THE BREEDING BIOLOGY AND BEHAVIOUR OF GREAT BLACK-BACKED GULLS (LARUS MARINUS L.) IN NEWFOUNDLAND

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THE BREEDING BIOLOGY AND BEHAVIOUR OF GREAT BLACK-BACKED GULLS (*Larus marinus* L.) IN NEWFOUNDLAND

BY

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ABSTRACT

The application of Game Theory to the study of behaviour has shown that it is possible, in theory, to have stable equilibria with individuals in a population behaving in different ways. In order to test for colony type selection or "nesting strategies" in this species, breeding success, site tenacity and mate selection should be monitored on a long term basis. An investigation of the reproductive biology and behaviour of Great Black-backed Gulls was undertaken to provide preliminary data to design such project.

The effects of habitat or colony type selection on reproductive output was assessed in a one year study by comparing the breeding biology and behaviour of Great Black-backed Gulls in two different environments, namely a mono-specific and a mixed-species colony. Many aspects of the breeding biology of Great Black-backed Gulls were similar between colonies but important behavioural differences were observed.

There is some evidence that colony type selection fits the model of "ideal free distribution" (Fretwell and Lucas, 1970) and acts as a "breeding strategy" in Great Black-backed Gulls. However, energetic studies should be undertaken to assess costs and benefits of the proposed strategies.

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Nicole A. Roy

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LIST OF ABBREVIATIONS

CD	Culmen Depth
CL	Culmen Length
HL	Head Length
ITS	Index of Territory Size
MB	Mating Behaviour
PB	Parental Behaviour
RB	Reproductive Behaviour
SM	Self Maintenance
TD	Territorial Defence
TL	Tarsometatarsus Length
WT	Body Weight

1.0 - INTRODUCTION

Gulls (Larus spp.) are probably the most common seabirds along world coastlines and often, well inland. In recent decades, the numbers of certain species have exploded, primarily due to changes in waste management procedures that have resulted in increased food availability (eg. Kadlec and Drury, 1968; Harris, 1970; Kihlman and Larsson, 1974). Graham (1975) described the adaptability of gulls to their environment in the following way:

> "It is their capacity to utilize whatever is in the landscape that has allowed gulls, like the brown rat and the German cockroach, to spread and thrive. It gives them an advantage over most other creatures in a world so drastically altered by man. Under so-called natural conditions Herring Gulls, California Gulls and others function as both predators and scavengers. The latter trait has served them well in this 'effluent' society, helping a greater number of young to survive the first year of their lives and swelling the population to what humans prefer to think is pest proportions."

In Atlantic Canada, Herring Gulls (L. argentatus Pont.) are the most numerous larids but the Great Black-backed Gull (L. marinus L.) population is rapidly increasing in numbers and expanding its range (Gross, 1945; Parnell and Souts, 1975; Southern, 1980).

Competition between the two species on the nesting grounds has been assessed by McGill (1977) but comparatively

few studies have been done on the breeding biology of Great Black-backed Gulls (Bergman, 1972; Verbeek, 1979; Butler and Trivelpiece, 1981; Butler and Janes-Butler, 1982, 1983), especially in Canada (Threlfall, 1968; Haycock, 1973). Similar breeding biology and habitat requirements between Herring Gulls and Great Black-backed Gulls (Harris, 1964; Erwin, 1971) may promote interspecific competition and influence their reproductive success in densely populated colonies where the availability of suitable nesting sites is limited. The advantages and handicaps of coloniality are summarized in Welty (1982):

> "Close nesting increases a bird's competition for nest-sites and nesting materials and increases opportunities for intraspecific fighting, for infanticide, and for the transmission of parasites and diseases. On the other hand, colonial living improves defence against predators, provides group stimulation and synchronization in breeding, promotes education of the young, and enhances communication about sources of danger or food."

Based on sexual selection arguements, colonially nesting gulls may be viewed as a complex array of individuals competing to propagate their own genes. Therefore, to maximize their success, they should behave and time their activities according to ecological characteristics of their environment and according to the behaviour of their competitors. Thus, the type of colony in which a Great Black-backed Gull nests may influence, to some extent, its futur reproductive

success.

The application of Game Theory (see Krebs and Davies, 1981) to the study of behaviour has shown that it is possible, in theory, to have stable equilibria with individuals in a population behaving in different ways; for example, selecting different types of colony.

In order to test for the existence of colony type selection or "nesting strategies" in this species, breeding success, site tenacity and mate selection should be monitored over many consecutive years. Thus a long term banding program of both adults and chicks would provide baseline data for such study by ensuring individual recognition of all gulls in the population and providing the nesessary information on age of partners and age at first breeding, duration of pair bonds, lifetime reproductive performance, yearly location of nests and recruitment.

An investigation of the reproductive biology and behaviour of Great Black-backed Gulls was undertaken to provide preliminary data for such long term project. The effects of habitat selection on reproductive output was assessed by studying and comparing the breeding biology and the behaviour of Great Black-backed Gulls in two different environments, namely a monospecific and a mixed-species colony. To do so, territorial attributes were compared. Time-activity budgets, breeding success and chick growth rates were also monitored throughout the reproductive season.

2.0 - METHODS AND MATERIALS

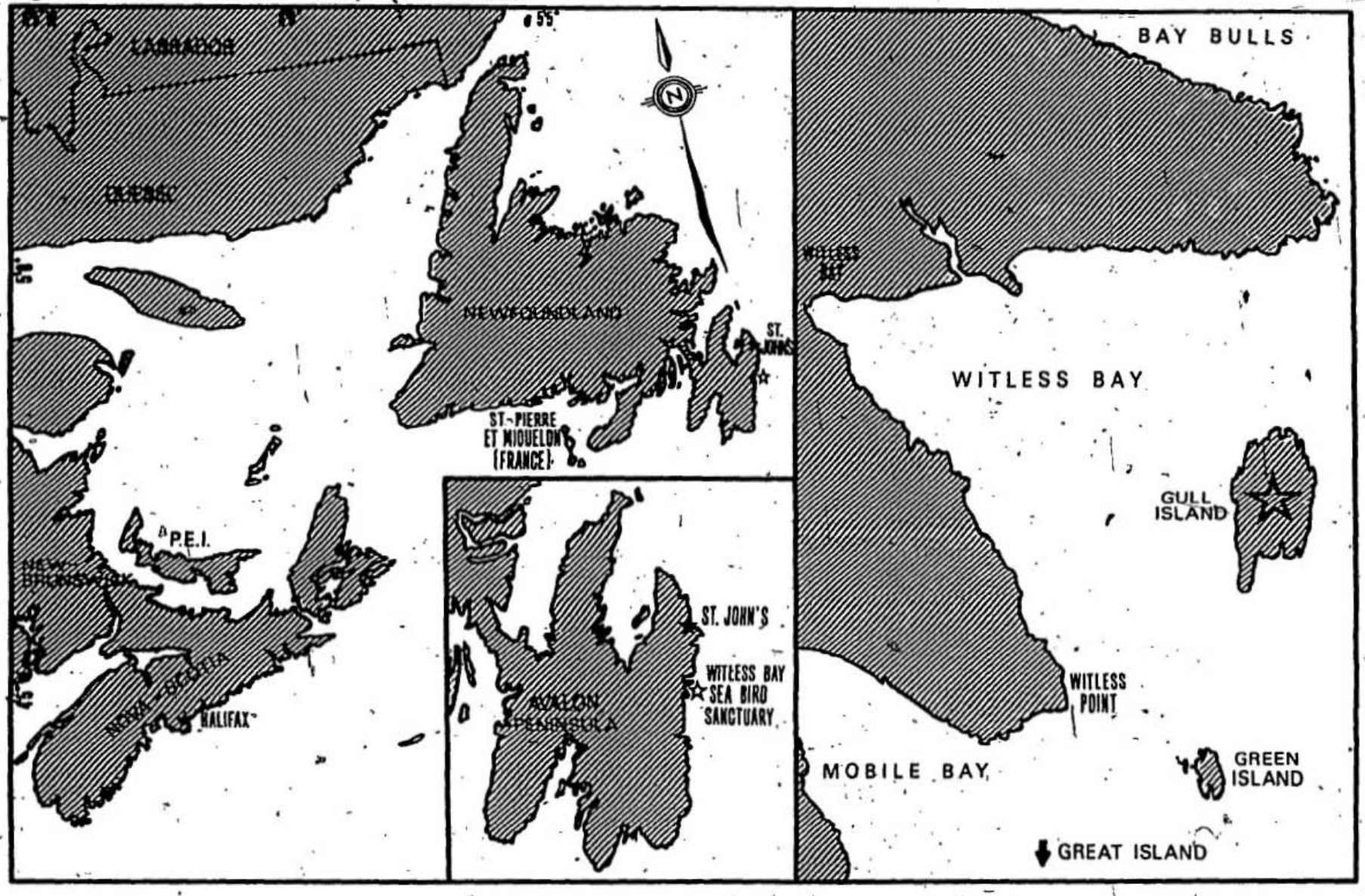
2.1 - Study area:

The present study of Great Black-backed Gulls was carried out on Gull Island (47°15'31" N, 52°46'26" W), the northernmost of three islands in the Witless Bay Sea Bird Sanctuary on the east coast of Newfoundland (Fig. 1). The experiments reported in this manuscript were performed between May 13 and August 5, 1984. Earlier access to the study site was prevented by arctic pack-ice around the island.

Gull Island is a small rocky island (1.2 X 0.8 km) located 23 km south of St. John's, and 2.5 km off the coastline. A distinctive peninsula, the Point, extends southwards from the Southwest corner. The island is bordered by high cliffs (30 m) and is covered with a thick layer of peat. At the top of the cliffs, wide grassy slopes extend to a dense spruce-fir forest covering most of the island (see Haycock, 1973, for a detailed description of Gull Island).

No mammals live on the island but the avifauna is abundant and diverse. Leach's Storm-Petrels (Oceanodroma leucorhoa (Vieillot)) and various bird species, especially passerines (Appendix 1), inhabit the tree zone. Black-legged Kittiwakes (Rissa tridactyla (L.)), Common Murres (Uria aalge (Pont.)), Razorbills (Alca torda L.), and Black Guillemots

Figure 1. Location of Gull Island, Newfoundland.



(Cepphus grylle (L.)) nest at different heights on cliffs. Atlantic Puffins (Fratercula arctica (L.)) and Leach's Storm-Petrels nest in burrows dug out in grassy slopes while Great Black-backed and Herring Gulls nest in close proximity on those grassy areas. Herring Gulls also nest on rocky outcrops and in wooded areas of low tree density such as forest edges, trails and clearings.

Approximately half of the population of Great Black-backed Gulls (60 pairs) nests in a monospecific colony established on a southern rocky outcropping: the Point (Fig. 2). They breed in a dense colony where only a few Herring Gulls manage to establish small territories among unused boulders and stones. The Great Black-backed Gulls nest on grass-covered peat while Herring Gulls form a distinctive colony on the surrounding bare bedrock.

The mixed-species colony is subdivided into two areas: the South and the East side and the monospecific colony is established in two distinct areas on the Point. These areas are physically separated by a deep and wide dent in the bedrock in which Herring Gulls nest. Nine pairs of Great Black-backed Gulls nest at the base of the Point while 51 pairs form the main colony on the southern extremity of the Point.

