayflies and lepidoptera larvae being quite abundant in some samples (see Appendix 7).

Fish comprised the bulk of food brought to chicks on Granite Island (see Appendix 7). Trout perch (*Percopsis omiscomaycus*) were the most common fish species and were found in samples throughout the sampling period. Smelt (*Osmerus mordax*) were also present throughout, but were most common in samples from early June. Stickleback (*Pungitius pungitius*) and Yellow Perch (*Perca flavescens*) were each found in only three samples. All 4 fish species were represented in both normal and superclutch samples.

In addition to fish and insects, a single Crayfish (*Orconectes virilis*) was found in a sample from a normal chick. A few small sticks, and some other vegetation were found, but they occurred infrequently and in small amounts (see Appendix 7).

3.6 MORPHOLOGY AND PHYSIOLOGY OF FEMALE-FEMALE PAIR MEMBERS

3.6.1 SIZE, WEIGHT, SEX AND CONDITION OF SUPERCLUTCH ATTENDANTS

Females trapped on normal clutches and superclutches during 1979 and 1980 did not differ significantly in any measure of size, weight or condition (using the Condition Index)(Table 7). The sex of birds trapped on superclutches and normal clutches is shown in Table 8. The birds collected were 3 males and 2 females, as their measurements had indicated.

3.6.2 APPEARANCE OF BROOD PATCHES

Females of heterosexual bonds and female-female pair members had similar brood patch development. During the latter part of the first week of incubation all females examined had defeathered, well-vascularized patches. During the latter part of the third week feather papillae appeared on the edges of the brood patches. I saw only extensive refeathering in birds that were feeding young.

3.6.3 AGE

The only bird trapped that possessed any sign of immature plumage was a male captured in 1979 on a superclutch. During the study, 14 previously banded females were trapped on superclutches. Five had been banded as chicks on Granite Island and hence were of known age. The average age of these females was 6.0 ± 1.9 years. The other nine previously banded birds trapped on superclutches had been banded as adults. They ranged in age from 4+ to 12+ (Appendix 8), assuming that they all developed mature plumage at three years of age.

Females of known age trapped on normal clutches averaged 6.0 ± 1.3 years of age while males averaged 3.8 ± 1.4 years (Appendix 9). All

Table 7

Size, weight and condition index of female Ring-billed Gulls attending superclutches and normal clutches, Granite Island, 1979, 1980.

		Normal	Super	T or Z value[a]
Weight (g)				
	1979	510.3 ± 32.9 (4)[b]	486.0 ± 28.0 (56)	1.66, p>.05
	1980	462.1 ± 29.6 (24)	458.4 ± 31.9 (57)	0.94, p>.05
Gonys (mm)				
	1979	12.3 ± 0.4 (4)	12.5 ± 0.5 (56)	1.79, p>.05
	1980	12.8 ± 0.5 (27)	12.6 ± 0.4 (58)	1.79, p>.05
Gape (mm)				
	1979	57.5 ± 3.6 (4)	57.9 ± 2.8 (56)	0.71, p>.05
	1980	57.7 ± 1.6 (27)	57.9 ± 2.0 (58)	0.65, p>.05
Tarsus (mm)				
	1979	—	62.1 ± 2.3 (56)	—
	1980	62.3 ± 1.7	62.6 ± 3.3 (57)	0.02 , p>.05
Size[c]	1979	15.6 ± 0.5 (4)	15.8 ± 0.5 (56)	0.81, p>.05
	1980	15.9 ± 0.4 (27)	15.8 ± 0.4 (58)	0.94, p>.05
Condition Index	1979	4.29 (3)	4.19 (10)	, p>.05

[a] Tests were done according to sample size (see Section 2.3)

[b] Mean ± S.D. (Sample size)

[c] Size calculated according to discriminant function in Ryder (1978).

Table 8

Sex of trapped birds incubating superclutches and normal clutches of Ring-billed Gulls, Granite Island, 1979, 1980.

		Normal	Super
1979	Males	7 (63.6)[c]	2[a] (3.6)
	Females	4 (36.4)	56 (96.4)
1980	Males	17 (38.6)	8 (11.8)
	Females	27[b] (61.4)	60[b] (88.2)

[a] One male was known to be a member of a polygynous group

[b] Four of these females were members of (2) female-female pairs. These birds are considered with superclutch attendants.

[c] The number in parenthesis is a percent of the total

Note: The number of recaptured females trapped while incubating superclutches is illustrated in Table 11.

birds had been banded on Granite Island by J.P. Ryder.

3.6.4 INTRAPAIR SIZE VARIATION

The average difference in size between members of individual female-female pairs was 0.384 ±0.302 (N=30). This was significantly smaller than the average difference of 0.609 ±0.404 (N=30) calculated for numerically randomly paired females ($t=2.44$, $df=58$, $p<.05$).

3.6.5 METABOLITE AND HORMONE LEVELS IN BLOOD PLASMA

Levels of blood chemistry parameters are illustrated in Tables 9 and 10. The only consistent differences were low cholesterol and elevated progesterone levels in female-female pair members, compared to females involved in heterosexual pairs.

3.7 NEST-SITE TENACITY AND MATE-FIDELITY IN FEMALE-FEMALE PAIRS

Table 11 presents the numbers of captured females attending superclutches, divided into captured pairs and nests at which only one member of the pair was trapped. Three birds (one single individual and one pair) captured in 1978 during the study of Ryder and Somppi (1979) were recaptured at the same sites in 1979. The recaptured pair was composed of the same marked individuals. Neither member of this pair was recaptured in 1980, but the individual bird that had been captured in 1978 and 1979 was trapped in 1980 as was its mate of that year.

In 1980, two pairs relocated at the same site they had used in 1979. Two additional pairs, although nesting with the same mates in 1980 as in 1979, moved to other areas of the colony in 1980.

Seventeen individuals of female-female pairs were recaptured in two

Table 9

Blood hormone levels in the plasma
of Ring-billed Gulls attending superclutches and normal clutches,
Granite Island, 1979, 1980.

	1979			1980		
	Normal	Super		Normal	Super	
Estrogen ng/ml	2.0 ± 0.4 (3)[a]	3.8 ± 2.5 (9)	S	1.0 ± 0.5 (4)	1.5 ± 0.9 (11)	NS
Androgens pg/ml	202.0 ± 144.4 (3)	453.8 ± 242.3 (10)	NS			
Progesterone ng/ml	1.7 ± 0.7 (3)	4.8 ± 1.5 (10)	S	1.6 ± 1.0 (9)	4.9 ± 1.4 (14)	S
Corticosterone ng/ml	18.9 ± 0.5 (3)	19.5 ± 3.2 (10)		23.3 ± 15.3 (9)	35.1 ± 11.0 (15)	NS

[a] Mean ± S.D. (Sample size)

[b] S ($p<.05$) or NS ($p>.05$) according to Mann-Whitney U Test

Table 10

Blood metabolite levels in the plasma

of Ring-billed Gulls attending superclutches and normal clutches,

Granite Island, 1979, 1980.

	1979			1980		
	Normal	Super		Normal	Super	
Amino Nitrogen mg/100 ml	7.1 ± 2.0 (3)^a	7.1 ± 1.8 (10)	NS^b	4.3 ± 1.2 (9)	3.8 ± 1.1 (17)	NS
Urea mg/100 ml	3.7 ± 0.9 (3)	3.4 ± 1.3 (10)	NS			
Uric acid mg/100 ml	12.6 ± 6.4 (3)	12.4 ± 4.6 (10)	NS			
Total protein g/100 ml	4.8 ± 0.9 (3)	4.3 ± 0.5 (10)	NS			
Glucose mg/100 ml	445.0 ± 18.0 (3)	408.0 ± 88.8 (10)	NS			
Calcium mg/100 ml	10.6 ± 0.6 (3)	9.8 ± 1.1 (10)	S	9.6 ± 0.9 (9)	9.8 ± 1.4 (14)	NS
Cholesterol mg/100 ml	444.3 ± 142.3 (3)	307.3 ± 43.1 (10)	S	327.8 ± 37.5 (9)	286.0 ± 18.5 (14)	S
Triglycerides mg/100 ml	165.7 ± 122.0 (3)	70.3 ± 19.0 (10)	NS			
Thyroxine ng/ml	19.0 ± 3.1 (3)	15.0 ± 2.2 (10)	S	23.3 ± 15.3 (9)	17.2 ± 6.0 (17)	NS

[a] Mean ± S.D. (Sample size)

[b] S ($p<.05$) or NS ($p>.05$) according to Mann-Whitney U Test

Table 11

Female Ring-billed Gulls captured and recaptured while incubating superclutches, Granite Island.

Females captured	1978	1979	1980
Pairs	6[a]	14	22[c]
Singles	9[a]	28	16
Pairs recaptured from previous year		1	4[b]
Singles recaptured from previous year		1	7

[a] Data from Ryder and Somppi (1979)

[b] One individual recaptured 1978, 1979, and 1980.

[c] Includes 2 pairs of females incubating normal sized clutches.

consecutive seasons (Table 11). Ten (59%) used the same site in consecutive nesting seasons, two (12%) remained within two meters of the colony site used previously, and five (29%) moved to other areas of the colony. Breeding success and nest-site tenacity were not directly related. Three female-female pairs that experienced total egg loss in 1979 used the same nest sites in 1980. Six of seven individuals that moved to other sites in 1980 had produced young in 1979.

3.8 BEHAVIOUR OF FEMALE-FEMALE PAIRS

3.8.1 BEHAVIOUR OF FEMALE-FEMALE PAIRS OVER THE BREEDING SEASON

Table 12 shows rates of occurrence of behaviour of the Attending Bird during the 1979 and 1980 breeding seasons. For most behaviour categories, the results are consistent for the two years. Several categories during 1979 were influenced strongly by the lack of success by three homosexual pairs and the ultimate desertion of their nests. For example, Absent is over-estimated for female-female pairs and Brooding is underestimated. They were able to skew the data because of the small number of homosexual pairs observed during 1979.

Table 13 illustrates the behaviour of the Partner over the two breeding seasons. The only consistently significant difference between pair types during the two years when the data for each year is considered a single sample occurs for Moving Threat. Heterosexual pairs used this behaviour more frequently than did homosexual pairs in defending their territories.

The difference in 1979 for the category Standing (Table 13) is somewhat spurious, resulting from the Partner of female-female pairs being

Table 12

Behaviour of the Attending Bird

during the breeding seasons of 1979 and 1980 for

female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	1979			1980		
Behaviour	Normal	Female-female	T-value	Normal	Female-female	T-value
Incubation	13.91 ± 12.10^{a}	18.10 ± 10.90	3.68, $p<.05$	13.76 ± 16.5	16.70 ± 11.80	2.76, $p<.05$
Preening	1.23 ± 1.89	.80 ± 2.26	2.07, $p<.05$	1.82 ± 2.74	1.27 ± 2.18	3.35, $p<.05$
Sleeping	2.85 ± 5.05	2.99 ± 5.37	0.26, $p>.05$	4.36 ± 5.96	2.73 ± 4.41	4.71, $p<.05$
Turning Eggs	0.72 ± 0.95	0.64 ± 0.85	0.92, $p>.05$	0.43 ± 0.77	0.61 ± 0.84	3.24, $p<.05$
Nest Building	0.53 ± 1.11	0.81 ± 1.43	2.15, $p<.05$	0.43 ± 1.04	0.73 ± 1.32	3.59, $p<.05$
Change-over	0.21 ± 0.37	0.16 ± 0.32	1.50, $p>.05$	0.19 ± 0.39	0.20 ± 0.40	0.55, $p>.05$
Choking	0.01 ± 0.09	0.00 ± 0.00	1.59, $p>.05$	0.03 ± 0.15	0.02 ± 0.12	1.09, $p>.05$
Head Tossing	0.25 ± 0.45	0.22 ± 0.50	0.76, $p>.05$	0.32 ± 2.27	0.26 ± 0.59	0.59, $p>.05$
Threat	0.36 ± 0.68	0.36 ± 0.74	0.00, $p>.05$	0.28 ± 0.67	0.23 ± 0.67	1.15, $p>.05$

cont. . .

