The relationship of body size to time of nesting and mate preference in the Ring-billed Gull (*Larus delawarensis*)

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

Victoria Helen Johnston ©
Lakehead University
Thunder Bay, Ontario
May, 1988

ISBN 0-315-44782-6

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.

May, 1988

DEDICATION

This thesis is dedicated with love and gratitude to my uncle,

Stanley M. Teeple.

ABSTRACT

The first part of this thesis investigated the relationship between time of nesting and body size in Ring-billed Gulls (Larus delawarensis). There were no significant differences in skeletal measurements among birds from early, peak, post-peak, and late nesting periods. Discriminant function analysis failed to classify individuals by overall body size into groups defined by the periods in which they initiated nesting activities. Body condition was significantly lower in late-breeding birds compared to those from other nesting periods. Although there was a direct relationship between timing of nesting and body condition, no such relationship held with body size or individual skeletal variables.

The second part of this thesis examined the relationship between body size and mate preference in Ring-billed Gulls. A total of 16 skeletal measurements were taken on each bird from 108 mated pairs of gulls. Variance in skull and bill measures was significantly lower between mates than in randomly-generated pairs. However, correlation coefficients for all single skeletal characters between mates were low. High correlations were found between mates in body condition and fresh weight but not in random pairs. A significant positive correlation existed between overall body size within mated pairs but not within random pairs.

The results indicate that Ring-billed Gulls mate assortatively on the basis of body condition and to a lesser degree by overall body size. I postulate, however, that this assortative mating is not the result of active choice of similar-sized or quality mates. Ring-bill probably attempt to obtain the best quality mate possible, but because of the presence of higher-

quality competitors, actually obtain mates of comparable size and quality. This type of mate choice would appear as assortative mating in studies undertaken after mate selection was completed.

ACKNOWLEDGEMENTS

I extend appreciation to my supervisor Dr. John P. Ryder for financial and moral support during all phases of this study. The companionship of Beatrice Termaat, Liz Murray and Shelagh Hamer during the field seasons is gratefully acknowledged. Ray Trowbridge provided logistic support (and good conversation!) at Dorion; Alonzo Nuttall's dependable boat service and radio contacts greatly improved my stay on Granite Island. I thank Lynn Hauta for valuable discussions and advice pertaining to this thesis. The services of Walter Momot and Helve Hobe as committee members and Bruce McGillivray as external examiner are gratefully acknowledged.

I extend special and heartfelt thanks to Beatrice Termaat for guidance, support and friendship over the course of this study. I am indebted for her help above and beyond the call of duty!

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1. INTRODUCTION

In temperate latitudes, time constraints have a profound influence on reproduction of many bird species (Welty 1982). Well-defined breeding seasons have evolved with temporal limits set by photoperiod (Welty 1982:178), temperature (Lack 1968:303), and food availability (Perrins 1970). Synchrony in breeding is especially well-developed in colonial species where an entire colony may initiate clutches in two weeks (Gochfeld 1980).

Time of breeding within a season may affect an individual's reproductive success. Generally, birds breeding late in the season have smaller eggs and clutches (Black-legged Kittiwake (*Rissa tridactyla*), Coulson and White 1961; Arctic Tern (*Sterna paradisaea*), Lemmetyinen 1973; Herring Gull (*Larus argentatus*), Parsons 1975; Red-billed Gull (*L. novaehollandiae*), Mills 1979; Long-billed Curlew (*Numenius americanus*), Redmond 1986; see McCrimmon (1978) for review) and fledge fewer, lighter chicks than do earlier-nesting conspecifics (Manx Shearwater (*Puffinus puffinus*), Perrins 1966; Herring Gull, Nisbet and Drury 1972; Glaucous-winged Gull (*L. glaucescens*), Hunt and Hunt 1976; Ring-billed Gull (*L. delawarensis*), Chardine 1978; Black-headed Gull (*L. ridibundus*), Patterson (1965) and Viskne and Janaus (1980); see McCrimmon (1978) for review). Harris (1980) found, however, that Atlantic Puffin (*Fratercula arctica*) chick survival was not influenced by laying date. Davies and Lundberg (1985) also showed that Dunnock (*Prunella modularis*) clutch sizes were not correlated with time of laying. They conjectured that ad libitum food supplied to their experimental populations may have negated natural advantages to early breeding. Several authors have suggested that very early laying could have adverse effects on reproductive performance because of food scarcity and adverse weather conditions (e.g. Perrins 1970, Brooke 1978, Burger 1982). Sealy (1975) observed auklets (Aethia sp.) that built nests before snow melted suffered lower reproductive success than those birds that postponed breeding until the snow was gone. Morris and Chardine (1985) observed a similar occurrence on a Herring Gull (Larus argentatus) colony during a season in which ice melt was delayed.

An important question arising from the above observations is "what characteristics of late nesters make them poor reproducers?". Many studies have reported an age differential between peak and late nesters (Brooke 1978, Haymes and Blokpoel 1980, Mills and Shaw 1980; see Nelson (1986) for a review of the relationship between age and breeding in seabirds). Late nesters tend to be younger than earlier nesters. Davis (1976) found that age and breeding experience of Parasitic Jaegers (Stercorarius parasiticus) affected breeding date but the two factors were difficult to assess independently. Breeding experience was not significantly correlated with laying date in Northern Fulmars (Fulmaris glacialis; Ollason and Dunnet 1978) and Coulson (1966) suggested that the number of consecutive breeding seasons with the same mate was the important factor influencing laying date of Black-legged Kittiwakes. Younger kittiwakes were subject to competition for food and space by older neighbours; inexperienced birds lacked the motivation and skill necessary to successfully raise chicks (Coulson 1966).

A neglected line of inquiry has been to compare the physical characteristics of early and late nesters. The first part of this thesis reports on the relationship between relative time of nesting and body size in Ring-billed Gulls. Ring-billed Gulls are suitable for this study because a) their colonial habit facilitates collection of relatively large samples; b) social interactions among nesting pairs are accentuated because dense aggregations of nesting individuals occur; c) there has been chronological collection of nesting data on the study colony of Ring-bills for over 10 years. Specifically, I will test the null hypothesis that skeletal measurements and total body size of late-nesting birds are the same as those of early and peak-nesting birds.

Body size is arguably one of the most important physical parameters affecting the social and reproductive histories of individuals (Trivers 1985:228). It is possible that the poor success characteristic of late nesters could be due to their small body size relative to earlier-nesting conspecifics. Small size could be a disadvantage in two ways. First, small birds may be able to amass fewer nutrients than large birds and so lay smaller, poorer quality eggs (i.e. lower amounts of protein and lipids in yolk and albumen). Small, poorly nourished young may be produced and this could subsequently reduce fledging success. This is often seen in the third egg of gull clutches. Third-egg chicks are often smaller and lighter than their siblings and suffer a much higher mortality (Parsons 1970). Secondly, small body size may put late nesters at a competitive disadvantage with their neighbours. They may be compromised at feeding sites and could have a difficult time defending the nest site. Stress and distractions from neighbours could result in less attention neing directed to eggs or chicks and nest sucess would be reduced.

Alternately, small birds may have to "squeeze in" amongst larger pairs once they have established territories and begun incubation or when territories become vacant through nest failure (Burger 1980, 1984, Fetterolf et al 1984).

The second part of this thesis concerns mate selection. There is a large body of literature addressing this subject (e.g. Lack 1940, Warriner et al 1962, Cooke et al 1972, Coulson 1972, Emlen and Oring 1977, Hunt 1980, Burley 1981, Bateson 1983). Most authors agree that choice of a mate can, to a large degree, determine the future reproductive success of the individual. Procurement of a 'good' mate (one that will improve or at least maintain an individual's level of reproductive fitness) is important in biparental species. Through courtship feeding females may be able to discern which males would likely be best at food procurement (Nisbet 1977). Degree of aggressive territorial behaviour toward other birds and the prospective mate during the early stages of pair formation has also been suggested as a direct behavioural indicator of the quality of a potential mate (Spurr 1974).

The genetic makeup of a bird influences its reproductive potential since body size (Boag and Grant 1978, Smith and Zach 1979, Smith and Dhont 1980, Gustafsson 1985), clutch/egg size (VanNoordwijk et al 1980), and perhaps other breeding characteristics have heritable components. Phenotypic expression of genotypes could be useful markers in mate selection (Halliday 1983). Mate choice for superior genotypes is presently a hotly-debated topic (Parker 1983).

Preferential mating on the basis of phenotypic characters is common in polygamous and monogamous species (see Bateson 1983). Assortative mating occurs when pair bonds are formed between individuals possessing certain phenotypes more often than expected under random mating (Partridge 1983). Mates are chosen in relation to the phenotype of the chooser (Cooke and Davies 1983). There may be single or multiple traits under consideration (Burley 1981). The literature is replete with examples of assortative mating on discontinuous characters. A vast majority of these studies have reported positive assortative mating where phenotypically similar individuals pair. O'Donald et al (1974) found populations of Parasitic Jaegers where individuals mate assortatively on the basis of colour. Interestingly, only some colour morphs mated assortatively and mating preference varied among populations. Lesser Snow Goose (Anser caerulescens) populations also have high percentages of like-colour pairings (Cooke et al 1972, Cooke et al 1976, Cooke and Davies 1983). Individuals imprint on the plumage colour of their parents and choose mates of the same colour. There did not seem to be any selective advantage in mating with a bird of the same colour. Warriner et al (1962) found that assortative mating in pigeons (Columba livia) was influenced by parental colour. Brant (Branta bernicla) populations on Southampton Island, Northwest Territories, may mate assortatively by necklace pattern (Abraham et al 1983). Negative assortative mating (disassortative mating) is rare. The only documented avian example is that of British feral pigeons where individuals of four colour morphs mate with birds of a different colour than themselves (Murton et al 1973).

Assortative mating by continuous morphometric characters is not well documented in birds. Boag and Grant (1978) found significant correlations between mated Darwin's finches (Geospiza sp.) in bill and tarsus measurements which they considered indicative of assortative mating. Coulter (1986) concluded that Common Terns (Sterna hirundo) mate assortatively on the basis of bill size.

I postulate that overall body size as well as specific skeletal characters could be important variables in assortative mating. In many species, large body size is a preferred character in mate selection (Grey Treefrog (Hyla versicolor), Gatz 1981a; American Toad (Bufo americanus), Gatz 1981b; Lesser Snow Goose, Ankney 1977). In light of Coulson's (1972) and other's findings that mate compatability is an important requisite of successful breeding, it is possible that complementarity of size could also be desirable in mated pairs. Colonial birds are especially suited to utilize body size as a selection criteria because instantaneous comparison of body size of numerous potential mates is possible.

I investigated the relationship between body size and mate selection in Ring-billed Gulls. I will test the null hypothesis that mating in this species is random with respect to overall body size or specific skeletal characters.

2. METHODS AND MATERIALS

2.1 Definitions

Clutch size: The number of eggs laid in a nest that is attended by a mated pair (Boersma 1982).

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

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

Early breeding/nesting pairs: those birds initiating clutches before peak-nesting pairs.

Peak breeding/nesting pairs: those birds initiating clutches during 4 days centred around the modal date of clutch initiation.

Late breeding/nesting pairs: the last 10 per cent of all pairs to initiate clutches on the colony (Boersma and Ryder 1983).

Egg volume: klb^2 (k= .489, l is maximum length (cm) and b is maximum width (cm)) (Ryder 1975).

Adult: birds three years of age and older. The majority of nesting Ring-bills are adults (Ludwig 1974).

Immature (=subadult): birds less than three years of age. A small number of two year old Ring-bills are found in breeding populations (Ludwig 1974).

Renesting: The laying of a second clutch in a single season to replace an earlier, destroyed clutch (Johnston and Ryder 1987).

Assortative mating: pair bonds formed between individuals with certain phenotypes more frequently than expected under random mating (Partridge 1983).

2.2 Study Area

I conducted the study on Granite Island, Black Bay, northern Lake Superior (48°43'N, 88°29'W), located approximately 80 km northeast of Thunder Bay, Ontario (Fig. 1). The island is a 60 ha granite outcrop 402 m by 102 m with steeply inclined slopes rising to about 30 m above water level (Ryder and Carroll 1978). Approximately 50 per cent of the island is covered with vegetation (see Kovacs-Nunan (1982) for description). The summit and northeastern slopes are mostly bare granite with soil-filled depressions that contain Rough Cinquefoil (Potentilla norvegica) and Kentucky Blue-grass (Poa pratensis). This portion of the island supports the majority of the nesting Ring-billed Gulls (Fig. 2). The north and northwest sides of Granite Island are steep and rocky. In 1986, 109 pairs of Herring Gulls nested on these slopes (B. Termaat, pers. comm.).

The number of Ring-billed Gulls nesting on Granite Island has increased markedly over the past decade. In 1973, Ryder (1975)

Figure 1. Location of Granite Island in northern Lake Superior (from Meathrel 1986).

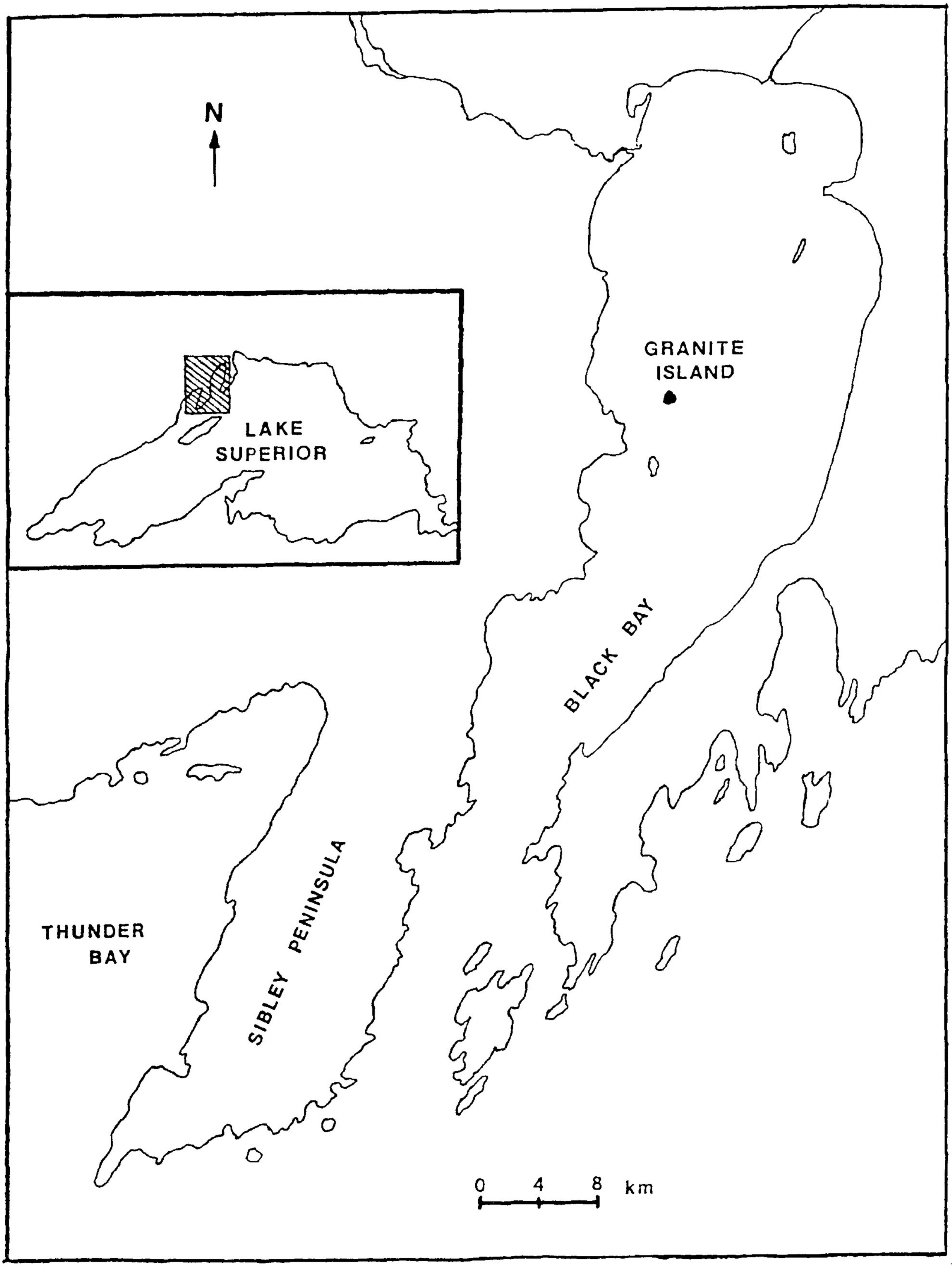
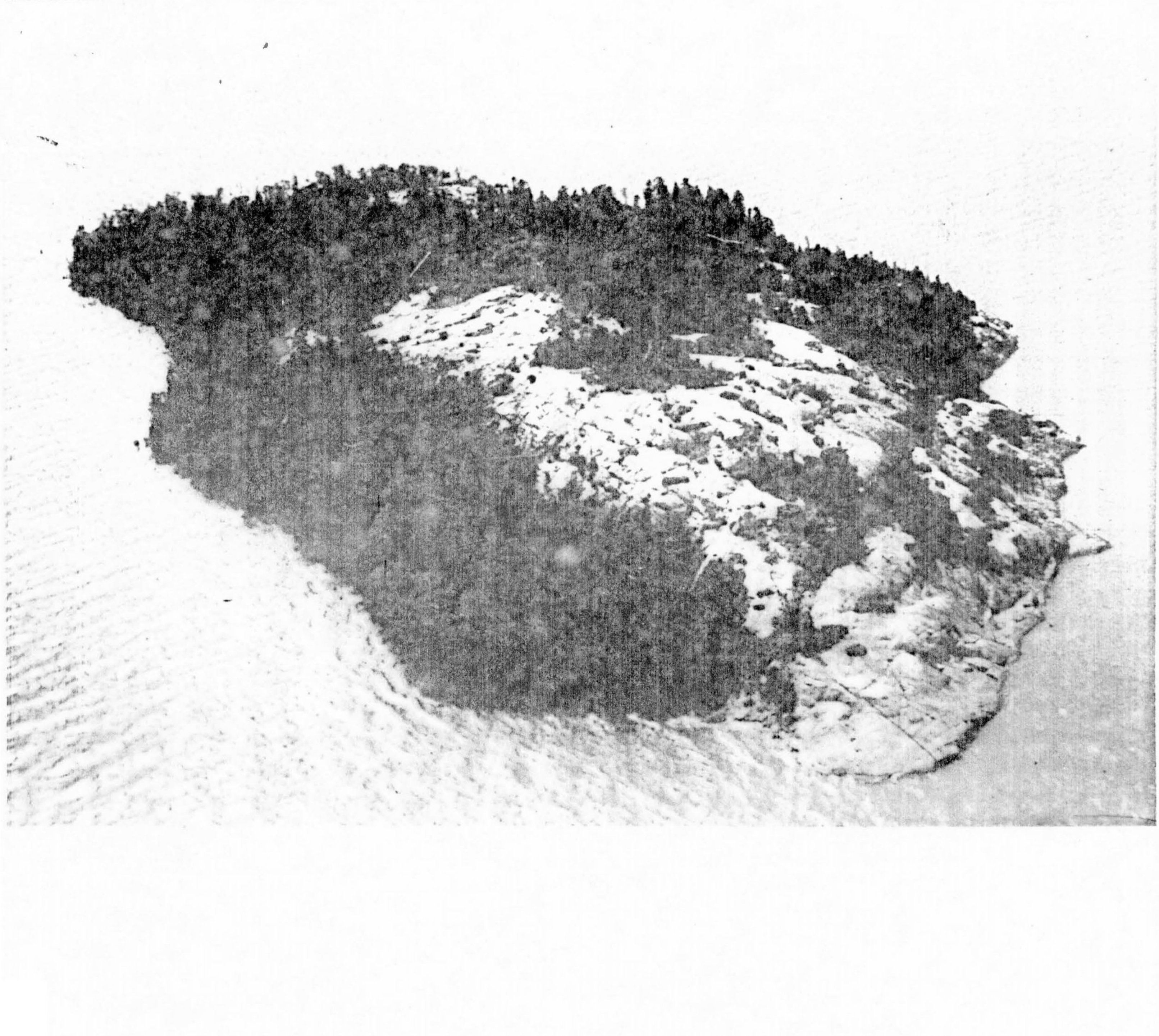

N
LAKE
SUPERIOR
GRANITE
ISLAND
BLACK BAY
THUNDER
BAY
SIBLEY PENINSULA
0
4
8
km

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



reported 800 pairs; four years later, Somppi (1978) estimated 1600 pairs. Kovacs-Nunan (1982) counted 2600 nests in 1980. In 1985, there were approximately 4800 nests on Granite Island (pers. obs.). An additional 50 species of birds were observed on and immediately adjacent to the island during this study.

I used four subsections of the Ring-bill nesting colony as study areas (Fig. 3). Two summit areas, one section of the northeastern slope, and the lower part of the northeastern slope were used to obtain data on early and peak-breeding birds. I used both summit and slope areas for data collection to minimize any potential intra-colony differences in gull morphology, physiology, and behaviour that might bias results. The entire colony (except the very steep slope areas below the summit) served as a study area for late-nesting birds. This was necessary because late nests were scattered throughout the colony. Renesting studies were conducted in the same areas.

2.3 Nesting Data

In 1985 I arrived on Granite Island on 8 May. The earliest clutches (62) had already been initiated. I marked all nests in my study areas that contained one egg by placing a numbered wooden block adjacent to each nest. Newly initiated clutches were marked each day until egg-laying was completed (to 24 June 1985). Three weeks after the peak of clutch initiation I searched the entire colony daily for late nests and marked them the same way as early and peak nests.

In 1986 I arrived on Granite Island on 3 May; the first clutches were initiated the following day. Study areas and the method of recording nests were consistent with those of 1985. I continued daily

Figure 3. Study areas on Granite Island, 1985 and 1986 (modified from Boersma 1982).

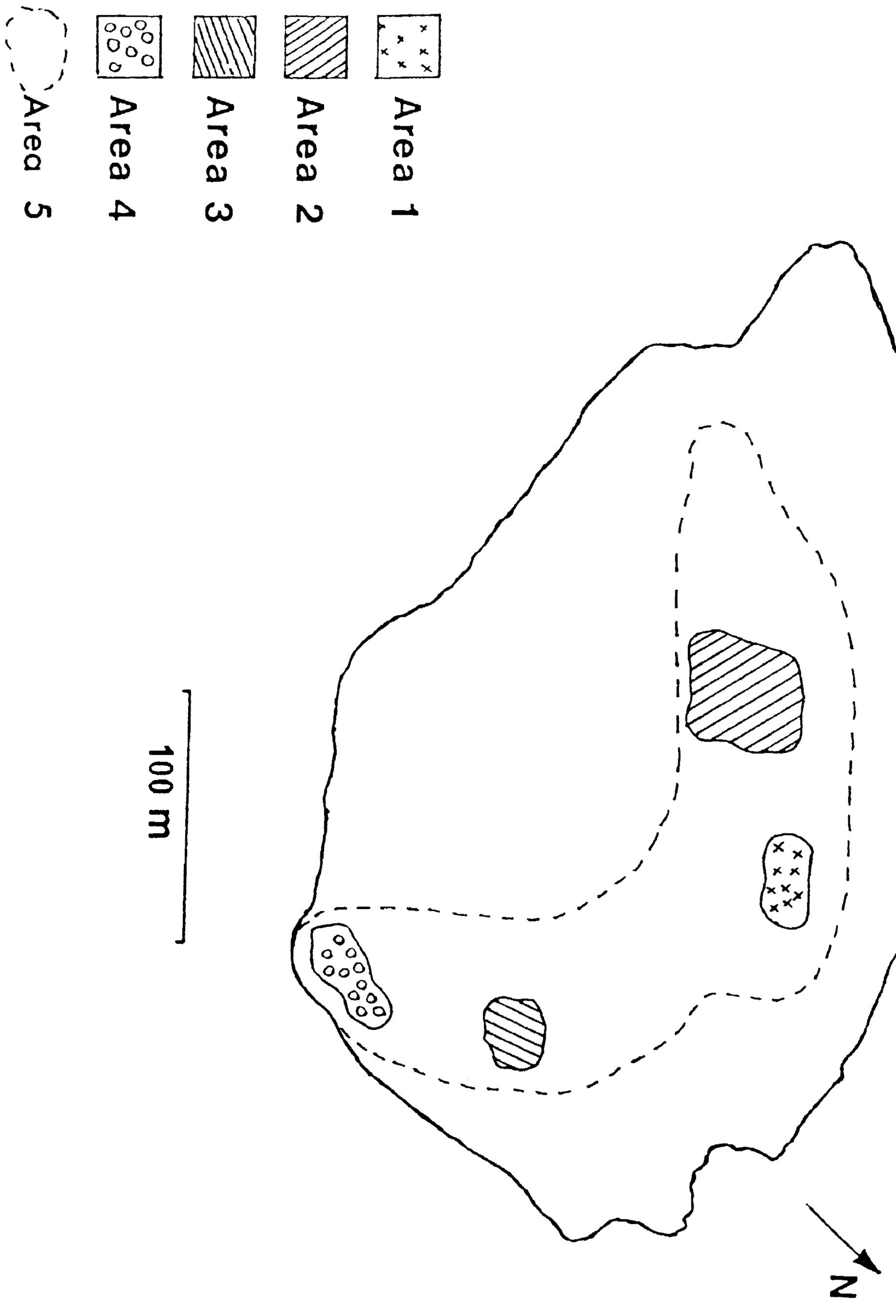
Area 1: Summit area 1.