The rest of the Great Black-backed Gulls (53 pairs) breed in sympatry with Herring Gulls along the grassy slopes surrounding the island. Isolated pairs are scattered through

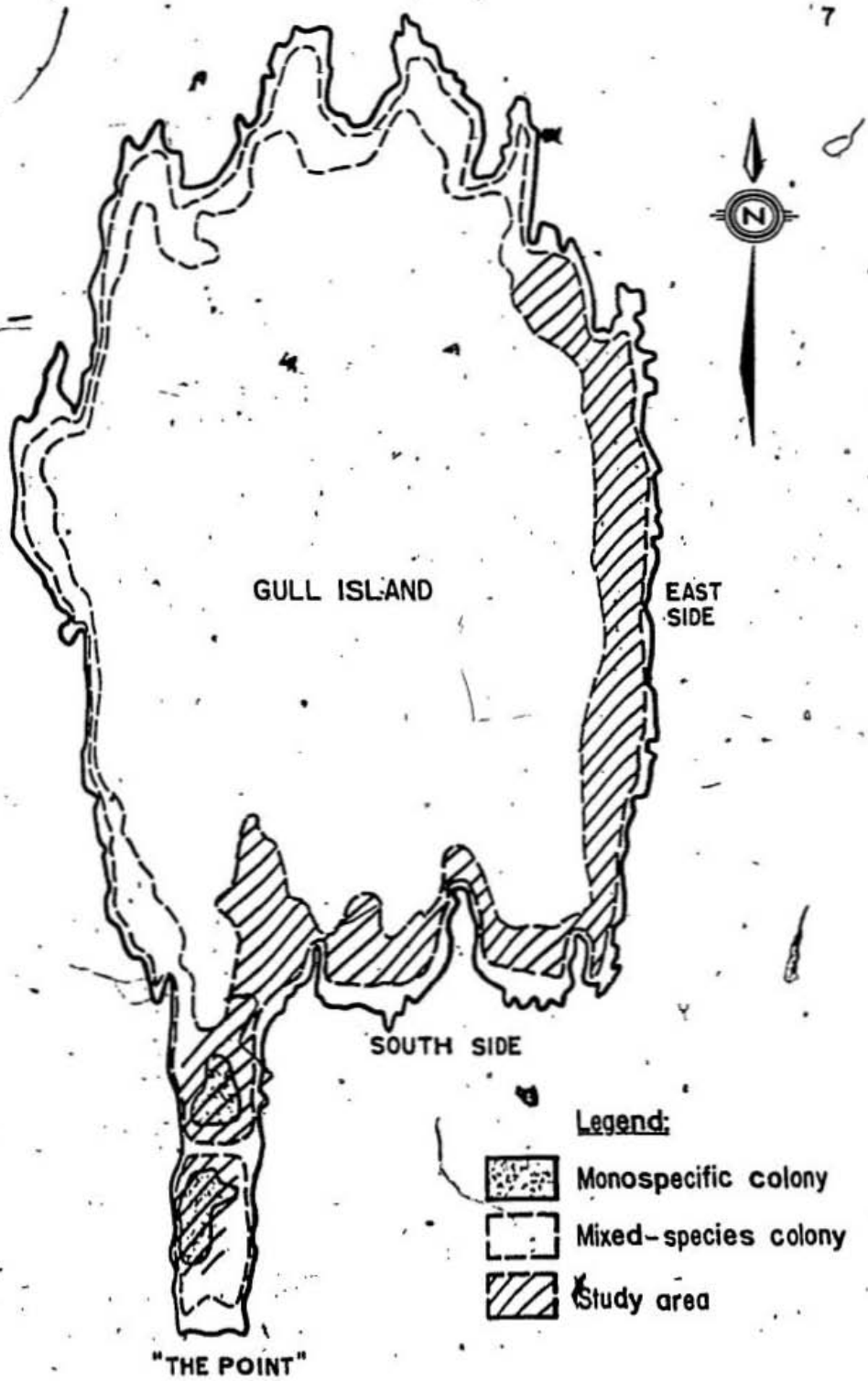


Figure 2. Location of gulleries and study area, 1984.

out the Herring Gull colonies but groups of 2, 3 or 4 pairs of Great Black-backed Gulls may form sporadic nuclei. The majority of Great Black-backed Gulls nesting among Herring Gulls are found on the South and East sides of the island.

2.2 - Experimentation:

2.2.1 - Breeding biology:

The breeding biology of Great Black-backed Gulls was monitored immediately after first arrival on the island (May 13, 1984), with egg laying being found to be well advanced. In order to minimize human disturbance during this early stage of the reproductive season, no attempt was made to record further egg layings. The timing of this activity was estimated from hatching dates using the species' mean incubation period on Gull Island (Haycock, 1973). Hatching, nestling and fledging periods were monitored during regular surveys of the colonies (see section 2.2.3).

2.2.2 - Clutch and egg size:

Just before hatching, all Great Black-backed Gull nests on the Point, South and East sides were marked with a numbered tag and clutch size was recorded. Maximum egg length and maximum transverse breadth were measured on all eggs to the nearest 0.1 mm using Vernier calipers.

2.2.3 - Chick identification and growth rate:

Great Black-backed Gull chicks were individually marked at hatching with a numbered spaghetti-tag inserted through the humeral patagium (Fig. 3). When they became large enough (approximately 21 days old or 850g), a USFWS band was fixed to the right tarsometatarsus ("tarsus"). Growth rates of 393 marked chicks were estimated from repeated measurements of 5 body parameters (weight, tarsus length, culmen length and depth, total head and bill length; Fig. 4) recorded at various time intervals depending on individual rates of recapture. Again, to reduce disturbance to breeding birds, only chicks that were easily found and/or caught were measured during a particular visit. Three or four replicates of these measurements were usually recorded before fledging.

2.2.4 - Territorial attributes:

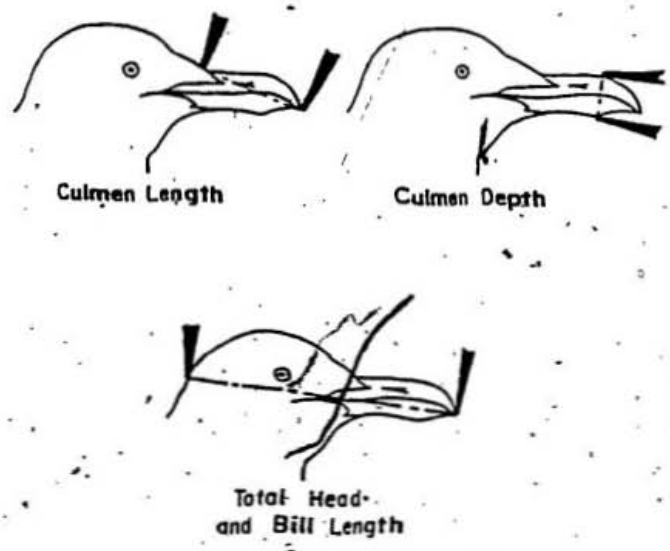
Territories were mapped during the fledging period. The abundance and identity of neighbours were recorded at the same time. Inter-nest distances (±5 cm) and angles relative to Magnetic North were measured for each territory.

Since it was impossible to identify territorial boundaries without behavioural observations and since these limits may have changed as the breeding season progressed (Hunt and Hunt, 1976; Burger, 1980), a standardized index of territory size (ITS) was developped. This method provided a minimum estimate of territory size that was consistent among

1 day old chick.

7 days old chick.

Figure 3. Spaghetti-tag fixed to the humeral patagium of Great Black-backed Gull chicks.



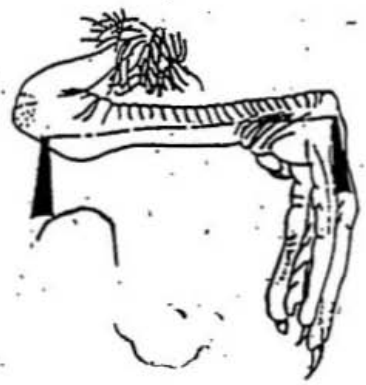


Figure 4. Body measurements taken on Great Black-backed Gull chicks.

most pairs.

If two opponents were of equal competitive capacity, the limits of the nesting area defended by each gull would be located halfway between their respective nests. Similarly, the size of their territory would be equal to the sum of the sectors formed by two consecutive inter-nest vectors and the segment uniting their halfpoint (Fig. 5).

By definition, the area of a triangle is:

$$A = 1/2\ (a)\ (b)\ \sin\theta$$

where θ is the angle between 2 adjacent sides, a and b. Thus,

$$ITS = \sum 1/2\ (D_i/2)\ (D_{i+1}/2)\ |\sin\theta_{i.i+1}|$$

$$= \sum 1/8\ (D_i)\ (D_{i+1})\ |\sin\theta_{i.i+1}|$$

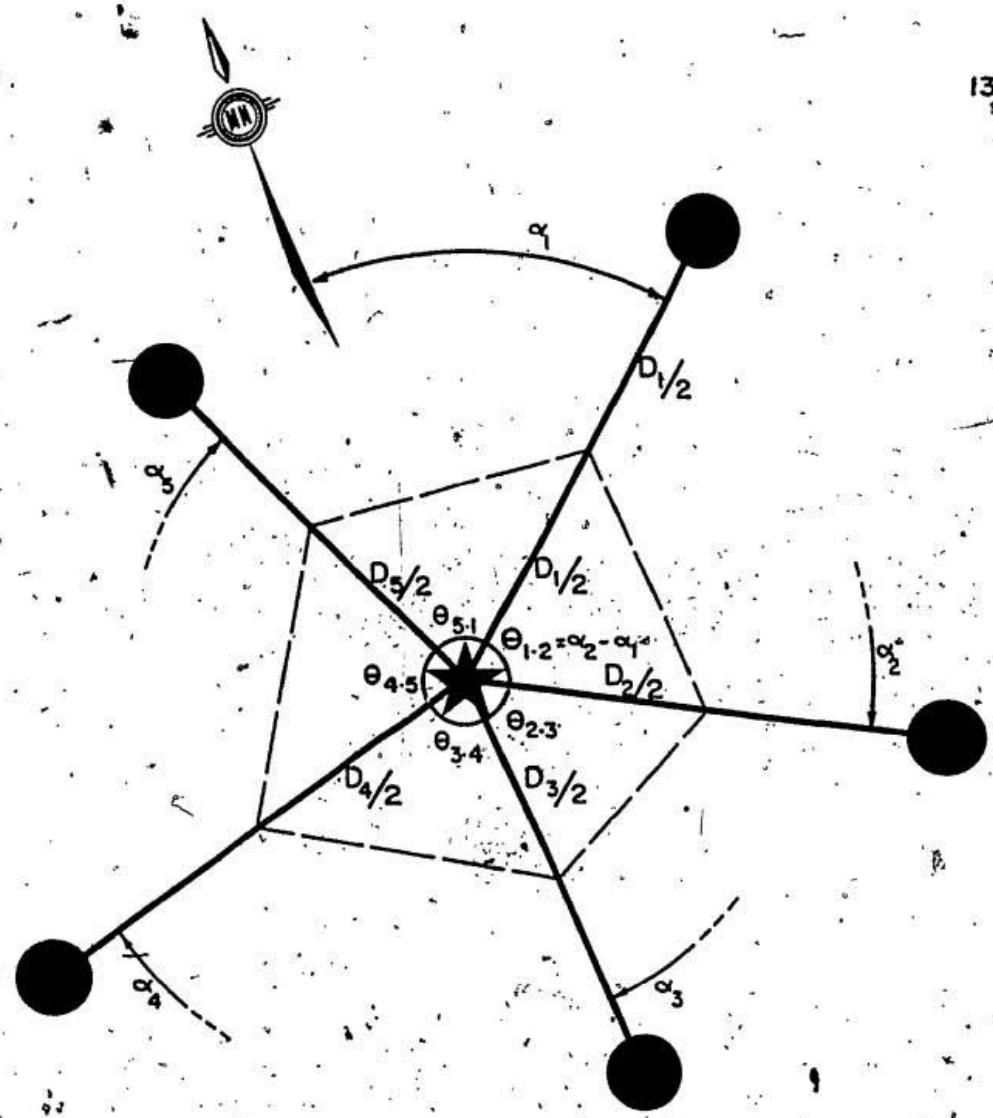
$$= 1/8 \sum\ (D_i)\ (D_{i+1})\ |\sin\theta_{i.i+1}|$$

where ITS is an estimate of the territory size,
D_i is the actual distance to the i^{th} neighbour,
$\theta_{i.i+1}$ is the angle between two consecutive D_i-vectors.

Two logical restrictions apply to this model:

1- Except when geographical constraints such as cliff edges, rocks or ponds influence nest spacing, neighbouring pairs should be evenly distributed around a territory, as opposed to grouped on one side.

2- The number of nests surrounding a territory should be at least 3; more accuracy is gained as the number of neighbours increases and $\theta_{i.i+1}$ decreases.



$$ITS = 1/8 \sum D_i (D_{i+1}) \left|\sin \theta_{i\cdot i+1}\right|$$

α_i = angle relative to magnetic North

$\theta_{i\cdot i+1}$ = angle between consecutive D_i vectors

D_i = actual distance to a neighbour

[ ] = area represented by ITS

Figure 5. Index of territory size, ITS.