Fighting	0.02 ± 0.11	0.00 ± 0.00	1.81, p>.05	0.03 ± 0.19	0.01 ± 0.13	1.45, p>.05
Brooding	1.74 ± 5.77	0.00 ± 0.04	5.62, p<.05	2.13 ± 6.55	2.10 ± 6.65	0.07, p>.05
Feeding	0.29 ± 0.78	0.03 ± 0.24	5.50, p<.05	0.40 ± 0.92	0.27 ± 0.86	2.13, p<.05
Standing	7.23 ± 10.60	2.79 ± 7.08	5.51, p<.05	6.41 ± 9.19	4.68 ± 8.91	2.81, p<.05
Absent	0.58 ± 2.60	3.41 ± 8.90	3.87, p<.05	1.47 ± 4.90	0.65 ± 2.99	3.14, p<.05

---

[a] Mean rate of occurrence per hour = S.D.

Table 13

Behaviour of the Partner

during the breeding seasons of 1979 and 1980 for

female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	1979			1980		
Behaviour	Normal	Female-female	T-value	Normal	Female-female	T-value
Preening	0.80 ± 2.16[a]	1.36 ± 3.56	1.79, p>.05	1.70 ± 3.79	1.69 ± 3.64	0.03, p>.05
Sleeping	0.11 ± 0.80	0.06 ± 0.35	0.96, p>.05	0.09 ± 0.73	0.05 ± 0.35	1.12, p>.05
Bringing Nest Material	0.02 ± 0.13	0.06 ± 0.30	1.70, p>.05	0.05 ± 0.26	0.07 ± 0.31	0.87, p>.05
Choking	0.04 ± 0.20	0.03 ± 0.13	1.19, p>.05	0.04 ± 0.20	0.02 ± 0.12	1.69, p>.05
Head Tossing	0.07 ± 0.47	0.05 ± 0.23	0.71, p>.05	0.05 ± 0.28	0.03 ± 0.18	0.82, p>.05
Threat	0.02 ± 0.12	0.02 ± 0.10	0.53, p>.05	0.15 ± 0.55	0.10 ± 0.36	1.85, p>.05
Moving Threat	0.34 ± 0.72	0.19 ± 0.51	2.65, p<.05	0.05 ± 0.31	0.01 ± 0.12	2.64, p<.05
Fighting	0.02 ± 0.12	0.01 ± 0.10	0.61, p>.05	0.02 ± 0.14	0.01 ± 0.07	1.52, p>.05
Feeding	0.01 ± 0.09	0.00 ± 0.00	1.57, p>.05	0.02 ± 0.21	0.01 ± 0.13	1.23, p>.05
Standing	9.57 ± 9.37	7.54 ± 8.97	2.26, p<.05	4.08 ± 6.55	4.17 ± 6.06	0.22, p>.05
Absent	18.20 ± 10.30	19.92 ± 10.70	1.70, p>.05	24.28 ± 12.00	23.93 ± 8.68	0.50, p>.05

[a] Mean rate of occurrence per hour ± S.D.

slightly more active Preening, and Bringing Nesting Material. Note that there is no significant difference between the two pair types in the amount of time spent on/off the territory by the Partner (see Table 13, Absent).

3.8.2 COURTSHIP AND EGG LAYING PERIOD

Six female-female pairs were observed from before they had initiated nest scrapes. Both members of each pair participated in Choking over the future nest site and Bringing Nesting Materials to the site. Female-female pairs participated in courtship activities, consisting of bouts during which both members Tipped while circling each other. Intra-pair Mountings were seen involving three female-female pairs. One pair was observed Mounting twice. The two females alternated their relative positions. In all observed cases the mock copulation attempts ended at this point. I did not observe females Tail-wagging or otherwise attempt to make cloacal contact. Courtship Feeding between members of any female-female pair was not observed.

I observed five double-banded females copulating with males of neighbouring territories. I saw three other copulations involving double-banded females and males but I was not able to identify the males in these cases. All of these copulations were actively solicited by the females, and did not take place on the females' territory. Early in the season pairs of females defended the area around their chosen nest-site against either sex. If challenged by males, however, they backed up and faced away.

Most males were very cooperative in mating extramaritally. A soliciting female was only driven away by a male if his mate got off the nest upon intruder's arrival or during the ensuing interactions. Forced copulation attempts (Figure 17) occurred commonly during the early egg laying period. Few were successful. I never observed a male attempt a forced copulation with a female-female pair member.

3.8.3 BEHAVIOUR OBSERVED DURING PERIOD 1 (12-16 MAY 1980)

Territories had been established by this time although later nesting birds did encroach into the observation areas later in the season. Egg laying was still occurring although some birds were incubating completed clutches.

The behaviour of homosexual and heterosexual pairs did not however differ significantly during this period (Table 14).

3.8.4 BEHAVIOUR OBSERVED DURING PERIOD 2 (17-21 MAY 1980)

Heterosexual pairs initiating clutches during this time period were predominantly those in which the male had subadult plumage; often possessing a full dark tail band. During this time period homosexual pair members incubating their clutches Slept less than did control birds, and their Partners performed fewer Threat postures (Table 15).

3.8.5 BEHAVIOUR OBSERVED DURING PERIOD 3 (22-27 MAY 1980)

Females attending superclutches spent more time Turning Eggs, Settling, and Nest-Building than normal pairs. They also differed from normal pairs in the rate of performance of Threat postures

Partners of female-female pairs brought nesting materials more often than normal pair members. This usually served as an inducement for the incubating bird to get off the nest. Changeovers did present difficulties for some female-female pairs. Occasionally mild pushing matches occurred over the nest between the members of a pair

Figure 17. Forced copulation attempt by a male Ring-billed Gull, Granite Island, 1980.

1

2

3

4

Table 14

Behaviour of the Attending Bird and Partner during Period 1 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	23.59 ± 6.93[a]	25.28 ± 4.95	0.88, p>.05			
Preening	0.25 ± 0.68	0.05 ± 0.21	1.78, p>.05	0.47 ± 1.03	0.73 ± 2.15	0.46, p>.05
Sleeping	3.66 ± 6.39	1.78 ± 3.80	1.42, p>.05	0.13 ± 0.83	0.20 ± 0.78	0.28, p>.05
Turning Eggs	0.65 ± 1.10	0.74 ± 1.01	0.32, p>.05			
Nest Building	0.74 ± 1.75	1.31 ± 2.00	1.08, p>.05			
Bringing Nest Material				0.13 ± 0.39	0.27 ± 0.80	0.65, p>.05
Changeover	0.22 ± 0.48	0.07 ± 0.26	1.60, p>.05			
Choking	0.06 ± 0.24	0.00 ± 0.00	0.94, p>.05	0.08 ± 0.43	0.07 ± 0.10	0.10, p>.05
Head Tossing	0.45 ± 1.19	0.33 ± 1.29	0.34, p>.05	0.11 ± 0.42	0.07 ± 0.26	0.53, p>.05
Threat	0.50 ± 1.00	0.77 ± 1.47	0.68, p>.05	0.32 ± 1.07	0.13 ± 0.52	0.94, p>.05

cont. ..

Moving Threat				0.15 ± 0.46	0.13 ± 0.52	0.13, p>.05
Fighting	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	0.04 ± 0.19	0.70 ± 0.26	0.48, p>.05
Standing	0.23 ± 0.92	0.05 ± 0.21	1.28, p>.05	7.22 ± 8.96	3.99 ± 7.70	1.27, p>.05
Absent	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	21.96 ± 10.57	24.45 ± 10.69	1.02, p>.05
Mounting	0.04 ± 0.19	0.00 ± 0.00	0.76, p>.05			
Tipping	0.13 ± 0.52	0.00 ± 0.00	0.99, p>.05	0.04 ± 0.19	0.00 ± 0.00	0.76, p>.05
Courtship Feeding	0.06 ± 0.24	0.00 ± 0.00	0.94, p>.05	0.06 ± 0.23	0.00 ± 0.00	0.93, p>.05
Begging	0.04 ± 0.28	0.00 ± 0.00	0.53, p>.05	0.02 ± 0.11	0.00 ± 0.00	0.53, p>.05
Time on eggs (minutes)	57.40 ± 5.34	58.73 ± 2.30	1.41, p>.05			

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[a] Mean rate of occurrence per hour ± S.D.

Table 15

Behaviour of the Attending Bird and Partner during Period 2 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	20.35 ± 7.40	23.25 ± 5.59	2.43, p<.05			
Preening	0.91 ± 1.30	0.71 ± 1.35	0.83, p>.05	2.65 ± 4.51	2.11 ± 4.02	0.69, p>.05
Sleeping	7.35 ± 7.45	4.07 ± 5.10	2.74, p<.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Turning Eggs	0.62 ± 0.60	0.80 ± 0.94	1.22, p>.05			
Nest Building	0.64 ± 1.08	1.09 ± 1.73	1.64, p>.05			
Bringing Nest Material				0.06 ± 0.21	0.05 ± 0.26	0.31, p>.05
Changeover	0.14 ± 0.30	0.14 ± 0.32	0.06, p>.05			
Choking	0.05 ± 0.20	0.00 ± 0.00	1.75, p>.05	0.06 ± 0.22	0.00 ± 0.00	1.99, p<.05
Head Tossing	0.05 ± 0.21	0.13 ± 0.31	1.48, p>.05	0.02 ± 0.12	0.00 ± 0.00	0.90, p>.05

cont. .

Threat	0.21 ± 0.46	0.20 ± 0.76	0.06, p>.05	0.21 ± 0.41	0.08 ± 0.29	2.06, p<.05
Moving Threat				0.01 ± 0.10	0.02 ± 0.14	0.30, p>.05
Fighting	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Standing	0.11 ± 0.75	0.19 ± 0.81	0.54, p>.05	5.14 ± 6.30	3.43 ± 4.60	1.70, p>.05
Absent	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	22.01 ± 9.29	24.61 ± 7.57	1.65, p>.05
Time on eggs (minutes)	58.28 ± 2.26	57.94 ± 2.72	0.62, p>.05			

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[a] Mean rate of occurrence per hour ± S.D.

with both females attempting to get over the eggs (Figure 18). Again Partners of homosexual pairs were less aggressive defending the territory than normal pairs' Partners (Table 16).

3.8.6 BEHAVIOUR OBSERVED DURING PERIOD 4 (28 MAY - 1 JUNE 1980)

A superclutch was initiated, completed and deserted during this interval. The two females were present only sporadically and both left the nest site the day after the sixth egg was laid. All the eggs were eaten by the next day. The Attending Birds of other superclutches continued to Turn Eggs more often than birds incubating normal clutches (Table 17).

3.8.7 BEHAVIOUR OBSERVED DURING PERIOD 5 (2-6 JUNE 1980)

Period 5 marked the start of the hatching period in the observation areas. Because of the prolonged incubation necessary for eggs in superclutches (see Section 3.1.3), female-female pairs had hatched relatively fewer young than normal pairs by the end of this period. Hence, significant differences occurred in the rate of occurrence of Incubation, Brooding, Feeding ,Standing and Time on eggs (Table 18). Birds attending normal clutches performed significantly more Comfort Movements over their eggs or young than did superclutch attendants (included in Turning Eggs, Table 18).

3.8.8 BEHAVIOUR OBSERVED DURING PERIOD 6 (7-12 JUNE 1980)

The Attending Bird on superclutches Headtossed significantly more than did the Attending Bird of normal clutches. This was in response to intrusions by aggressive parents and young chicks from neighbouring heterosexual pairs' territories (Table 19).

Figure 18. Pushing match over the nest by members of a female-female pair of Ring-billed Gulls, with both birds attempting to get over the eggs, Granite Island, 1979.

Table 16

Behaviour of the Attending Bird and Partner during Period 3 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

Behaviour	Attending Bird			Partner		
	Normal	Super	T-value	Normal	Super	T-value
Incubation	22.35 ± 6.59	22.94 ± 5.13	0.61, p>.05			
Preening	0.79 ± 1.28	0.96 ± 1.80	0.67, p>.05	4.48 ± 5.91	4.34 ± 5.17	0.15, p>.05
Sleeping	4.77 ± 6.09	3.20 ± 4.45	1.78, p>.05	0.06 ± 0.37	0.07 ± 0.42	0.15, p>.05
Turning Eggs	0.56 ± 0.56	0.79 ± 0.78	2.05, p<.05			
Nest Building	0.87 ± 1.35	1.47 ± 1.70	2.27, p<.05			
Bringing Nest Material				0.07 ± 0.27	0.21 ± 0.41	2.36, p<.05
Changeover	0.22 ± 0.35	0.25 ± 0.40	0.42, p>.05			
Choking	0.02 ± 0.10	0.05 ± 0.15	1.24, p>.05	0.05 ± 0.19	0.06 ± 0.19	0.46, p>.05
Head Tossing	0.07 ± 0.24	0.06 ± 0.21	0.29, p>.05	0.04 ± 0.18	0.01 ± 0.06	1.46, p>.05

cont. . .