Area 2: Summit area 2.

Area 3: Middle northeast slope.

Area 4: Lower northeast slope.

Area 5: Entire colony (for sampling late nesters).


Area 1
Area 2
Area 3
Area 4
Area 5
100 m
N

searches of the colony for late nests until 26 June.

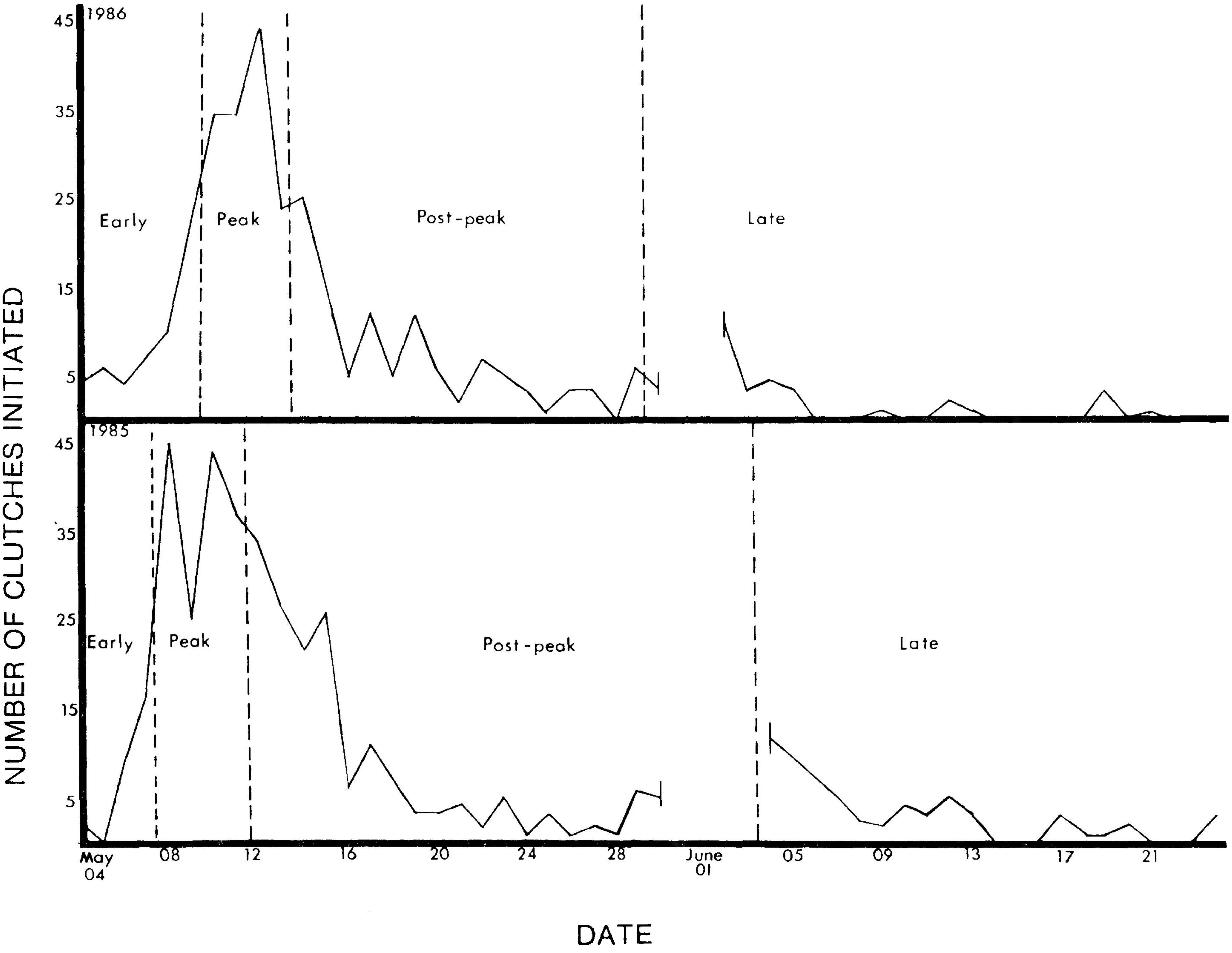
I marked eggs in study nests in the order laid by placing dots of red nail polish on the blunt end of the egg (the a-egg, b-egg, c-egg, and d-egg refer to the first, second, third and fourth egg laid in a clutch respectively). Eggs were weighed to the nearest 1 g with a 100 g Pesola spring scale within 23 h of being laid. Length and width of all eggs in a nest were taken (to the nearest 0.1 mm) with Vernier calipers 5 days after the last egg was laid in each clutch. This staggered weighing and measuring of eggs and reduced disturbance among the other nesters.

2.4 Categorization of Birds

It was important to accurately and consistently define birds as early, peak, or late nesters (hereafter, the terms egg-laying period and nesting period are used synonymously). By recording the number of nests initiated each day, the peak egg-laying period could be determined a few days after it was over. I decided on a four day peak nesting period because each year the steepest slopes on each side of the peak occurred at roughly four-day intervals (Fig. 4). By truncating the peak nesting period at 4 days I also hoped to accentuate any difference that might exist between peak and late-nesting birds.

To maximize contrasts between late birds and peak nesters, I considered the last 10 per cent of birds initiating nests to be late nesters. However, they could not be identified as late birds until nest initiation on the colony was completed. Many birds initiated clutches after the peak of nesting but were not the last 10 per cent of the population to do so. I follow Chardine (1978) and call these birds "post-peak" nesters.

Figure 4. Number of clutches initiated by Ring-billed Gulls during early, peak, post-peak, and late nesting periods on Granite Island, 1985 and 1986.


1986
1985
NUMBER OF CLUTCHES INITIATED
45
35
25
15
5
Early
Peak
Post-peak
Late
May 04
08
12
16
20
24
28
June 01
05
09
13
17
21
DATE

2.5 Collection of Adults

Each year, attending adults were captured on their nests with drop traps approximately 5 days after clutch completion (Mills and Ryder 1979). After one pair member was caught, the trap was reset to catch the mate. Once captured, birds were removed from the colony and placed in a plastic bag containing a small amount of ether. This is a humane and economical collection method; yhr nitfd firf wuivkly (less than 30 seconds) and 1L of ether lasted the entire season. The sex and body condition of each bird was determined from external measurements using the methods of Ryder (1978) and Meathrel (1986) respectively. Birds were weighed to the nearest gram on a Testut Electronique balance and marked with a numbered web-tag (National Band and Tag Co.) for future identification. All specimens were frozen on dry ice and transported to freezers at Lakehead University.

2.6 Age of Nesting Pairs

The age of some birds was determined from USFW aluminum bands that had been applied when the birds were chicks. Unbanded birds were aged as adult or immature on the basis of plumage (refer to Grant (1982) for a discussion of Ring-billed Gull plumage). Ring-billed Gulls are considered to be subadult if their plumage exhibits one or more of the following characteristics (Ryder 1975):

a) buffy coverts on the primaries; b) complete or partial subterminal tail band; c) lack of white spots on the primaries.

2.7 Renesting Experiments·

It was important to determine whether my sample consisted of late-nesters or renesters from earlier nesting periods. In 1986 I devised an experiment to discover the proportion of Ring-bills that naturally renest (i.e. discounting egg destruction by experimenters) during the late-breeding period.

I marked 27 birds chosen at random from my study areas. Five early nesters, 10 peak birds and 12 post-peak birds were marked with yellow dye (picric acid mixed with 70 per cent ethanol) on the capitum and nape (Fig. 5). Dyed birds were readily distinguishable three weeks after marking.

During the late-nesting period I scanned the colony for dyed birds attending nests other than the one they had when marked. Birds renesting in the same nest would be noticed because daily nest checks were made of all study areas.

Theoretically, the number of dyed birds that renest during late period/number of birds dyed is proportional to the total number of birds renesting during the late period/number of birds in colony. From this proportionality, I estimated the probability of categorizing renesting birds as late nesters.

2.8 Preparation of Skeletons

Birds were thawed and major soft tissue masses removed. They were then placed in an enzyme digest solution (Termaat and Ryder 1984), sealed, and held at 40°C for 2-4 days. The bones were placed in a solution of Ammodet amd water for degreasing. After 2 days they were rinsed and placed in a 3% bleach solution for 1-2 days, then rinsed and

Figure 5. Ring-billed Gull exhibiting marking technique used in renesting experiments.

dried.

2.9 Skeletal Measurements

I measured 16 skeletal characters for each specimen (see Appendix 1 and Figs. 6, 7 and 8). Character descriptions followed those of Schnell (1970) with the exception of bill width and synsacrum width. All measurements were taken with Vernier calipers to 0.01 mm.

Each character met the following criteria for use in the analysis:

a) Each major body region (see below) should be represented by one or more characters (Termaat and Ryder 1984). This criterion is especially important in this study where I wanted to obtain an accurate appraisal of the size and shape of each bird. Head, wings, legs, and trunk comprise the major body regions of a gull and each was represented in characters chosen for measurement.

b) Only one character should be chosen from a set of highly correlated characters. The use of correlated characters may lead to redundancy in the character set which may in turn lead to erroneous data interpretation (Rohlf 1967). I excluded external keel and bill measurements from analysis because they were highly correlated with internal measures of the same structures (Appendix 2).

c) Only those characters that were available for the majority of individuals should be used because discriminant tests eliminate individuals with missing data from analyses (Termaat and Ryder 1984). Only four (0.02 per cent) of 272 specimens had missing characters.

d) Characters which were easy to measure were used. A subsample of skeletons were remeasured and average per cent difference between the two sets of measures were calculated to quantify the repeatability of

Figure 6. Illustration of skull measurements. (A) Skull, dorsal view; (B) Skull, posterior view; (C) Skull and lower mandible, side view. (After Termaat and Ryder 1984; see Appendix 1 for descriptions).

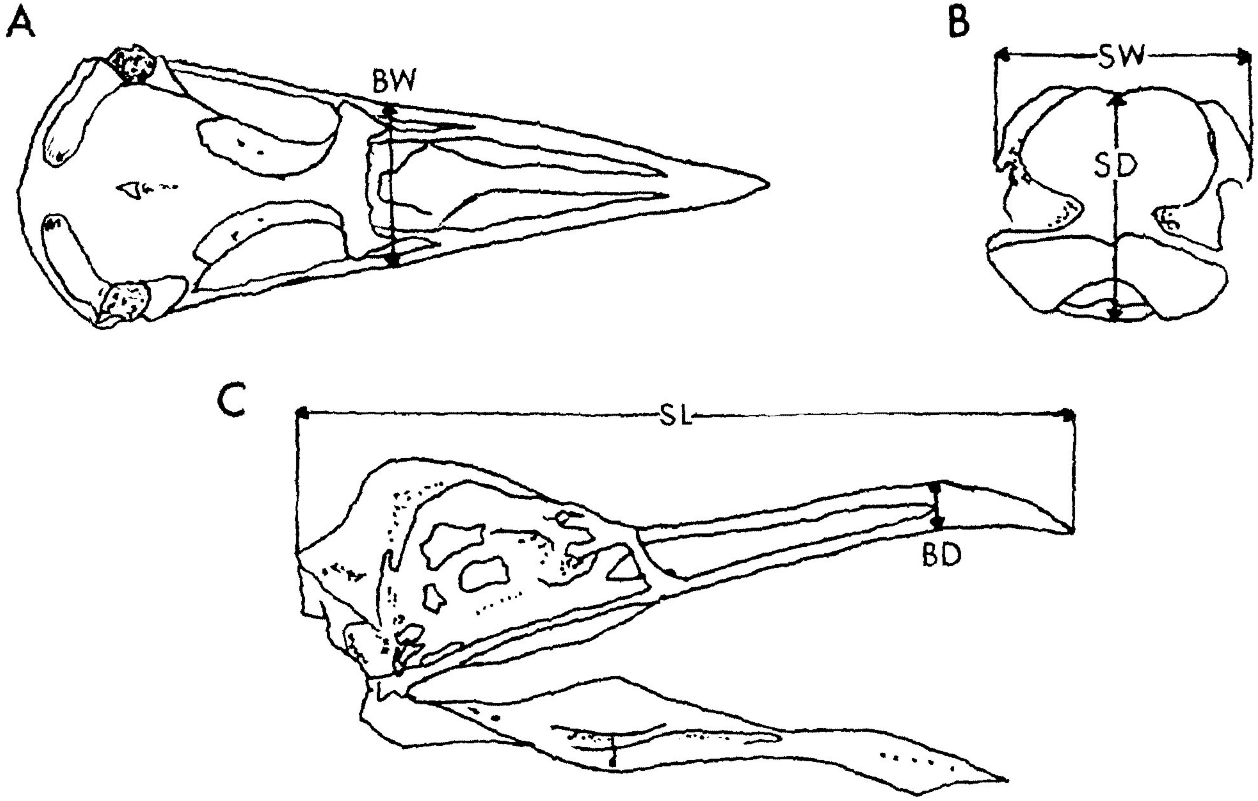

A
BW
B
SW
SD
C
SL
BD

Figure 7. Illustration of body skeletal measurements. (A) Furcula, dorsal view; (B) Sternum, lateral view; (C) Sternum, ventral view; (D) Synsacrum, dorsolateral view; (E) Synsacrum, dorsal view. (After Termaat and Ryder 1984; see Appendix 1 for descriptions).

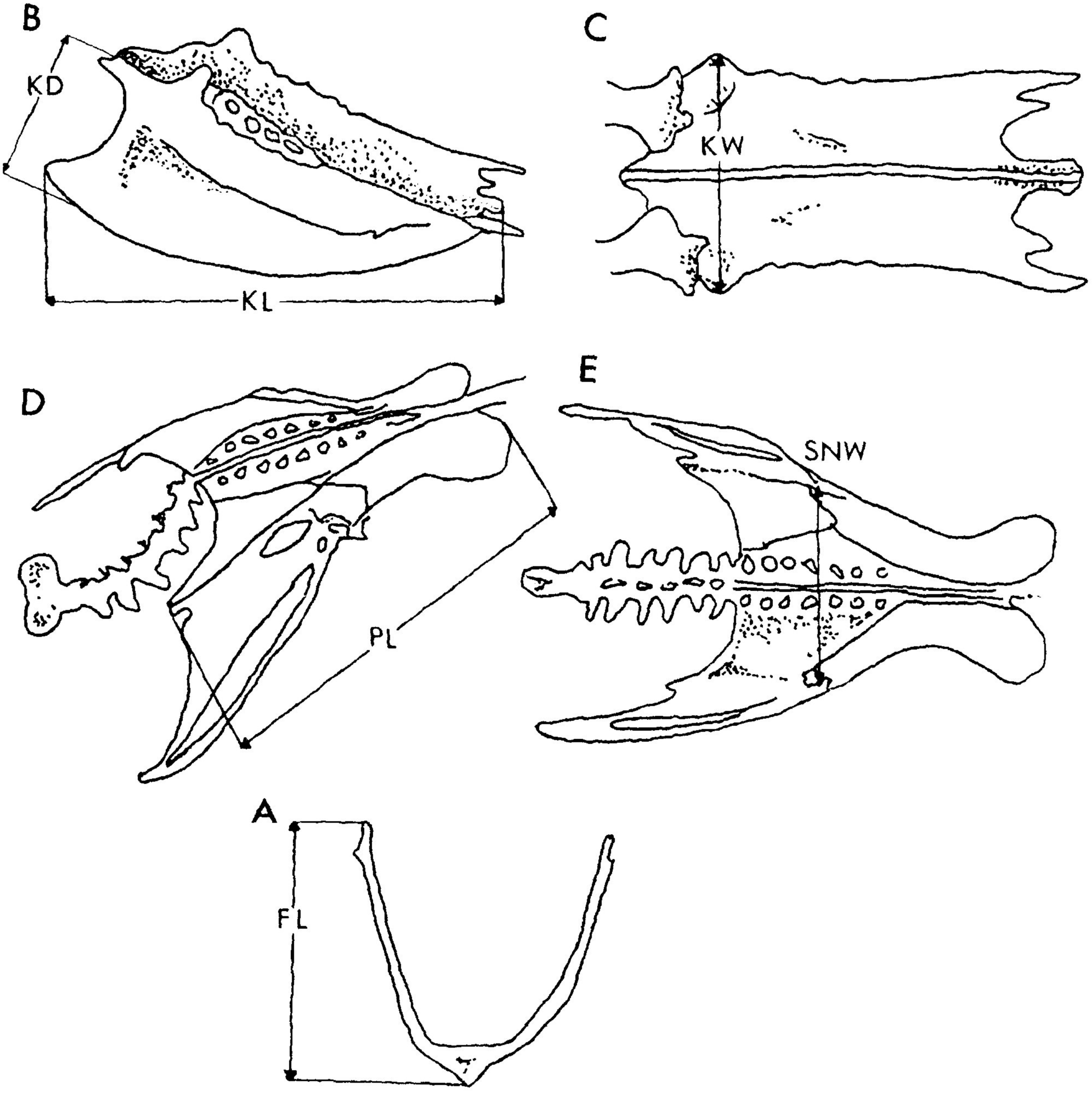
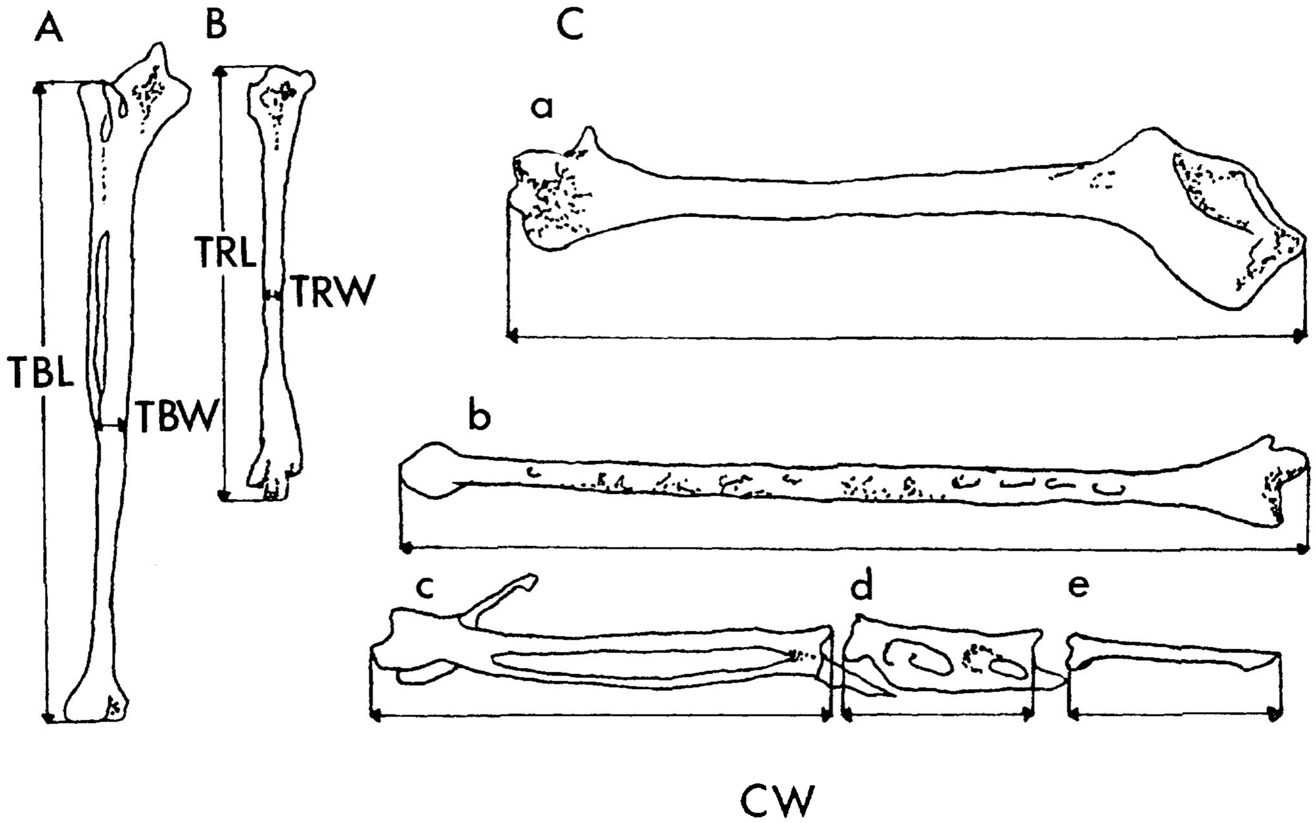

B
KD
KL
C
KW
D
PL
E
SNW
A
FL

Figure 8. Illustration of leg and wing measurements. (A) Tibiotarsus anterior view; (B) Tarsometatarsus, anterior view; (C) Composite wing measurement composed of (a) Humerus, palmar view; (b) Ulna, lateral view; (c) Carpometacarpus, lateral view; (d) Phalynx, lateral view; (e) Pollex, lateral view. (After Termaat and Ryder 1984; see Appendix 1 for descriptions).


A
B
C
TBL
TBW
TRL
TRW
a
b
c
d
e
CW

measurements.

e) It was preferable to use measurements that have been frequently used in the literature. Thirteen of 16 characters I used have been described and used by Schnell (1970) and Termaat and Ryder (1984). I changed character abbreviations from the SK format used by these authors to descriptive short forms (e.g. SL for skull length) to facilitate easier interpretation of character abbreviations.