2.2.5 - Time-activity budgets:

The time-activity budgets of nesting gulls was divided into the following categories of behaviour: reproductive behaviour (RB), territorial defence (TD) and self maintenance (SM). For the purpose of this study, RB refers to all behaviours concerned with reproduction. It is divided into mating and parental behaviours (MB and PB). MB comprises all behaviours aimed at establishing and reinforcing a pair bond and PB refers to behaviours concerned with provisioning and rearing the offspring. Furthermore, it is assumed that MB, PB, TD and SM are mutually exclusive, that is, a gull cannot perform activities included in different behavioural categories at the same time. Table I lists the various activities included in each behavioural category.

2.2.5.1 - Behavioural observations:

Thirteen pairs of Great Black-backed Gulls on the Point and eight on the East side were observed from blinds. The East side blind was located on top of a cliff near the forest edge and was easily accessible without disturbing the gulls. Observations required either a 15-60X telescope or a pair 7-12 X 30 binoculars. Access to the blind located on the Point caused considerable disturbance because the observer had to walk through the colony. Thus, behavioural observations began when "normal" activities had resumed, at least

Table 1. Classification of activities into behavioural categories.

BEHAVIOURAL CATEGORY	ACTIVITY
1. REPRODUCTIVE BEHAVIOUR (RB)	
1a. Mating behaviour (MB)	- choking[1]
	- gathering of nest material
	- nest building
	- nest relief
	- begging
	- courtship feeding
	- copulation
1b. Parental behaviour (PB)	- incubation
	- brooding
	- chick feeding
2. TERRITORIAL DEFENCE (TD)	- choking[1]
	- guard[2]
	- upright threat
	- posture
	- grass pulling
	- fighting
3. SELF MAINTENANCE (SM)[3]	- preening
	- resting
	- sitting (not brooding or incubating)
	- sleeping

[1]Depending on the circumstances and the sequence of behaviours, choking is used either (i) to indicate the location of the nest and to reinforce pair bonds, MB or (ii) to indicate the location of territorial limits to potential intruders (TD). In the first case, choking is performed at the nest, by both mates simultaneously. In contrast, the same behaviour taking place away from the nest by either or both mates standing in front of an opponent clearly functions as a territorial display (Tinbergen, 1960).

[2]"Guard" is a posture intermediate between the upright threat posture and the resting position in which the neck is tucked in. This posture clearly indicates awareness and aggressiveness.

[3]Self maintenance include activities centered on the individuals themselves and having no apparent social implication.

30 min after entering the blind. No visual aid was required on the Point since only nests located within 50 m of this hiding structure were observed.

Territories were scanned every 5 min: behaviours were coded and recorded for each member of a pair (Appendix 2). Data collected were then classified into the four behavioural categories described earlier.

Ninety-nine hours of observation in the mixed-species colony and 85.5 hours on the Point were gathered by two observers (N.A. Roy and S.B. Will) between May 27 and July 26; 1984; 37.5 hours overlapped. Observation periods usually lasted 4 to 6 hours but one dawn-to-dusk watch (16 hrs) was performed in the two sites simultaneously. The schedule of observations is given in Appendix 3.

The 184.5-hour period spent recording behavioural data on nesting gulls is defined as "real observation time" as opposed to "total observation time:nest" which refers to the summation of "real observation time" on each nest. For example if one had observed 10 nests during 3 periods of 5 hours, the "real observation time" would be 3 X 5 = 15 hours but the "total observation time·nest" would equal 3 X 5 X 10 = 150 hours.

The "total observation time·nest" represented 1727 hours or 103620 min of data collection on 21 nests; 76.3% (79200 min) of which was performed on sexed birds. For the purpose of this study, the analysis of behavioural

observations will be restricted to sexed animals only.

Since the duration of observation periods and the number of nest observed during each period were not always the same, the total time spent observing each nests was different. It varied, for sexed birds, from 1440 to 5580 min. Even though it was not statistically different between colonies ($U = 73$, $n_1 = 8$ and 13, $P > .10$), further analysis and comparisons will be based on "mean observation time/nest". Mean observation time/nest is defined as the mean duration of observations on individual nests per mean observation period.

2.2.5.2 - Identification and sexing of adults:

Each pair of gulls was sexed primarily on relative body size, with the females usually being smaller than their mates (Tinbergen, 1953), and on behaviours such as courtship feeding, copulation (rarely seen) and aggressiveness; males being generally more aggressive than females (Butler and Janes-Butler, 1983). When possible, one mate was colour marked with a saturated solution of picric acid in 70% alcohol using a device placed close to the nest (Figs. 6, 7).

In order to validate the sexing method, 10 adults (5 males and 5 females) were captured, banded and colour marked. Trapping was done during the fledging period using baited drop traps (Fig. 8). Baits used were thawed capelin and

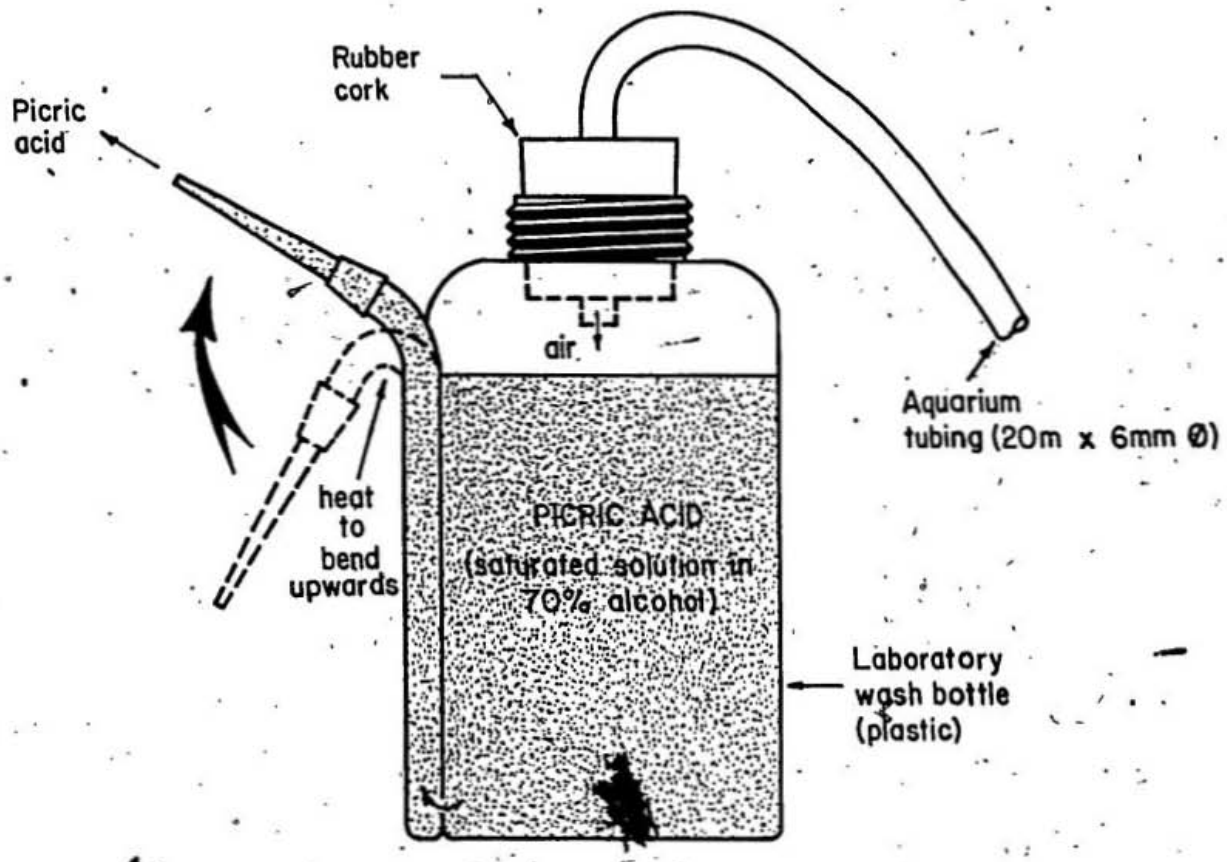


Figure 6. Apparatus used to colour mark adult gulls (Modified from Moseley and Mueller, 1975).

Figure 7. Adult Great Black-backed Gull marked with picric acid while incubating (note the colour-marking device hidden close to the nest).

Baited drop traps with triggering mechanism cocked.

Adult male caught in drop trap.

Figure 8. Baited drop traps used to capture adult Great Black - backed Gulls (Modified from Mills and Ryder, 1979).

fresh cod scraps.

Weight, tarsus length, culmen length, culmen depth, and wing chord, as well as presumed sex, were recorded for each bird. These data were compared to a control sample using a discriminant analysis (Shugart, 1977). The control sample consisted of 25 Great Black-backed Gulls (18 males and 7 females) killed in the Witless Bay Seabird Sanctuary between 1966 and 1969, and sexed during necropsy (Threlfall, pers. comm.).

Prior to the analysis, a series of t-tests were performed on the control sample (1966-69) to establish its relevance in sexing this species (Table 2). Since significant differences between sexes were found for all variables, none was rejected. T-tests were also used to compare the control and the test samples (Table 3). Except for tarsus length, no significant difference in body measurements was computed between the two samples. Thus, only four parametres provided reliable information to sex adult Great Black-backed Gulls from the test sample. The canonical equation used to confirm the sex of the gulls studied was:

$$SEX = 0.3693\,CD + 0.2348\,CL + 0.0012\,WT + 0.0385\,WC - 46.1166$$

where CD= culmen depth, CL= culmen length, WT= weight, WC= wing chord

(Female: $SEX \leq -1$; Male: $SEX > -1$)

Table 2. Comparisons of selected body measurements between sexes within a control sample of adult Great Black-backed Gulls (1966-69).

VARIABLE	SEX	N	MEAN	S.D.	T-VALUE	DF	P
WEIGHT (g)	M	18	1927.53	239.73	3.95	24	<0.001
	F	7	1536.71	165.83			
TARSUS	M	18	82.74	3.80	3.54	24	<0.002
LENGTH (mm)	F	7	77.14	2.76			
CULMEN	M	18	67.58	2.80	5.43	24	<0.001
LENGTH (mm)	F	7	60.71	3.04			
CULMEN	M	18	27.21	1.62	6.10	24	<0.001
DEPTH (mm)	F	7	23.74	1.55			
WING	M	18	490.56	12.06	5.10	23	<0.001
CHORD (mm)	F	7	457.86	19.58			

Table 3. Comparisons of selected body measurements between a control sample (1966-69) and a test sample (1984) of adult Great Black-backed Gulls.

VARIABLE	YEAR	N	MEAN	S.D.	T-VALUE	DF	P
WEIGHT (g)	84	10	1693.00	226.17	1.30	34	>0.2
	66-9	25	1822.31	281.47			
TARSUS	84	10	77.59	4.27	2.35	35	<0.025
LENGTH (mm)	66-9	25	81.23	4.32			
CULMEN	84	10	65.66	4.75	0.04	35	>0.9
LENGTH (mm)	66-9	25	65.73	4.18			
CULMEN	84	10	25.36	2.36	1.20	35	>0.2
DEPTH (mm)	66-9	25	26.28	2.01			
WING	84	10	482.36	11.47	0.14	34	>0.5
CHORD (mm)	66-9	25	481.40	20.58			

Although culmen depth appeared to be the best measurement available to sex Great Black-backed Gulls, Coulson et al. (1981) observed an age-related increase in culmen depth in Herring Gulls up to about nine years. This measurement should therefore be used with caution when sexing other gull species.

Differences in "tarsus" lengths and sex ratios between the control and the test samples were methodological in origin. Threlfall recorded a modified tarsus measurement, taken in a straight line from the distal end of the tarsometatarsus (the digits having been pushed down) to the end of the tibiotarsus including the full thickness of the medial malleolus[1] whereas a true tarsometatarsus length was measured in 1984.

Similarly the method used to capture adult gulls differed between investigators. Birds from the control sample having been collected for parasitological studies, were simply shot when they swooped at an investigator walking through the colony. It is believed that males, being generally more aggressive towards intruders than their mates, were more prone to be shot. In contrast, gulls from the test sample had to be caught alive and kept injury-free since they were involved in behavioural investigations.

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[1]The medial malleolus is the prominent distal end of the tibiotarsus. It forms the cranial boundary of a groove (sulcus mallealaris) for the tendon of the flexor digitorium longus.

Baited drop traps placed within nesting territories caused little disturbance and both sexes were equally attracted to the bait.

Results show that the actual sex of the control sample corresponded exactly to that predicted by the canonical equation. Also, the presumed sex of the test-sample matched that predicted by the same equation in all cases (Fig. 9). Thus the sexing method used during behavioural observations was considered to be reliable. In comparison, Coulson et al. (1983) reported more than 97% accuracy when using total head and bill length to sex Great Black-backed Gulls and additionnal body measurements did not improve significantly the exactitude of the sexing method.