Threat	0.42 ± 0.87	0.18 ± 0.39	2.12, $p<.05$	0.26 ± 0.51	0.29 ± 0.60	0.31, $p>.05$
Moving Threat				0.06 ± 0.18	0.01 ± 0.06	2.20, $p<.05$
Fighting	0.00 ± 0.00	0.00 ± 0.00	0.00, $p>.05$	0.02 ± 0.10	0.01 ± 0.06	0.90, $p>.05$
Standing	0.01 ± 0.06	0.05 ± 0.23	1.58, $p>.05$	6.71 ± 6.73	7.34 ± 6.08	0.58, $p>.05$
Absent	0.39 ± 1.25	0.59 ± 1.62	0.82, $p>.05$	18.17 ± 12.22	17.63 ± 9.89	0.29, $p>.05$
Time on eggs (minutes)	57.87 ± 2.77	57.11 ± 2.73	1.65, $p>.05$			

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[a] Mean rate of occurrence per hour ± S.D.

Table 17

Behaviour of the Attending Bird and Partner
during Period 4 of the 1980 breeding season for female-female pairs
and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	21.88 ± 6.73	23.78 ± 5.30	1.35, $p>.05$			
Preening	0.45 ± 0.85	0.53 ± 1.03	0.35, $p>.05$	3.26 ± 5.15	3.25 ± 5.54	0.01, $p>.05$
Sleeping	5.64 ± 5.60	3.94 ± 5.53	1.34, $p>.05$	0.17 ± 1.02	0.23 ± 0.76	0.29, $p>.05$
Turning Eggs	0.48 ± 0.63	0.98 ± 0.80	3.19, $p<.05$			
Nest Building	0.95 ± 1.26	1.09 ± 1.13	0.50, $p>.05$			
Bringing Nest Material				0.11 ± 0.44	0.06 ± 0.25	0.62, $p>.05$
Changeover	0.37 ± 0.60	0.23 ± 0.51	1.08, $p>.05$			
Choking	0.02 ± 0.14	0.00 ± 0.00	0.81, $p>.05$	0.02 ± 0.14	0.00 ± 0.00	0.81, $p>.05$
Head Tossing	0.11 ± 0.43	0.05 ± 0.20	0.95, $p>.05$	0.00 ± 0.00	0.02 ± 0.11	1.23, $p>.05$

CONT. . .

Threat	0.05 ± 0.22	0.02 ± 0.11	0.86, p>.05	0.28 ± 0.84	0.11 ± 0.40	1.24, p>.05
Moving Threat				0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Fighting	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	0.08 ± 0.35	0.00 ± 0.00	1.35, p>.05
Standing	0.00 ± 0.00	0.07 ± 0.26	1.76, p>.05	5.59 ± 7.16	5.05 ± 5.98	0.42, p>.05
Absent	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05	24.13 ± 26.98	21.74 ± 10.4	0.56, p>.05
Time on eggs (minutes)	58.65 ± 1.60	57.06 ± 4.59	1.88, p>.05			

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[a] Mean rate of occurrence per hour ± S.D.

Table 18

Behaviour of the Attending Bird and Partner
during Period 5 of the 1980 breeding season for female-female pairs
and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	11.70 ± 12.27[a]	23.10 ± 7.76	6.20, $p<.05$			
Preening	0.55 ± 1.04	0.99 ± 2.17	1.36, $p>.05$	1.76 ± 3.22	1.01 ± 2.30	1.41, $p>.05$
Sleeping	5.63 ± 7.55	3.18 ± 4.38	2.22, $p<.05$	0.09 ± 0.50	0.04 ± 0.16	0.75, $p>.05$
Turning Eggs	1.10 ± 1.27	0.60 ± 0.85	2.58, $p<.05$			
Nest Building	0.37 ± 7.30	0.58 ± 1.05	1.21, $p>.05$			
Bringing Nest Material				0.07 ± 0.32	0.05 ± 0.38	0.25, $p>.05$
Changeover	0.29 ± 0.50	0.25 ± 0.56	0.49, $p>.05$			
Choking	0.06 ± 0.21	0.01 ± 0.09	1.54, $p>.05$	0.03 ± 0.14	0.01 ± 0.10	0.75, $p>.05$
Head Tossing	0.14 ± 0.39	0.19 ± 0.66	0.55, $p>.05$	0.05 ± 0.27	0.01 ± 0.10	0.84, $p>.05$

cont. .

Threat	0.23 ± 0.79	0.13 ± 0.40	0.89, $p>.05$	0.17 ± 0.57	0.00 ± 0.00	2.13, $p<.05$
Moving Threat				0.13 ± 0.74	0.00 ± 0.00	1.29, $p>.05$
Fighting	0.02 ± 0.12	0.00 ± 0.00	0.91, $p>.05$	0.00 ± 0.00	0.00 ± 0.00	0.00, $p>.05$
Standing	1.03 ± 3.40	0.00 ± 0.00	2.22, $p<.05$	3.48 ± 5.39	5.42 ± 7.87	1.49, $p>.05$
Brooding	8.54 ± 11.09	1.20 ± 5.17	4.79, $p<.05$			
Feeding	0.40 ± 0.71	0.02 ± 0.18	3.83, $p<.05$	0.15 ± 0.59	0.00 ± 0.00	1.82, $p>.05$
Absent	0.00 ± 0.00	0.00 ± 0.00	0.00, $p>.05$	23.94 ± 8.80	23.45 ± 9.16	0.29, $p>.05$
Time on eggs (minutes)	35.54 ± 28.69	56.33 ± 11.59	4.84, $p<.05$			

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[a] Mean rate of occurrence per hour ± S.D.

Table 19

Behaviour of the Attending Bird and Partner during Period 6 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	1.87 ± 6.95	13.53 ± 14.06	3.82, p<.05			
Preening	1.30 ± 1.80	0.70 ± 1.48	1.53, p>.05	0.47 ± 1.86	0.71 ± 1.92	0.51, p>.05
Sleeping	1.98 ± 3.66	0.58 ± 1.75	1.82, p>.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Turning Eggs	0.15 ± 0.33	1.05 ± 0.95	4.65, p<.05			
Nest Building	0.14 ± 0.63	0.12 ± 0.33	0.20, p>.05			
Bringing Nest Material				0.03 ± 0.17	0.02 ± 0.13	0.12, p>.05
Changeover	0.28 ± 0.38	0.22 ± 0.38	0.54, p>.05			
Choking	0.00 ± 0.00	0.03 ± 0.14	1.04, p>.05	0.03 ± 0.17	0.02 ± 0.13	0.12, p>.05
Head Tossing	0.15 ± 0.33	0.52 ± 0.71	2.44, p<.05	0.16 ± 0.69	0.00 ± 0.00	1.26, p>.05

cont. .

Threat	0.15 ± 0.33	0.23 ± 0.57	0.69, p>.05	0.03 ± 0.17	0.13 ± 0.43	1.26, p>.05
Moving Threat				0.03 ± 0.17	0.00 ± 0.00	0.91, p>.05
Fighting	0.06 ± 0.23	0.00 ± 0.00	1.37, p>.05	0.03 ± 0.17	0.00 ± 0.00	0.91, p>.05
Standing	12.90 ± 10.70	3.73 ± 8.30	3.49, p<.05	2.15 ± 4.50	3.19 ± 5.78	0.82, p>.05
Brooding	10.28 ± 12.04	9.15 ± 12.03	0.34, p>.05			
Feeding	1.16 ± 1.30	0.98 ± 1.65	0.44, p>.05	0.02 ± 0.12	0.00 ± 0.00	0.91, p>.05
Absent	0.15 ± 0.65	0.00 ± 0.00	1.21, p>.05	27.06 ± 5.93	26.26 ± 6.46	0.53, p>.05
Time on eggs (minutes)	10.94 ± 22.65	30.53 ± 29.19	3.07, p<.05			

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[a] Mean rate of occurrence per hour ± S.D.

3.8.9 BEHAVIOUR OBSERVED DURING PERIODS 7-10 (13 JUNE- 3 JULY 1980)

Female-female pairs were slightly out of phase with heterosexual pairs. Because of the slightly later hatching time homosexual pairs were caring for younger chicks during each of the remaining time periods. Their behaviour reflects this asynchrony (Tables 20-23).

Young once present were cared for in a normal manner by homosexual pairs, compared to heterosexual pairs (see Standing, Brooding, Feeding, and Absent in Tables 20-23).

During Periods 8 and 9 the rate of occurrence of Feeding is lower for homosexual pairs because fewer of them had chicks at these times than did normal pairs due to a higher mortality rate (see Section 3.4.6).

3.8.10 TERRITORY SIZE OF FEMALE-FEMALE PAIRS

Territory maps of areas occupied during 1979 in my two observation areas are illustrated in Figures 19 and 20. Territories held by female-female pairs were much smaller than those held by heterosexual pairs.

3.9 BEHAVIOUR (AND SUCCESS) OF POLYGYNOUS GROUPS

The small sample sizes for nests that were known to be attended by trios does not allow for statistical analyses. Four polygynous groups were monitored in the observation areas during 1979 and 1980. Two had figure 8 nest arrangements. The other two used single nest cups. The relationships in all cases proved to be unstable compared to heterosexual or female-female pairs. Females in trios did not cooperate well (Figure 21). One group dispersed shortly after the clutch had been completed. The eggs were eaten, presumably by neighbouring adults. The other three clutches hatched one, three and three chicks respec-

Table 20

Behaviour of the Attending Bird and Partner
during Period 7 of the 1980 breeding season for female-female pairs
and normal pairs of Ring-billed Gulls, Granite Island.

Behaviour	Attending Bird			Partner		
	Normal	Super	T-value	Normal	Super	T-value
Incubation	2.28 ± 7.90[a]	7.35 ± 12.31	1.76, p>.05			
Preening	2.43 ± 2.67	1.00 ± 2.30	2.06, p<.05	0.27 ± 1.09	0.09 ± 0.27	0.80, p>.05
Sleeping	0.99 ± 1.95	0.26 ± 0.86	1.71, p>.05	0.05 ± 0.26	0.00 ± 0.00	1.02, p>.05
Turning Eggs	0.04 ± 0.20	0.53 ± 0.88	2.74, p<.05			
Nest Building	0.08 ± 0.31	0.25 ± 0.67	1.20, p>.05			
Bringing Nest Material				0.03 ± 0.14	0.00 ± 0.00	1.02, p>.05
Changeover	0.10 ± 0.23	0.16 ± 0.28	0.92, p>.05			
Choking	0.00 ± 0.00	0.04 ± 0.20	0.98, p>.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Head Tossing	0.14 ± 0.27	0.29 ± 0.54	1.21, p>.05	0.00 ± 0.00	0.03 ± 0.14	0.98, p>.05

cont. . .

Threat	0.12 ± 0.44	0.14 ± 0.60	0.13, p>.05	0.02 ± 0.10	0.03 ± 0.14	0.21, p>.05
Moving Threat				0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Fighting	0.06 ± 0.22	0.00 ± 0.00	1.39, p>.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Standing	16.78 ± 9.40	7.97 ± 9.96	3.24, p<.05	1.51 ± 3.38	1.57 ± 3.10	0.06, p>.05
Brooding	3.86 ± 6.88	11.38 ± 11.80	2.80, p<.05			
Feeding	0.44 ± 0.71	0.53 ± 0.92	0.41, p>.05	0.02 ± 0.10	0.10 ± 0.41	1.01, p>.05
Absent	3.31 ± 6.25	0.67 ± 2.47	1.97, p>.05	28.14 ± 4.47	28.15 ± 3.56	0.01, p>.05
Time on eggs (minutes)	4.68 ± 16.20	13.50 ± 25.15	1.49, p>.05			

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[a] Mean rate of occurrence per hour ± S.D.