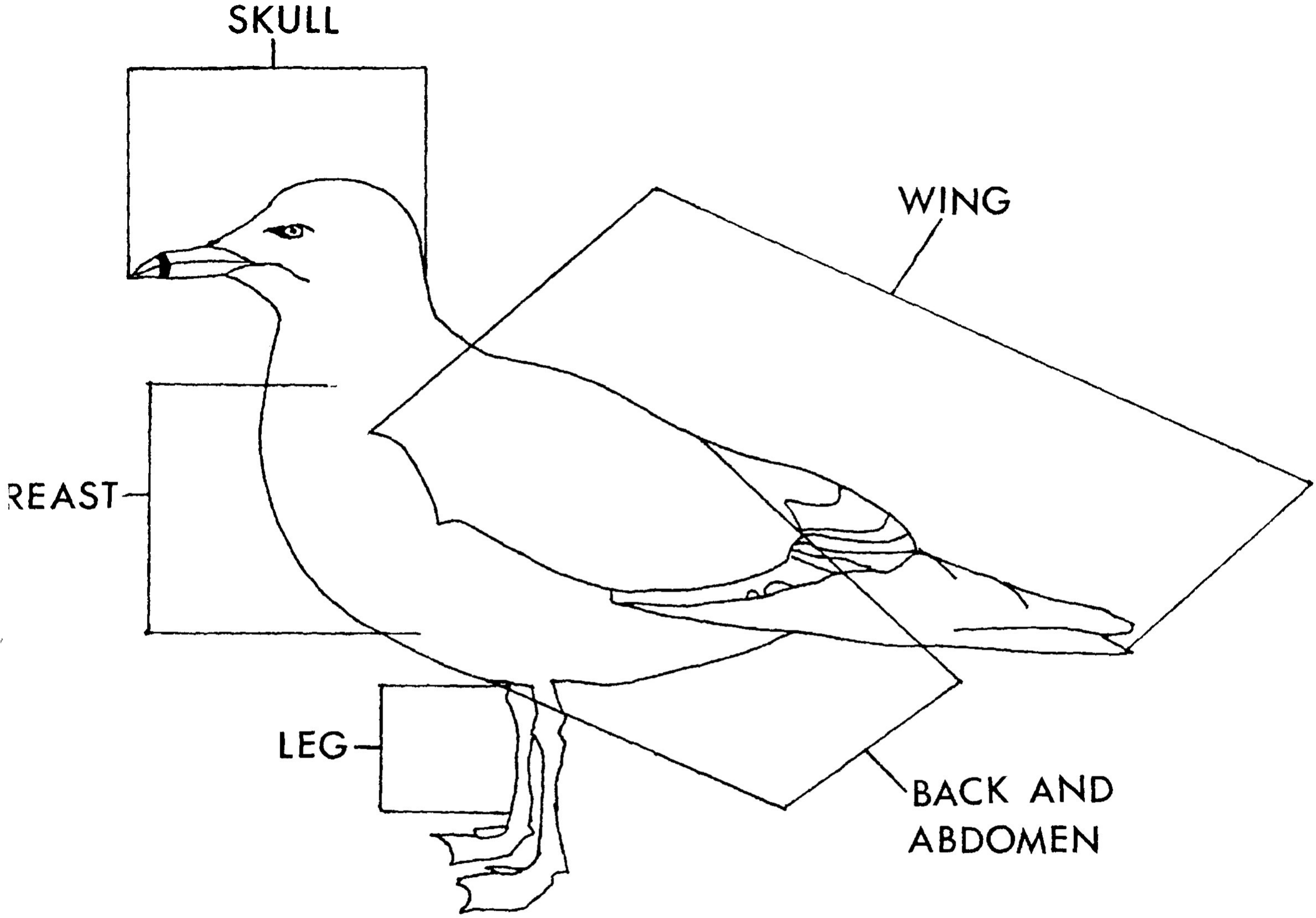
I chose characters that would reflect the size and shape of a Ring-billed Gull as seen by its conspecifics (Fig. 9). For example, femur length would be an inappropriate character to use because the femur is hidden from view by feathers and torso on a living gull. Similarly, widths of wing bones would be inappropriate measurements because feathers obscure the true width of these bones. Tibiotarsus length (TBL), on the other hand, would be an appropriate character for use because it contributes directly to the visual impression of height on a living specimen.

There has been some concern that skeletal specimens may shrink when stored for long periods of time. If there were differential periods of storage time for skeletons before they were measured, a bias could be introduced into the measurements. My calculation of measuring error (see Section 3.7) quantified this possible source of error.

2.10 Statistical Procedures

Data were entered into the VAX computer system for analysis using SPSS (Nie et al 1970) and SPSSX (SPSSX User's Guide, 1986) programs. Statistical procedures followed Sokal and Rohlf (1981) and Pimentel (1979). Differences in mensural characters between sexes, years and

Figure 9. Major body regions covered by skeletal measurements in adult Ring-billed Gulls.


SKULL
WING
REAST
LEG
BACK AND ABDOMEN

nesting periods were examined using one-way analyses of variance. Two-way analysis of variance was used to determine the relative contributions of year and season to differences in skeletal measurements. Pearson product moment correlations and average linkage cluster analysis were used to define relationships between measurements; Kolmogorov-Smirnov tests determined normality of sample populations. F-tests were used to check for assortative mating on a character-by-character basis, and Stepwise Discriminant Function Analysis was performed to a) determine if early, peak, and late-nesting birds differed in overall size, and b) compute a discriminant function that separated males and females by skeletal characters to determine if assortative mating occurs with respect to overall body size. Significance was assumed at $p < 0.05$.

3. RESULTS

3.1 Egg-laying

In 1985 the egg-laying period extended from 4 May to 24 June. A total of 380 nests were marked. Forty per cent were considered peak nests and 11 per cent late nests (Table 1). In 1986, egg-laying began on 4 May and extended to 21 June. Forty-one per cent of marked nests (n = 331) were designated peak and 11 per cent late (Fig. 4).

3.2 Clutch and egg characteristics

In both years, one-egg clutches were more frequent in late nests than in the earlier periods (Table 2). Three eggs formed the modal clutch size in early, peak, and post-peak nesting periods. Nest destruction increased with nesting period (Table 2).

Egg lengths, widths, weights, and volumes are summarized in Tables 3 and 4. Egg weight differed significantly between years except in d-eggs where length differed (Table 5). In light of these findings, egg variables were tested separately by year in subsequent analyses.

In 1985, late a-eggs were significantly smaller from those in other periods in all parameters except weight. Late b-eggs were smaller than peak b-eggs in width only. C- and d-eggs were similar over all nesting periods (Table 6).

Late 1986 a-,b-, and c-eggs were significantly smaller in most parameters than their counterparts in other periods. Only d-eggs were similar over all nesting periods. Post-peak eggs also differed from peak eggs in several variables (Table 6). Egg lengths of b- and c-eggs were different over periods but Scheffe's test could not separate any

Table 1. Egg-laying dates on Granite Island, 1985 and 1986.

Nesting period	Date of laying period	Number of pairs initiating clutches (%)
1985		
Early	May 04 - May 07	19 (5)
Peak	May 08 - May 11	148 (40)
Post-peak	May 12 - June 03	171 (45)
Late	June 04 - June 24	42 (11)
1986		
Early	May 04 - May 09	54 (16)
Peak	May 10 - May 13	136 (41)
Post-peak	May 14 - May 28	104 (32)
Late	May 29 - June 21	37 (11)

Table 2. Clutch size and nest destruction on Granite Island, 1985 and 1986.

Nesting period	Clutch size 1	2	3	4	5	Nest destruction (%)[1]
1985						
Early	0	1	17	1	0	5
Peak	5	9	122	10	2	17
Post-peak	22	22	116	9	2	22
Late	29	8	5	0	0	44
1986						
Early	3	4	41	5	0	6
Peak	8	9	109	8	2	8
Post-peak	19	26	53	4	2	19
Late	22	12	2	1	0	68

[1] nests destroyed within 2 weeks of clutch initiation

Table 3. Mean lengths, widths, weights and volumes of eggs on Granite Island, 1985.[1]

Nesting period	Length (cm)	Width (cm)	Weight (g)	Volume (cm^3)
1985				
Early				
A (n= 19)	5.88 (.21)	4.23 (.09)	58.1 (2.87)	12.1 (.45)
B (n= 19)	5.92 (.10)	4.21 (.09)	57.4 (2.15)	12.2 (.46)
C (n= 18)	5.80 (.11)	4.14 (.10)	56.4 (3.09)	11.6 (.46)
D (n= 0)	–	–	–	–
Peak				
A (n= 148)	5.91 (.27)	4.22 (.12)	58.6 (3.00)	12.2 (.67)
B (n= 143)	5.91 (.21)	4.20 (.11)	58.3 (3.88)	12.1 (.59)
C (n= 134)	5.81 (.27)	4.14 (.11)	56.0 (3.64)	11.8 (.68)
D (n= 10)	5.99 (.19)	4.13 (.19)	57.2 (5.86)	12.1 (.82)
Post-peak				
A (n= 171)	5.86 (.25)	4.17 (.11)	57.4 (4.13)	12.0 (.67)
B (n= 149)	5.87 (.21)	4.20 (.10)	58.0 (3.47)	12.0 (.59)
C (n= 127)	5.86 (.21)	4.15 (.12)	56.6 (3.56)	11.9 (.61)
D (n= 9)	5.90 (.24)	4.10 (.11)	55.6 (1.16)	11.4 (.67)
Late				
A (n= 42)	5.91 (.25)	4.05 (.13)	60.0 (5.05)	11.7 (.71)
B (n= 13)	5.92 (.18)	4.09 (.10)	56.4 (3.40)	11.8 (.63)
C (n= 5)	5.75 (.31)	4.05 (.08)	55.7 (1.16)	11.4 (.82)
D (n= 0)	–	–	–	–
Total				
A (n= 380)	5.89 (.26)	4.19 (.12)	58.0 (4.31)	12.1 (.68)
B (n= 324)	5.89 (.21)	4.20 (.11)	58.0 (3.65)	12.1 (.59)
C (n= 284)	5.83 (.24)	4.14 (.11)	56.0 (3.56)	11.8 (.64)
D (n= 19)	5.95 (.21)	4.12 (.16)	56.0 (5.11)	12.0 (.75)

[1] standard deviation in parentheses

Table 4. Mean lengths, widths, weights and volumes of Ring-billed Gull eggs on Granite Island, 1986.[1]

Nesting period	Length (cm)	Width (cm)	Weight (g)	Volume (cm^3)
Early				
A (n= 53)	5.88 (.27)	4.20 (.12)	58.9 (4.00)	12.1 (.68)
B (n= 50)	5.86 (.19)	4.20 (.09)	50.4 (3.28)	12.0 (.53)
C (n= 46)	5.76 (.26)	4.14 (.09)	56.0 (3.66)	11.6 (.66)
D (n= 5)	5.76 (.22)	4.12 (.04)	54.4 (3.85)	11.6 (.53)
Peak				
A (n= 136)	5.89 (.22)	4.22 (.09)	59.6 (3.34)	12.2 (.55)
B (n= 128)	5.92 (.34)	4.24 (.08)	60.2 (3.32)	12.3 (.80)
C (n= 119)	5.87 (.22)	4.18 (.09)	57.9 (3.07)	12.0 (.55)
D (n= 10)	5.75 (.20)	4.12 (.19)	56.8 (5.19)	11.6 (.81)
Post-peak				
A (n= 104)	5.03 (.24)	4.15 (.14)	57.4 (4.22)	11.8 (.71)
B (n= 85)	5.83 (.21)	4.17 (.14)	57.6 (4.19)	11.9 (.70)
C (n= 59)	5.85 (.22)	4.13 (.18)	56.4 (4.49)	11.8 (.82)
D (n= 6)	5.89 (.10)	4.21 (.05)	59.2 (2.17)	12.1 (.32)
Late				
A (n= 37)	5.71 (.11)	4.05 (.14)	55.3 (3.67)	11.3 (.31)
B (n= 15)	5.56 (.07)	4.01 (.05)	53.2 (3.03)	10.9 (.18)
C (n= 3)	5.64 (.12)	3.87 (.11)	54.0 (3.56)	10.6 (.22)
D (n= 0)	-	-	-	-
Total				
A (n= 330)	5.87 (.24)	4.19 (.12)	58.0 (4.01)	12.0 (.65)
B (n= 278)	5.88 (.29)	4.21 (.11)	59.2 (3.95)	12.1 (.75)
C (n= 227)	5.84 (.24)	4.16 (.12)	57.1 (3.76)	11.9 (.67)
D (n= 21)	5.78 (.18)	4.14 (.14)	57.0 (4.30)	11.7 (.67)

[1] standard deviation in parentheses

Table 5. Differences in egg measurements of Ring-billed Gulls, Granite Island, between 1985 and 1986.

	Student's t	Probability level[1]
A-egg		
length (cm)	1.19	.236
width (cm)	-0.49	.623
weight (g)	-2.49	.013*
volume (cm^3)	0.66	.515
B-egg		
length	0.61	.508
width	-1.38	.168
weight	-2.53	.012*
volume	-0.18	.845
C-egg		
length	-1.21	.227
width	-0.57	.572
weight	-1.52	.004*
volume	-0.16	.322
D-egg		
length	2.74	.011*
width	-0.46	.647
weight	-0.22	.829
volume	1.25	.223

1 * denotes significance at the 0.05 level

Table 6. Differences in egg measurements between nesting periods, 1985 and 1986.[1]

Egg measure[2]	1985 Anova (F)	1985 p[3]	1986 Anova (F)	1986 p
A				
length	.809	.4987	2.141	.096
width	10.748	<.0001	10.335	<.0001
weight	15.344	<.0001	14.291	<.0001
volume	12.418	<.0001	28.041	<.0001
B				
length	0.915	.4343	2.866	.0373
width	2.886	.0360	10.197	<.0001
weight	0.956	.4136	18.782	<.0001
volume	0.563	.6398	26.811	<.0001
C				
length	0.650	.5834	2.764	.0429
width	1.316	.2696	4.472	.0045
weight	0.517	.6706	4.210	.0064
volume	0.383	.7651	7.655	<.0001
D				
length	0.649	.4349	0.810	.4645
width	0.131	.7321	0.497	.6189
weight	0.407	.5325	1.047	.3987
volume	0.832	.3751	2.912	.0655

1 Scheffe's range tests show: 1985, late a-eggs differ from other nesting periods in width, weight, and volume; late b-eggs differ from peak b-eggs in width. 1986, late a-eggs and late b-eggs differ from other nesting periods in width, weight, and volume; early c-eggs differ from peak c-eggs in weight; late c-eggs differ from all others in volume

2 length and width in cm, weight in g, volume in cm^3

3 significance assumed at $p < 0.05$

two periods that differed significantly.

3.3 Age of trapped individuals

Fifteen trapped birds were banded previously as chicks on Granite Island. Banding data showed that their ages ranged from 4-10 years (Table 7). One member of a mated pair that I trapped was over 4 years old and the other member was 9 years old. No birds trapped were classed as subadult based on plumage characteristics. Observations in my study areas did not reveal any immature-plumaged nesters.

3.4 Trapping of adults

A total of 272 birds were collected over both years of the study (123 mated pairs and 26 birds whose mates avoided the traps; Table 8). One pair which had been designated as male and female were found by gonadal inspection to be two males. It is possible one male was caught while robbing the nest. This pair and one female trapped from a superclutch were excluded from the analyses.

3.5 Adult body condition

Body condition indices were significantly lower in females than in males ($t=6.81$, $p< 0.0001$) but were similar between years ($t=0.80$ (male), 0.47 (female), $p> 0.05$). Late-nesting birds had significantly lower body condition indices than birds from other nesting periods ($F=$ 9.65 (male), 8.78 (female), $p< 0.001$; Table 9).

Table 7. Ages of banded gulls trapped on Granite Island, 1985 and 1986.

Nesting period trapped in	Age (years)	Frequency of age group found (n= 15)
Early	4+	1
Peak	4+	7
	5+	1
	10	1
Post-peak	4+	1
	5	1
	8	1
	9	1
Late	8	1

Table 8. Summary of Ring-billed Gulls trapped on Granite Island, 1985 and 1986.

Nesting period	Number of pairs trapped			Number of single birds trapped		
	1985	1986	Total	1985	1986	Total
Early	12	14	26	1	2	3
Peak	24	14	38	2	2	4
Post-peak	33	7	40	9	3	12
Late	13	5	18	4	3	7

Table 9. Mean body condition indices of Ring-billed Gulls on Granite Island, 1985 and 1986.

Nesting period	Mean body condition indices[1]					
	1985		1986		Total	
	♂	♀	♂	♀	♂	♀
Early	4.28	3.87	4.11	3.85	4.20	3.86
Peak	4.14	3.89	4.28	4.00	4.21	3.95
Post-peak	4.30	3.11	3.97	3.70	4.13	3.41
Late	3.76	3.61	3.66	3.33	3.71	3.47

[1] Anovas tested for differences between breeding periods: F (males) = 9.651, $p < 0.0001$, F (females) = 8.775, $p < 0.0001$. Scheffe's range tests showed differences to lie between late nesters and all others.

3.6 Renesting experiments.

Renesting experiments in 1986 showed no evidence of renesting during the late period. Twenty-seven birds were dyed; five of these birds subsequently deserted their nests and remained near the colony but were not found renesting. It appeared, however, that some renesting occurred in 1986 during peak and post-peak periods (10-28 May). There was unseasonal cold and wet weather during this time. Several clutches were destroyed and new clutches were laid in the same nests a few days later. The original pairs probably deposited the new clutches because I noticed no absence of nest defence in interim periods between original and replacement clutches. This was not seen during the renesting experiment; I was primarily concerned with peak or post-peak birds renesting during the late period and so did not dye the majority of birds until the middle of the peak period.

Results of this experiment suggest that the numbers of peak and post-peak birds renesting during the late nesting period are negligible.

3.7 Measurements and measuring error

Means, standard deviations, and numbers of measurements for skeletal characters of Ring-billed gulls are presented in Tables 10-13.

I estimated measurement error of skeletal characters by remeasuring 20 per cent (n = 60) of randomly-chosen skeletons. The average per cent difference between two sets of measurements gives an estimate of measurement precision (McGillivray 1985). Only sternum width (3.3 per cent) and tibiotarsus length (4.6 per cent) had high measuring error (Table 14). Sternum width was deleted from analysis; tibiotarsus

Table 10. Means of 16 skeletal measurements (cm) and fresh weight (g) of male Ring-billed Gulls, Granite Island, 1985.

Measure[1]	Nesting Period			
	Early	Peak	Post-peak	Late
FWT	557±46.1 (12)[2]	536±35.2 (27)	531±50.3 (26)	490±33.6 (10)
SL	9.65±.30 (12)	9.54±.24 (27)	9.50±.18 (26)	9.62±.23 (10)
SW	3.25±.12 (12)	3.23±.08 (27)	3.22±.07 (26)	3.25±.04 (10)
SD	2.52±.09 (12)	2.52±.07 (27)	2.54±.07 (26)	2.55±.08 (10)
BW	1.47±.12 (12)	1.45±.07 (27)	1.44±.08 (26)	1.45±.07 (10)
BD	0.54±.02 (12)	0.53±.04 (27)	0.53±.02 (26)	0.54±.02 (10)
KL	6.45±.15 (12)	6.41±.22 (27)	6.31±.20 (26)	6.43±.20 (10)
KW	3.69±.13 (12)	3.66±.14 (27)	3.62±.12 (26)	3.69±.11 (10)
KD	3.01±.11 (12)	2.97±.11 (27)	2.96±.10 (11)	2.82±.10 (10)
SNW	3.08±.11 (12)	3.04±.10 (27)	3.03±.09 (26)	3.06±.06 (10)
PL	5.65±.17 (12)	5.68±.20 (27)	5.60±.20 (26)	5.74±.10 (10)
FL	4.32±.18 (12)	4.28±.12 (27)	4.28±.12 (26)	4.33±.09 (10)
CW	33.3±.55 (11)	33.0±.80 (27)	33.2±1.0 (25)	33.4±.91 (10)
TBL	8.65±.29 (12)	8.63±.24 (27)	8.62±.24 (26)	8.71±.18 (10)
TBW	0.43±.05 (12)	0.43±.03 (27)	0.42±.03 (26)	0.41±.03 (10)
TRL	5.74±.22 (12)	5.74±.16 (27)	5.70±.24 (26)	5.69±.39 (10)
TRW	0.29±.02 (12)	0.30±.02 (27)	0.29±.02 (26)	0.29±.02 (10)

1 measurements described in Appendix 1
2 values are means ± s.d. with sample sizes in parentheses

Table 11. Means of 16 skeletal measurements (cm) and fresh weight (g) of male Ring-billed Gulls, Granite Island, 1986.

Measure[1]	Nesting period			
	Early	Peak	Post-peak	Late
FWT	529±32.8 (15)[2]	549±40.0 (14)	510±28.8 (09)	465±48.2 (05)
SL	9.65±.22 (15)	9.62±.19 (14)	9.51±.30 (09)	9.47±.31 (05)
SW	3.24±.06 (15)	3.23±.07 (14)	3.18±.09 (09)	3.20±.05 (05)
SD	2.50±.06 (15)	2.52±.07 (14)	2.52±.07 (09)	2.45±.08 (05)
BW	1.46±.07 (15)	1.56±.03 (14)	1.41±.09 (09)	1.38±.02 (05)
BD	0.56±.02 (15)	0.56±.03 (14)	0.54±.02 (09)	0.52±.04 (05)
KL	6.50±.16 (15)	6.49±.21 (14)	6.34±.34 (09)	6.34±.33 (05)
KW	3.68±.14 (15)	3.70±.11 (14)	3.62±.22 (09)	3.62±.07 (05)
KD	3.07±.09 (15)	3.01±.11 (14)	3.05±.08 (09)	3.03±.08 (05)
SNW	3.06±.10 (15)	3.11±.09 (14)	3.06±.11 (09)	3.01±.11 (05)
PL	5.65±.24 (15)	5.77±.18 (14)	5.74±.18 (09)	5.60±.29 (05)
FL	4.33±.10 (15)	4.29±.10 (14)	4.31±.13 (09)	4.32±.11 (05)
CW	33.4±.72 (15)	33.2±.75 (14)	32.9±.76 (09)	32.9±1.4 (05)
TBL	8.79±.28 (15)	8.62±.24 (14)	8.72±.30 (09)	8.64±.30 (05)
TBW	0.43±.02 (15)	0.41±.03 (14)	0.39±.03 (09)	0.42±.02 (05)
TRL	5.84±.25 (15)	5.75±.20 (14)	5.78±.20 (09)	5.81±.36 (05)
TRW	0.30±.02 (15)	0.29±.02 (14)	0.30±.02 (09)	.029±.01 (0)

[1] measurements described in Appendix 1

[2] values are means ± s.d. with sample size in parentheses

Table 12. Means of 16 skeletal measurements (cm) and fresh weight (g) of female Ring-billed Gulls, Granite Island, 1985.

Measure[1]	Nesting period			
	Early	Peak	Post-peak	Late
FWT	468±36.1 (12)[2]	464±39.6 (27)	456±46.5 (28)	430±32.6 (08)
SL	8.77±.19 (12)	8.78±.19 (27)	8.84±.28 (28)	8.86±.08 (08)
SW	3.03±.03 (12)	3.02±.07 (27)	3.00±.10 (28)	3.03±.04 (08)
SD	2.38±.06 (12)	2.40±.09 (27)	2.42±.07 (28)	2.42±.06 (08)
BW	1.40±.16 (12)	1.31±.07 (27)	1.33±.09 (28)	1.35±.05 (08)
BD	0.49±.03 (12)	0.48±.03 (27)	0.48±.02 (28)	0.48±.03 (08)
KL	6.05±.13 (12)	6.03±.13 (27)	5.98±.22 (28)	6.00±.13 (08)
KW	3.42±.13 (12)	3.53±.59 (27)	3.41±.13 (28)	3.44±.12 (08)
KD	2.82±.05 (12)	2.82±.09 (27)	2.80±.11 (28)	2.84±.07 (08)
SNW	2.92±.10 (12)	2.90±.09 (27)	2.89±.09 (28)	2.92±.13 (08)
PL	5.23±.30 (12)	5.17±.26 (27)	5.12±.56 (28)	5.24±.18 (08)
FL	3.99±.10 (12)	3.91±.36 (27)	4.01±.17 (28)	3.94±.10 (08)
CW	31.3±.63 (12)	31.2±.74 (27)	31.3±.96 (26)	31.3±.79 (07)
TBL	8.22±.18 (12)	8.18±.25 (27)	8.18±.24 (28)	8.24±.27 (08)
TBW	0.41±.03 (12)	0.39±.03 (27)	0.38±.03 (28)	0.40±.02 (08)
TRL	5.46±.20 (12)	5.44±.22 (27)	5.36±.17 (28)	5.41±.02 (08)
TRW	0.28±.02 (12)	0.27±.02 (27)	0.27±.02 (28)	0.27±.01 (08)

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[1] measurements described in Appendix 1

[2] values are means ± s.d. with sample size in parentheses

Table 13. Means of 16 skeletal measurements (cm) and fresh weight (g) of female Ring-billed Gulls, Granite Island, 1986.

Measure[1]	Nesting period			
	Early	Peak	Post-peak	Late
FWT	459±34.8 (15)[2]	479±34.1 (17)	434±48.2 (09)	398±32.6 (07)
SL	8.79±.23 (15)	8.85±.19 (17)	8.75±.15 (09)	8.81±.25 (07)
SW	3.05±.07 (15)	3.05±.07 (17)	3.06±.06 (09)	3.08±.08 (07)
SD	2.43±.05 (15)	2.44±.07 (17)	2.41±.05 (09)	2.46±.04 (07)
BW	1.35±.05 (15)	1.32±.07 (17)	1.36±.06 (09)	1.32±.04 (07)
BD	0.51±.02 (15)	0.51±.02 (17)	0.49±.02 (09)	0.51±.03 (07)
KL	6.06±.20 (15)	6.05±.18 (17)	6.01±.13 (09)	6.19±.12 (07)
KW	3.38±.15 (15)	3.41±.12 (17)	3.31±.09 (09)	3.34±.13 (07)
KD	2.90±.07 (15)	2.87±.08 (17)	2.83±.09 (09)	2.87±.09 (07)
SNW	2.87±.10 (15)	2.89±.11 (17)	2.86±.13 (09)	2.90±.10 (07)
PL	5.24±.18 (15)	5.29±.26 (17)	5.25±.20 (09)	5.17±.12 (07)
FL	4.00±.19 (15)	3.40±.13 (17)	3.96±.09 (09)	4.01±.11 (07)
CW	30.9±.81 (15)	30.9±.71 (17)	30.9±1.2 (09)	31.3±.82 (07)
TBL	8.11±.26 (15)	8.13±.06 (17)	8.13±.37 (09)	8.18±.25 (07)
TBW	0.40±.05 (15)	0.38±.02 (17)	0.38±.02 (09)	0.38±.02 (07)
TRL	5.33±.21 (15)	5.31±.21 (17)	5.37±.31 (09)	5.33±.09 (07)
TRW	0.27±.02 (15)	0.27±.01 (17)	0.28±.01 (09)	0.29±.03 (07)

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1 measurements described in Appendix 1
2 values are means ± s.d. with sample size in parentheses

Table 14. Repeatability of skeletal measurments[1].