2.2.6 Statistical analysis:

Behavioural data were compiled and analysed on an IBM PC/XT microcomputer equiped with a 20 megabits hard disk, using the SPSS/PC statistical package (Norusis, 1984). Analysis of variance (ANOVA) were used to assess the variance in behavioural data within each colony while non-parametric statistics (Mann-Whitney U-test) were used when comparing the variance between colonies as well as the variance between sexes.

Pearson's correlation coefficients (r) and computer generated scatterplots were used to measure the strength of linear associations between breeding success and the various

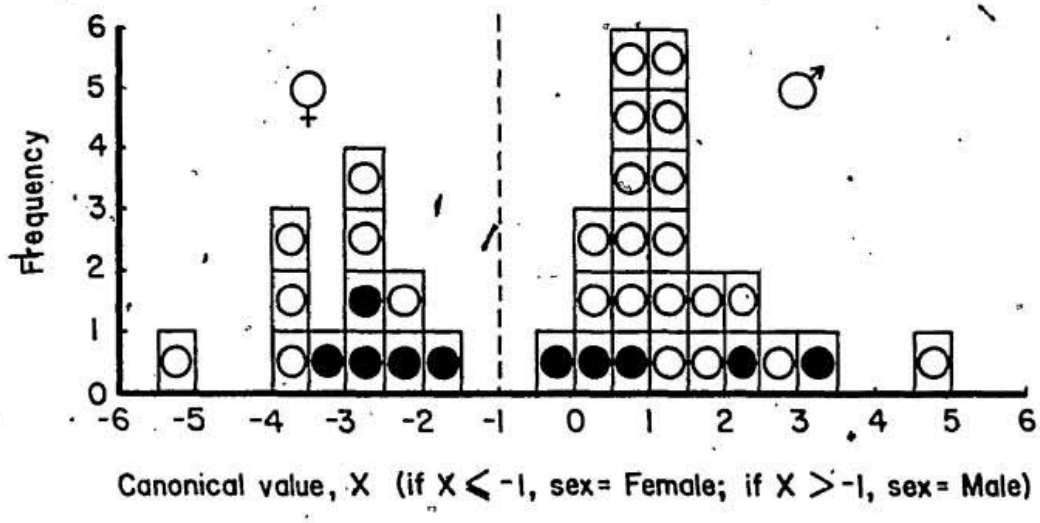

Figure 9. Sexing adult Great Black-backed Gulls according to body measurements.

biological and behavioural factors studied. Care had to be taken in interpreting correlation coefficients since a strong r does not necessarily imply causation. For example two variables can be highly correlated but for practical reasons, be independent of each others while being related to a third variable that may not be included in the analysis.

These simple tests were favoured because of the exploratory nature of the project. Based on the results obtained, it will be possible to develop more sophisticated methods keeping, adding or removing other variables.

3.0 - RESULTS

3.1 - Breeding biology:

The breeding biology of Great Black-backed Gulls was monitored on 99 of the 113 nests present on Gull Island in 1984. The breeding success of this population is summarized in Table 4.

3.1.1 - Clutch and egg size:

A total of 251 eggs were laid in 99 nests in 1984. Clutch size ranged from 1 to 3 and averaged[1] 2.5 (Table 5). Mean[1] clutch sizes were not significantly different between the monospecific and the mixed-species colonies ($t = 1.72$, $DF = 97$, $P > .05$) but the distribution of clutches was different ($G = 8.911$, $DF = 2$, $P < .025$). Eight nests containing only one egg were found in the mixed-species colony compared to one on the Point.

There was no difference in clutch size between sub-colonies despite the large difference in the number of nests involved. Clutch size averaged 2.6 at the base of the Point compared to 2.7 eggs per nest in the main colony ($t = 0.50$, $DF = 53$, $P > 0.5$). Similarly, individuals nesting on the South side of Gull Island laid slightly more eggs ($\bar{X} = 2.9$) than those nesting on the East side ($\bar{X} = 2.3$) but the differ-

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[1] Throughout the manuscript, "average" and "mean" will refer to the arithmetic mean of a sample, "$\bar{X}$". Means will be given $\pm$ one standard deviation as follow: $\bar{X} \pm$S.D.

ua s mse ves an av ng no appare.

Table 4. Breeding success of Great Black-backed Gulls on Gull Island, 1984.

AREA	NESTS	EGGS LAID	CHICKS HATCHED	CHICKS FLEDGED	HATCHING SUCCESS[1]	FLEDGING SUCCESS[2]	NESTLING SUCCESS[3]
POINT	55	145	104	57	0.72	0.39	0.55
colony	46	122	88	50	0.72	0.41	0.57
base	9	23	16	7	0.70	0.30	0.44
SIDES	44	106	74	49	0.70	0.47	0.66
south	8	23	11	9	0.48	0.39	0.82
east	36	83	63	40	0.76	0.48	0.63
ISLAND	99	251	178	106	0.71	0.42	0.60

[1] Hatching success = chicks hatched / eggs laid
[2] Fledging success = chicks fledged / eggs laid
[3] Nestling success = chicks fledged / chicks hatched.

Table 5. Distribution of clutches in the monospecific colony (the Point) and the mixed-species colony (South and East sides), 1984.

AREA	CLUTCH SIZE 1	2	3	MEAN CLUTCH
POINT	1	18	36	2.6
colony	1	14	31	2.7
base	0	4	5	2.6
SIDES	8	10	36	2.4
south	0	1	7	2.9
east	8	9	19	2.3
ISLAND	9	28	62	2.5

ence was not significant ($t = 1.91$, $DF = 42$, $P > .05$). Thus no distinction will be made between sub-colonies when comparing reproductive success of gulls nesting in the different types of coloniality.

Egg size was generally more variable in the mixed-species colony than in the monospecific colony: except for maximum egg length, all extreme values of the parameters measured were recorded in the mixed-species colony (Table 6). Maximum egg length was significantly larger on the Point than in the mixed-species colony ($t = 2.87$, $DF = 255$, $P < 0.005$) but maximum transverse breadth was similar ($t = 0.56$, $DF = 255$, $P > .5$). Furthermore, no significant difference was found in egg volume ($t = 1.81$, $DF = 255$, $P > 0.05$).

3.1.2 - Incubation period:

Haycock (1973) found that the incubation period of Great Black-backed Gulls on Gull Island averaged 30 days after laying (1st egg, 31.5 $\pm$1 day; 2nd egg, 29.8 $\pm$1 day; 3rd egg, 30.0 $\pm$1 day). The distribution of egg laying dates in 1984 was estimated by subtracting Haycock's figure from hatching dates (section 3.1.3). Egg laying occured between April 25 and May 26, and culminated during the second week of May; one unsuccessful renest (2 eggs) was recorded in the monospecific colony on June 6.

A chronological difference between the two colonies such as that observed in hatching dates can not be inferred

Table 6. Mean values of various measurements taken on 257 Great Black-backed Gull eggs on Gull Island, 1984.

AREA	NUMBER EGGS	MAXIMUM LENGTH (mm)	MAXIMUM TRANVERSE BREADTH (mm)	VOLUME[1] (cc)
POINT	155	76.81	53.31	104.03
(S.D.)		3.02	1.44	7.67
(range[2])		68.0-84.9	49.0-56.3	80.7-119.8
SIDES	102	75.69	53.20	102.17
(S.D.)		3.17	1.57	8.53
(range[2])		64.9-83.1	45.9-56.4	67.5-120.2
TOTAL	257	76.37	53.27	103.30
(S.D.)		3.12	1.49	8.08
(range[2])		64.9-84.9	45.9-56.4	67.5-120.2

[1] Egg volume= $D^2L(0.476)/1000$ (Harris, 1964; Parsons, 1972).

[2] Maximum and minimum values are underlined.

since different environmental, biological and behavioural factors might have influenced the duration of the incubation period (MacRoberts and MacRoberts, 1972; Parsons, 1972). Furthermore, there is no estimate of laying dates of 73 eggs that did not hatch.

3.1.3 — Hatching period:

Although 178 out of 251 eggs hatched successfully (Table 4) hatching dates were recorded on 145 chicks. The first chick hatched on May 25 and the last one, on June 21 (Fig. 10). Estimates of hatching dates for 24 chicks of unknown age extend the hatching period to June 24 with a wide peak between June 6 and June 14. The ages of these chicks were estimated from multiple regression equations generated from data on known-age chicks.

The Point:

AGE = −33.1148 + .3508 HL + 1.1614 CD − .2145 TL + .5022 CL

(R= .98, F= 1458.12, DF= 4 and 199, P< .0001)

South and East sides:

AGE = −34.5885 + .4235 HL + 1.2298 CD − .2758 TL + .4272 CL

(R= .98, F= 1209.96, DF= 4 and 168, P< .0001)

where HL= head length CL= culmen length
CD= culmen depth TL= tarsus length

Body weight was not entered in the equations since

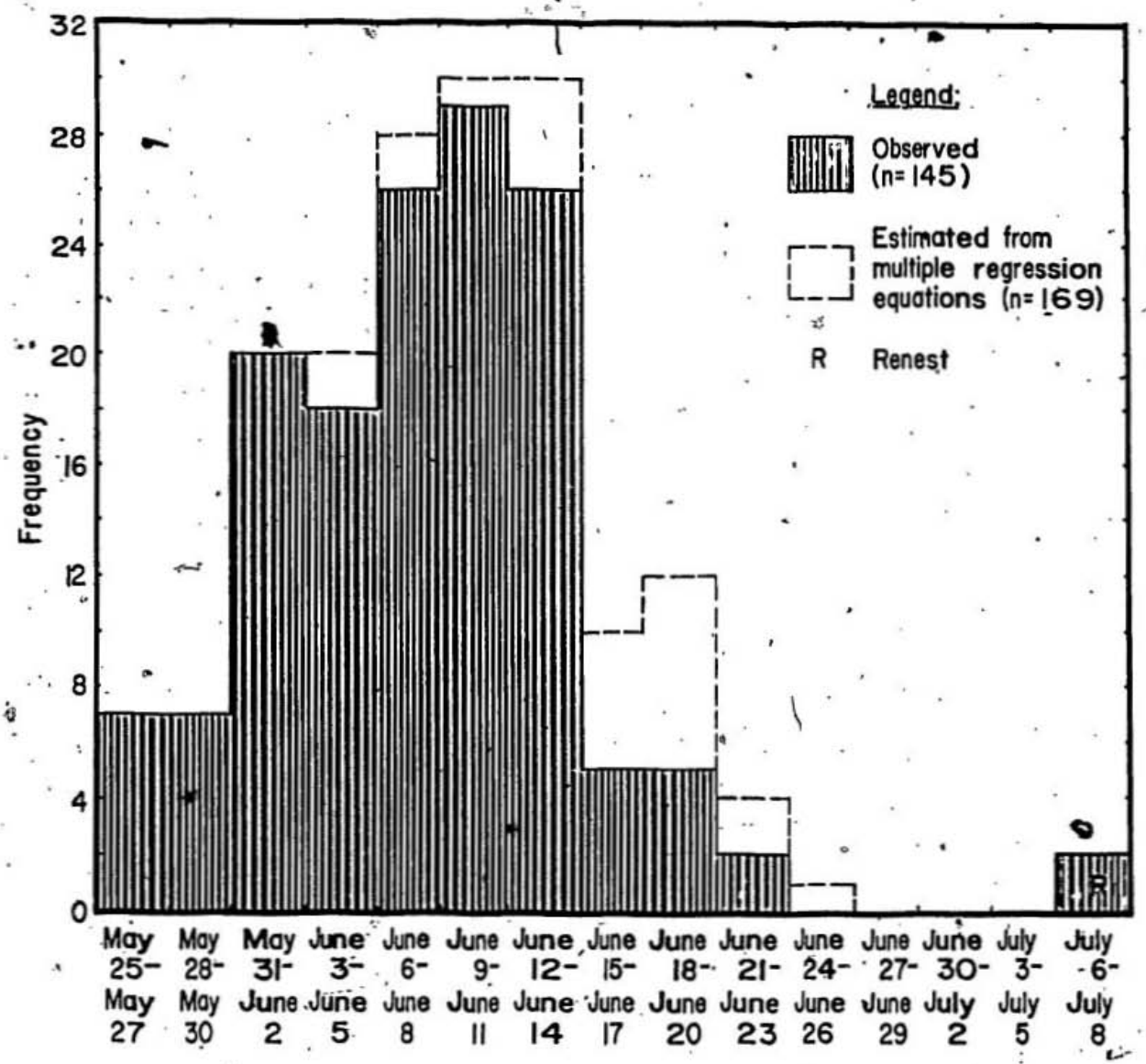

Figure 10. Distribution of hatching dates on Gull Island, 1984.

it did not add significant improvement in fit over the linear models (Zar, 1974). The large variability observed in body weight especially in the latter part of the nesting season may have been caused by the irregular occurrence of regurgitation and/or defecation when the chicks were handled. Other factors contributing to this variability include the time elapsed since the last meal and, possibly, sexual dimorphism (especially during the few weeks prior to fledging).