Table 21

Behaviour of the Attending Bird and Partner during Period 8 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	1.44 ± 5.47[a]	5.70 ± 10.73	2.11, p<.05			
Preening	2.49 ± 2.39	1.83 ± 2.23	1.24, p>.05	0.07 ± 0.45	0.15 ± 0.70	0.57, p>.05
Sleeping	2.98 ± 4.45	2.11 ± 3.67	0.93, p>.05	0.02 ± 0.15	0.00 ± 0.00	0.88, p>.05
Turning Eggs	0.03 ± 0.13	0.14 ± 0.32	1.83, p>.05			
Nest Building	0.05 ± 0.18	0.39 ± 0.78	2.48, p<.05			
Bringing Nest Material				0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Changeover	0.07 ± 0.32	0.20 ± 0.36	1.69, p>.05			
Choking	0.01 ± 0.08	0.00 ± 0.00	0.88, p>.05	0.02 ± 0.15	0.00 ± 0.00	0.88, p>.05
Head Tossing	1.36 ± 7.59	0.39 ± 0.10	0.85, p>.05	0.05 ± 0.30	0.00 ± 0.00	0.88, p>.05

cont. .

Threat	0.20 ± 0.31	0.26 ± 0.93	0.40, p>.05	0.01 ± 0.08	0.00 ± 0.00	0.88, p>.05
Moving Threat				0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Fighting	0.15 ± 0.52	0.10 ± 0.39	0.42, p>.05	0.01 ± 0.08	0.00 ± 0.00	0.88, p>.05
Standing	11.81 ± 8.33	12.48 ± 11.56	0.28, p>.05	0.38 ± 1.22	0.34 ± 0.94	0.15, p>.05
Brooding	0.06 ± 0.21	4.61 ± 9.32	2.82, p<.05			
Feeding	1.38 ± 1.95	1.21 ± 1.77	0.39, p>.05	0.02 ± 0.15	0.00 ± 0.00	0.88, p>.05
Absent	9.68 ± 10.90	1.09 ± 3.68	4.89, p<.05	30.00 ± 4.67	29.60 ± 1.07	1.23, p>.05
Time on eggs (minutes)	2.68 ± 12.43	10.53 ± 23.03	1.79, p>.05			

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[a] Mean rate of occurrence per hour ± S.D.

Table 22

Behaviour of the Attending Bird and Partner during Period 9 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	1.13 ± 5.15	5.96 ± 10.46	2.66, $p<.05$			
Preening	4.20 ± 3.36	2.56 ± 2.58	2.59, $p<.05$	0.32 ± 0.89	0.25 ± 0.51	0.51, $p>.05$
Sleeping	2.94 ± 4.02	2.89 ± 5.32	0.05, $p>.05$	0.30 ± 1.51	0.04 ± 0.26	1.39, $p>.05$
Turning Eggs	0.03 ± 0.18	0.09 ± 0.33	0.95, $p>.05$			
Nest Building	0.01 ± 0.09	0.11 ± 0.41	1.42, $p>.05$			
Bringing Nest Material				0.00 ± 0.00	0.00 ± 0.00	0.00, $p>.05$
Changeover	0.08 ± 0.21	0.30 ± 0.38	3.36, $p<.05$			
Choking	0.03 ± 0.14	0.04 ± 0.18	0.31, $p>.05$	0.03 ± 0.13	0.02 ± 0.08	0.98, $p>.05$
Head Tossing	0.42 ± 0.63	0.53 ± 0.64	0.82, $p>.05$	0.02 ± 0.10	0.06 ± 0.22	1.17, $p>.05$

cont. .

Threat	0.38 ± 0.62	0.36 ± 0.72	0.14, p>.05	0.06 ± 0.26	0.03 ± 0.12	0.95, p>.05
Moving Threat				0.01 ± 0.08	0.00 ± 0.00	0.77, p>.05
Fighting	0.03 ± 0.16	0.00 ± 0.00	1.35, p>.05	0.00 ± 0.00	0.00 ± 0.00	0.00, p>.05
Standing	16.73 ± 7.30	15.67 ± 10.68	0.54, p>.05	1.81 ± 3.78	3.07 ± 5.05	1.40, p>.05
Brooding	0.70 ± 3.76	0.83 ± 3.38	0.17, p>.05			
Feeding	0.84 ± 0.91	0.46 ± 0.65	2.45, p<.05	0.00 ± 0.00	0.03 ± 0.20	1.30, p>.05
Absent	2.44 ± 5.34	0.70 ± 2.50	2.22, p<.05	27.49 ± 5.54	26.33 ± 5.37	1.09, p>.05
Time on eggs (minutes)	2.47 ± 11.89	16.55 ± 26.49	3.87, p<.05			

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[a] Mean rate of occurrence per hour ± S.D.

Table 23

Behaviour of the Attending Bird and Partner during Period 10 of the 1980 breeding season for female-female pairs and normal pairs of Ring-billed Gulls, Granite Island.

	Attending Bird			Partner		
Behaviour	Normal	Super	T-value	Normal	Super	T-value
Incubation	0.00 ± 0.00[a]	4.63 ± 9.39	3.64, $p<.05$			
Preening	5.33 ± 3.96	3.33 ± 3.29	2.47, $p<.05$	0.88 ± 2.28	1.19 ± 2.17	0.55, $p>.05$
Sleeping	3.74 ± 4.54	2.24 ± 3.67	1.55, $p>.05$	0.03 ± 0.18	0.06 ± 0.22	0.71, $p>.05$
Turning Eggs	0.08 ± 0.34	0.26 ± 0.82	1.12, $p>.05$			
Nest Building	0.02 ± 0.10	0.19 ± 0.70	1.37, $p>.05$			
Bringing Nest Material				0.02 ± 0.15	0.04 ± 0.19	0.38, $p>.05$
Changeover	0.15 ± 0.29	0.13 ± 0.30	0.35, $p>.05$			
Choking	0.02 ± 0.11	0.03 ± 0.15	0.21, $p>.05$	0.04 ± 0.16	0.03 ± 0.15	0.30, $p>.05$
Head Tossing	0.47 ± 0.64	0.49 ± 0.68	0.16, $p>.05$	0.07 ± 0.25	0.26 ± 0.47	1.96, $p>.05$

cont. .

Threat	0.36 ± 0.72	0.42 ± 0.76	0.38, $p>.05$	0.00 ± 0.00	0.08 ± 0.34	1.65, $p>.05$
Moving Threat				0.06 ± 0.21	0.00 ± 0.00	1.35, $p>.05$
Fighting	0.03 ± 0.15	0.04 ± 0.14	0.27, $p>.05$	0.00 ± 0.00	0.04 ± 0.13	1.89, $p>.05$
Standing	16.62 ± 6.78	13.81 ± 9.60	1.42, $p>.05$	3.64 ± 8.92	4.71 ± 7.20	0.53, $p>.05$
Brooding	1.69 ± 5.58	0.00 ± 0.00	1.65, $p>.05$			
Feeding	0.50 ± 0.62	0.12 ± 0.38	3.44, $p<.05$	0.04 ± 0.14	0.00 ± 0.00	1.57, $p>.05$
Absent	1.35 ± 3.91	4.07 ± 8.11	1.72, $p>.05$	26.47 ± 6.36	23.73 ± 9.35	1.35, $p>.05$
Time on eggs (minutes)	0.00 ± 0.00	8.48 ± 20.76	2.78, $p<.05$			

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[a] Mean rate of occurrence per hour ± S.D.

Figure 19. Territories held in Observation Area 1, by female-female pairs and heterosexual pairs of Ring-billed Gulls, Granite Island, 1979. Broken lines indicate the edge of a territory that was not disputed often enough to determine the exact location of the boundary line. This map was drawn during the third week of incubation, for most clutches illustrated.

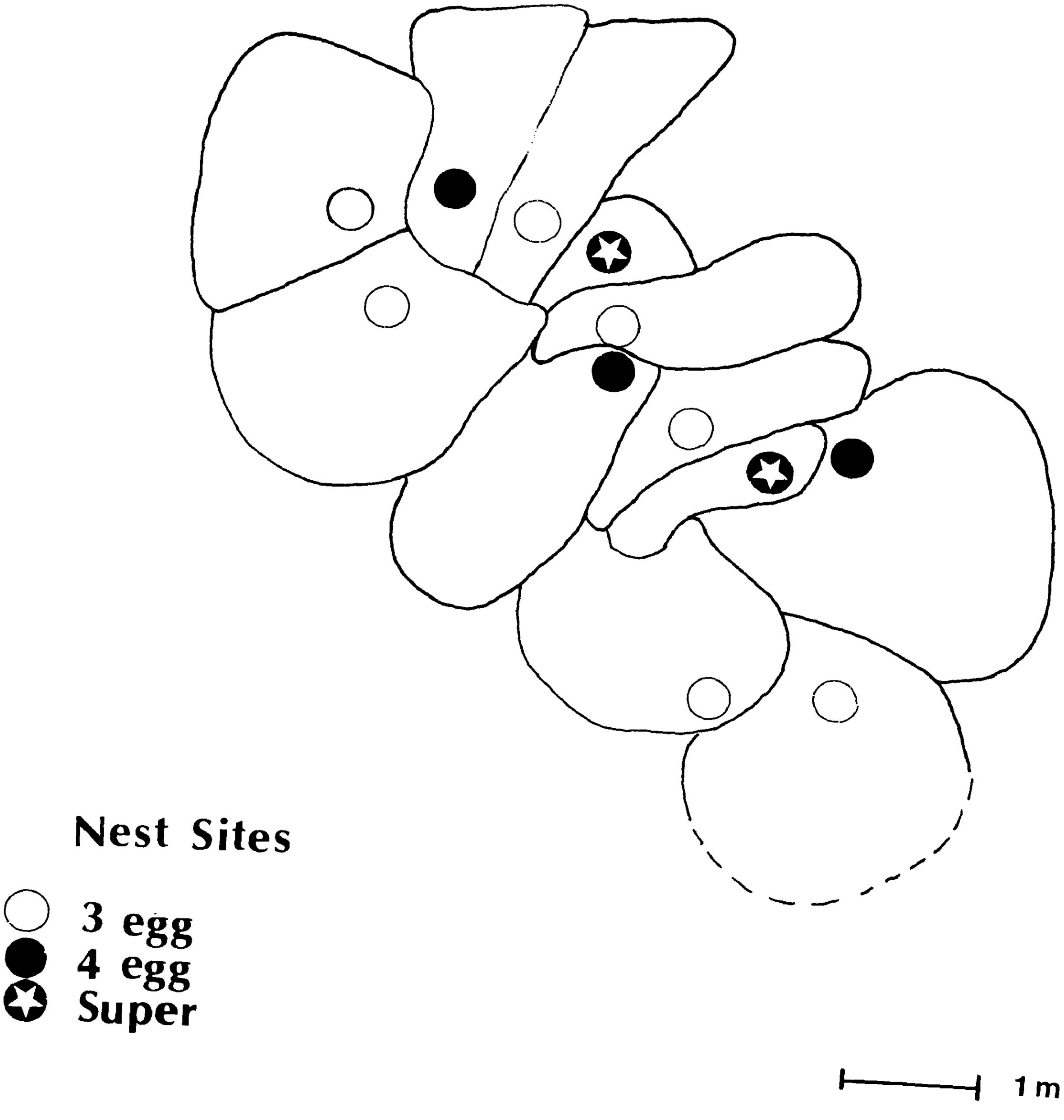
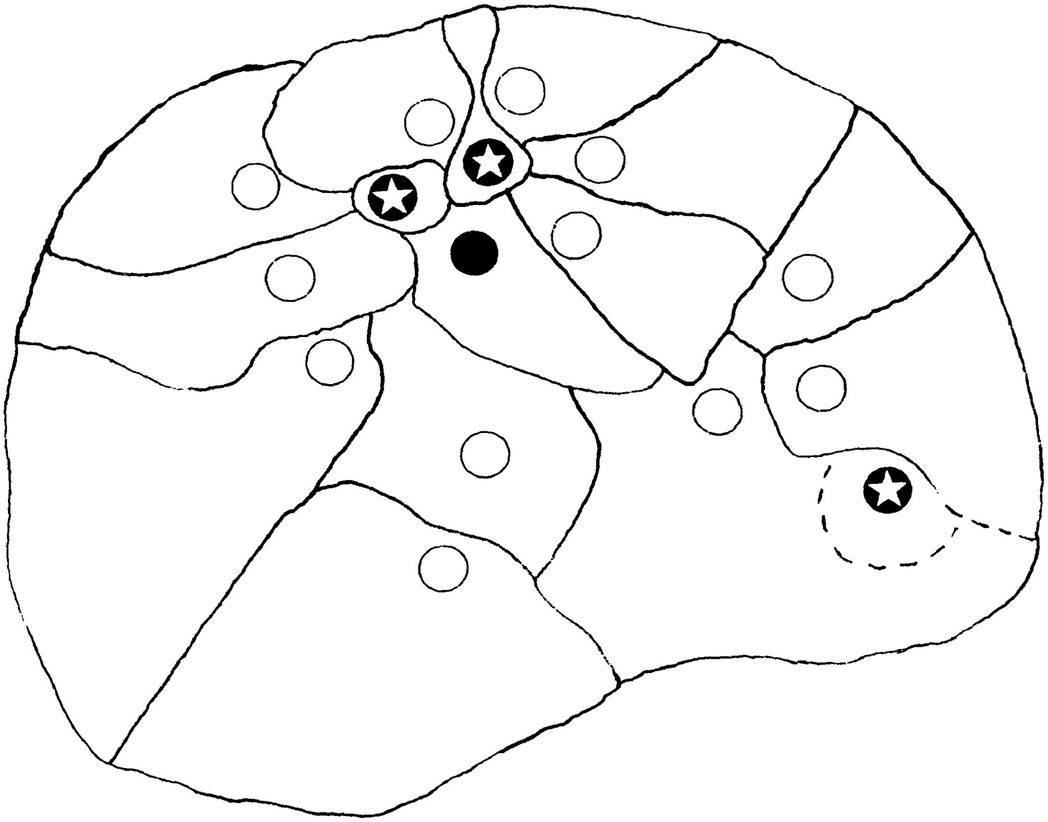