Skeletal character	Repeatability (%)
SL	0.2
SW	0.3
SD	1.3
BD	0.2
BW	0.3
KL	0.5
KW	3.3
KD	1.6
SNW	0.2
PL	0.4
FL	0.2
CW	0.2
TBL	4.6
TBW	0.5
TRL	0.4
TRW	1.0

[1] repeatability = average mean difference between two sets of measures on a skeletal character. Keel width and tibiotarsus length were considered to have unacceptable levels of measurement uncertainty. KW was deleted from analysis; TBW was retained because it is the major measure of lower body height.

length was retained because I considered it to be a good field indicator of body height.

3.8 Male-Female comparisons

In previous studies on Granite Island male Ring-billed Gulls were on average 11 per cent larger than females (Ryder 1978). Sexual size dimorphism was confirmed in this study. One-way analyses of variance showed highly significant differences between all male and female measurements ($p< 0.001$; Table 15). In light of these findings, further analyses were conducted separately by sex.

3.9 Comparisons between years

Two variables on males (BD, KD) and six variables on females (SW, SD, BD, KD, CW, TRL) differed significantly between years (Appendices 3 and 4). Two-way analyses of variance showed these differences were caused by sampling variation between years and not differences in nesting period within the breeding season (Table 16). All subsequent analyses comparing skeletal characters by nesting period were performed separately by year.

3.10 Univariate comparisons between nesting periods.

There were no significant differences in skeletal measurements between nesting periods in either year or sex (Tables 17 and 18). Upper mandible depth differed significantly among 1986 males, but Scheffe's range test failed to determine which nesting period differed from the others. Fresh weight was significantly different between nesting periods for each sex and year except 1985 females. Late

Table 15. Mean male and female measurements and differences in measurements by sex.[1]

Measure[2]	male	female	F[3]
FWT	527.50	455.50	165.8
SL	9.58	8.81	685.6
SW	3.23	3.04	414.2
SD	2.52	2.41	138.8
BW	1.42	1.33	79.7
BD	0.54	0.49	176.4
KL	6.41	6.03	209.1
KW	3.66	3.42	61.6
KD	3.01	2.84	159.4
SNW	3.06	2.89	157.3
PL	5.65	5.21	175.5
FL	4.31	3.97	225.1
CW	33.17	31.11	345.1
TBL	8.67	8.16	231.5
TBW	0.42	0.39	57.3
TRL	5.76	5.37	169.5
TRW	0.29	0.27	69.1

1 1985 and 1986 data combined
2 FWT in g; all others in cm
3 all significant at $p < 0.001$

Table 16. F-values partitioning the effects of year and nesting period on variation in skeletal measurements[1].

Skeletal measure	Year		Nesting period		Year X Nesting period	
	F	p[2]	F	p	F	p
BD ♂	6.416	.013	1.703	.171	1.700	.171
KD ♂	7.840	.006	1.239	.299	0.192	.902
SW ♀	7.473	.007	0.378	.769	0.407	.748
SD ♀	6.747	.012	0.908	.440	0.773	.511
BD ♀	13.328	.0001	0.445	.722	0.427	.734
KD ♀	11.368	.001	1.027	.384	0.336	.800
CW ♀	5.136	.025	0.116	.950	0.038	.990
TRL ♀	4.985	.028	0.435	.728	0.840	.475

1 skeletal characters presented here were significantly different between years according to one-way analyses of variance.
2 significance assumed at $p < 0.05$

Table 17. Univariate comparisons between nesting periods of male Ring-billed Gulls, 1985 and 1986.

Skeletal character	F	
	1985	1986
FWT	4.793[1]	7.259[1]
SL	1.139	1.193
SW	0.636	2.014
SD	0.685	1.454
BW	0.307	1.793
BD	0.269	3.375[2]
KL	1.852	1.235
KW	1.148	0.701
KD	0.602	0.889
SNW	1.072	1.459
PL	1.546	1.255
FL	0.681	0.375
CW	0.871	0.981
TBL	0.326	1.011
TBW	0.665	2.497
TRL	0.215	0.350
TRW	0.868	0.363

[1] $p < 0.01$

[2] $p < 0.05$

Table 18. Univariate comparisons between nesting periods of female Ring-billed Gulls, 1985 and 1986.

Skeletal character	F	
	1985	1986
FWT	1.692	8.893[1]
SL	0.601	0.551
SW	0.415	0.371
SD	1.020	1.016
BW	2.344	1.469
BD	0.085	1.046
KL	0.699	1.584
KW	0.543	1.345
KD	0.725	1.206
SNW	0.411	0.201
PL	0.277	0.597
FL	0.869	0.329
CW	0.033	0.113
TBL	0.200	0.089
TBW	2.757	0.900
TRL	1.187	0.161
TRW	0.564	1.284

[1] $p < 0.0001$

nesters weighed less than early and peak nesters and 1986 post-peak females weighed less than peak females. Late breeding birds had significantly lower body condition indices than individuals from other nesting periods (Table 9, Fig. 10).

3.11 Multivariate comparisons of size differences between nesting periods

Discriminant analysis was performed only on 1985 skeletal data because late samples from 1986 were too small (five pairs). Combined data from both years were not used because of significant differences in some measurements between years.

Discriminant functions with significant chi-square statistics were generated in males and females. Overall size seemed to be the major basis for discrimination in both sexes as was evinced by the uniformity of sign in the first canonical functions (Tables 19 and 20). The first function for males showed postorbital width and leg length characters to be the most important discriminating variables. In females, most of the characters I measured contributed to the function; CW, SL, KL, FL, and TBL were especially important in differentiating between nesting periods.

Although the discriminant functions were significant, they failed to correctly classify birds into their proper nesting periods (Table 21, Fig. 11). Scatterplots (Figs. 12 and 13) showed that while group centroids may have been separable, overlap in size of birds from all nesting periods was so great that the discriminant functions were meaningless.

I attempted a two-group discriminant analysis to accentuate any

Figure 10. Mean body condition indices of Ring-billed Gulls from Granite Island over the breeding season. M = male, F = female; bars denote standard deviations about means.

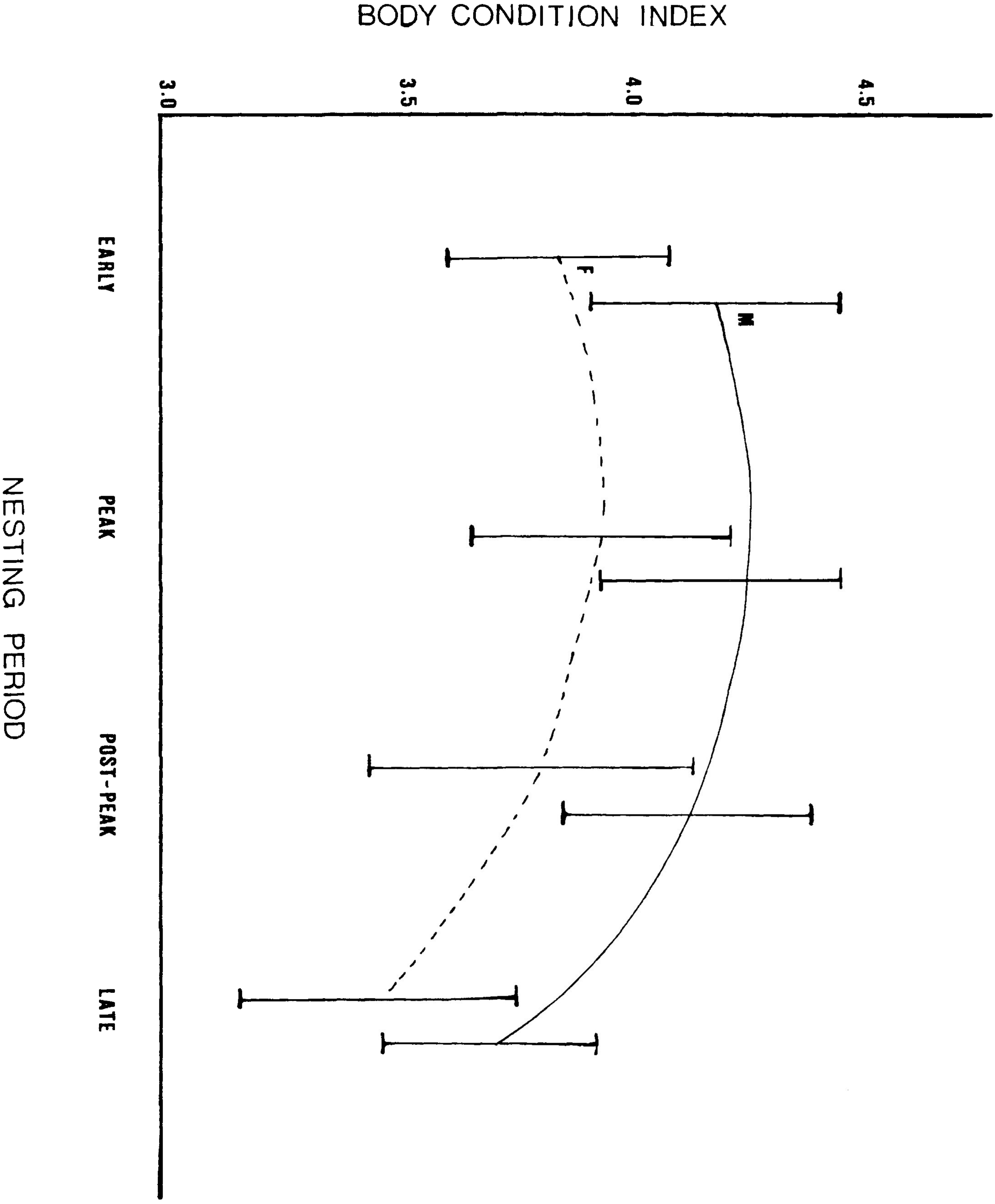

BODY CONDITION INDEX
3.0
3.5
4.0
4.5
EARLY
PEAK
POST-PEAK
LATE
F
M
NESTING PERIOD

Table 19. Standardized discriminant functions for separating male Ring-billed Gulls by nesting period[1].

Skeletal character	Standardized coefficients		
	Function 1[2]	Function 2[3]	Function 3[4]
SL	0.23127	0.68051	0.75229
SW	1.08730	0.45397	0.49746
KL	0.06592	1.02856	0.14196
KW	0.11918	0.12353	0.73945
CW	0.55052	1.31216	0.64735
TBL	0.79410	0.60527	0.04563
TRL	0.57748	0.21764	0.51413

1 according to first function, overall size is the basis of discrimination with skull, wing and leg characters contributing most to separation.
2 Wilks lambda = .1576392, χ^2= 43.415, p = 0.0028
3 Wilks lambda = .3697800, χ^2= 23.379, p = 0.0247
4 Wilks lambda = .6889674, χ^2= 0.755, p = 0.1192

Table 20. Standardized discriminant functions for separating female Ring-billed Gulls by nesting period.[1]

Skeletal character	Standardized Coefficients		
	Function 1[2]	Function 2[3]	Function 3[4]
SL	4.53226	0.85920	0.28200
SW	1.30169	0.30186	0.09544
SD	0.75708	0.21032	0.24841
BW	0.54830	1.09942	0.35843
KW	1.35992	0.05717	0.04112
SNW	1.96258	0.54896	0.52616
KD	2.60624	-1.23244	0.45624
FL	2.40451	0.10824	1.23625
PL	1.55094	0.07041	0.30739
CW	4.28771	0.89605	0.31849
TBL	2.85252	-0.75690	0.52571
TBW	0.39874	1.42622	0.18078
TRW	0.94677	0.82626	0.27690

[1] according to first function, overall size is the basis of discrimination; wing length and skull length are the most important contributors to separation.
[2] Wilks lambda = 0.0343778, χ^2= 62.351, p = 0.0102
[3] Wilks lambda = 0.2907216, χ^2= 22.855, p = 0.5824
[4] Wilks lambda = 0.7279529, χ^2= 5.8741 p = 0.8816

Table 21. Classification results of male and female Ring-billed Gull discriminant analysis[1].

Actual group	Number of individuals	Predicted group membership	
		Correct (%)	Incorrect (%)
MALES			
Early	11	7 (63.6)	4 (36.4)
Peak	27	13 (48.1)	14 (51.8)
Post-peak	25	11 (44.0)	14 (56.0)
Late	10	2 (20.0)	8 (80.0)
Total	73	33 (45.2)	40 (54.8)
FEMALES			
Early	12	7 (58.3)	5 (41.7)
Peak	26	17 (65.4)	9 (34.6)
Post-peak	26	11 (42.3)	15 (55.6)
Late	7	3 (42.8)	4 (57.1)
Total	71	38 (53.5)	33 (46.5)

1 only birds from 1985 were used in generation of discriminant function

Figure 11. Mean discriminant scores of Ring-billed Gulls from Granite Island over the breeding season. M = male, F = female; bars denote standard deviations about means. Scores computed from first canonical functions based on skeletal measurements.

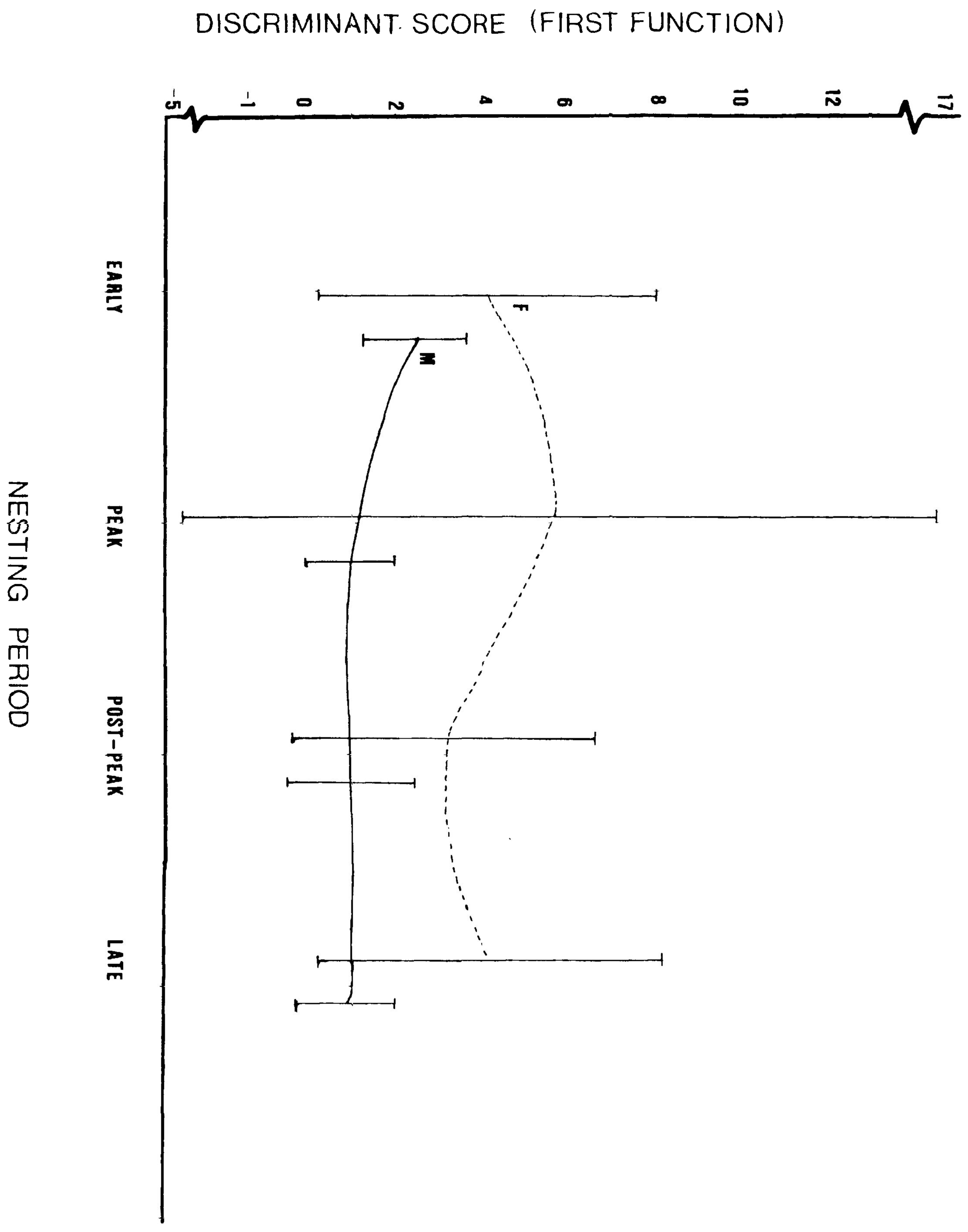

DISCRIMINANT SCORE (FIRST FUNCTION)
-5
-1
0
2
4
6
8
10
12
17
F
M
EARLY
PEAK
POST-PEAK
LATE
NESTING PERIOD

Figure 12. Scatterplot showing relationship between male Ring-billed Gulls from different nesting periods according to first two canonical functions from discriminant function analysis. Functions were based on skeletal measurements; 1 = early nester, 2 = peak nester, 3 = post-peak nester, 4 = late nester.

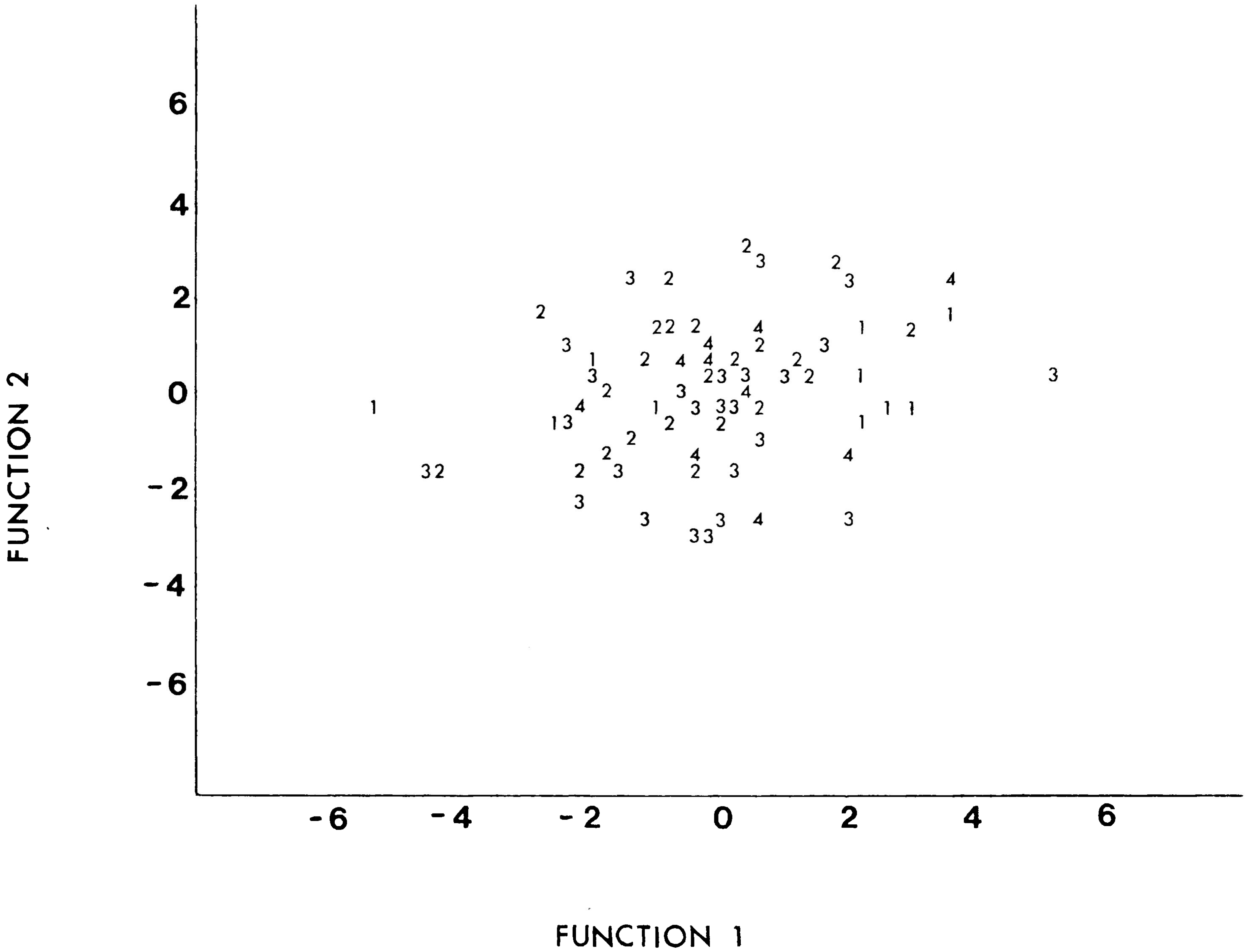
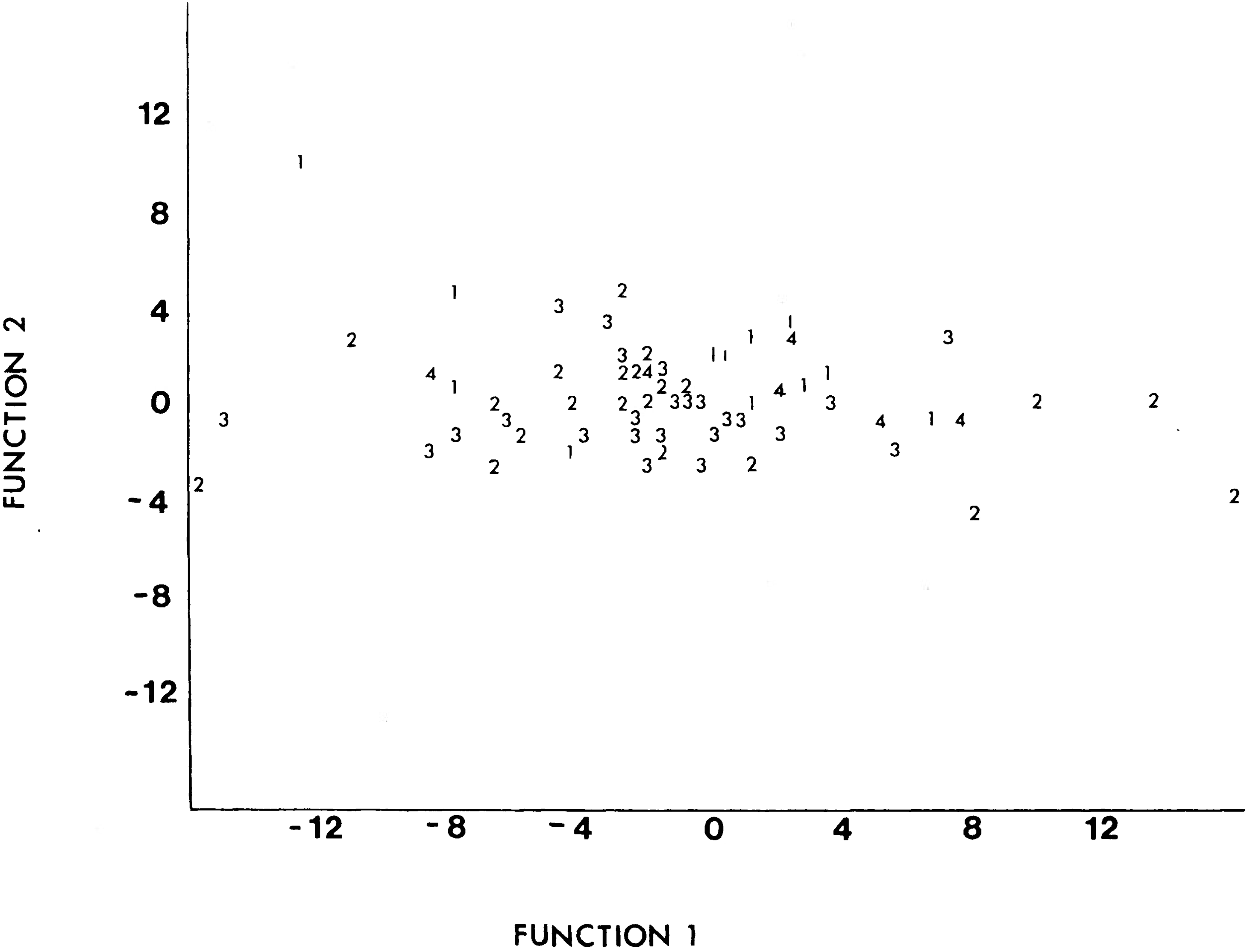

FUNCTION 2
6
4
2
0
-2
-4
-6
-6
-4
-2
0
2
4
6
FUNCTION 1

Figure 13. Scatterplot showing relationship between female Ring-billed Gulls from different nesting periods according to first two canonical functions from discriminant function analysis. Functions were based on skeletal measurements; 1 = early nester, 2 = peak nester, 3 = post-peak nester, 4 = late nester.