Although the numbers of chicks hatched in each colony were similar (Table 7), hatching occured significantly earlier in the monospecific colony (May 25 to June 18, $\bar{X}$= June 6 $\pm$6.5 days) than in the mixed-species colony (June 1 to June 21, $\bar{X}$= June 9 $\pm$4.5 days; t= 2.52, DF= 143, $P<0.02$; Fig. 11). This difference was further enhanced when the estimated hatching dates of the unknown-age chicks were incorporated into the distributions (monospecific: unchanged; mixed-species: ~~June 1~~ to June 24, $\bar{X}$= June 11 $\pm$6.0 days; t= 4.72, DF= 167, $P<0.0001$).

3.1.4 - Nestling period:

3.1.4.1 - Chick mortality:

Of the 178 chicks hatched in 1984 (Table 4), 72 died before fledging: 47 in the monospecific colony and 25 in the mixed-species colony (Table 8). There was no difference in the total number of chicks dead before fledging in the two

Table 7. Fate of eggs on Gull Island, 1984.

AREA	No. EGGS LAID	No. CHICKS HATCHED[1]	NO. EGGS NOT HATCHED[2] missing	rotten	TOTAL
POINT	145	104	32	8	40
SIDES	106	74	28	5	33
TOTAL	251	178	60	13	73

[1] $\chi^2 = 0.11$, DF = 1, $P > .50$
[2] $\chi^2 = 1.10$, DF = 1, $P > .25$

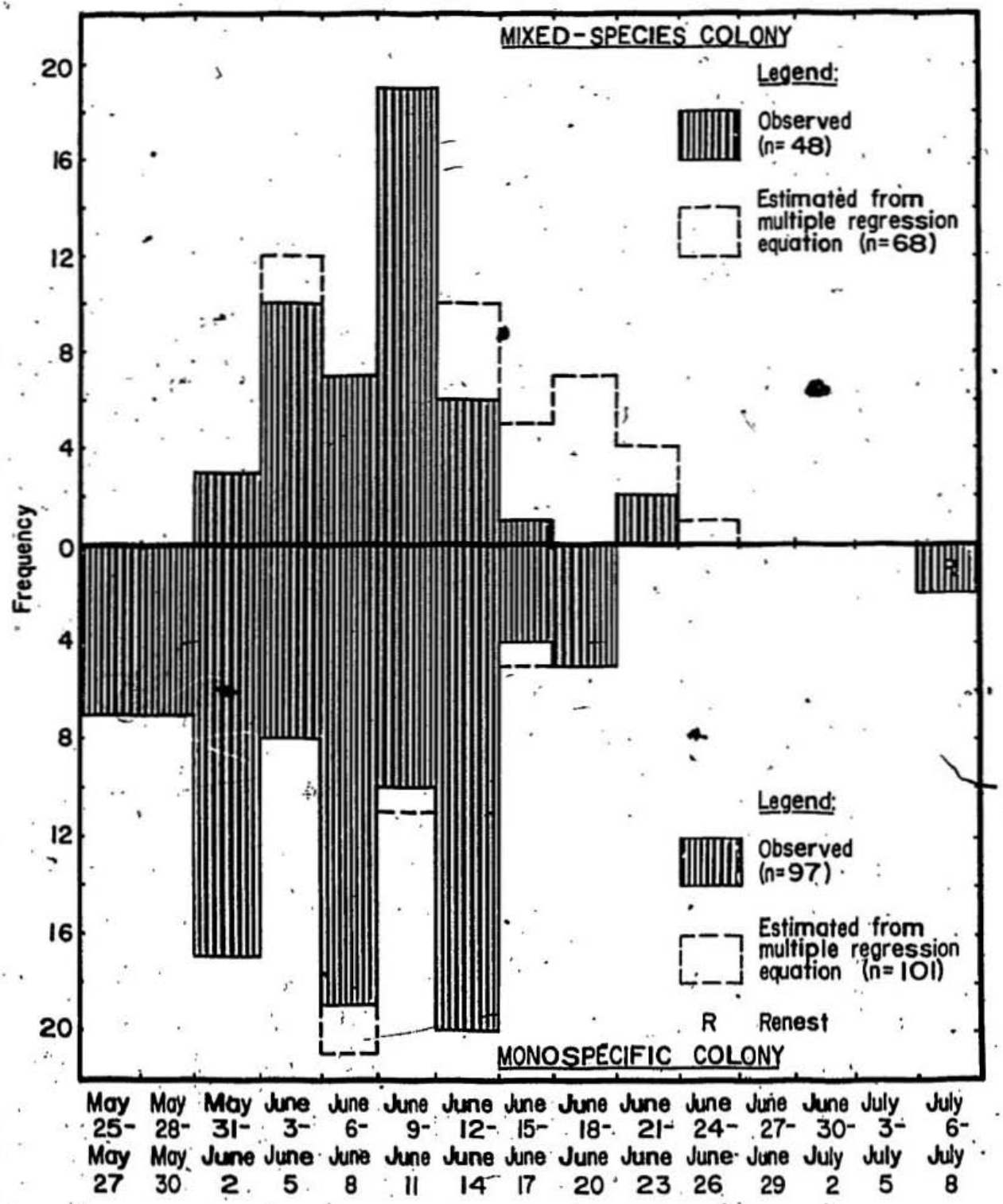

Figure 11. Distributions of hatching dates in the mixed-species and the monospecific colony, 1984.

Table 8. Observed frequencies of chick mortality in the monospecific colony (the Point) and in the mixed-species colony (South and East sides), 1984.

	AREA		
	POINT	SIDES	TOTAL
NUMBER OF NESTS INVOLVED			
Total number of nests	55	44	99
Nests with mortality[1]	32	16	48
NUMBER OF CHICKS INVOLVED			
Total number of chicks	104	74	178
Chicks in nests with mortality[2]	72	40	112
Chicks dead[3]	47	25	72

[1] $\chi^2 = 4.66$, DF= 1, $P < .05$*
[2] $\chi^2 = 4.14$, DF= 1, $P < .05$*
[3] $\chi^2 = 2.34$, DF= 1, $P > .10$

colonies but the number of nests in which mortality occurred and the size of the broods affected were significantly different.

In the monospecific colony, mortality occurred in 58% of the nests. Broods of 3 and 2 chicks were the most affected with 53% and 34% loosing at least one chick respectively. Furthermore, 62.5% of the broods affected lost only one chick and 28% lost two siblings.

In the mixed-species colony, mortality occurred in 36% of the nests; 50% of which hatched 3 chicks. Broods of 2 and 1 chicks were equally affected. Furthermore, although 50% of the broods affected lost only one chick, 44% lost two siblings.

These results indicate that there may have been a selection pressure that affected broods differently in the two colonies. In the monospecific colony 2/3 of the broods were affected but and brood size was generally reduced by 1. In the mixed-species colony 1/3 of the broods were affected but they generally suffered a greater loss. Such selection pressure may be linked to many components of the environment (eg. territory size) and/or to behavioural factors such as competition and experience.

The occurrence of mortality per age class was similar in the two colonies ($G = 9.918$, $DF = 8$, $P > .25$; Table 9) and 73.7% of the chicks that did not survive to fledging died during the first 14 days of life. After 35 days of age,

Table 9. Observed frequencies of chick mortality per age class.

AGE CLASS:	1	2	3	4	5	6	7	8	9		
AGE (DAYS):	0-7	8-14	15-21	22-28	29-35	36-42	43-49	50-56	57+	?	TOTAL
AREA											
POINT	25	8	3	3	0	1	2	1	1	3	47
(%)	53.2	17.0	6.4	6.4		2.1	4.3	2.1	2.1	6.4	100.0
SIDES	15	5	1	3	1	0	0	0	0	0	25
(%)	60.0	20.0	4.0	12.0	4.0						100.0
TOTAL	40	13	4	6	1	1	2	1	1	3	72
(%)	55.6	18.1	5.6	8.3	1.4	1.4	2.7	1.4	1.4	4.1	100.0

mortality was only observed in the monospecific colony. At the age of 35 days, Great Black-backed Gull chicks weigh about 1300g which is the average weight of male Herring Gulls (Threlfall and Jewer, 1978). In contrast, male Great Black-backed Gulls weighed, on average, more than 1900g. Hence Great Black-backed Gull chicks were better able to defend themselves against aggressive neighbours in the mixed-species colony than on the Point.

It was not always possible to determine the causes of mortality: only 17 corpses were found on the island and 7 showed signs of injuries such as broken wings or damaged skulls. These nestlings died between 5 and 51 days after hatching but most (11) were older than 21 days. Fifty-five chicks "disappeared" from the area where they hatched and were assumed to be victims of crows or cannibalistic gulls. Of these, 18 chicks (32.7%) were seen for the last time when wing-tagged; 13 at the age of 2 days or less and five between 5 and 18 days old. Since the spaghetti-tags were hidden under the wing and did not make the chicks more conspicuous than unmarked ones, it is suspected that perturbations caused by investigators may have been a major cause of chick mortality.

The effects of human disturbance on colonially nesting birds are reviewed in Lamoureux, et al. (1985): human disturbance causes a reduction in breeding success through changes in adult behaviour. In the current study, the

presence of investigators in the colonies during the nestling period caused the adults to temporarily abandon their territories. Chicks left without surveillance were more vulnerable to predation during the first 14 days after hatching and, to aggression by neighbours after this period. Also, prolonged exposure to extreme temperatures may have reduced the survival of very young hatchlings when the colonies were disturbed since young gulls were not fully able to thermoregulate during the first few days after hatching (Howell et al., 1974, in Hand, 1980).

3.1.4.2 - Chick growth rate:

The multiple regression equations used to predict the age of chicks of unknown hatching dates according to location (section 3.1.3) were not statistically different from each other ($F = .230$, $DF = 5$ and 367, $P > .50$). In other words, the type of coloniality in which young Great Black-backed Gulls were raised did not appear to influence their overall physical development. But since chick growth rates eventually reached a plateau, these linear equations quickly lost their predictive value as nestlings grew older. Growth rates were therefore monitored through the development of each growth parameter, taken separately.

Except for body weight which will be discussed later, the shape of the curves that best described the relationships between particular growth parameters and chick age

was similar to a second order (quadratic) function:

$$Y = b_0 + b_1(AGE) + b_2(AGE)^2 \qquad (1)$$

where Y is the predicted value of the parameter studied.

A curve representing the general equation was fitted to the data by plotting the expected values of Y corresponding to 0, 5, 10, 15, 20, ... , 65, 70 days of age.