Nest Sites
3 egg
4 egg
Super
1 m

Figure 20. Territories held in Observation Area 2, by female-female pairs and heterosexual pairs of Ring-billed Gulls, Granite Island, 1979. Brocken lines indicate the edge of a territory that was not disputed often enough to determine the exact location of the boundary line. This map was drawn during the third week of incubation, for most clutches illustrated.



Nest Sites

○ 3 egg
● 4 egg
✪ Super

Figure 21. Members of a polygynous group of Ring-billed Gulls, Granite Island, 1979. The females of the trio are involved in a mild grabbing match.

tively. None of the chicks survived to the age of 7 days.

4. DISCUSSION

4.1 FREQUENCY AND SEASONAL DISTRIBUTION OF SUPERCLUTCHES

Superclutches in larids were reported as early as 1942 (Moffit, Nethersole-Thompson and Nethersole-Thompson), and 1954 (Johnston and Foster), before the recent proliferation of reports (Schreiber 1970, Vermeer 1970, Hunt and Hunt 1973, 1977, Merilees 1974, Ryder 1975, Morris and Haymes 1977, Shugart and Southern 1977, Somppi 1978, Southern 1978, Conover _et_ _al_. 1979, Ryder and Somppi 1979, Hand 1980, Koonz 1980, Shugart 1980, Kovacs and Ryder 1981, Ryder and Ryder 1981). The recent reports probably represent actual increases in the incidence of this phenomenon, as it is difficult to believe that superclutches have been overlooked by researchers in the past. They have been attributed to human disturbance (Merilees 1974), accidental laying in a nest by more than one female (Vermeer 1970), larger than normal clutch size produced by a single bird (Moffit 1942, Koonz 1980) and more commonly recently, to female-female pairing (Hunt and Hunt 1977, Conover et al. 1979, Ryder and Somppi 1979, Kovacs and Ryder 1981) and polygynous groups (Nethersole-Thompson and Nethersole-Thompson 1942, Shugar and Southern 1977, Conover _et_ _al_. 1979, Shugart 1980)

Studies that documented female-female pairing and/or polygyny reported frequencies of superclutches to be 8-14% (Hunt and Hunt 1977; Western Gulls), 1.3% (Conover _et_ _al_. 1979; Ring-billed Gulls), 1.7% (Conover et al. 1979; California Gulls), 1.9% (Ryder and Somppi 1979; Ring-billed Gulls) and 0.7% (Shugart 1980; Herring Gulls). Data for

Western Gulls, California Gulls and Herring Gulls included 4-egg clutches. Only clutches of 5 or more eggs were considered to be the result of female-female pairing for Ring-billed Gulls.

The frequency of superclutches has varied from year to year on Granite Island. Ryder (1975) reported that the frequency of superclutches was 9.4% in 1973 and 12.1% in 1977 (Somppi 1978). Ryder and Somppi's (1979) study of the same Ring-billed Gull population in 1978 reported a 1.9% frequency of superclutches compared to my findings of 4.1% in 1979 and 2.8% in 1980.

It is difficult to ascertain the exact frequency of female-female pairing or polygyny. Hunt and Hunt (1977), Conover et al. (1979) and I have found low incidences of female-female pairs incubating normal clutches, and male-female pairs incubating superclutches. Ryder and Somppi (1979) discussed the difficulty of distinguishing nests that had received dumped eggs from superclutches produced by homosexual pairs. Additionally, it is difficult to separate female-female pairs from polygynous groups, unless all of the attendants are trapped. Conover et al. (1979) found no double-nests but did trap three females and one male using a single nest-cup. I observed single and double nest-cup arrangements used by polygynous groups. In one instance a female-female pair's nest became double-cupped in response to two eggs rolling out of the nest, and the females building the nest-cup so that it went around them. This may have been the case for the birds described by Southern (1978).

Somppi (1978) and Ryder and Somppi (1979) reported that all superclutches attended by female-female pairs were initiated early in the season. Monitoring clutch completion dates I found that some superclutches were completed after peak completion dates for normal clutches. This does not necessarily mean that our studies disagree. Superclutches completed late in the season may have been initiated early, by the first laying female of a pair. Evidence for asynchrony within some pairs of females is largely circumstantial, but examining eggs in superclutches that had been abandoned after chicks hatched in the clutch I often found that the remaining eggs contained developed embryos of very similar ages that had been incubated for only 10-20 days (following the descriptions in Ryder and Somppi 1977). These eggs may have been laid later by a second female or may have developed more slowly because they spent more time on the edge of the nest. Also, my normal sample was a subsample within a single area of the colony, whereas my superclutches were complete samples that were distributed throughout the colony.

4.2 EGG CHARACTERISTICS AND CLUTCH SIZE

The slightly smaller size of eggs laid by females of homosexual pairs of Ring-bills may be due to a lack of Courtship Feeding of these birds, as was suggested by Hunt and Hunt (1977) for homosexual pairs of Western Gulls that laid smaller eggs than heterosexually paired females. However, correlation between the nutritional status of females at the time of laying and its effects on egg size is somewhat controversial. Some researchers considered that nutritional status and food availability at the time of laying are factors in the determination of egg size (Scott 1973, Lemmetyinen 1973, Murton *et al.* 1974, Mills 1979, Schreiber *et al.* 1979), while others have shown or felt that it is not (Coulson *et al.* 1969, Parsons 1975, Bryant 1975). Some studies have stated directly that a male's ability to courtship feed the female may influence egg size (Cullen and Ashmole 1963, Lack 1966, 1968, Nelson 1966a, Royama 1966, Brown 1967 , Nisbet 1973, Mills 1973, 1979, Murton et al. 1974, Davis 1975). Several of these investigators have noted extensive courtship feeding in several species of larids and have suggested that this may be an important source of energy to the female during egg formation.

Schreiber et al. (1979) suggested that stress, resulting from high population density in a colony of Laughing Gulls, may have caused a reduction in egg size. If stress can reduce egg size, it may be a factor influencing the size of eggs laid by female-female pairs. This is assuming that the females involved in these pairs may undergo stress while establishing and defending a territory, which is usually done more by male gulls (see below).

The shape of individual bird's eggs is dictated to some extent by the general physiological condition of the reproductive system, and particularly muscul tone the oviduct (Romanoff and Romanoff 1949). The width of a given female's eggs increases over the first few breeding seasons resulting in older birds laying more spherical eggs (Richdale 1955, Coulson 1963).

The lack of any difference in egg shape between eggs from normal and superclutches may reflect a similar age and reproductive condition, at least of the oviduct, of birds in normal and female-female pairs.

The smaller average clutch size per female may result from females in female-female pairs being influenced by their mate's eggs, in that three or more eggs already in the nest may cause a female to stop laying

(Paludan 1951, Parsons 1976).

4.3 INCUBATION PERIOD

Modal incubation periods for normal clutches are comparable to incubation durations reported for Ring-billed Gulls by Vermeer (1970; 25 days), Hunter et al. (1979; 25.3 days) and Ryder and Somppi (1977; 25-27 days).

Ryder and Somppi (1979) noted retarded development in embryos from eggs in superclutches, which corresponds to my findings of a prolonged incubation period for these eggs, of up to 42 days. They suggested that the retardation was due to less heat received by eggs toward the outside edge of superclutches. Although not working with female-female pairs, Schreiber (1970), Shugart and Southern(1977), Coulter (1973) and Barrett (1980) all suggested that prolonged incubation of enlarged clutches may be due to insufficient heat transfer. The possession of three distinct brood patches by adult Ring-billed Gulls may affect a parent's ability to cover more than three eggs effectively. My limited data on nest-cup temperatures support these hypotheses.

That female-female pair members continue to incubate longer than the normal incubation period is not unusual. Prolonged incubation when eggs fail to hatch in the normal period of time has been documented for a variety of bird species (Skutch 1962, Harris 1969, Holcomb 1970, Beck and Brown 1972). An extension of 50-100% of the normal incubation time can occur before incubation of unhatched eggs is terminated. I saw one superclutch destroyed by the attending parent after 42 days of incubation. The incubating bird stood up and pecked her single remaining egg. She and her female partner remained on territory for several days and returned periodically over the next week. The egg contained a well developed embryo, approximately 23 days old according to Ryder and Somppi's (1977) descriptions. This response was probably the result of hormone levels reaching a threshold level, such that the sight of an egg in the nest no longer provided a stimulus to incubate, but rather it was seen as a food item.

4.4 EGG POSITION AND EGG ROTATION DURING INCUBATION

Egg Turning behaviour is important to the survival of the embryo in most bird species although there are exceptions such as the Kiwi (*Apteryx australis mantelli*)(Rowe 1978). One result of such behaviour is the shifting of eggs relative to one another in the nest (Springarn 1934, Kossack 1947, Kessler 1960, Tinbergen 1960, Drent 1973, 1975, this study). This behaviour functions to promote an even distribution of heat among the eggs of a clutch. Because of the larger number of eggs in superclutches, their eggs remain in the same position more than eggs in normal clutches do. This results in eggs on the edge of the nest cup in superclutches tending not to be moved into the center of the where the temperature is higher. This may prevent embryos in the eggs on the edge of superclutches from developing at the same rate as those located in the center.

Rotation of individual eggs is also important during incubation, to prevent adhesions involving the extra-embryonic membranes (Robertson 1961). It is also important during later incubation to allow the egg to assume its equilibrium position which is important for the attainment of the correct position for hatching by the developing embryo (Lind, cited in Drent 1973). Eggs in superclutches were rotated on average the same amount per egg as those in normal clutches. This requires a higher frequency of Egg Turning because of the larger number of eggs in superclutches, compared to normal clutches. This may cause slight imbalances in temperature.

4.5 NEST AND NEST-SITE CHARACTERISTICS

Nests function to enhance incubation effectiveness by providing thermal insolation rendering protection from predation and in helping to maintain optimal positioning of the egg (Drent 1975). Although nests containing superclutches were well constructed their large size relative to those containing normal clutches could provide more space for air circulation and hence excessive heating or cooling of eggs, especially those on the edge. Although limited, my temperature data support this suggestion.