FUNCTION 2
12
8
4
0
-4
-8
-12
-12
-8
-4
0
4
8
12
FUNCTION 1

differences that might exist between late and peak nesters. Early and peak birds were lumped together as the "early" group; post-peak birds were excluded from analysis. No significant discriminant function was obtained for the males (Wilk's lambda= 0.442, χ^2= 11.41, p= 0.076). Although a significant function was calculated for female Ring-bills (Wilk's lambda= 0.248, χ^2= 16.70, p= 0.010), classification proved it to be of no value in separating birds from different nesting periods.

3.12 Univariate tests for assortative mating

I used F-tests to test the hypothesis that variances between male and female measurements were greater in randomly created pairs than in mated pairs. By this test I could determine if mating was random with respect to specific skeletal characters. Results are mixed; some measures (particularly skull and bill characters) exhibited significantly greater variance in randomly assigned pairs (Table 22). Scatter diagrams did not suggest either a linear or a non-linear relationship between paired male and female measurements (Appendices 5 to 22). Significant regressions were calculated within pairs for SL, CW, and TBW, but correlation coefficients were very low (Table 23). Body condition and fresh weight were also significantly different between real and random pairs. Although scatter diagrams did not show any obvious relationships in intra-pair fresh weights and condition indices, significant regressions within pairs were computed with moderately high significance of r (FWT= 0.47, BC= 0.43; Table 23). In general it seems that non-random mating occurs by body condition and fresh weight but not by single skeletal characters.

Table 22. Mean differences between male and female measurements in randomly-generated and actual pairs of Ring-billed Gulls.

Variable[1]	Mean difference (cm)[2]		F
	Random pairs[3]	Actual pairs	
FWT	71.954	68.704	1.84[4]
SL	0.754	0.748	1.41[5]
SW	0.207	0.196	1.33[6]
SD	0.113	0.101	1.10
BW	0.135	0.125	1.73[4]
BD	0.053	0.048	2.00[4]
KL	0.393	0.359	1.22
KW	0.242	0.222	1.00
KD	0.158	0.156	1.40[6]
SNW	0.138	0.160	1.18
PL	0.408	0.452	1.01
FL	0.352	0.325	1.02
CW	2.682	1.888	2.04[4]
TBL	0.486	0.470	1.04
TBW	0.028	0.030	1.50[5]
TRL	0.327	0.351	1.03
TRW	0.020	0.021	1.00
BC[7]	1.759	1.116	1.58[5]

---

1 FWT in g; all others except BC in cm
2 mean difference = male measure - female measure within a pair
3 randomly-generated pairs of gulls
4 $p < 0.005$
5 $p < 0.025$
6 $p < 0.05$
7 BC = body condition index

Table 23. Regression analysis on variables that differed between actual and randomly-mated pairs of Ring-billed Gulls.

Variables	a-intercept	b (slope)	r[1]	p
BC	24.66	0.43	0.43	0.0001
FWT	294.66	0.51	0.47	0.0001
SL	7.01	0.29	0.25	0.004
SW	3.20	0.008	0.008	0.470
SD	2.65	-0.060	-0.050	0.290
BW	1.62	-0.110	-0.070	0.230
BD	0.48	0.120	0.110	0.130
KD	2.36	0.220	0.100	0.020
CW	25.76	0.240	0.240	0.010
TBW	0.34	0.200	0.180	0.030

[1] magnitude of r indicates the strength of association between the variable under consideration and mate choice in Ring-billed Gulls

3.13 Multivariate tests for assortative mating

Discriminant analysis was used to produce a function that best discriminated between male and female gulls (Table 24). The function was highly significant (2.49(SL) + 5.11(SW) + 1.42(SD) + 1.52(BW) + 0.77(FL) + 0.76(PL); $p < 0.0001$) and assigned only three per cent of individuals to the wrong sex. A discriminant score was calculated for each bird; these scores were then run through Pearson correlation analyses where each female's score was matched with her mate's score. A significant but low positive correlation resulted between male and female size within pairs (Pearson coefficient= 0.2675, p= 0.003). In random pairs, correlation of male and female scores was not significant (Pearson coefficient= 0.0709, p= 0.232). It appears that there is positive assortative mating by body condition and to a lesser degree by total body size between male and female Ring-billed Gulls.

Table 24. Discriminant function calculated to separate Ring-billed Gulls by sex.

Skeletal character	Standardized coefficients[1]
SL	2.488312
SW	5.114329
SD	1.422474
BW	1.520279
FL	0.768807
PL	0.759330

[1] Wilks lambda = 0.2128, = 357.41, $p < 0.0001$

4. DISCUSSION

4.1 Size and body condition, reproductive success, and nesting period

4.1.1 Differences in reproductive success between nesting periods

A comparison of reproductive success among pairs nesting at different times in the breeding season was not possible because most late nesters were collected prior to egg hatch. However, early indications of reproductive success (small egg and clutch size, nest destruction) showed that late nesters were less successful than earlier-nesting conspecifics (Tables 2 and 6). Previous data from the Granite Island colony suggested that the trends outlined above continue through hatching and fledging. Boersma and Ryder (1983) reported that late nesters fledged fewer young than early nesters. Ryder (1975) demonstrated poorer nest success in late breeders, and Ryder and Ryder (1981) found that all parameters of reproductive success were directly influenced by time of nesting. Meathrel (1986) noted poor hatching success among her late-nesting sample on Granite Island.

Differences in reproductive success between early and peak nesters were not found in this or other studies on the island. This is, perhaps, to be expected since early nesters in this colony precede peak nesters by only a few days. By contrast, late nesters may lay as much as six weeks after the majority of pairs have initiated their clutches. Climate-related restrictions on breeding site suitability and food supply simply do not allow a substantial number of pairs to nest well ahead of the mean. I suggest that in colonies with protracted laying at the beginning of the season, demarcation of early nesters is artificial.

4.1.2 Size and body condition differences between nesting periods

Univariate comparisons showed that gulls from different nesting periods are not distinguishable by any single skeletal measurement (Tables 17 and 18). Similarly, birds from different nesting periods could not be differentiated on the basis of overall body size and/or shape (Table 21). Small physical size, then, cannot explain the markedly poorer reproductive success exhibited by late nesters. Jarvinen and Vaisanen (1984) found no size differences between early and late breeding Pied Flycatchers (Fidecula hypoleuca). They based this conclusion, however, on only one external body measurement (wing length). Wing length alone may not provide an adequate assessment of body size. Coulson (pers. comm.) did not find a relationship between body size and reproductive success or time of breeding in kittiwakes. The most successful female in his colony was actually below average size. Body fat content is an indicator of an individual's condition and quality (Coulson and Thomas 1985, Bailey 1979). Perhaps body quality (based on body condition) and not body size influences an individual's reproductive success.

Murphy (1986) found that variation in time of breeding in Eastern Kingbirds (Tyrannus tyrannus) was significantly correlated with estimates of body size based on skeletal measurements and muscle weights. Small females of this species bred earlier and laid larger eggs than did larger females. He pointed out, however, that there was at best a weak relationship between body size and breeding date when muscle weight was held constant. Because muscle is an actively metabolizing tissue that can be quickly influenced by nutrient supply and general health of the organism, it is a crude estimate of body condition. Murphy (1986) also found that egg size (but not clutch size) was a function of muscle weight/body condition.

Murphy's results are in accordance with my findings. Univariate analysis showed that Granite Island Ring-bills of both sexes vary in fresh weight and body condition according to the time of season in which they nest (Tables 5, 17 and 18). I focus attention here on body condition because body weight is subject to daily variation (sample birds in this study were not eviscerated prior to weighing). Meathrel (1986) found that gulls on this colony decrease in body condition but not in external measures of body size as they nest progressively later in the season. It is tempting to suggest that differences in reproductive success between earlier and later nesters are due to differences in body condition. However, a cause and effect relationship cannot be invoked with certainty.

The observed variability in body condition may be the true cause of variability in reproductive performance or it may simply be a measurable symptom of other differences between peak and late breeders. For example, age differences between nesting pairs could manifest themselves as differences in body condition. There are numerous examples in the literature where younger birds showed poor reproductive success and/or low body condition indices (Coulson and White 1958, Horobin 1966, Mills 1973, Ryder 1980, Nisbet et al 1984, Perrins and McCleery 1985). Low body condition in young birds can be caused by foraging inefficiency (Tolonen 1976, Ulfstrand 1979, Pugesek 1983, Maclean 1986). Coulson (pers. comm.) found that in Herring Gulls and Kittiwakes, the late breeding segment of the population was composed of physically inferior young birds and poor quality older birds. He did not find any biometrical characteristics that would distinguish good and poor quality individuals. He also reported no obvious size differences between younger and older breeders. I did not find any late breeding Ring-bills in immature plumage, but Ryder (1975) found 36 (22 per cent) nests in his Granite Island study areas were attended by at least one parent in immature plumage. Boersma (1982) found no adult:adult plumaged late pairs (n=14) on the same colony. It is likely that at least some birds in my late sample were young individuals that had attained full adult plumage.

Low body condition indices could also be caused by a lack of breeding experience. Inexperience in itself can lead to poor reproductive success (Ollason and Dunnet 1978, Ryder 1980) and inexperienced breeders often nest later than experienced birds (Coulson and White 1960, Rechten 1986). First or second time breeders, regardless of age, may underestimate the energetic demands of reproduction and fail to amass sufficient food resources before nesting (Tolonen 1976). By the incubation period these birds (especially females) may be in poor condition.

There is also the possibility that other factors unrelated to body condition are causes of the poor reproductive performance typical of late breeders. In colonial situations, group synchronization forces could affect breeding success. Boersma (1982) recorded suboptimal incubation behaviour in late-nesting Ring-bills. She postulated that late breeders may have been affected by cues from their peak-breeding neighbours. Copulation and courtship displays by some individuals can stimulate changes in hormonal secretions in neighbouring birds (Lehrman 1959) and induce them to engage in the same activities (Emlen and Miller 1969, Southern 1974). Late nesters may inadvertently be thrown out of synchrony with their own reproductive activities by the behaviour of neighbouring peak pairs.

While the thesis outlined above may explain at least in part the association between late nesting and poor reproductive success, it cannot account for the relationship exhibited in my study between nesting period and body condition. At its simplest, anything that impairs foraging efficiency or nutrient absorption will leave a bird in poor condition. Age, foraging and breeding experience, intra-specific interactions, and disease are all variables that could affect body condition. Poor quality birds tend to breed later in the season and have lower reproductive success than the colony average. Size does not seem to be relevant.

4.2 Body size, body condition, and assortative mating

Results are equivocal regarding assortative mating by single skeletal characters. It is not surprising that skull and bill characters contrasted the greatest amount between real and randomly-assigned pairs because these measures contributed the most to size differences between the sexes. It is difficult to interpret the results of regressions of male on female characters (Table 23). Skull and wing length are characters that intuitively seem to be good indicators of body size. However, it is unlikely that gulls are able to discern differences in tibiotarsus width with enough accuracy to use it as a criterion in mate selection. In any case, correlation coefficients for all single characters were so low that it would be misleading to try to explain their role in the mate selection process. The final interpretation must be that Ring-bills do not mate assortatively to any extent by single skeletal characters.

Ring-billed Gulls may mate assortatively on the basis of overall body size. My correlation between male and female size within pairs (r= 0.2675, p= 0.003) is lower than that which Coulter (1986) found between paired male and female bill size in Common Terns (r= 0.46). He considered his correlation to be indicative of positive assortative mating. I view mine as evidence of weak assortative mating because the same test with randomly-assigned pairs produced a very low, non-significant correlation (r= 0.07, p=0.23).

Body condition appears to be a stronger basis for assortative mating than did any skeletal measures tested. The correlation (r= 0.43, p< 0.0001) between paired male and female body condition indices indicates that high quality birds tended to pair together. Randomly-assigned pairs had low, non-significant correlation coefficients (r= 0.08, p= 0.21).

At this point, two questions may be raised: 1) Why is body condition more important in mate selection than body size? and 2) What are the consequences of assortative mating to Ring-billed Gull pairs? Body size may act in concert with body condition. It is often the case that large individuals are socially dominant to smaller birds (Pettingill 1970, Kalinoski 1975, Saitou 1979), but body condition has rarely been examined in the same context. Ankney (1977) found non-random mating by body size among Lesser Snow Geese (Anser caerulescens) and concluded that a male's large size improves its mates chance of reproducing successfully. He did not, however, look for any relationship between body condition, mate choice, and reproductive success. Generally, high quality birds lay larger, high quality eggs and clutches (Coulson 1968, Drent and Daan 1980, Houston et al 1983) although Meathrel and Ryder (1987) stated that egg size and composition were not satisfactory predictors of female body condition in Ring-billed Gulls. My own data shows significant but low correlations between egg size and female body condition (Appendix 23). It would not be surprising if many large birds were also of high quality given the food procurement advantages that even slightly larger chicks have over their siblings at hatch (Young 1963, Johnson and Sloan 1978, Welty 1982).

Occasionally, there have been reports of small individuals being preferred as mates. Petrie (1982) showed that female Moorhens (Gallinula chloropus) preferred small, fat males as mates. He postulated that the higher fat content (and better body condition) of the small males made them more efficient incubators. Coulson (pers. comm.) stated that the most successful reproducers in his Kittiwake colony were not average-sized but were of high quality. They also laid the largest eggs. In situations where there are no great differences in size between small and large individuals, preference for mates in good condition may be a better strategy than choice on the basis of body size.

To procure a full evaluation of the consequences of assortative mating to Ring-billed Gulls, it would be necessary to follow pairs of known size and condition throughout the breeding season and monitor their reproductive sucess. This would be a logical continuation of the present study where identification of assortative mating's parameters necessitated collection of birds before breeding was completed.

Cooke and Davies (1983) proposed guidelines for those researchers attempting to demonstrate mate choice and its evolutionary consequences. They were originally put forth with general non-random mating in mind but are suitable for studies on assortative mating. I apply these guidelines to evaluate the meaning and significance of my own results.

1) Is there evidence of assortative mating in relation to some phenotypic character?

My results indicate that there is assortative mating by body condition and to a lesser extent by overall body size.

2) Does the assortative mating necessarily imply mate choice?

It is possible that the mating patterns observed do not imply mate choice. Differing body condition or size of individuals may create temporal or spatial barriers during the breeding season. Norton-Griffiths (1968) decided that non-random pairing by prey preference in Oystercatchers (Haematopus ostralegus) occurred simply because birds with certain foraging techniques and prey specializations tended to encounter others of their own kind in their feeding areas. In Ring-billed Gulls, time of northern migration and arrival at the breeding colony may be influenced by physical condition. It is reasonable to assume that birds would tend to choose a mate from conspecifics that arrived at roughly the same time as themselves. It is still not known with certainty when or where Ring-bills form pair bonds (Ryder, pers. comm.).

Ring-billed Gulls may also mate assortatively according to their location on the breeding colony. Coulson (1968) found that Kittiwakes that bred on the edge of a colony were of poorer quality (= body condition) than individuals nesting in the centre. If this is the case on Granite Island, perhaps high and low quality Ring-bills are spatially segregated and mate assortatively by default. Somppi (1978), however, found no differences in reproductive success between central and peripheral nesters on Granite Island. My results have intimated that poor reproducers (late nesting sample) were in poor body condition so Coulson's (1968) results may not be applicable in this case. At any rate, if Ring-bills pair before spring migration, both of the preceeding mechanisms for assortative mating by "default" could be discounted.

3) Is the choice based on the character itself?

Are Ring-bills actually choosing mates on the basis of body condition and size or are these merely visible artifacts of their choice for some other character? I believe that body condition is the key character being chosen. In some cases it is possible to experimentally verify the validity of the choosing character. Cooke and McNally (1975) designed an experiment that confirmed their thesis that colour itself was the character being chosen in Snow Geese. It would be difficult to validate my results in this manner because body condition is a continuous variable. Cooke and McNally (1975) were dealing with two discrete colour morphs. One could, however, test for dominance of condition over size in the mate choice process. Members of one sex could be allowed to choose between large, low quality mates and small, high quality mates. By forcing birds to choose between extremes of the two variables, the relative importance of each could be assessed.

4) Is there genetic variability for the character?

Genetic variability is the raw material upon which natural selection operates. It is only possible to discuss the evolutionary consequences of mate selection if selected characters vary genetically (Cooke and Davies 1983).

Inheritance of body size variables is well documented (e.g. Leamy 1974, Boag and Grant 1978, Smith and Zach 1979, Smith and Dhont 1980). Thus it is possible that there could be evolutionary consequences to mate choice based on body size. It is uncertain, however, if organisms can inherit body condition *per se*. In controlled laboratory situations it has been shown that organisms of low viability and vigour combine to produce sickly offspring (Farnesworth 1978). Occasionally some genes contributing to poor condition and health have been isolated, but so many genetic and environmental factors influence an organism's general condition that a complete assessment is presently impossible. In natural populations, animals must attain a certain threshold of health or they simply do not survive. Above this survival threshold there are varying degrees of healthiness or body condition that are undoubtedly affected by genes controlling size and strength (important in social interactions), speed and visual acuity (foraging skills), and other physical qualities. Behavioural traits are probably also influenced by genetic make-up (Dobzhansky 1964). Rowher and Rowher (1978), through manipulation of plumage patterns, showed that the external markings of dominance (size, plumage pattern) did not assure an individual of a high place in the dominance hierarchy. The appropriate behavioural patterns must also be exhibited.

Because body condition relies on nutritional intake, the many environmental factors that determine food abundance must largely influence each bird's condition. The relative contribution of environment and genes to body condition is yet to be established.

5) Is there a selective advantage in making the correct choice?

This question is the crux of most mate choice problems. If there is a selective advantage in mating assortatively by body size/condition, then presumably this mating pattern would persist and perhaps even intensify until time and energy expended in attaining a mate of comparable status was no longer equalled by benefits accruing from such an effort. If a selective advantage did not exist, there would be no point in mating assortatively. Unfortunately, long-term monitoring of reproductive success of assortatively-mated pairs and their offspring would be necessary to verify the existence of a selective advantage.

It is impossible to answer this question with the data I have collected. However, I advance a possible explanation of the assortative mating observed for future testing. It seems unlikely that there is a selective advantage to mating assortatively by body condition. In such a system, those birds in good condition would certainly reap selective benefits since their mates would also be in good condition. Birds in poor condition, however, would be at an extreme disadvantage if they sought out mates of their own status. Similarly, birds of average quality could do no more than maintain their reproductive status quo by mating assortatively. There is almost certainly no genetic penalty assessed to birds that take mates in better condition than themselves. Perhaps the assortative mating pattern I uncovered is an artifact of a posteriori investigation techniques. Each bird may in reality be striving to obtain the highest quality mate possible. Its chances of doing so are very low, however, because there are many other birds of higher quality following the same strategy. The net result of such a selection process would be mated pairs whose members are more similar to each other in body condition than to other birds of the opposite sex. A field study that is conducted after mate choice is completed would deliver data that seemed to indicate assortative mating by body condition. I term this mating pattern passive assortative mating because it occurs between individuals that are not actively attempting to mate assortatively. Passive assortative mating provides a mechanism by which a mating regime with no selective advantage can persist in a population.

To circumvent the problem of investigation after the fact, researchers need to make careful field observations during the mate choosing period on a marked population of birds. By recording the number, duration, and results of courtship attempts made by and toward low and high quality individuals, one could determine if active or passive assortative mating occurred. In Ring-billed Gulls the logistics of such a study would be difficult given the uncertainty surrounding the location and timing of pair bond formation. Without this information, the passive assortative mating hypothesis remains untestable.

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Appendix 1. Definitions of skeletal characters.

SL[1] (skull length)- medially, from posterior part of supraoccipital to anterior tip of premaxilla.

SW[1] (postorbital width)- transversly, the maximum dimension between postorbital processes of frontal.

SD[1] (skull depth)- medially, from sphenoidal rostrum to dorsal region of frontal.

BW (bill width)- transversly, from junction of the right jugal and nasal to junction of the left jugal and nasal.

BD[1] (upper mandible depth)- medially, the maximum depth at anterior edge of narial opening.

KL[1] (keel length)- medially, from posterior edge of sternum to anterior edge of keel.

KW[1] (sternum width)- transversely, maximal dimension between sterno-coracoidal processes.

KD[1] (keel depth)- medially, from dorsal edge of ventral manubrial spine to ventral edge of keel.

FL[1] (furcula length)- lateromedially, from furcular process to centre of coracoidal facet.

SNW[1] (synsacrum width)- transversely, minimum dimension between acetabula as seen from dorsal view.

PL (pelvis length)- maximal dimension from posterior edge of antitrochanter to posterior notch of synsacrum.

CW[1] (composite wing)- humerus length (maximum dimension from head to internal condyle) + ulna length (maximum dimension from olecranon to external condyle) + caropmetacarpus length (maximum dimension from carpal trochlea to facet for digit 3) + phalynx length (maximum dimension from digital facet to metacarpal facet) + pollex length (maximum dimension from digital facet to distal end).

TBL[1] (tibiotarsus length)- maximum dimension from articular surfaces to external condyle.

TBW[1] (tibiotarsus width)- minimum dimension of tibia near end of spine of fibula.

TRL[1] (tarsometatarsus length)- maximum dimension from proximal end of trochlea for digit 3.

TRW[1] (tarsometatarsus width)- transversely, minimum dimension.

1-from Schnell (1970).

2-Schnell's (1970) humerus length + ulna length + carpometacarpus length + phalynx length + pollex length.

Appendix 2. Pearson correlation coefficient matrix showing degree of relationship between skeletal measurements.

	FWT	KLE	BLE	BDE	SL	SW	SD	BD	BW	KL	KW	KD	SNW	PL	FL	CW	TBL	TBW	TRL	TRW
FWT	1																			
KLE	.61	1																		
BLE	.67	.63	1																	
BDE	.65	.61	.73	1																
SL	.71	.71	.90	.77	1															
SW	.60	.64	.72	.67	.79	1														
SD	.45	.42	.56	.54	.63	.59	1													
BD	.56	.56	.66	.67	.73	.62	.56	1												
BW	.38	.37	.46	.46	.51	.40	.37	.46	1											
KL	.56	.82	.68	.60	.77	.70	.50	.63	.39	1										
KW	.37	.47	.46	.43	.47	.39	.37	.37	.30	.47	1									
KD	.51	.60	.61	.58	.69	.64	.53	.60	.32	.69	.45	1								
SNW	.57	.53	.64	.55	.67	.63	.49	.52	.43	.61	.46	.56	1							
PL	.52	.54	.62	.56	.68	.59	.42	.49	.39	.60	.40	.51	.55	1						
FL	.56	.51	.67	.64	.74	.66	.54	.59	.37	.58	.37	.58	.56	.55	1					
CW	.66	.67	.77	.73	.85	.71	.54	.64	.44	.72	.44	.62	.67	.78	.72	1				
TBL	.58	.58	.72	.64	.79	.65	.49	.57	.37	.63	.40	.59	.62	.63	.64	.87	1			
TBW	.42	.44	.44	.39	.49	.46	.30	.38	.25	.48	.33	.37	.38	.40	.38	.44	.37	1		
TRL	.54	.58	.67	.62	.72	.59	.44	.55	.39	.61	.38	.53	.56	.57	.57	.72	.86	.34	1	
TRW	.39	.43	.42	.40	.49	.49	.38	.37	.34	.42	.28	.42	.39	.42	.38	.43	.38	.32	.39	1

Appendix 3. Mean male measurements (1985 and 1986) and F-values from Anovas testing for differences between years.