Assuming that this model is a good approximation of the reality, the development of a particular growth parameter is completed when the curve reaches a plateau, that is, when its slope (or first derivative) equals zero. This point indicates the age at which the maximum value of the parameter studied is achieved. Thus,

$$Y' = 0 = b_1 + 2b_2(AGE) \qquad (2)$$

and,

$$AGE = -b_1/2b_2 \qquad (3)$$

Combining equations (1) and (3),

$$\begin{aligned} Y_{max} &= b_0 + b_1 (-b_1/2b_2) + b_2 (-b_1/2b_2)^2 \\ &= b_0 - b_1^2/2b_2 + b_1^2/4b_2 \\ &= b_0 - 1/4 (b_1^2/b_2) \end{aligned} \qquad (4)$$

The relationship between body weight and chick age was best represented by a third order (cubic) function:

$$Y = b_0 + b_1 (AGE) + b_2 (AGE)^2 + b_3 (AGE)^3 \qquad (5)$$

The maximum weight achieved was computed in a similar manner as above that is, by setting the first derivative of equation (5) equal to 0, estimating the corresponding age (from successive trials in this case) and inserting its value in the original equation.

$$Y' = 0 = b_1 + 2b_2 (AGE) + 3b_3 (AGE)^2 \qquad (6)$$

Also, the maximum rate of weight gain which corresponds to the inflection point of the curve could be calculated by setting the second derivative of equation (5) equal to zero:

$$Y'' = 0 = 2b_2 + 6b_3 (AGE) \qquad (7)$$

and,

$$AGE = -b_2/3b_3 \qquad (8)$$

Combining equations (6) and (8),

$$\begin{aligned} Y'_{max} &= b_1 + 2b_2 (-b_2/3b_3) + 3b_3 (-b_2/3b_3)^2 \\ &= b_1 - 2b_2^2/3b_3 + b_2^2/3b_3 \\ &= b_1 - b_2^2/3b_3 \end{aligned} \qquad (9)$$

Figures 12 to 16 show the developmental curves of five growth parameters monitored on chicks from the two colonies. The polynomial equations representing the best fitted curves were compared to determine whether they were estimating a unique population. The method used to determine whether two multiple regression equations are estimating the same population regression function is outlined in Zar

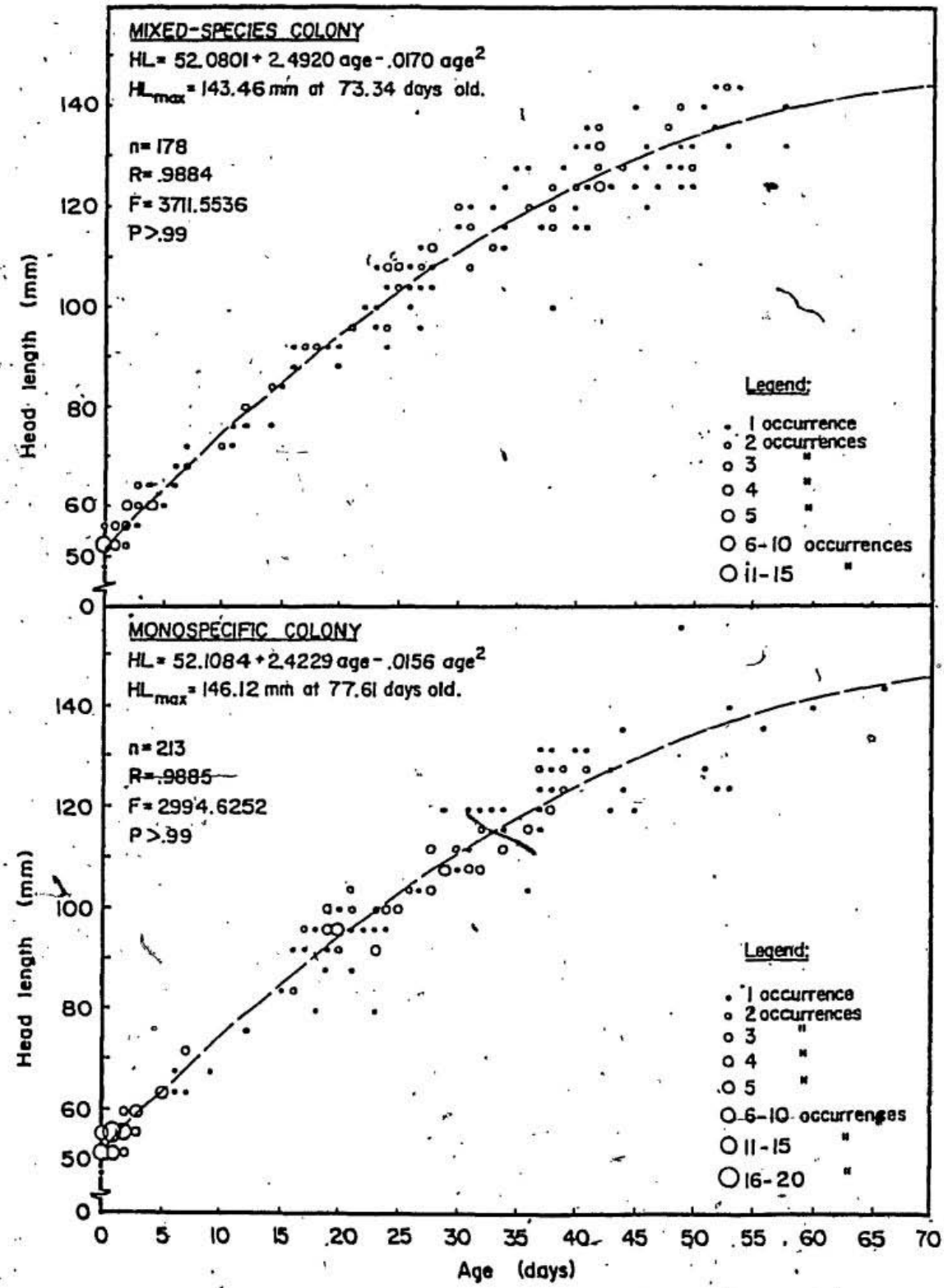

Figure 12. Increase in head length of chicks raised in the mixed-species and in the monospecific colony.

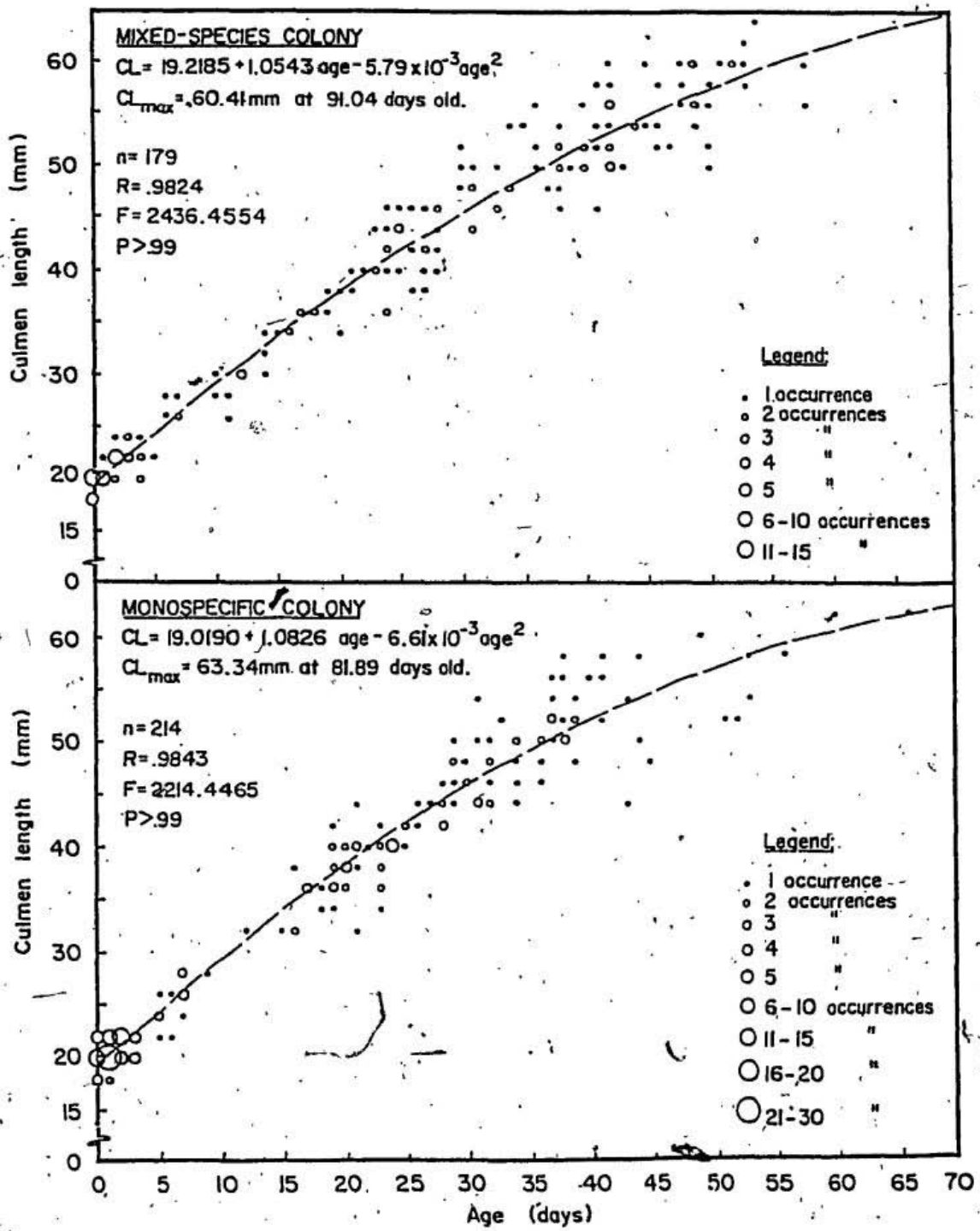

Figure 13. Increase in culmen length of chiks raised in the mixed-species and in the monospecific colony.

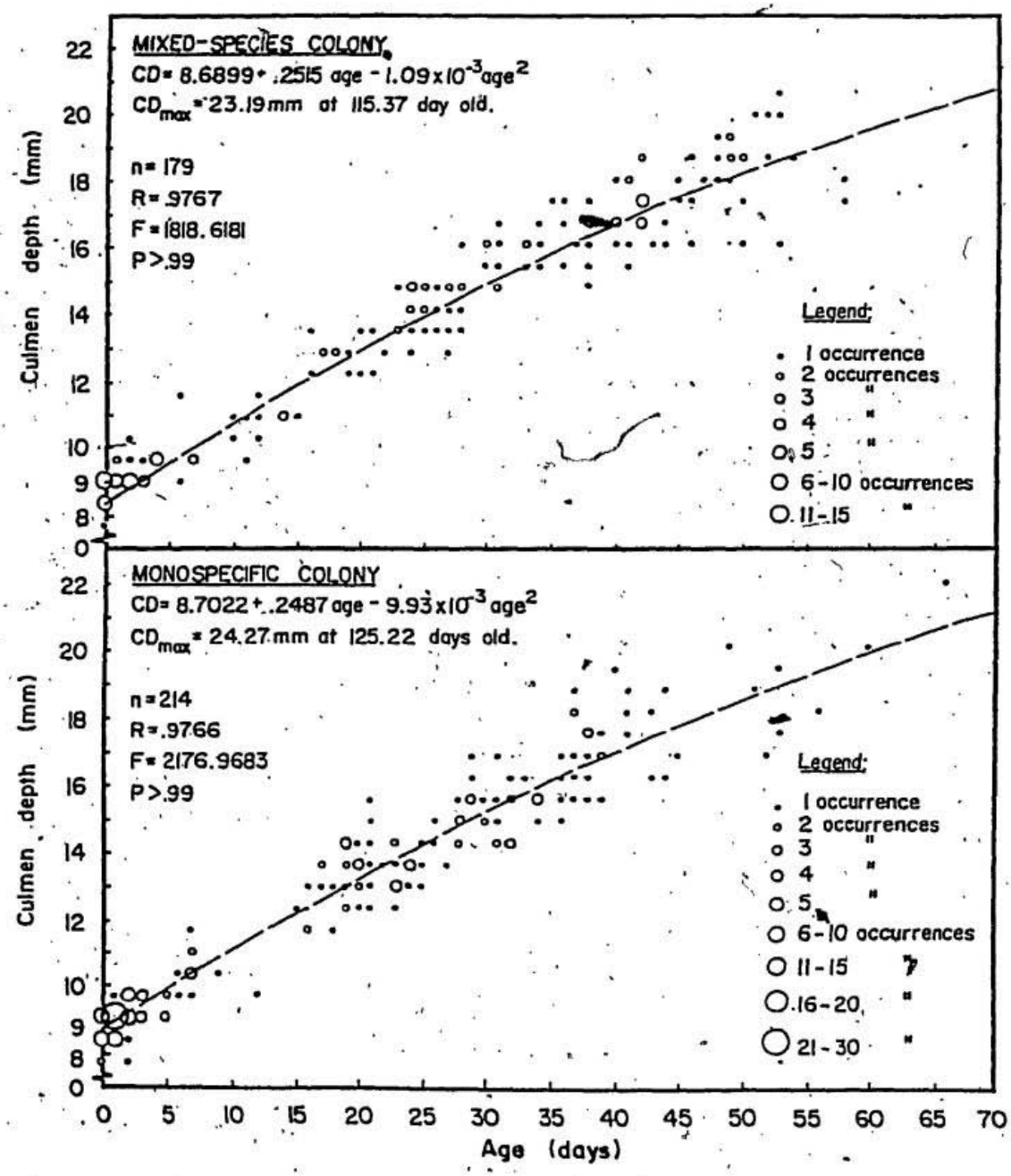

Figure 14. Increase in culmen depth of chicks raised in the mixed-species and in the monospecific colony.