Superclutches do not appear to be differentially located compared to normal clutches, according to density, substrate or colony location. Internest distances for normal nests during 1980 were comparable to those reported by Somppi (1978) (83 cm vs 86 cm) and greater than those found by Vermeer (1970) for Ring-billed Gulls (60 cm). The latter measured from nest rim to rim, rather than from center to center as Somppi and I did. The similarity of nearest-neighbour distance and nest density between normal clutches and superclutches indicates that female-female pairs were not forced into suboptimal habitat within the colony. Finally Somppi's (1978) and my findings that most superclutches were centrally located serves as further evidence that female-female pair members were not younger birds or birds of inferior quality that were forced to locate in suboptimal areas within the colony (see Patterson 1965, Nelson 1966a,b, Coulson 1968, Coulson et al. 1969, Tenaza 1971, Buckley and Buckley 1972, Burger 1974, Dexheimer and Southern 1974, Ludwig 1974, Southern 1974, Spurr 1974, 1975, Montevecchi 1975, Ryder 1975, Wooler and Coulson 1977).

4.6 REPRODUCTIVE SUCCESS

4.6.1 EFFECTS OF HUMAN DISTURBANCE

Human disturbance has a negative effect on the reproductive success of gulls (Kadlec and Drury 1968, Harper 1971, Hunt 1972, Robert and Ralph 1975, Gillett et al. 1975, Schreiber et al. 1979, Hand 1980). Although I tried to minimize disturbance in all possible ways, I am sure that my presence and especially my trapping efforts had a negative effect on reproductive success. However, I do not believe that I affected normal clutches and superclutches differentially.

4.6.2 NEST SUCCESS

The percentage of nests that were successful is similar to that found for Ring-billed Gulls (Somppi 1978) and Laughing Gulls (Schreiber et al. 1979). That superclutches and normal clutches did not differ significantly in this measure of success is a reflection that female-female pairs are as attentive as normal pairs (virtually 100% during incubation), and do not have a higher rate of desertion.

4.6.3 HATCHING SUCCESS

The mean hatching success for normal clutches in my study was within the range reported for Ring-billed Gulls by Vermeer (1970, 86%, 16%), Dexheimer and Southern (1974, 63%, 60%), Ryder (1975, 52%), Baird (1976, 34%, 41%), Somppi (1978, 61-71%), Southern _et al_.(1979, 75%), and Ryder and Ryder (1981, 59%).

Ryder and Somppi (1979) reported a 21% maximum hatching success for female-female pairs, if collected fertile eggs had hatched. I found a 33% (1979) and 30% (1980) hatching success for superclutches not counting fertile eggs in the three clutches incubated by the birds that I collected. Other studies, although not working with female-female pairs also have found that larger than normal clutch sizes had a negative effect on hatching success (Schreiber 1970, Hunt and Hunt 1973, Ryder 1975, Ryder and Ryder 1981).

The large difference in hatching success between normal clutches in 1979 and 1980 is due mainly to a difference in sampling. As mentioned in Section 2.4 only peak nests were used in 1979's normal sample, whereas in 1980 I used early, peak, and late nests. Timing of laying effects hatching success, with those eggs laid during the peak laying period being the most likely to hatch (Paynter 1949, Paludan 1951, Kadlec and Drury 1968, Vermeer 1963, 1970, Erwin 1971, Ryder 1975, Morris _et al_. 1976, Hunt and Hunt 1976, Morris and Haymes 1977, Somppi 1978, Ryder and Ryder 1981). Different levels of predation also may have had some influence between the two years. Crows were seen taking eggs infrequently during 1979 and 1980, and an otter also was seen swimming near the island at dusk both years, although I never saw it on the colony. During 1980, a Snowy Owl caused major losses in some areas of the colony, taking one or two adults a night for several weeks. In addition, egg predation by Herring Gulls and by Ring-bills was more prevalent in 1980.

4.6.4 FATE OF EGGS

The *Disappearance* of eggs was a major cause of eggs not hatching . Others working with Ring-billed Gulls also have found this to be the case (Vermeer 1970, Somppi 1978).

The higher incidence of eggs *Rolled* from the nest cup or *Buried* in superclutches compared to normal clutches also was reported by Ryder and Somppi (1979). Coulter (1973) also found this to be the case for superclutches of Western Gulls. This may be because of crowding in the nest-cup, and because of the increased rate of occurrence of *Egg Turning* and *Settling* by birds incubating these clutches. Eggs were *Buried* because of the difficulty of moving them around inside the crowded nest-cup.

The frequency of abandoned eggs was higher in superclutches than in normal clutches because of the higher potential for the eggs in a superclutch to vary in the length of time they were incubated. If females of a pair laid asynchronously, the chicks from the first clutch might hatch before the embryos of the second clutch were developed fully. The females I observed reduced the time spent incubating eggs to feed and care for young that had hatched, leaving remaining eggs unattended.

4.6.5 FERTILITY OF EGGS

Many authors do not report fertility rates, because of the difficulty in differentiating between infertile eggs and those in which embryos died at a young age. Fertility of eggs belonging to heterosexual pairs is usually assumed to be quite high (80-100%). Hunt and Hunt (1977) reported that 81.5% of eggs in 3-egg clutches of Western Gulls showed development. They also found that superclutches in that species showed only 13% development. Conover et al. (1979) reported 65-70% of the eggs in 5-egg and 6-egg clutches of Ring-billed Gulls showed development, and nine of ten eggs examinined from 4-egg clutches of California Gulls proved fertile. Ryder and Somppi (1979) found a similar fertility of 66% for Ring-billed Gull superclutches.

The fertility rates I determined for superclutches are higher than those reported by Conover et al. (1979) and Ryder and Somppi (1979) for Ring-billed Gulls. However, I was not able to determine fertility for all of the eggs in 1979 or 1980, because many Disappeared and others were addled by the time I checked them, so my sample may not be representative for all superclutches.

4.6.6 FLEDGING SUCCESS

Studies on Ring-billed Gulls report a wide range of fledging success, (Emlen 1956, 22%; Vermeer 1970, 40%; Dexheimer and Southern 1974, 10%, 80%; Ryder and Ryder 1981, 55%). The fledging rates calculated for normal pairs during 1979 and 1980 were above average for Ring-billed Gulls. This may be due in part to differing definitions or methods of calculation for fledging, as Emlen (1956) and Vermeer (1970) do not define the criteria they used . Seasonal variation also might be a factor.

In both years, the fledging success for chicks hatching from superclutches was approximately 50% of that determined for normal clutches. This is primarily because of differential mortality during the first week following hatching (discussed below, Section 4.6.7).

4.6.7 MORTALITY OF CHICKS

I found, as have others working with Ring-billed Gulls (Vermeer 1970, Somppi 1978, Ryder and Ryder 1981), that well over 50% of the total chick mortality occurred during the week post hatch. Early mortality was most pronounced for chicks hatching from superclutches, which had a substantially higher death rate. Their slightly smaller egg size and lower hatching weight may result in more deaths occurring during the first week post hatch. This has been reported to be the case for chicks from normal pairs of gulls (Parsons 1970, Nisbet 1973, Coulter 1980, Lundberg and Vaisaner 1981). The relatively smaller size of territories held by female-female pairs may also influence the number of chicks killed by neighbours (Hunt and Hunt 1976, Butler and Trivelpiece 1981). The higher frequency of death by crushing in the nest in superclutches compared to normal clutches leads me to believe that female-female pair members may have more difficulty making the transition from incubating to brood rearing. If the females of a pair laid asynchronously, the female that laid last may not have sufficiently high prolactin and low progesterone levels to change from incubation to brood rearing activities.

Working with Western Gulls, Pierotti (1981) found that females spent most of their time brooding during the week following hatching while their mates did most of the feeding of the young. If this is the case for Ring-billed Gulls, it may have a negative influence on the survival rate for young belonging to female-female pairs, because they may not be provided with adequate food by their two female parents during the first week post hatch.

There have been few published reports on the growth rates of Ring-billed Gull chicks. Kirkham and Morris (1979) refer to growth of seven early and six late chicks but do not provide the actual weight data. According to weight data collected in 1979 and 1980 and Vermeer's (1970) report on Ring-billed Gulls, they have a standard (sigmoid) growth curve, defined by Ricklefs (1968). Unfortunately, my sample sizes are small as the asymptote of the curve is approached. Those chicks that I did manage to catch after 20 days were substantially heavier than weights reported by Vermeer (1970) for chicks of the same ages.

Although the hatching weight is slightly lower than normal for chicks in superclutches, they achieve the same fledging weight (statistically). The slightly faster growth rate experienced by the chicks from superclutches could be a result of reduced brood size. Although the same average number of chicks hatch per brood in the two clutch types, mortality during the first week is higher for chicks from superclutches; therefore, female-female pairs raise fewer chicks during the second and third weeks post hatch. Vermeer (1970) found that single chick broods grew more quickly than did those containing two or three.

The normal or slightly faster rate of growth for chicks from superclutches reflects the ability of the two female parents to provide sufficient food for their normal sized broods.

4.6.8 REGURGITATION SAMPLES

Studies of the food types of Ring-billed Gulls report that they consume fish, insects, earthworms, grains, grasses, corn, crayfish, eggs, birds, spiders, rodents, refuse, fiddlercrabs and date fruits (Munro 1936, Pettingill 1958, Meyerriecks 1965, Mueller and Berger 1965, Ludwig 1966, 1974, Vermeer 1970, Miller and Emlen 1975, Allan 1978, Chudzik 1978, Southern et al. 1976, Jarvis and Southern 1976, Haymes and Blokpoel 1978, Grant 1979, Kirkham and Morris 1979).

Jarvis and Southern (1976) suggested that the reliance of Ring-billed Gulls on insects as an energy source is a recent innovation that has been increasing in frequency during the recent enlargement of the population (Ludwig 1974). They also noted that significant differences exist between the food habits of Ring-billed Gulls breeding in eastern and western portions of North America.

My regurgitation samples provided only qualitative data on the various food types. The results correspond very closely to other studies done on Ring-billed Gulls' feeding habits in northeastern North America (Chudzik 1978, Jarvis and Southern 1976, Southern et. al. 1976, Haymes and Blokpoel 1978, Kirkham and Morris 1979). Ring-billed Gulls on Granite Island fed their young primarily fish and insects. The absence of refuse is likely a function of relative abundance of preferred food items, and the long distance of the colony from any major human settlement. The absence of earthworms, grains and corn is probably a matter of availability. Northern Ontario produces few agricultural crops and consequently little soil is cultivated.

The similarity between food types brought to chicks from normal and superclutches, as well as growth data and weight at the time of fledging leads me to believe that female-female pairs of Ring-billed Gulls are as capable as male-female pairs at providing food for the young, although Pierotti (1981) found that male Western Gulls feed their chicks significantly more often and brought larger food items than did females.

4.7 MORPHOLOGY AND PHYSIOLOGY OF FEMALE-FEMALE PAIR MEMBERS

All measurements of size indicate that female-female pair members fall within the normal size range. Their weights, which can be considered an index of metabolic resources (Korschgen 1977) are normal compared to heterosexually paired females as are their condition indices, which adjust for structural size differences and hence are considered a more accurate reflection of relative fitness (Bailey 1979).

The similarity of size between members of individual female-female pairs supports the suggestion of Hunt (1980) that if one of the characteristics of normal mate choice in gulls is size, if males are not available, then females would choose to pair with the largest females available. In female-female pairs, because both females will be seeking large mates, the largest mate that either could get might be a bird its own size. In this case, members of female-female pairs would be, as I have found, of similar size.

Sample sizes and lack of experimental design, especially in 1979, prevent me from drawing conclusions about the effect of metabolite and hormone levels. Because of the general void of information in this area for wild birds, and because of the interesting trends, I believe that several brief and speculative comments are appropriate.

There appears to be only one consistent difference in metabolite levels between females in homosexual pairs and those in heterosexual pairs, namely the low cholesterol level found in female-female pair members. The low cholesterol level is especially interesting in the light of the elevated progesterone levels found for members of female-female pairs during both years of study because cholesterol serves as a precursor for the synthesis of estrogens (Turner and Bagnara 1976). Progesterone seems to be involved in defeathering of the brood patch (Jones 1971), and it acts synergistically with estrogen to elicite nest building and incubation behaviour (Cheng and Silver 1975). The elevated levels of progesterone in female-female pairs might be caused by or a result of the pair bond and close proximity of the two females, or because of a visual or tactile superstimulus provided by superclutches. Social control of hormone levels has been documented for mice (*Mus mus*)(Lamond 1959), rats (*Rattus norvegicus*)(McClintock 1978) and humans (McClintock 1971, 1981). Excitement and attraction of larger than normal clutch-size during the incubation period has been reported for gulls (Baerands 1959, Beer 1961, 1965), indicating that superclutches cause at least a more extreme psychological attraction than a normal clutch.