Skeletal measure[1]	1985 (± s.d)	1986 (± s.d)	F
FWT	531±45.3	524±43.4	.398
SL	9.56±0.23	9.59±0.24	.396
SW	3.23±0.08	3.22±0.07	.862
SD	2.53±0.07	2.51±0.07	3.543
BW	1.45±0.08	1.47±0.03	.706
BD	0.54±0.04	0.55±0.19	9.036[2]
KL	6.38±0.21	6.44±0.24	1.893
KW	3.66±0.13	3.67±0.15	.249
KD	2.98±0.10	3.04±0.10	10.705[2]
SNW	3.04±0.09	3.07±0.10	2.301
PL	5.66±0.19	5.64±0.49	1.352
FL	4.29±0.13	4.32±0.11	.875
CW	33.14±0.87	33.19±0.83	.062
TBL	8.64±0.24	8.70±0.28	1.576
TBW	0.42±0.04	0.41±0.03	1.745
TRL	5.72±0.23	5.79±0.23	2.503
TRW	0.29±0.02	0.30±0.02	.104

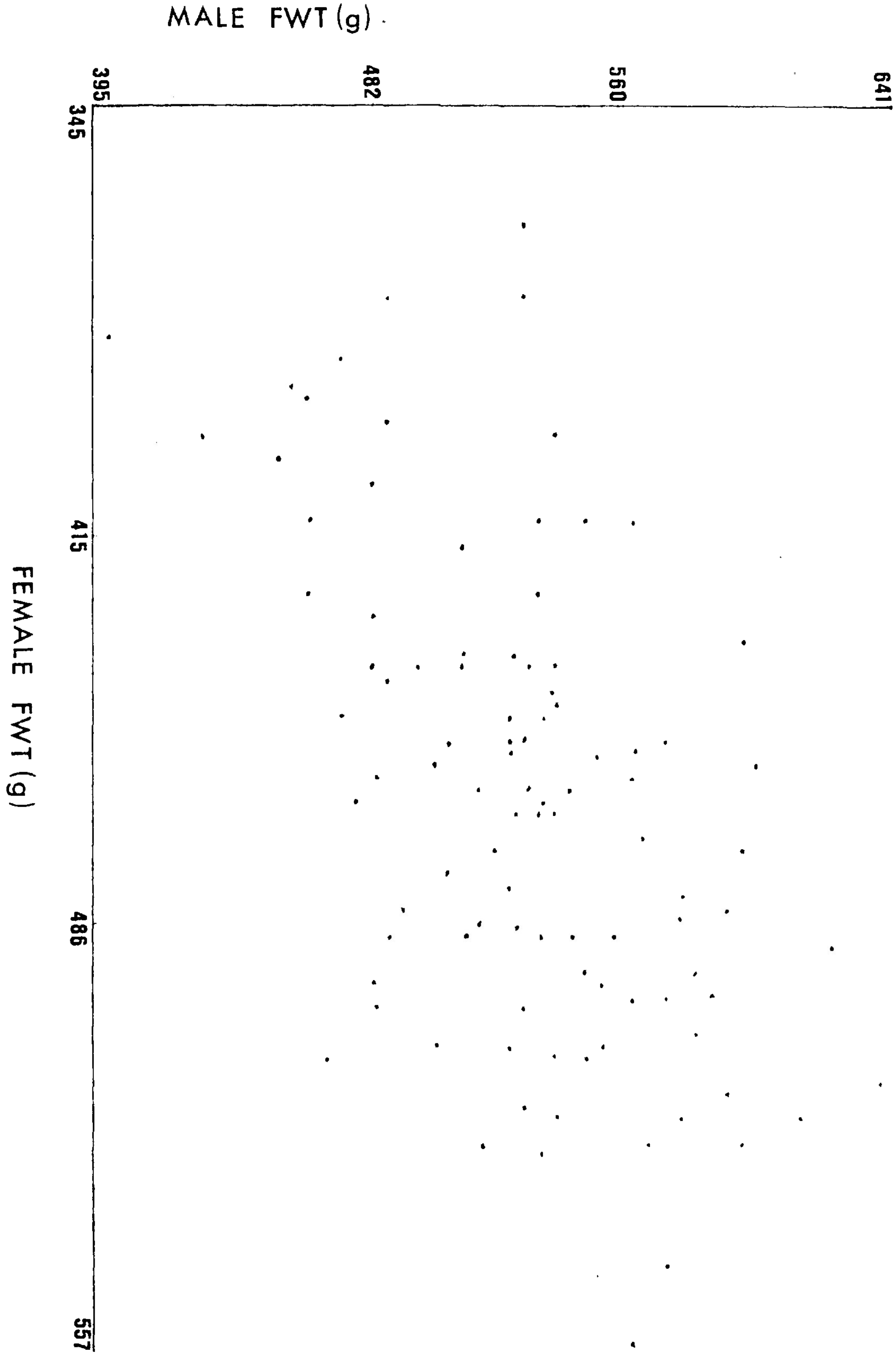
1 FWT in g; all others in cm
2 $p < 0.01$

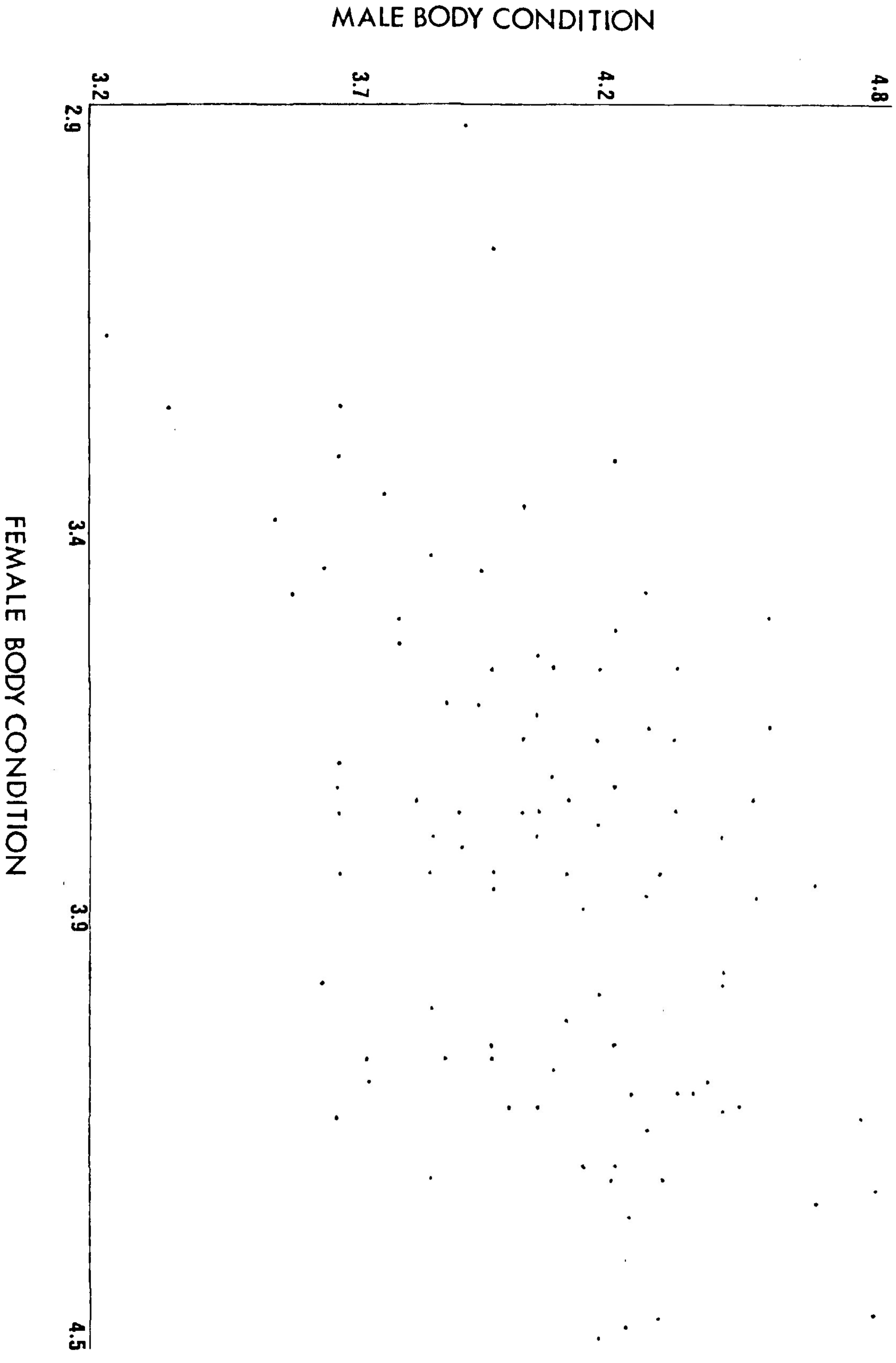
Appendix 4. Mean female measurements (1985 and 1986) and F-values from Anovas testing for differences between years.

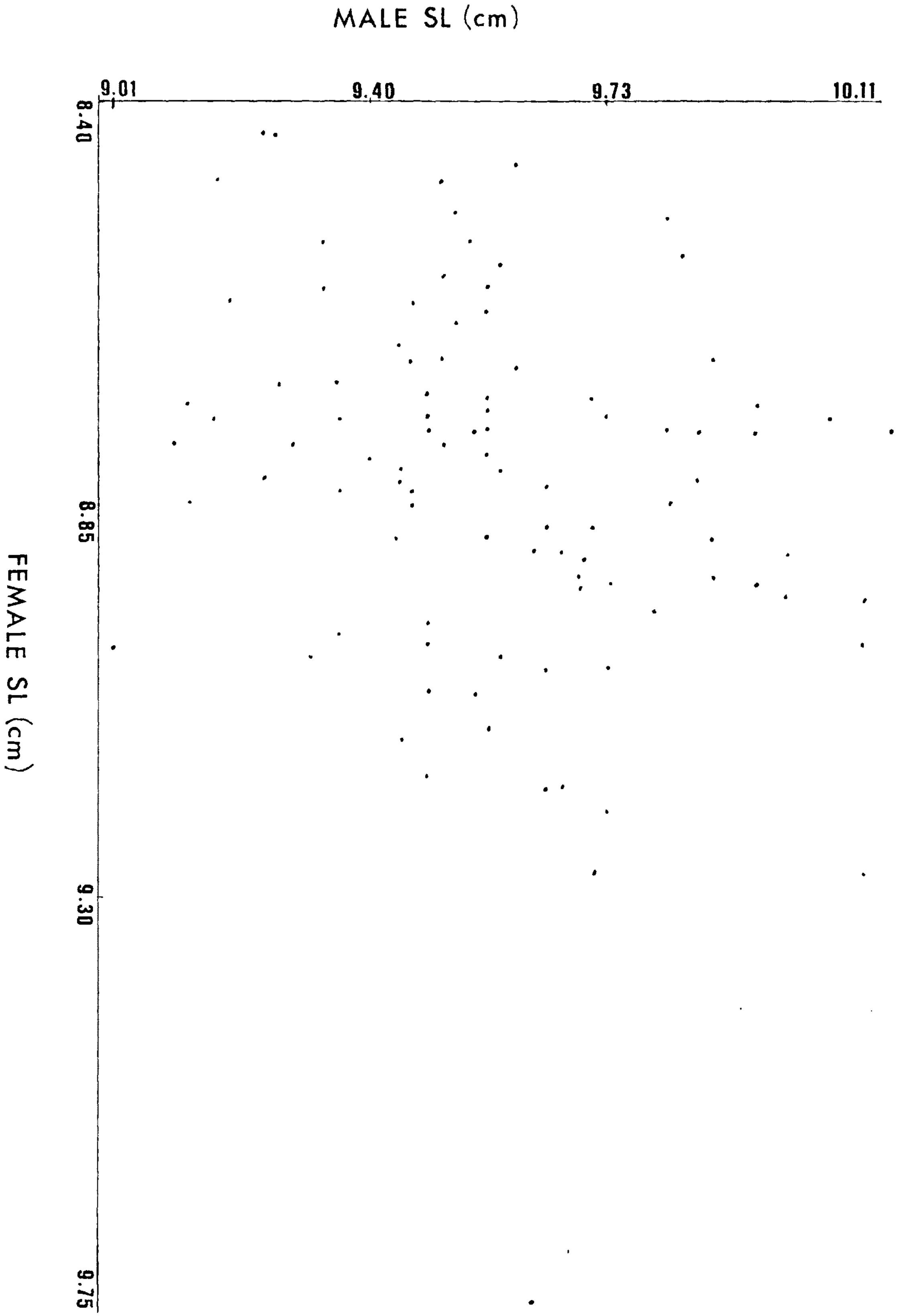
Skeletal measure[1]	1985 (± s.d.)	1986 (± s.d.)	F
FWT	458 (41.84)	453 (45.47)	0.492
SL	8.81 (0.22)	8.81 (0.21)	0.013
SW	3.02 (0.08)	3.06 (0.07)	9.806[2]
SD	0.48 (0.03)	0.50 (0.02)	5.564[3]
BW	2.40 (0.07)	2.43 (0.06)	0.001
BD	1.33 (0.10)	1.33 (0.06)	17.747[2]
KL	6.01 (0.18)	6.06 (0.17)	2.519
KW	3.46 (0.36)	3.37 (0.13)	2.690
KD	2.81 (0.09)	2.88 (0.08)	15.198[2]
SNW	2.90 (0.10)	2.88 (0.11)	1.196
PL	5.17 (0.39)	5.25 (0.21)	1.774
FL	3.96 (0.25)	3.99 (0.04)	0.713
CW	31.28 (0.78)	30.93 (0.84)	5.499[3]
TBL	8.20 (0.24)	8.13 (0.27)	1.884
TBW	0.39 (0.03)	0.39 (0.03)	0.012
TRL	5.41 (0.20)	5.33 (0.21)	4.291[3]

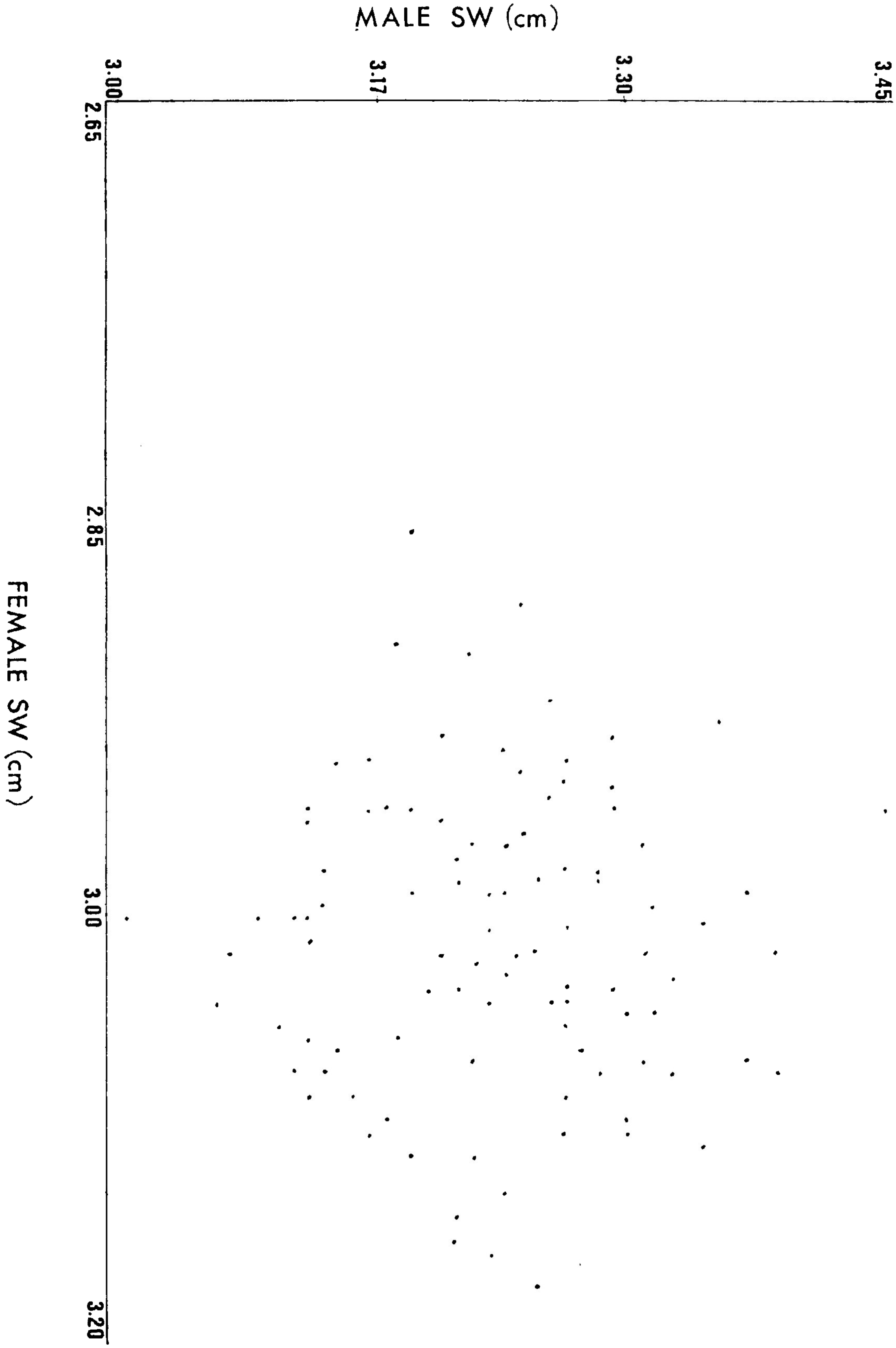
1 FWT in g; all others in cm
2 $p < 0.01$
3 $p < 0.05$

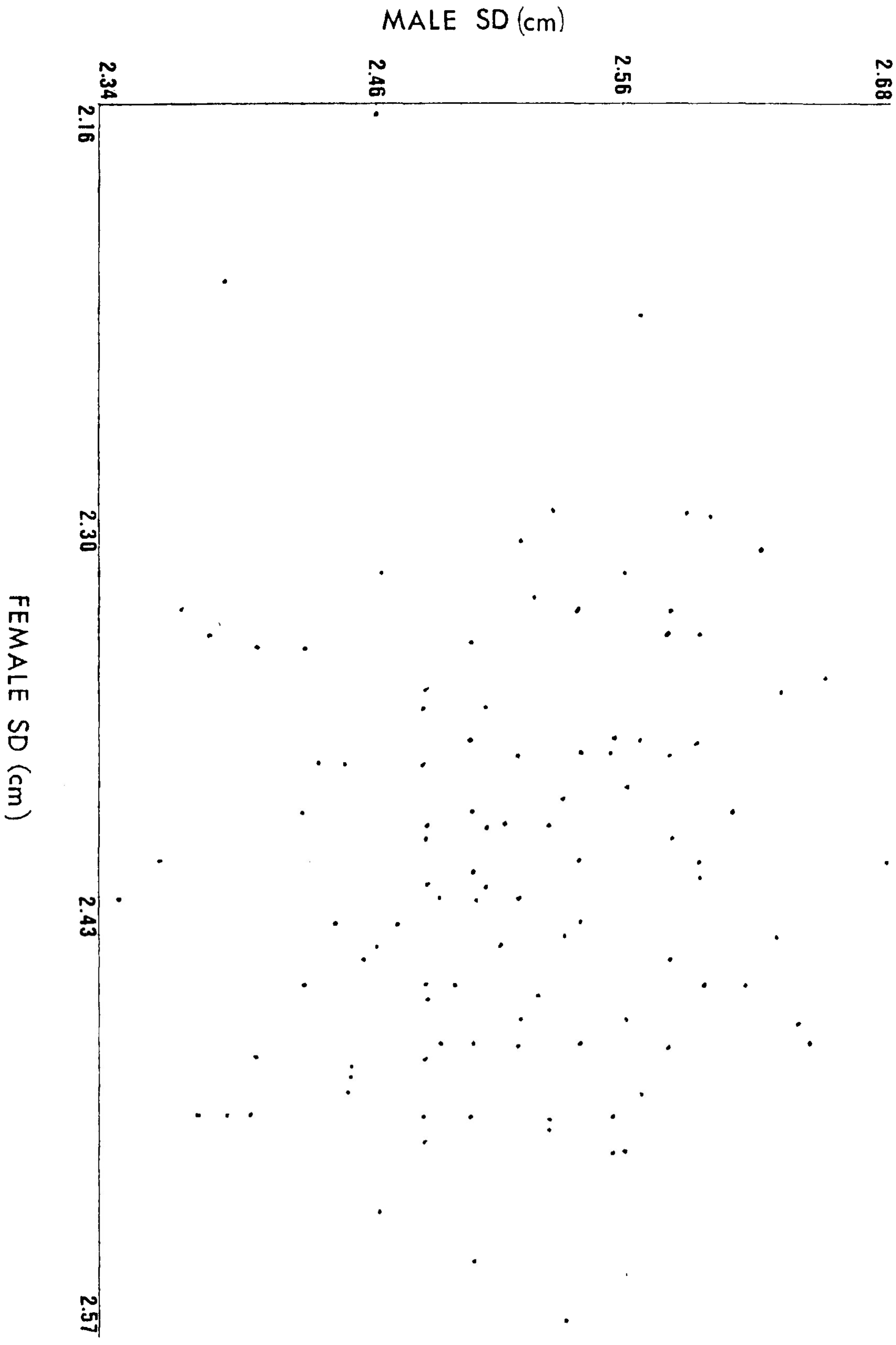
Appendices 5 to 22. Scattergrams showing relationships between paired male and female measurements.