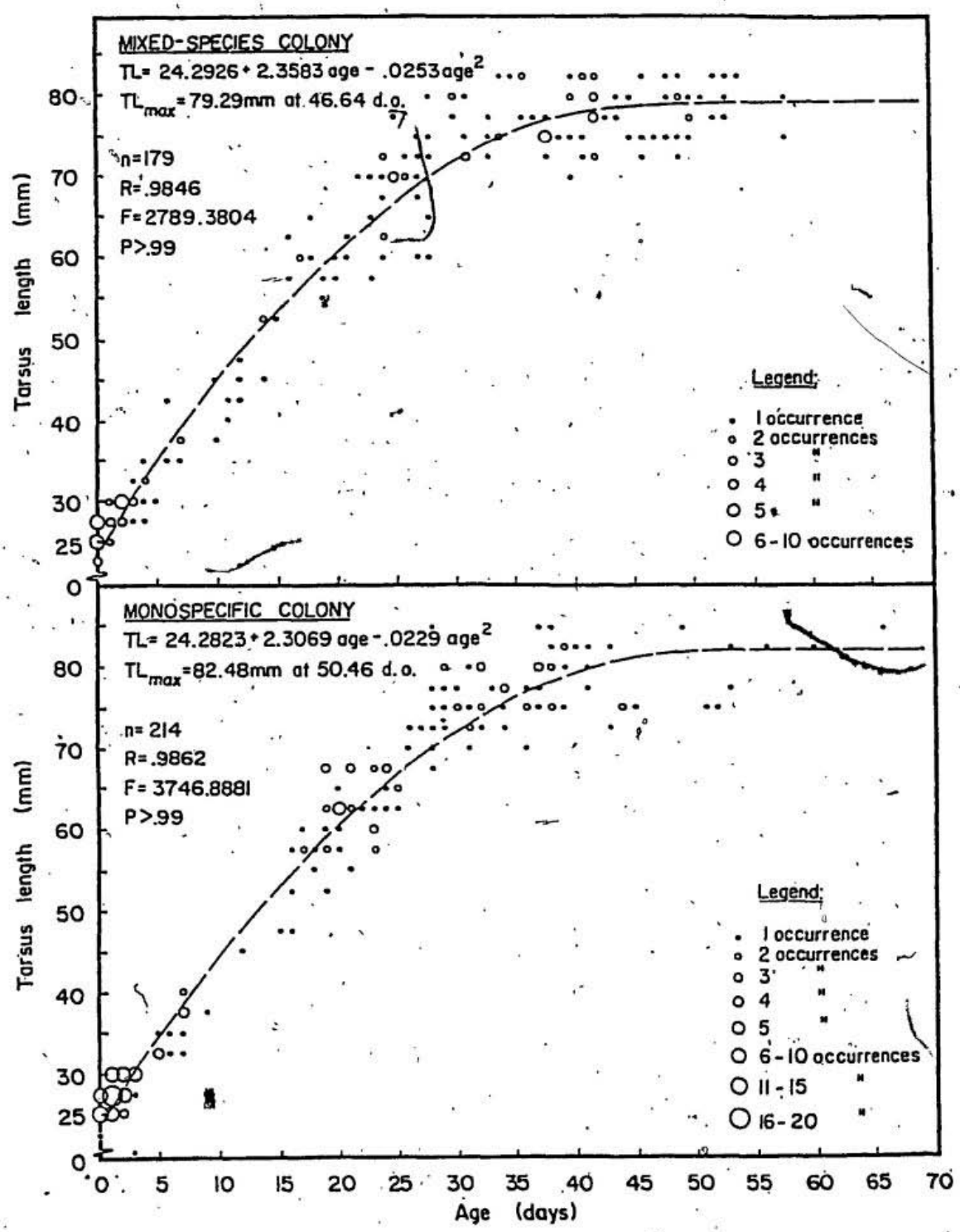

Figure 15. Increase in tarsus length of chicks raised in the mixed-species and in the monospecific colony.

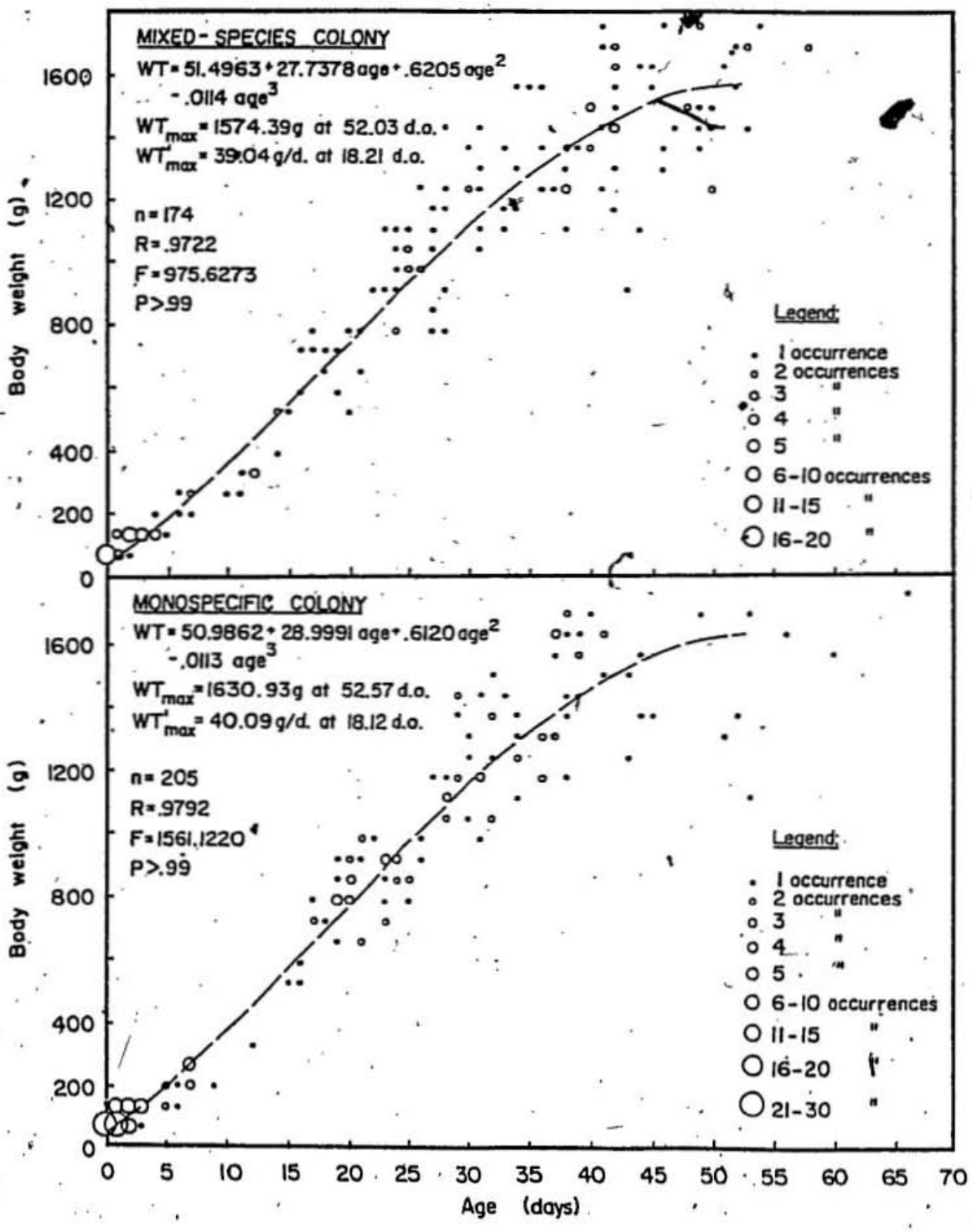

Figure 16. Increase in weight of chicks raised in the mixed-species and in the monospecific colony.

(1974). There was no statistical difference between equations representing the development of head length, culmen length, culmen depth and body weight between the two colonies, but a significant difference was found in growth rates of the tarsometatarsus (Table 10). Although tarsus length at hatching were similar in the two colonies (24.3 mm), a faster growth rate (especially after the age of 25 days) spread over a longer period of time in the monospecific colony resulted in a maximum tarsus length of 82.5 mm reached at 50.5 days compared to 79.3 mm, 46.6 days after hatching in the mixed-species colony. However, it was not possible to see if such morphological difference would persist until the age of reproduction because of the small samples involved (monospecific colony: 3 males and 3 females; mixed-species colony: 2 males and 2 females).

3.1.5 - Fledging period:

Since gull chicks do not usually leave the colony until several days after they are able to fly and continue to be fed by their parents during this time, young Great Black-backed Gulls were considered to be fledged at their first strong flight (Moreau, 1946; Drent et al., 1964; Haycock, 1973).

Of the 178 chicks hatched in 1984, 106 fledged: 57 in the monospecific colony and 49 in the mixed-species colony (Table 4). This difference was not significant (χ^2-

Table 10. Comparison of growth equations between the monospecific colony (the Point) and the mixed-species colony (South and East sides).

Y	AREA	Y_0	Y_{max}	AGE_{Ymax}	F	DF	P
HL (mm)	Point	52.1	146.1	77.6	0.48	3, 385	>.50
	Sides	52.1	143.5	73.3			
CL (mm)	Point	19.0	63.3	81.9	0.58	3, 387	>.50
	Sides	19.2	60.4	91.0			
CD (mm)	Point	8.7	24.3	125.2	0.08	3, 388	>.50
	Sides	8.7	23.2	115.4			
TL (mm)	Point	24.3	82.5	50.5	4.34	3, 387	=.01
	Sides	24.3	79.3	46.6			
WT[1] (g)	Point	51.0	1630.9	52.6	1.22	4, 371	>.50
	Sides	51.5	1574.5	52.0			

[1] maximum rate of weight gain:
Point: 40.09 g/day, 18.1 days after hatching.
Sides: 39.04 g/day, 18.2 days after hatching.

2.336, DF= 1, P>.10; see section 3.1.4.1).

Because of the difficulty in finding and catching nestlings as they grew older, and because of the occurrence of a severe moult in late July (Roy, et al., in press) that retarded fledging of 13 chicks (4 in the mixed-species colony and 9 in the monospecific colony), fledging data were recorded on 72 of the 106 fledglings: 35 on the Point and 37 on the South and East sides.

Fledging[1] started on July 10 in the monospecific colony and on July 15 in the mixed-species colony; the majority of chicks were flying by August 5 (Fig. 17). This 5 days delay in fledging in the mixed-species colony was also observed for hatching dates and, as expected, the mean fledging dates were significantly different between the two colonies (monospecific: $\bar{X}$= July 21 $\pm$7.6 days; mixed-species: $\bar{X}$= July 27 $\pm$7.4 days; t= 3.74, DF= 70, P<0.0005).

The age at first flight varied greatly in both colonies but was not statistically different (t= 1.82, DF= 66, P>.05). In the monospecific colony, fledging age varied from 40 to 54 days and averaged 47.5 $\pm$3.4 days compared to ages ranging from 38 to 60 days with a mean of 49.6 $\pm$5.4 days in the mixed-species colony.

---

[1]The occurrence of a wide gap in the distributions of fledging dates does not necessarily reflect a break in the rate of fledging but a change in searching and catching effort since the mapping of territories (section 2.2.4) and the capture of adult Great Black-backed Gulls (section 2.2.5.2) were performed during this period.