The normal level of androgens found in these birds also was reported for female-female pair members in Western Gulls (Wingfield *et al*. 1980a,b) indicating that female-female pair members were not hormonally abnormal in this parameter.

4.8 BEHAVIOUR

Courtship activities between female-female pairs of Ring-billed Gulls were somewhat different than those described for Western Gulls by Hunt and Hunt (1977). They observed females regurgitate food in response to repeated *Head-tossing* by the partner. I observed *Head-tossing*, *Tipping*, and *Begging* between females, but never saw females *Courtship Feeding* each other. *Mounting* attempts were seen by Hunt and Hunt (1977), and me. I saw a single pair in which both females interchanged *Mounting* position.

I do not feel that the courtship activities between females were due to a masculinization of one or both birds, as Hunt and Hunt (1977) suggested. Rather I believe that their function was purely pair-bond reinforcement, and that each female was responding to the behaviour of its mate.

Mounting behaviour by female Ring-billed Gulls has been reported before, but in a different context. Kinkel and Southern (1978) and I (this study) have witnessed known adult females mount juveniles that were from 14 to 21 days old. As Kinkel and Southern implied, the endogenous state of the females that perform such behaviour and the stimuli given by chicks that may elicit such responses are unkown. The fact remains that females can be prompted to perform male sexual behaviour. The striking similarities between the food-begging posture and vocalizations of juveniles and those of courting females lead me to believe that the causal factors involved in the observed mounting incidents may be somewhat the same.

Promiscuous behaviour by male gulls has been reported for the Herring Gull (Tinbergen 1960, MacRoberts 1973), Black-headed Gull (L. ridibundus) (Tinbergen 1959, Beer 1961, 1962), Laughing Gull (Burger and Beer 1975), Lesser Black-backed Gull (L. fuscus)(MacRoberts 1973), Western Gull (Hunt and Hunt 1977, Pierotti 1981), and Ring-billed Gull (Conover et al. 1979, this study). Gladstone (1979) pointed out that if a male can induce another female to make her large investment in his offspring he will be further ahead, provided that his promiscuity does not ensure disruption of his original pair bond and that the female(s) who is the object of his promiscuity has a good chance of raising the young to maturity. Female-female pairs of Ring-billed Gulls, to some degree meet these criteria for a promiscuous male.

Female-female pairs are extremely attentive but are generally more restless on the nest. They spend less time Sleeping and more time Fussing than do birds incubating normal clutches. This is not due to some inherent lack of quality in these females. It is a reported response to an enlarged clutch (Baerands 1959, Beer 1961, 1965, Coulter 1973). Discomfort produced by placing irregularly shaped objects in the nest resulted in the performance of similar behaviour (Moynihan 1953, Tinbergen 1960). Increased frequencies of Nest Building by female-female pairs is probably a displacement activity, as it occurs most often when both females want to be on the nest. The pushing matches I observed between female-female pairs are not exclusive to homosexual pairs. Moynihan (1953) and Tinbergen (1960) have documented almost identical sequences performed by heterosexual pairs under similar circumstances.

The low number of threat postures assumed by incubating female-female pair members and the general reduction of territorial defense by these pairs is not surprising. Tinbergen (1959, 1960), Moynihan (1958b), Baerands (1959), Burger and Beer (1975), Pierotti (1981), and Southern (1981) have all reported that male gulls are more aggressive and defend their territories more than females. Lack of defense by female-female pairs may result in the smaller territory size in dense areas of the colony, such as in my observation areas. The success experienced by some female-female pairs leads me to believe that the extremely small territories held in high density areas are not likely representative of those in lower density areas, where intrusion pressure would be lower.

4.9 NEST-SITE TENACITY AND MATE FIDELITY BY FEMALE-FEMALE PAIRS

Heterosexual pairs of Ring-billed Gulls exhibit nest-site tenacity and mate fidelity to varying degrees (Vermeer 1970, Southern 1977, Southern and Southern 1979, Blokpoel and Courtney 1980). I have found (this study) that homosexual pairs also exhibit these characteristics (see also Kovacs and Ryder 1981).

The benefits of nest-site tenacity remain enigmatic. It might serve to reunite pairs or to enhance reproductive performance by familiarizing the individuals with an area, particularly in stable habitats (McNicholl 1975) such as Granite Island. The selective advantages of mate fidelity are clear, for at the time and place of nesting birds exhibiting fidelity have a higher reproductive success relative to individuals that acquire new mates each year (Coulson 1966, 1972, Ryder 1980).

Although mate fidelity occurs in female-female pairs, nest-site tenacity is not likely a prerequisite. I do not know whether the pairs that moved nest sites in consecutive seasons initially returned to the site previously used. If they did their stays were brief because I watched these locations from hides extensively during the early part of the nesting season and did not observe them there.

The recapture in 1980 of birds trapped in 1979 incubating superclutches probably does not accurately indicate the return rate of female-female pairs to Granite Island. I concentrated my trapping efforts on superclutches, but these pairs did not always lay more than the normal number of three eggs (Hunt and Hunt 1977, Conover _et al_. 1979, this study). Consequently, some of the returning female-female pairs may have been overlooked, because rough terrain, dense vegetation, and potentially excessive disturbance limited searches for colour-banded birds.

4.10 GENERAL DISCUSSION

Several hypotheses have been suggested regarding the origin(s) of female-female pairing in gulls. Ryder (1978b) proposed three alternatives. The first involved a disproportionate mortality of mated males early in the breeding season, with stressed males leaving widowed fertilized females that form a bond with a similar conspecific. His second proposed circumstance suggested the existence of a disproportionate population sex ratio in favour of females. Lastly he proposed the possibility that female-female pairs originate from three member polygynous groups, with the death or desertion of the male leaving the two females to incubate and care for the young. Wingfield et al. (1980a) without reference to Ryder (1978b) suggested two possible hypotheses. The first was a sex ratio biased in favour of females. The second hypothesis was that female-female pairing was the result of modification of behaviour by abnormal hormone levels or cycles.

Regarding the last suggestion, the results of Wingfield et al. (1980a,b) and this study (although limited) provide no evidence of abnormal hormone levels in members of homosexual pairs that would indicate a masculinization of these birds. The other hypothesis of Wingfield et al. (1980a) and those of Ryder (1978b) all suggest or infer a skewed sex ratio in favour of females.

Hunt and Hunt's (1977) first study on female-female pairs of Western Gulls suggested that an aberrant sex ratio existed on Santa

Barbara Island. Since then evidence for their belief has been provided (Hunt et al. 1980, also see Pierotti 1981). The reason for such an imbalance was thought to be related to differential male mortality (Hunt 1980, Hunt et al. 1980). It has been suggested that toxic chemical contaminants may contribute to reduced male survivorship relative to females through physiological differences between sexes in lipid and lipophilic toxic chemical dynamics (Wurster et al. 1965, Gish and Chura 1970, see also Shugart 1980). Sex ratio alterations in a breeding population due to pesticide contamination is of particular significance in light of the result of Fry and Toone (1981). These investigators have demonstrated that injections of DDT into gull eggs at concentrations comparable to those found in contaminated seabird eggs induced abnormal development of testicular tissue such that it resembled ovarian tissue. This developmental feminization is associated with inability to breed as adults and the authors feel that this may explain the skewed functional sex ratio on Santa Barbara Island.

The case may be somewhat different for Ring-billed Gulls than for Western Gulls. Ryder and Somppi (1979) suggested that homosexual pairs were not of recent origin in Ring-bills, as had been suggested by Hunt and Hunt (1977) for Western Gulls, because reports of superclutches in Ring-billed Gulls go back to 1941 (Moffitt 1942), before the use of chemicals such as DDT. The sex ratio on Granite Island is unknown. It and the experimental testing of Ryder's (1978b) suggestions that female-female pairs may be the result of cooperating widowed females or broken polygynous groups will hopefully be the subject of future research.

If female-female pairing is a response to an aberrant sex ratio, whatever its cause, their adaptive significance appears to be obvious. Homosexual pairing would raise from zero the probability that excess females would raise offspring (Hunt and Hunt 1977, Conover _et al_. 1979, Ryder and Somppi 1979).

Hand (1981) proposed an extremely interesting hypothesis for the developmentof aberrant bonding under conditions of skewed sex ratios based on positive psychological reinforcement. She states that a bond will be formed between members of the same sex, male or female, if the relationship provides sufficient psychological reinforcement compared to the available alternatives, viz., not bonding at all.

The low incidence of polygyny relative to female-female pairing on Granite Island is most likely due to past selection pressure on Ring-billed Gulls favouring monogamy. Fitch (1979) stated that territorial and courtship behaviour related to maintenance of long-term pair bonds in normally monogamous gulls may hinder but not prevent formation of polygynous groups.

I am not able to provide any reasons why these particular females are involved in homosexual pairing. They are normal adult females in almost every criteria measured. Their elevated progesterone and depressed cholesterol level are likely a result rather than a cause of their bond. The females appear to selectively pair according to size and presumably behavioural compatability. The mere existence of female-female pairing is a tribute to the plasticity of larids and the lability within their mating system.

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Appendix 1

Relative Prolactin Potency* of Ring-billed Gull Serum

	Females		Males	
Laying Period	Bird No.	%B	Bird No.	%B
	1	46.9	5	51.0
	2	48.2	6	48.9
	3	49.2	7	58.0
	4	48.1	9	45.8
	8	45.1		
	10	43.1		
	11	32.2		
$\bar{X}$ ± SD		44.7 ± 5.9		50.9 ± 5.2
Incubation Period	12	46.9	18	39.6
	13	38.0	19	41.4
	14	40.6	21	52.6
	15	28.1	22	44.0
	16	47.7		
	17	39.6		
	20	43.6		
X ± SD		40.6 ± 6.6		44.4 ± 5.8
Feeding Period	23	15.8	24	18.4
	25	45.2	29	42.2
	26	41.0	30	38.8
	27	43.8		
	28	43.1		
	31	45.7		
	32	40.8		
X ± SD		39.3 ± 10.6		33.1 ± 12.9

* %B = $\frac{\text{Amount of radioactive prolactin bound in the presence of gull serum}}{\text{Amount of radioactive prolactin bound with no prolactin containing sample}}$

All samples were run at 50, 25 and 12.5 µl. For simplicity, only the data from the 25 µl samples are shown. The lower the %B figure, the more immunoreactive "prolactin" in the sample. (Following methods of Burke and Dennison 1980).

Appendix 2

Weight (g) of chicks from superclutches and normal clutches of Ring-billed Gulls from the day of hatching until 22 days of age Granite Island, 1979.

Day	Normal	Super	T-value
1	41.4 ± 3.6 (101)[a]	39.9 ± 5.0 (143)	2.61, p<.05
2	47.9 ± 4.8 (87)	48.8 ± 9.4 (34)	0.51, p>.05
3	58.5 ± 7.2 (45)	53.2 ± 9.4 (50)	3.07, p<.05
4	72.8 ± 10.3 (33)	69.2 ± 16.5 (26)	1.21, p>.05
5	97.1 ± 10.8 (13)	86.5 ± 22.3 (28)	1.65, p>.05
6	119.6 ± 20.4 (34)	105.6 ± 24.1 (34)	1.90, p>.05
7	143.2 ± 15.0 (5)	119.2 ± 33.0 (19)	1.42, p>.05
8	162.4 ± 35.5 (7)	141.1 ± 31.8 (30)	1.47, p>.05
9	165.2 ± 38.5 (20)	171.2 ± 35.6 (20)	0.10, p>.05
10	189.4 ± 37.2 (27)	179.9 ± 42.2 (21)	0.93, p>.05
11	202.7 ± 54.5 (21)	217.2 ± 38.1 (22)	0.32, p>.05
12	241.3 ± 51.4 (19)	243.4 ± 35.0 (18)	0.38, p>.05
13	274.9 ± 28.5 (20)	269.4 ± 25.6 (17)	0.53, p>.05
14	282.2 ± 20.9 (13)	273.4 ± 56.7 (14)	0.51, p>.05
15	305.6 ± 33.8 (19)	295.1 ± 30.2 (14)	0.82, p>.05
16	338.9 ± 36.7 (13)	294.5 ± 60.3 (13)	2.22, p<.05
17	329.5 ± 38.1 (19)	336.7 ± 34.4 (14)	0.69, p>.05
18	348.9 ± 33.6 (16)	355.2 ± 50.3 (9)	0.48, p>.05
19	362.4 ± 30.8 (13)	385.1 ± 46.6 (7)	1.07, p>.05
20	392.7 ± 38,8 (8)	406.1 ± 45.8 (8)	0.94, p>.05
21	410.2 ± 45.1 (9)	405.4 ± 37.8 (9)	0.22, p>.05
22	364.6 ± 58.3 (10)	429.0 ± 18.2 (3)	2.29, p<.05

[a] Mean ± S.D. (sample size)

Appendix 3

Weight (g) of chicks from superclutches and normal clutches of Ring-billed Gulls from the day of hatching until 22 days of age Granite Island, 1980.