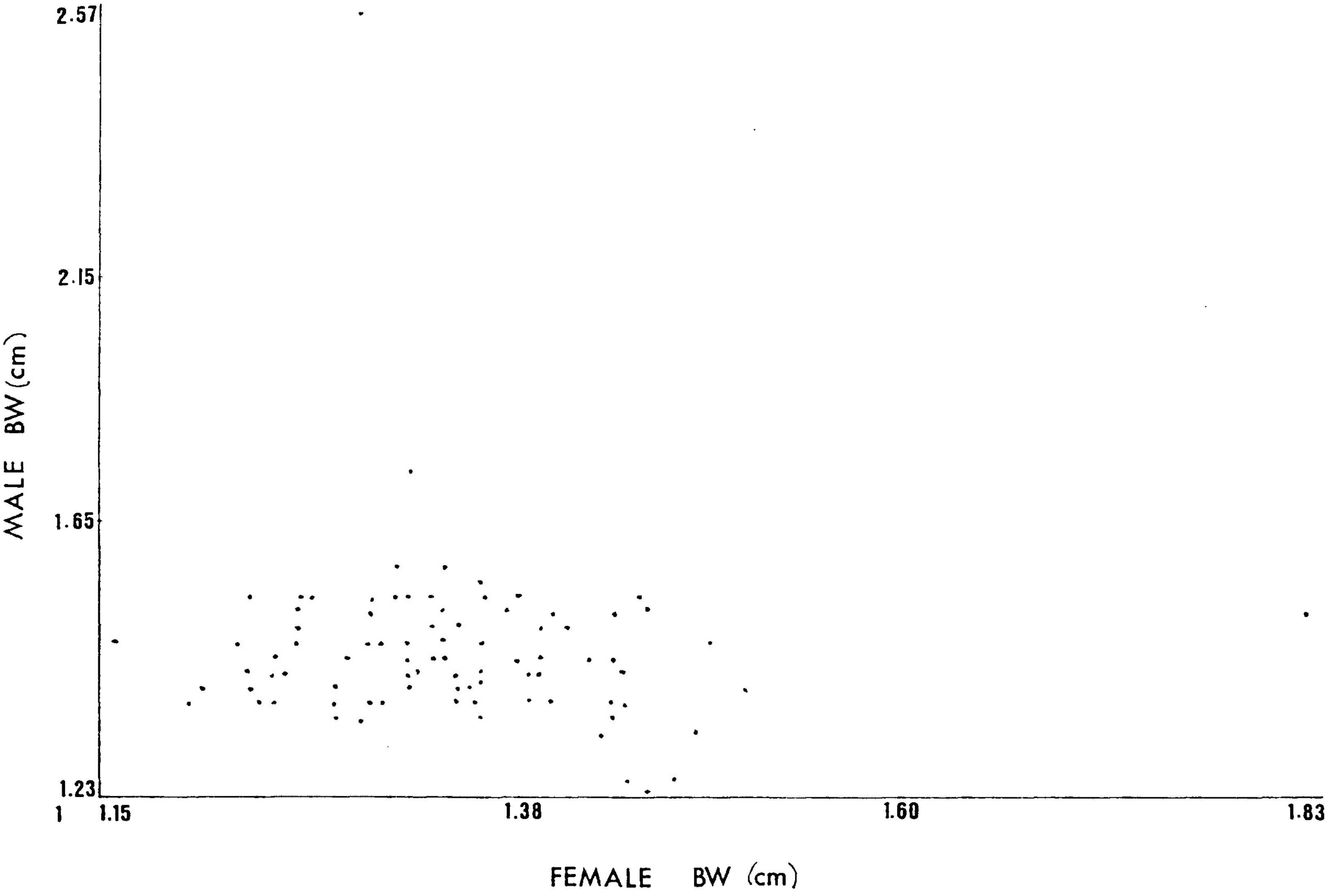

MALE FWT (g)
395
482
560
641
345
415
486
557
FEMALE FWT (g)

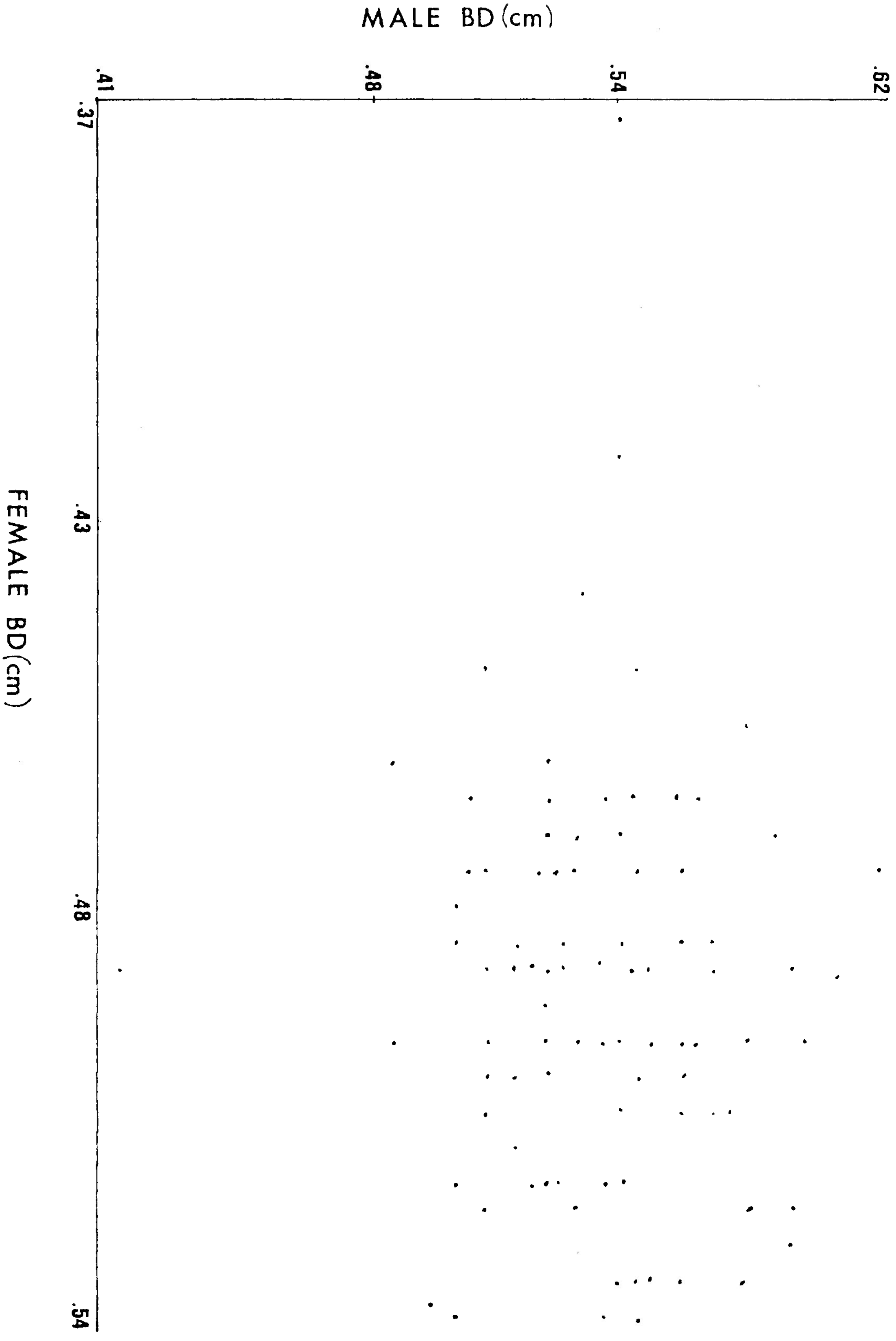

MALE BODY CONDITION
3.2
3.7
4.2
4.8
2.9
3.4
3.9
4.5
FEMALE BODY CONDITION

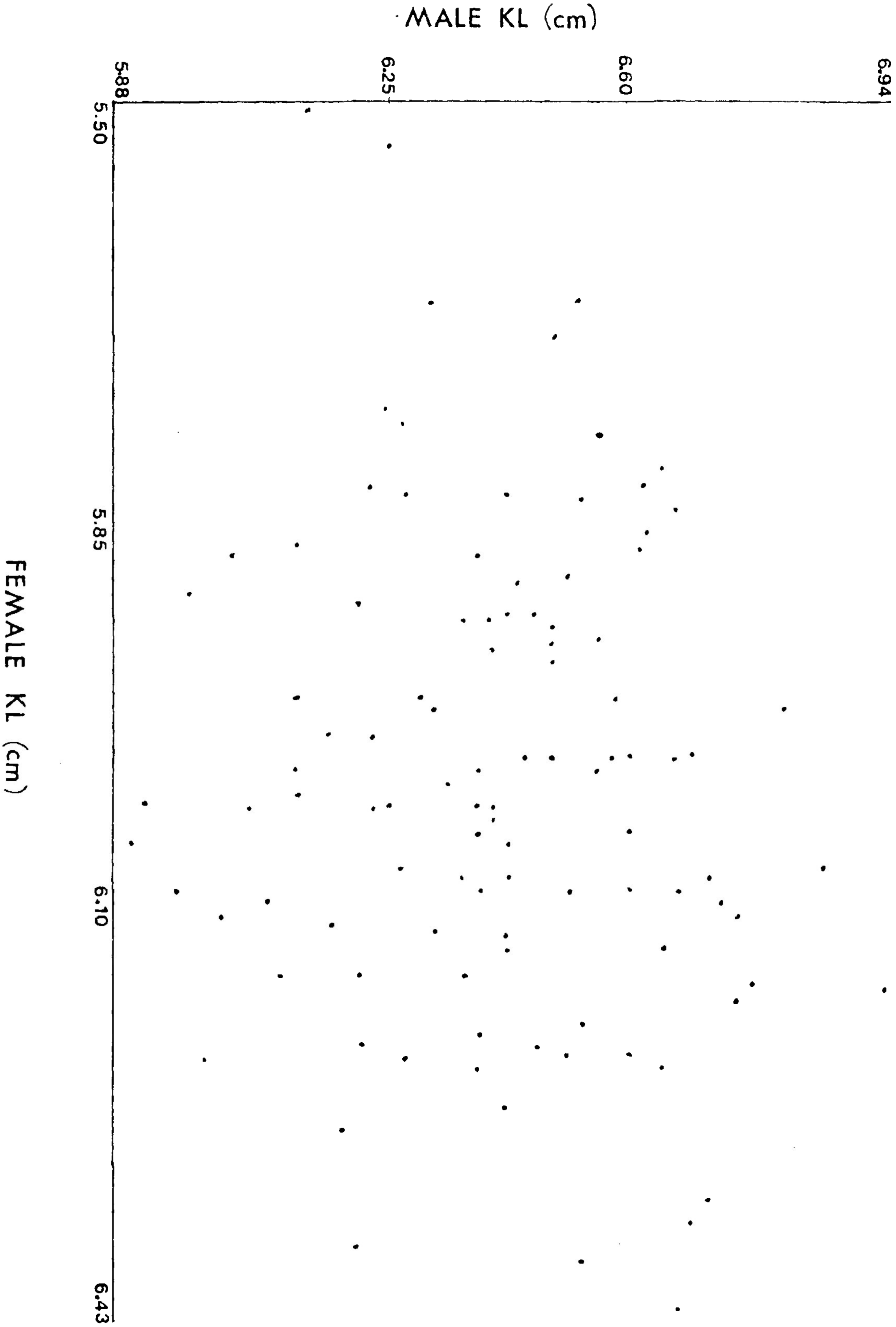

MALE SL (cm)
9.01
9.40
9.73
10.11
FEMALE SL (cm)
8.40
8.85
9.30
9.75

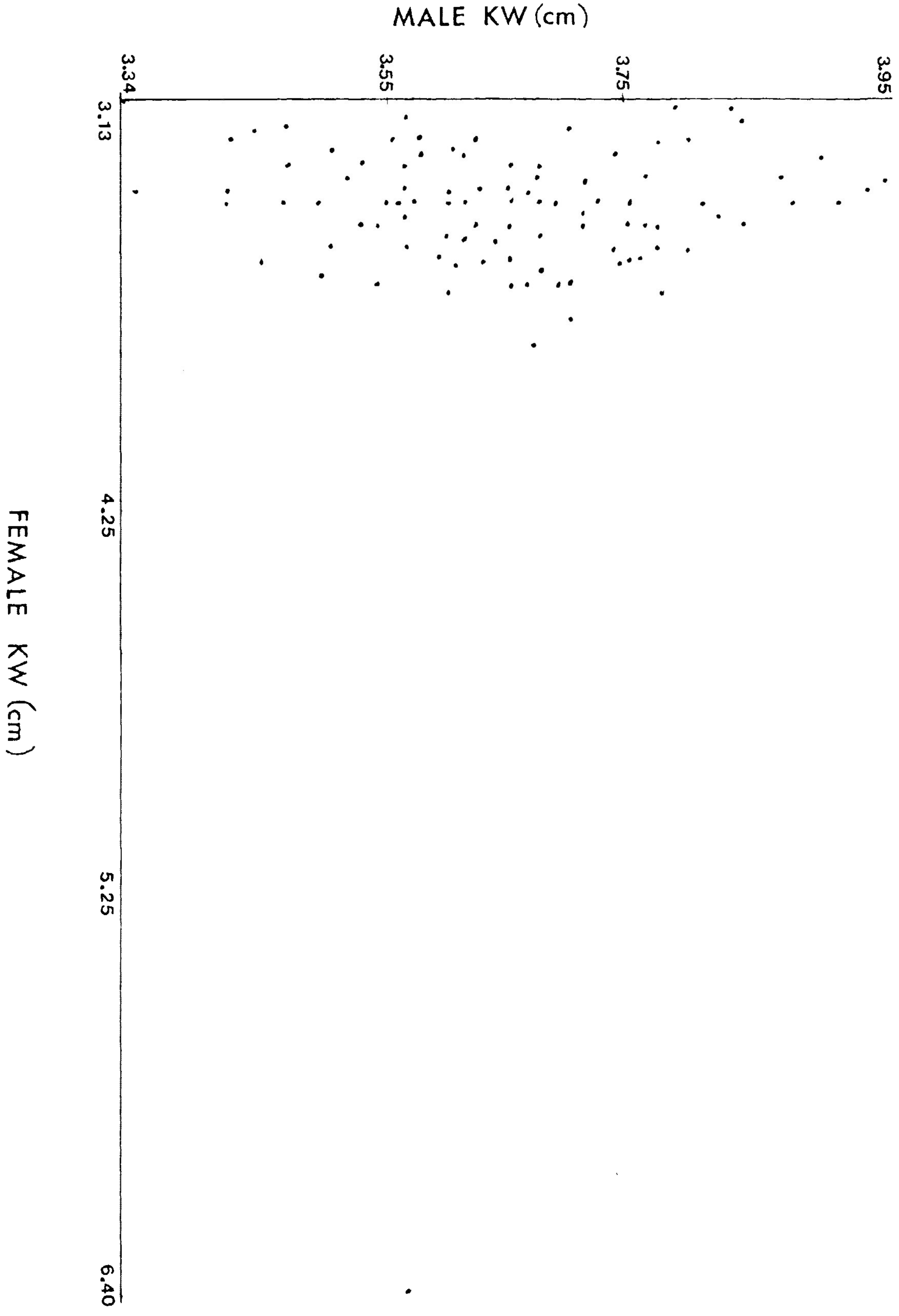

MALE SW (cm)
3.00
3.17
3.30
3.45
FEMALE SW (cm)
2.65
2.85
3.00
3.20

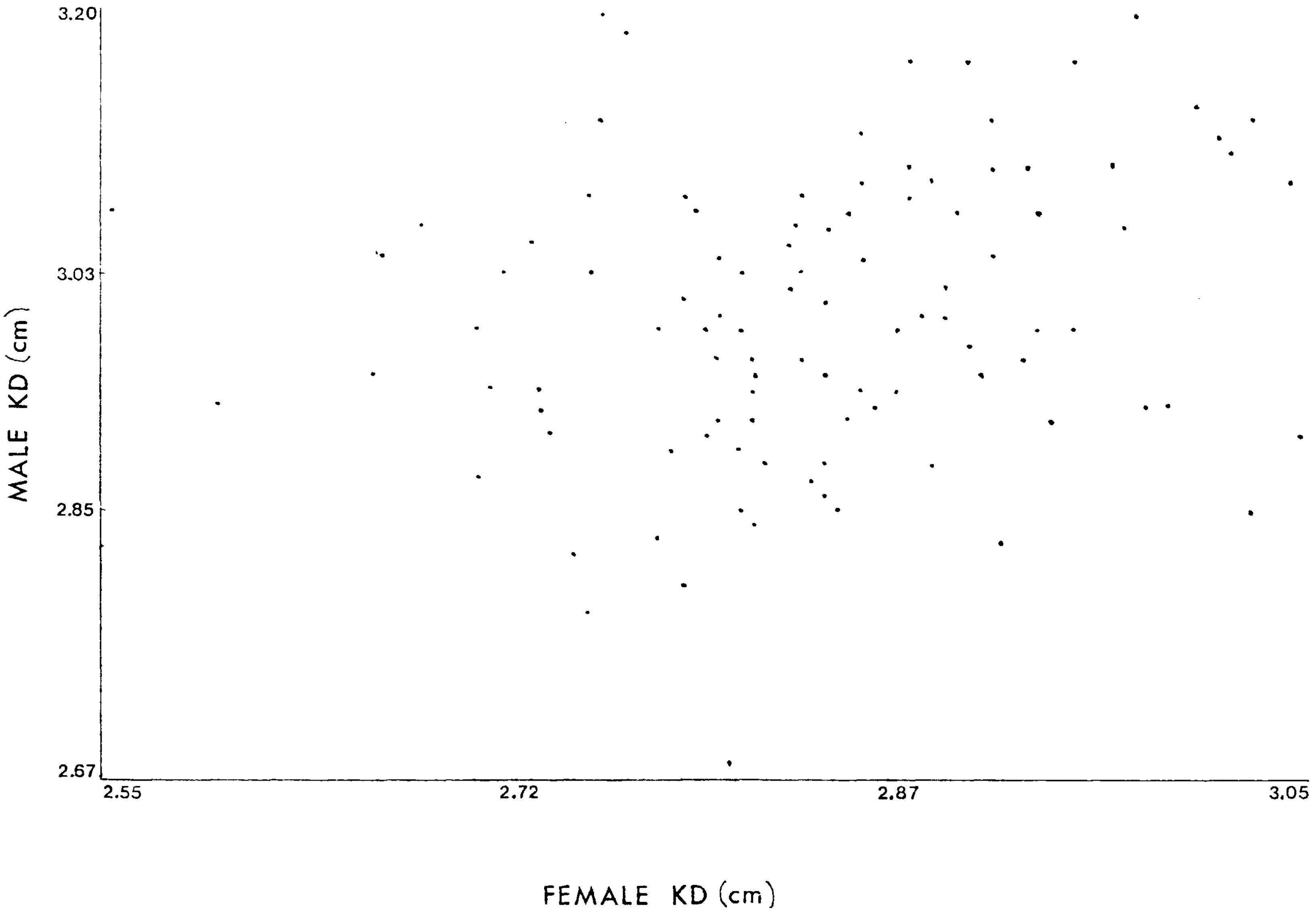

MALE SD (cm)
2.34
2.46
2.56
2.68
FEMALE SD (cm)
2.16
2.30
2.43
2.57

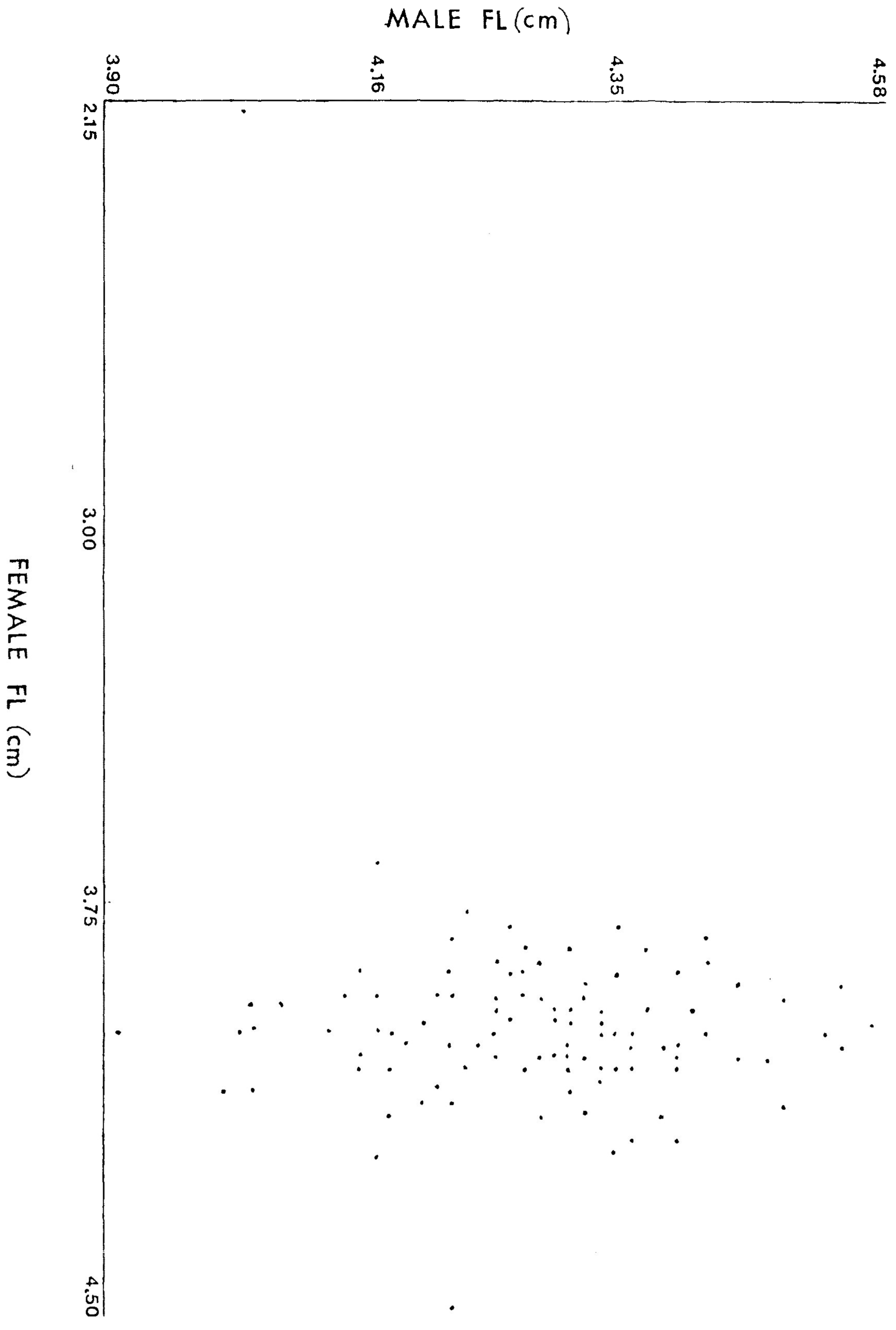

MALE BW (cm)
2.57
2.15
1.65
1.23
1
1.15
1.38
1.60
1.83
FEMALE BW (cm)

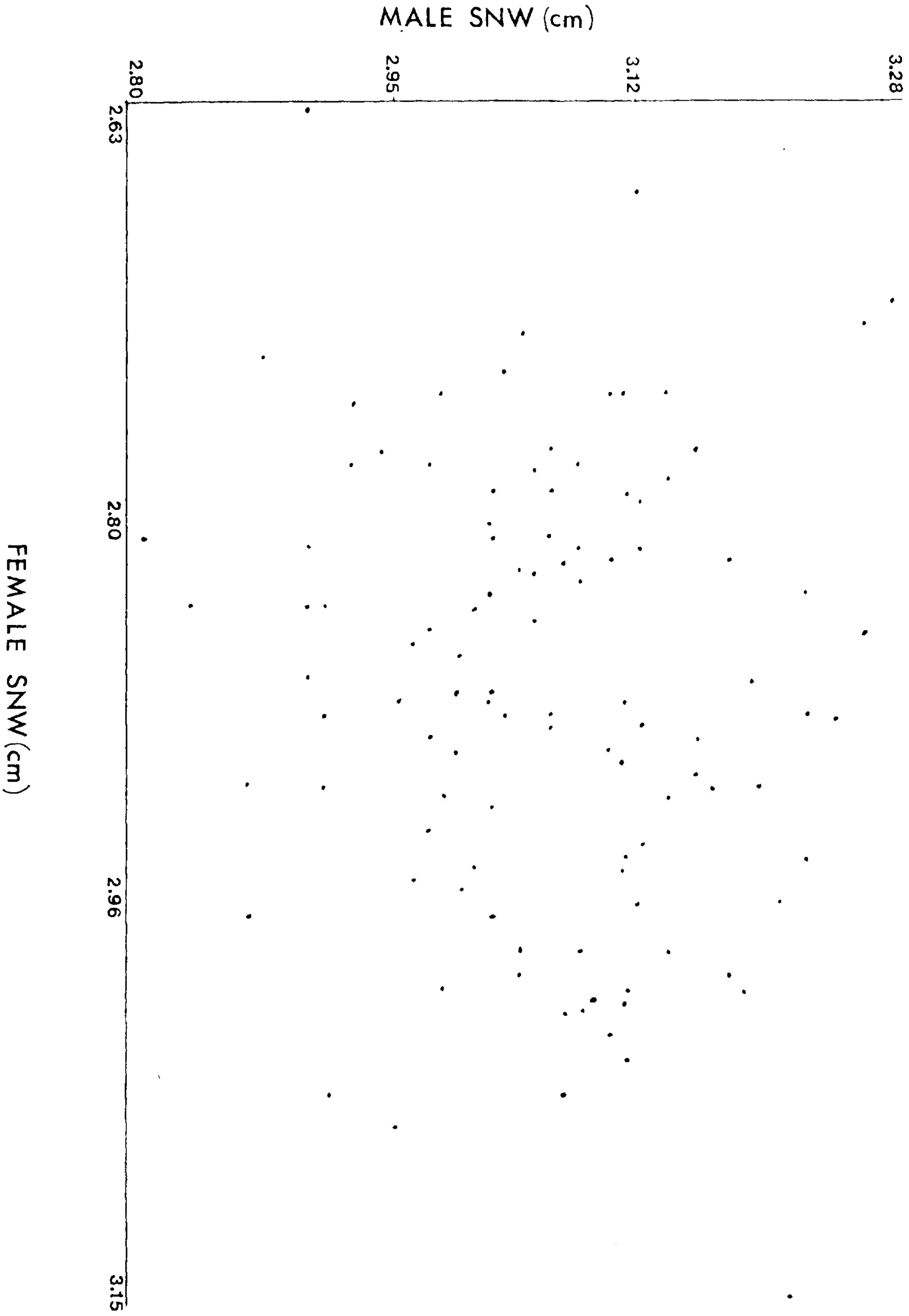

MALE BD (cm)
.41
.48
.54
.62
FEMALE BD (cm)
.37
.43
.48
.54

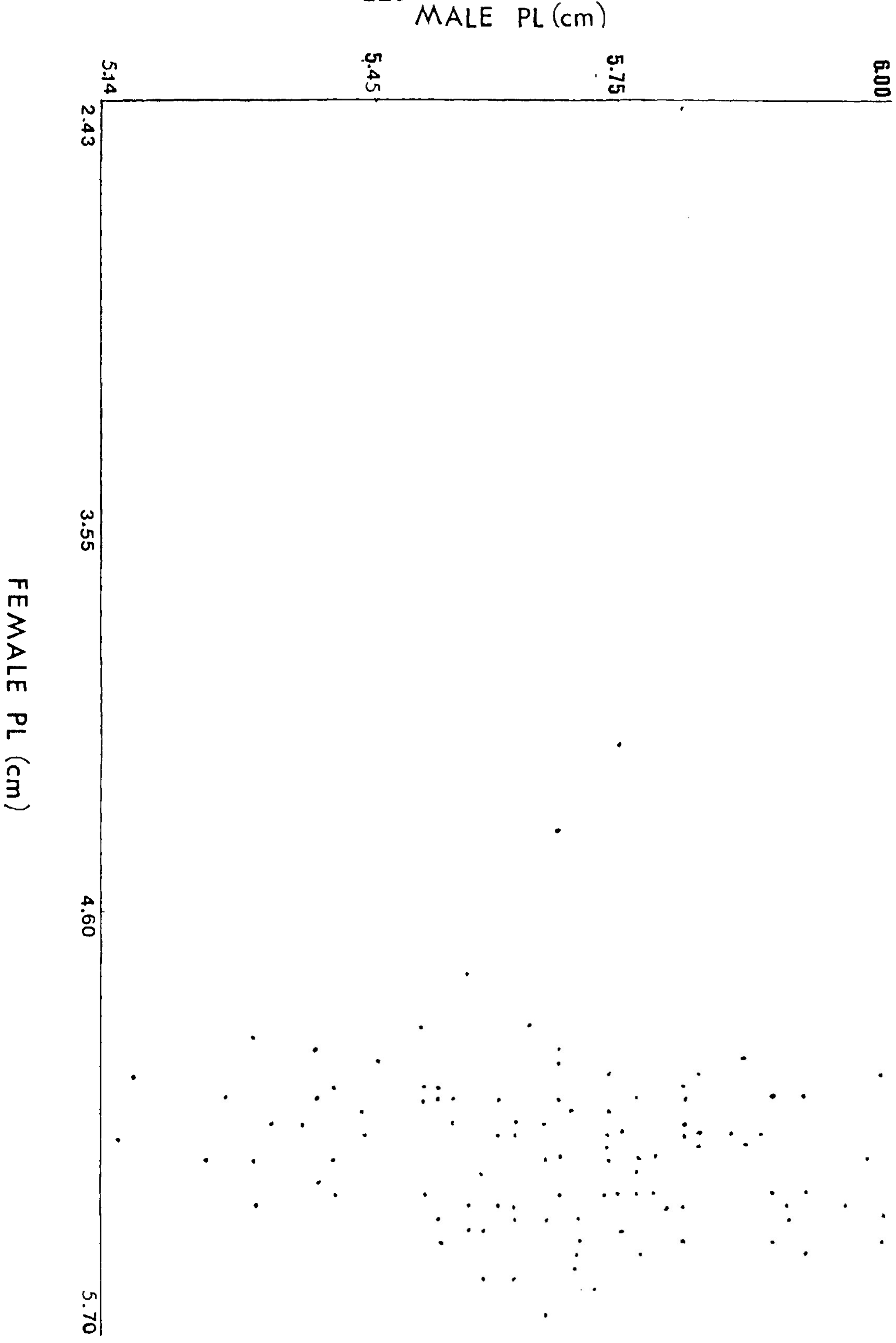

MALE KL (cm)
5.88
6.25
6.60
6.94
FEMALE KL (cm)
5.50
5.85
6.10
6.43

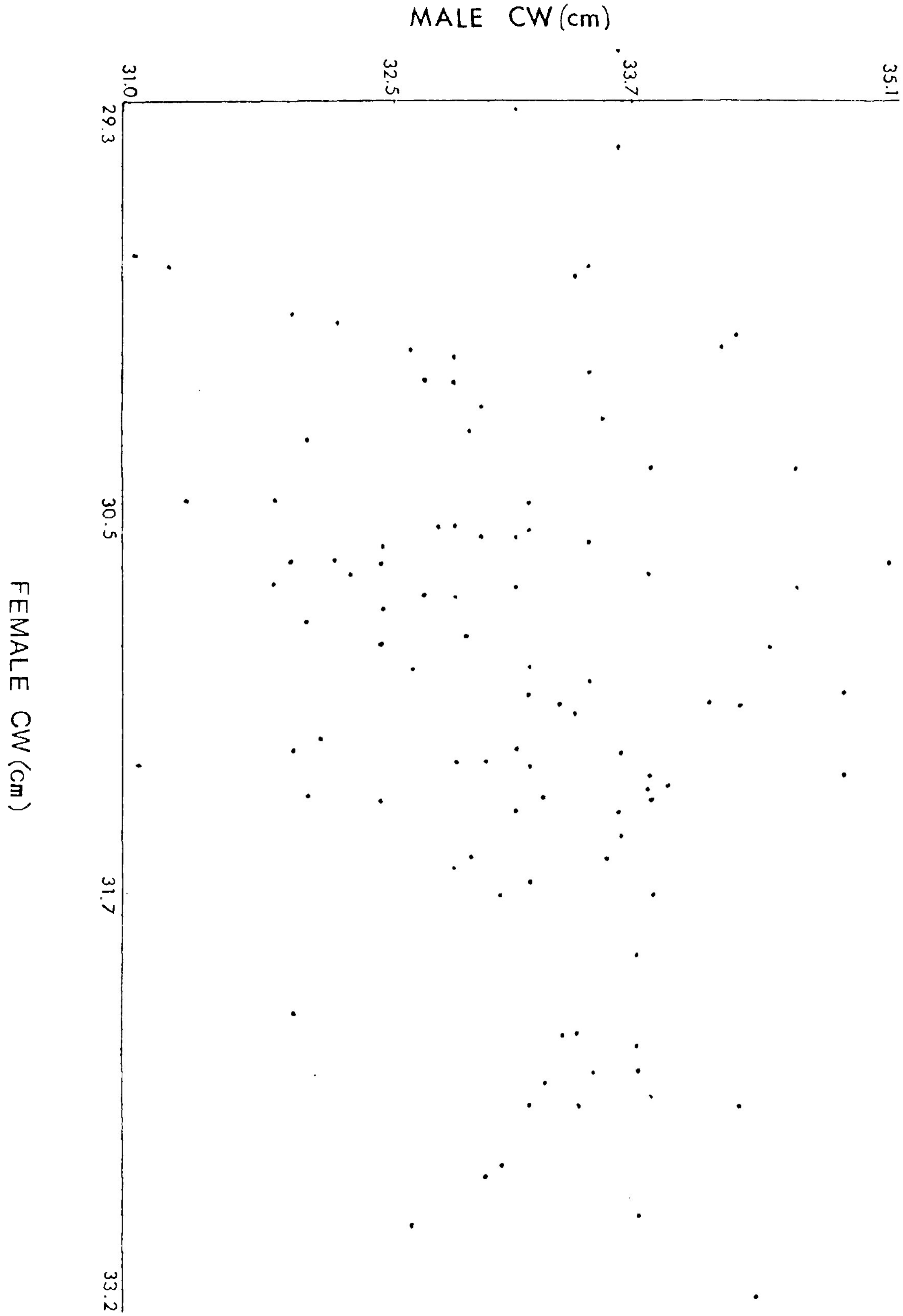

MALE KW (cm)
3.34
3.55
3.75
3.95
3.13
4.25
5.25
6.40
FEMALE KW (cm)

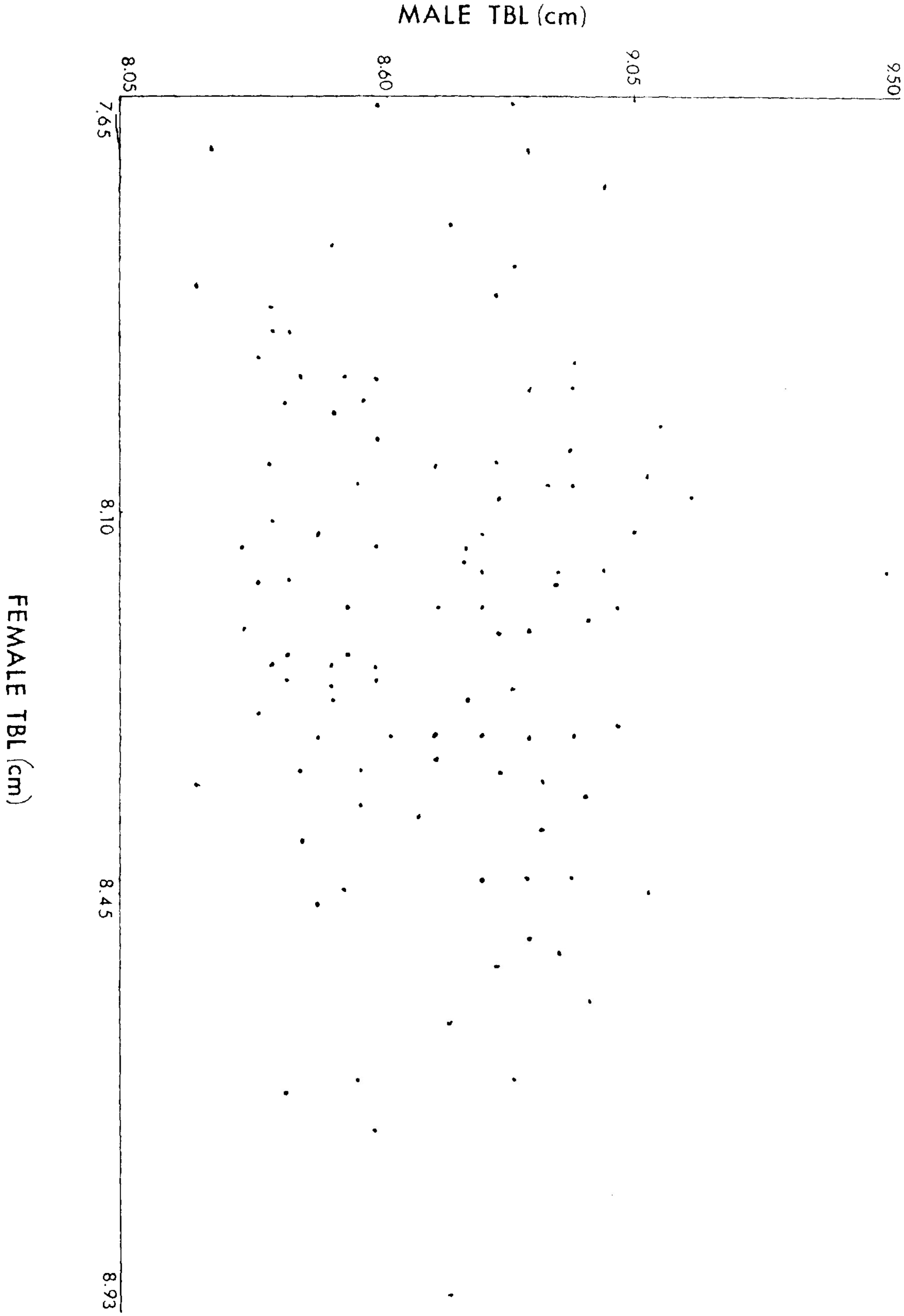

3.20
3.03
2.85
2.67
MALE KD (cm)
2.55
2.72
2.87
3.05
FEMALE KD (cm)

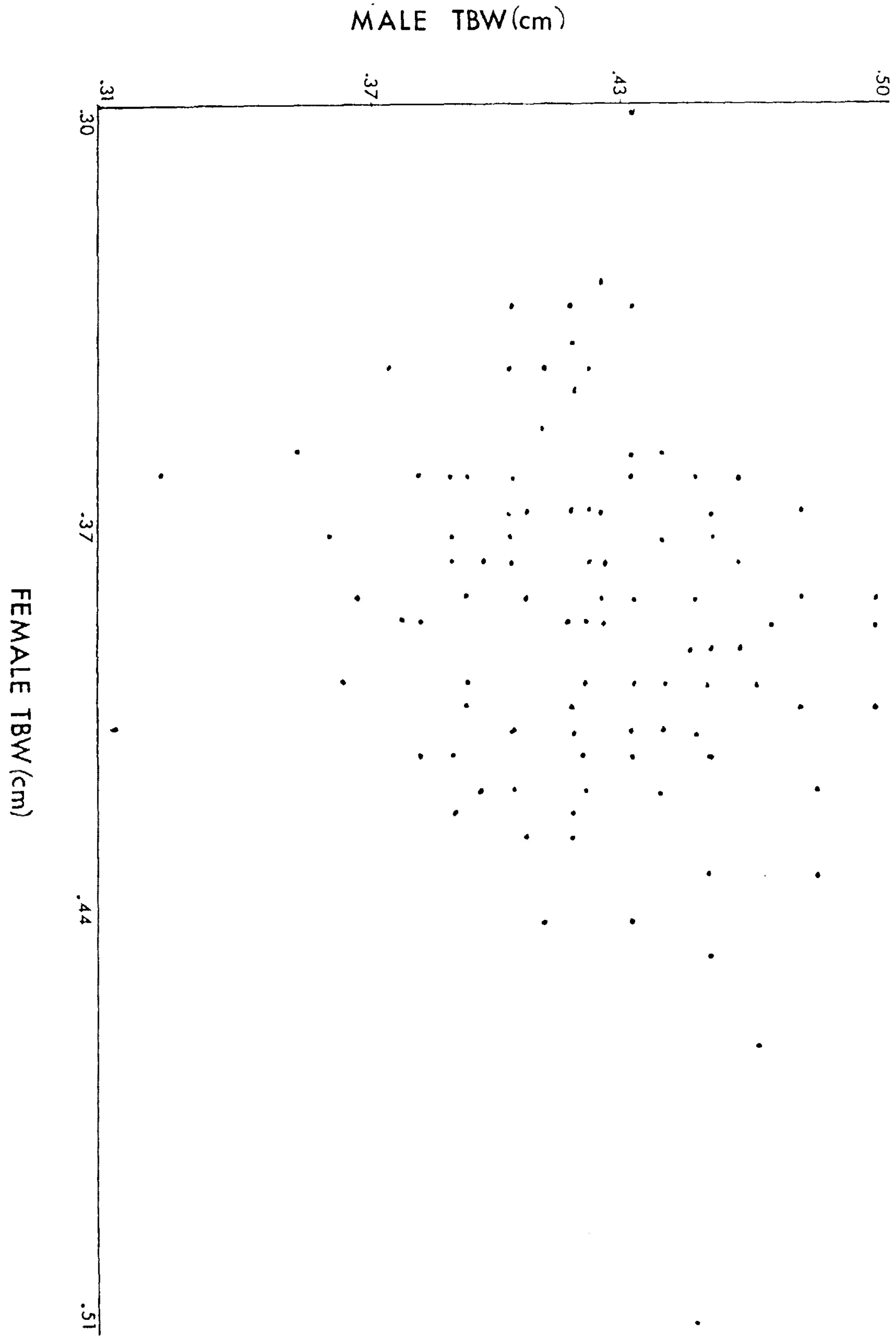

MALE FL(cm)
3.90
4.16
4.35
4.58
FEMALE FL (cm)
2.15
3.00
3.75
4.50

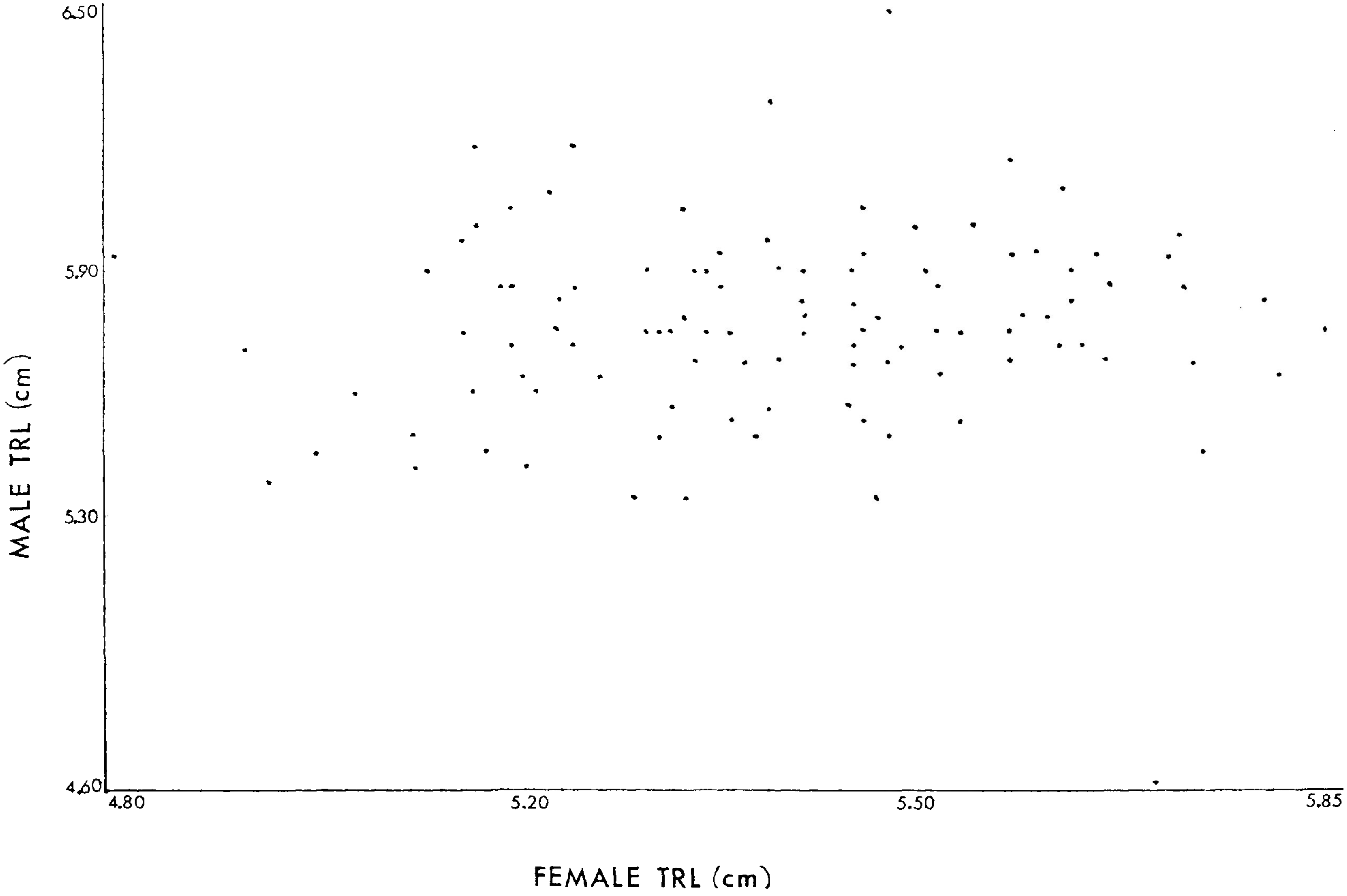

MALE SNW (cm)
2.80
2.95
3.12
3.28
FEMALE SNW(cm)
2.63
2.80
2.96
3.15

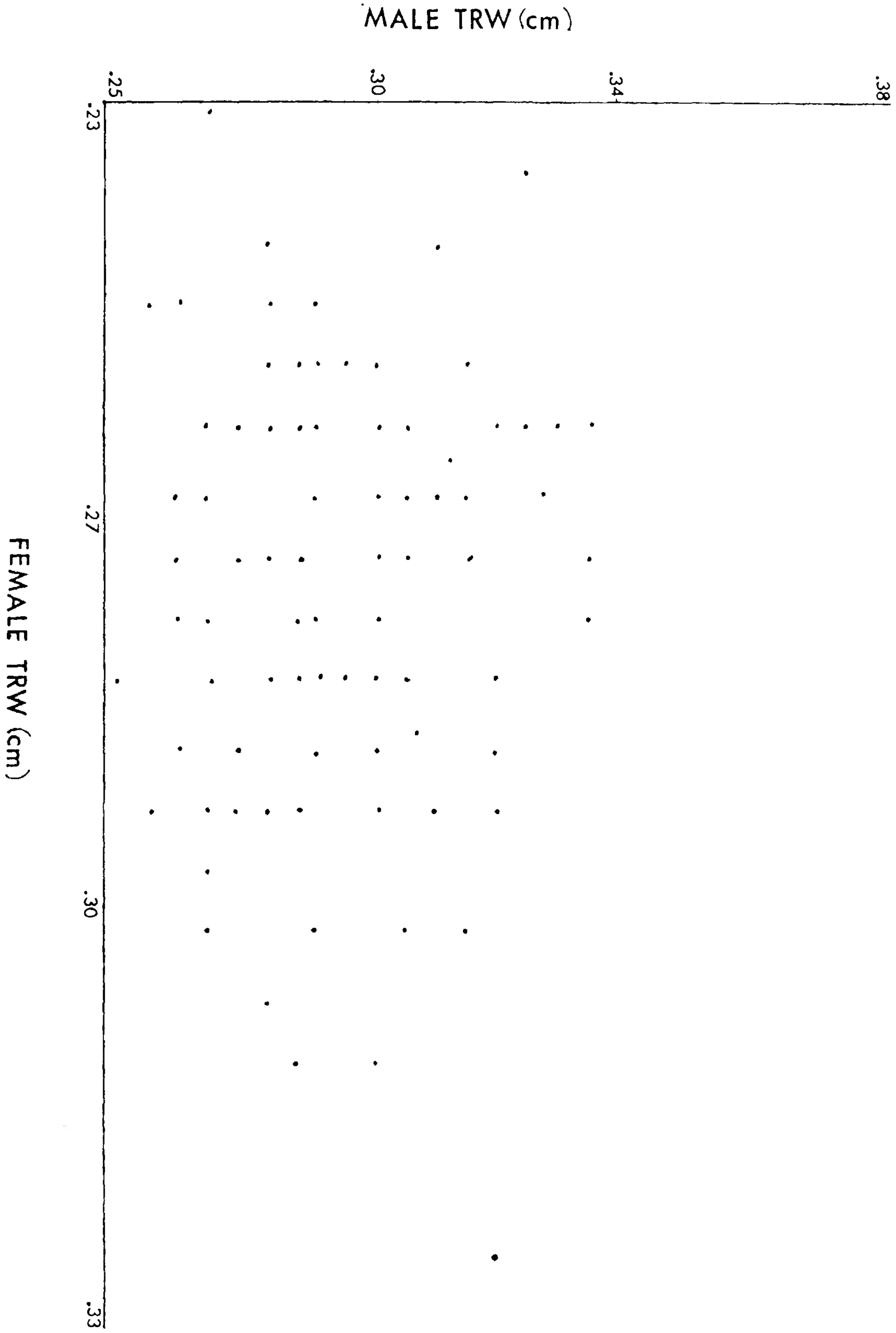

MALE PL (cm)
5.14
5.45
5.75
6.00
FEMALE PL (cm)
2.43
3.55
4.60
5.70


MALE CW (cm)
31.0
32.5
33.7
35.1
29.3
30.5
31.7
33.2
FEMALE CW (cm)


MALE TBL (cm)
8.05
8.60
9.05
9.50
7.65
8.10
8.45
8.93
FEMALE TBL (cm)


MALE TBW(cm)
.31
.37
.43
.50
.30
.37
.44
.51
FEMALE TBW(cm)


6.50
5.90
5.30
4.60
MALE TRL (cm)
4.80
5.20
5.50
5.85
FEMALE TRL (cm)


MALE TRW (cm)
.25
.30
.34
.38
FEMALE TRW (cm)
.23
.27
.30
.33

Appendix 23. Correlations between egg measurements and female body condition.[1]

Egg measurement	r	probability level[2]
a-egg		
length (cm)	0.05	0.002
width (cm)	0.19	0.002
weight (g)	0.17	0.003
b-egg		
length	0.13	0.030
width	0.19	0.002
weight	0.15	0.010
c-egg		
length	0.23	0.001
width	0.02	0.010
weight	0.19	0.004

[1] sample size too small to compute coefficients for d-eggs

[2] significance assumed at $p < 0.05$