Day	Normal	Super	T-value
1	41.8 ± 2.8 (171)[a]	38.2 ± 4.2 (67)	1.38, $p<.05$
2	53.6 ± 4.6 (73)	42.2 ± 5.7 (32)	1.55, $p<.05$
3	58.5 ± 10.5 (55)	49.9 ± 7.2 (19)	3.41, $p<.05$
4	71.1 ± 15.3 (43)	65.5 ± 9.0 (14)	1.13, $p>.05$
5	83.9 ± 16.3 (54)	74.4 ± 15.3 (10)	1.53, $p>.05$
6	97.2 ± 18.7 (30)	101.8 ± 20.8 (9)	0.77, $p>.05$
7	117.1 ± 22.3 (44)	112.4 ± 29.2 (12)	0.10, $p>.05$
8	129.5 ± 19.7 (30)	148.3 ± 26.9 (10)	1.78, $p>.05$
9	158.1 ± 27.6 (27)	150.8 ± 7.7 (5)	1.22, $p>.05$
10	175.0 ± 27.7 (21)	183.0 ± 27.8 (8)	0.68, $p>.05$
11	203.1 ± 36.6 (14)	188.0 ± 29.9 (5)	0.88, $p>.05$
12	225.7 ± 33.9 (9)	243.7 ± 19.8 (3)	1.02, $p>.05$
13	227.1 ± 50.8 (17)	225.0 ± 33.3 (6)	0.14, $p>.05$
14	272.5 ± 37.7 (17)	267.5 ± 22.2 (4)	0.45, $p>.05$
15	257.4 ± 31.7 (10)	288.7 ± 45.6 (7)	1.47, $p>.05$
16	299.7 ± 29.8 (11)	324.0 ± 33.9 (5)	1.19, $p>.05$
17	309.9 ± 59.2 (15)	310.0 ± 14.1 (2)	0.22, $p>.05$
18	315.6 ± 58.9 (13)	315.0 ± 34.2 (8)	0.22, $p>.05$
19	353.5 ± 39.2 (23)	354.3 ± 47.0 (4)	0.23, $p>.05$
20	357.0 ± 58.6 (10)	361.7 ± 50.6 (3)	0.09, $p>.05$
21	378.9 ± 52.0 (14)	349.0 ± 41.6 (8)	1.03, $p>.05$
22	384.9 ± 53.0 (17)	431.7 ± 36.2 (4)	2.19, $p>.05$

[a] Mean ± S.D. (sample size)

Appendix 4

Tarsus (mm) measurements of Ring-billed Gull chicks from superclutches and normal clutches from the day of hatching until 22 days of age, Granite Island, 1980.

Day	Normal	Super	T-value
1	27.5 ± 1.5 (149)[a]	26.7 ± 1.2 (51)	3.38, $p<.05$
2	29.6 ± 1.6 (57)	28.2 ± 1.2 (32)	4.30, $p<.05$
3	31.2 ± 2.1 (38)	29.9 ± 1.3 (23)	2.55, $p>.05$
4	32.9 ± 2.2 (41)	31.5 ± 2.3 (11)	1.60, $p>.05$
5	34.0 ± 2.2 (52)	33.3 ± 1.7 (10)	0.80, $p>.05$
6	35.6 ± 2.8 (30)	36.1 ± 2.5 (9)	0.67, $p>.05$
7	37.7 ± 2.9 (42)	37.5 ± 4.2 (13)	0.17, $p>.05$
8	39.6 ± 2.4 (31)	41.4 ± 2.2 (10)	1.77, $p>.05$
9	41.5 ± 2.6 (26)	39.0 ± 1.4 (5)	2.28, $p<.05$
10	44.5 ± 2.8 (21)	43.4 ± 2.0 (8)	1.20, $p>.05$
11	46.4 ± 4.1 (15)	43.9 ± 1.7 (5)	1.35, $p>.05$
12	48.2 ± 2.3 (10)	48.5 ± 1.4 (3)	0.42, $p>.05$
13	47.3 ± 4.4 (15)	46.4 ± 3.0 (6)	0.35, $p>.05$
14	50.6 ± 2.6 (18)	50.4 ± 2.6 (4)	0.04, $p>.05$
15	50.0 ± 2.6 (10)	50.9 ± 2.8 (7)	0.98, $p>.05$
16	53.0 ± 2.6 (11)	55.3 ± 1.5 (5)	1.57, $p>.05$
17	53.3 ± 3.6 (14)	55.2 ± 3.5 (2)	0.64, $p>.05$
18	54.5 ± 3.6 (12)	53.8 ± 2.7 (8)	0.19, $p>.05$
19	56.1 ± 3.0 (24)	54.8 ± 2.8 (4)	0.72, $p>.05$
20	55.1 ± 4.7 (13)	55.5 ± 3.1 (3)	0.47, $p>.05$
21	57.3 ± 3.1 (13)	56.0 ± 2.8 (8)	0.79, $p>.05$
22	57.2 ± 3.1 (17)	59.8 ± 3.5 (3)	1.33, $p>.05$

[a] Mean ± S.D. (sample size)

Appendix 5

Culmen (mm) measurements of Ring-billed Gull chicks from superclutches and normal clutches from the day of hatching until 22 days of age, Granite Island, 1980.

Day	Normal	Super	T-value
1	15.9 ± 4.5 (146)[a]	15.1 ± 0.7 (51)	1.93, $p>.05$
2	15.9 ± 1.1 (60)	15.8 ± 0.6 (32)	0.69, $p>.05$
3	17.0 ± 2.0 (39)	16.0 ± 0.7 (20)	2.98, $p<.05$
4	17.4 ± 1.8 (40)	17.1 ± 0.8 (13)	0.02, $p>.05$
5	18.3 ± 1.9 (53)	18.0 ± 0.9 (10)	0.08, $p>.05$
6	18.9 ± 1.2 (29)	18.7 ± 1.2 (9)	0.53, $p>.05$
7	19.9 ± 1.6 (43)	19.4 ± 1.0 (12)	0.69, $p>.05$
8	20.4 ± 1.1 (31)	21.1 ± 1.7 (10)	0.93, $p>.05$
9	21.4 ± 1.5 (26)	20.5 ± 0.8 (5)	1.51, $p>.05$
10	22.3 ± 1.1 (21)	21.9 ± 1.1 (8)	1.00, $p>.05$
11	23.7 ± 2.7 (15)	22.3 ± 0.6 (5)	1.17, $p>.05$
12	24.8 ± 3.1 (10)	23.4 ± 1.0 (3)	0.34, $p>.05$
13	24.2 ± 1.7 (15)	23.7 ± 1.6 (6)	0.56, $p>.05$
14	24.9 ± 1.1 (18)	25.3 ± 0.5 (4)	0.63, $p>.05$
15	24.3 ± 1.3 (10)	24.2 ± 1.7 (7)	0.49, $p>.05$
16	25.7 ± 0.9 (11)	25.6 ± 1.2 (5)	0.45, $p>.05$
17	26.2 ± 1.2 (14)	25.7 ± 0.1 (2)	0.37, $p>.05$
18	27.1 ± 2.6 (12)	25.5 ± 2.1 (8)	1.32, $p>.05$
19	26.7 ± 1.8 (24)	25.7 ± 0.6 (4)	1.28, $p>.05$
20	26.4 ± 2.3 (13)	27.2 ± 1.6 (3)	0.74, $p>.05$
21	28.3 ± 2.4 (13)	27.2 ± 1.6 (3)	1.39, $p>.05$
22	28.0 ± 1.5 (17)	29.4 ± 1.9 (3)	1.30, $p>.05$

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[a] Mean ± S.D. (sample size)

Appendix 6

Orders and families of insects found in regurgitation samples from Ring-billed Gull chicks, Granite Island, 1980.

Order	Family
Ephemeroptera (751)[a,b]	
Orthoptera (1)	
Plecoptera (59)	
Thysanoptera (2)	
Hemiptera (3)[b]	Pentatomidae
Neuroptera (5)	
Coleoptera (169)[b]	Carabidae
	Staphylinide
	Siphidae
	Scarabaeidae
	Byrrhidae
	Dryopidae
	Buprestidae
	Eliteridae
	Cantharidae
	Anobiidae
	Nitidulidae
	Tenebrionidae
	Cerambycidae
	Curculionidae
	Chrysomelidae

continued.....

Appendix 6 continued

Mecoptera (1)	Panorpidae
Tricoptera (17)[b]	
Lepidoptera (178)[b]	Noctuidae
Diptera (221)[b]	Tipulidae
	Chironomidae
	Anisopodidae
	Bibionidae
	Syriphidae
	Sciomyzidae
	Muscidae
	Sarcophagidae
Hymenoptera (24)[b]	Tenthredinoidae
	Braconidae
	Ichneumonidae
	Formicidae
	Vespidae

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[a] (total number of individuals per order)

[b] found in superclutch samples as well as normal samples

(classification followed Borror et al. 1976)

Appendix 7

Average percent of total volume

(measured by water displacement (ml^3)) fish/insects in composite samples from Ring-billed Gull chicks from superclutches and normal clutches, Granite Island, 1980.

Date June		2-8	9-15	16-22	23-30	July 2
Insects	S[1]		t[3]	100.0	27.0	
	N[2]	12.0	13.4	1.6	12.3	100.0
Fish	S		100.0	0.0	73.0	
	N	88.0 (0/6)[6]	82.5[4] (4/7)	98.4 (2/4)	71.3[5] (5/10)	0.0 (0/2)

[1] Chicks were from superclutches

[2] Chicks were from normal clutches

[3] Trace amounts were found (ie. insect legs)

[4] The additional 4.0% was 1.4% wood fragments and leaves and 2.6% was unidentifiable material.

[5] The additional 16.3% was a single crayfish (8.2%) and 8.1% unidentifiable material.

[6] (number of composite samples from superclutches/number of composite samples from normal clutches)

Appendix 8

Leg band numbers, sex and age of Ring-billed Gulls trapped on superclutches, Granite Island, 1979, 1980.

Leg Band Numbers	Year Banded	Sex	Age in 1979
725-77453	1972	female	8
755-42945	1973	female	9+[a]
786-31689	1978	female	4+
786-31692	1978	female	4+
786-31700	1978	female	4+
795-77004	1978	female	4+
795-77016	1978	female	4+
795-77034	1978	female	4+
			Age in 1980
725-74018	1971	female	12+
755-42507	1972	female	8
755-42945	1973	female	10+
765-58818	1975	female	5
765-59827	1975	female	5
765-62808	1976	female	4

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[a] + refers to gulls that were trapped as adults. They were considered at least 3 years old +, at the time of banding.

Appendix 9

Leg band numbers, sex and age of Ring-billed Gulls trapped on normal clutches, Granite Island, 1979, 1980.

Leg Band Numbers	Year Banded	Sex	Age in 1979
725-77111	1972	female	7
725-66579	1973	female	6
755-44947	1976	female	3
765-72425	1976	male	3
765-72471	1976	male	3
765-70333	1977	male	2
			Age in 1980
725-77164	1972	female	8
725-66619	1973	female	7
725-66997	1973	male	7
755-44544	1975	male	5
765-62620	1975	female	5
765-70300	1977	male	3