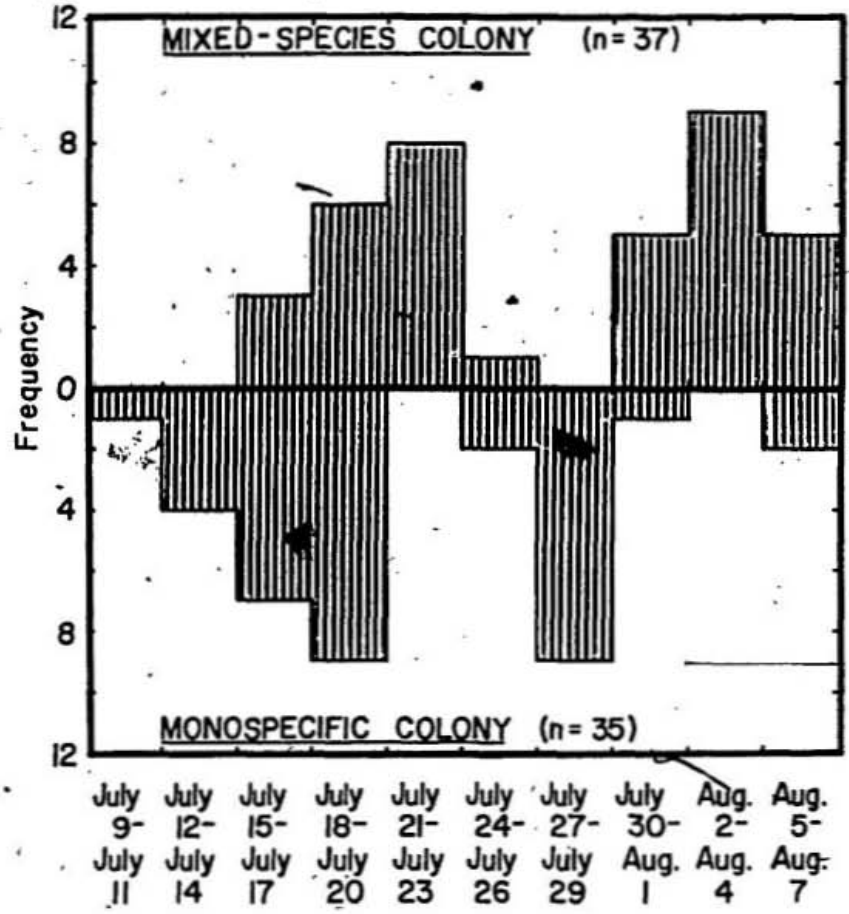

Figure 17. Distributions of fledging dates in the mixed-species and the monospecific colony, 1984.

Table 11 shows the fate of broods issued from different clutches as well as the number of fledglings produced per pair in relation to clutch size. The fate of 3-egg clutches was similar in the two colonies ($G = .584$, $DF = 3$, $P = .90$) but that of 2-egg clutches was better in the mixed-species colony ($G = 6.079$, $DF = 2$, $P < .05$).

Furthermore, in the monospecific colony, the production of fledglings per pair was largely based on 3-egg clutches. In contrast, the productivity of 2-egg clutches was almost as high as that of 3-egg clutches in the mixed-species colony. Thus, although 3-egg clutches were the most common and the most productive, the high success of 2-egg clutches in the mixed-species colony may indicate different uptimal clutch sizes in the two colonies. Testing this hypothesis requires comparative analysis of energy budgets of pairs producing clutches of 2 and 3 eggs within and between colonies.

3.2 - Territorial attributes:

Territorial attributes were recorded on 89 nests: 54 in the monospecific colony and 35 in the mixed-species colony.

3.2.1 - Territory size:

The index of territory size (ITS) was extremely variable, ranging from 1.98 to 215.72 m^2 (Fig. 18). The grand

Table 11. Numbers of chicks fledged (and chicks fledged/pair) in nests containing different clutches.

CLUTCH SIZE:	1		2			3			
CHICKS FLEDGED:	0	1	0	1	2	0	1	2	3
AREA:									
POINT	1	0	12	8	1	12	10	11	5
	(0.00)		(0.48)			(1.24)			
SIDES	4	4	3	3	4	9	7	6	5
	(0.50)		(1.10)			(1.30)			
TOTAL	5	4	15	11	5	21	17	17	10

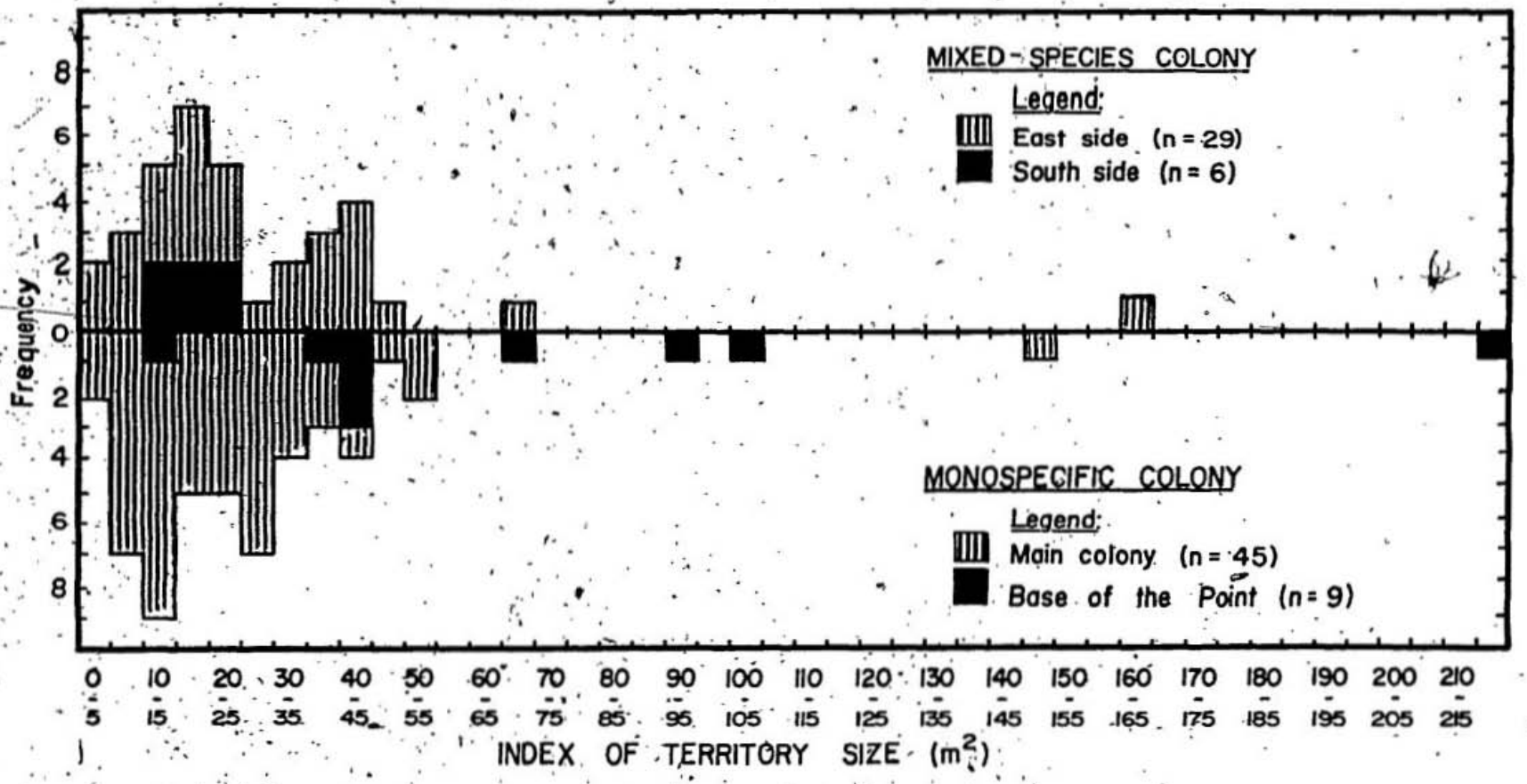

Figure 18. Distributions of territory sizes in the mixed-species and in the monospecific colony, 1984.

mean was estimated at 29.47 $\pm$30.83 m^2. This large variability in territory size was mainly due to the presence of unusually large territories at the base of the Point. Mean ITS at this subarea was 72.60 $\pm$60.83 m^2 compared to 22.22 $\pm$13.22 m^2 in the main colony. This difference was significant ($t = 5.11$, $DF = 51$, $P < .001$). Nevertheless, there was no significant difference between mean ITS in the monospecific colony and in the mixed-species colony where territories averaged 33.77 $\pm$32.84 m^2 and 27.43 $\pm$27.77 m^2 respectively ($t = 0.49$, $DF = 85$, $P > .50$).

The distributions of ITS in each colony were compared to a Poisson distribution using Chi-square to test for randomness. ITS were not randomly distributed in the mixed-species colony ($\chi^2 = 16.55$, $DF = 8$, $P < .05$). Figure 18 shows that Great Black-backed Gulls defended either small or large territories in this colony and rarely, medium sized territories. Although this might reflect the fitness of Great Black-backed Gulls nesting among Herring Gulls, ITS was not correlated with clutch size, number of chicks hatched, number of chicks fledged, hatching, nestling and fledging success.

Similarly, ITS were not randomly distributed in the monospecific colony ($\chi^2 = 37.74$, $DF = 8$, $P < .001$). The presence of extremely large territories at the base of the Point was, in part, responsible for this nonrandomness. ITS was also not correlated with the above reproductive param-

eters in the monospecific colony.

It is important to note that the statistics presented in this section were based on estimates of territory size and not actual sizes. This procedure, although providing interesting information about spacing of Great Black-backed Gulls, may have introduced some bias in the assessment of the relationships between breeding success and territory size.

3.2.2 - Identity and count of neighbours:

The mean number of neighbours surrounding Great Black-backed Gull territories was 6.0 $\pm$1.7 (range= 3 to 12). The number of neighbours was positively correlated with the number of chicks fledged ($r= .247$, $F= 5.72$, DF= 1 and 88, $P < .025$) and fledging success ($r= .256$, $F= 6.05$, DF= 1 and 86, $P < .025$).

In the monospecific colony, 3 to 11 neighbours were counted around Great Black-backed Gull nests; the mean was 5.6 $\pm$1.6. There were, however, major differences in territorial attributes between the two sub-colonies. In the main colony, 3 to 8 neighbours were counted around Great Black-backed Gull nests and 59% of the territories were surrounded by 5 or 6 neighbours ($\bar{X}= 5.4 \pm 1.3$). In most cases 3 to 5 pairs of Great Black-backed Gulls and no more than 2 pairs of Herring Gulls were found around Great Black-backed Gull nests. In addition, 25% of the Great Black-backed Gulls

were completely encircled by conspecifics but up to 7 pairs of Herring Gulls could be counted around peripheral nests.

At the base of the Point, a nucleus of 9 Great Black-backed Gull territories was surrounded by Herring Gulls who defended smaller territories. Qualitative estimates of the size of the Herring Gull territories varied from 10 to 20 m^2. These estimates are supported by Hunt and Hunt (1976). As a result, the average number of neighbouring Herring Gulls was very high compared to the main colony (main colony: $\bar{X}$= 1.7 $\pm$1.5; base of Point: $\bar{X}$= 5.4 $\pm$2.1; t= 6.31, DF= 56, P< .001). Moreover, since most of the territories found at the base of the Point were larger than average, more neighbours were counted around them (main colony: $\bar{X}$= 5.4 $\pm$1.3, base of Point: $\bar{X}$= 7.0 $\pm$2.2; t= 3.08, DF= 56, P<.005).

In the monospecific colony, a weak positive correlation was found between the number of neighbours and clutch size (r= .308, F= 4.84, DF= 1 and 46, P<.05); the presence Herring Gulls was positively correlated with the number of chicks fledged (r= .326, F= 5.23, DF= 1 and 45, P<.05) and fledging success (r= .312, F= 4.63, DF= 1 and 43, P<.05).

In the mixed-species colony, 4 to 12 neighbours were counted around Great Black-backed Gull nests; 79% of the territories were surrounded by no more than 8 neighbours ($\bar{X}$= 6.6 $\pm$1.8). Most Great Black-backed Gull territories (68%) were completely encircled by Herring Gulls but up to 2 pairs

of Great Black-backed Gulls could be present around nests of conspecifics, forming small nuclei within the Herring Gull colonies. No correlation between the six reproductive parameters listed earlier and the various territorial attributes was significant. Table 12 summarizes the results of section 3.2.

3.3 - Time-activity budgets of adults:

Figure 19a shows the total time spent observing each nest as well as the proportion of observations performed on sexed birds. The mean observation time/ nest on sexed birds (Fig. 19b) was generally uniform within colonies (monospecific: $\bar{X}$= 320.21 min, F= .17, DF= 12 and 131, P> .99; mixed-species: $\bar{X}$= 321.26 min, F= .15, DF= 7 and 95, P> .99) as well as between colonies (U= 53.5, n_1= 8 and 13, P> .20).

The histogram of Figure 19b is a reference template to subsequent figures in section 3.3.

3.3.1 - Occupancy of territories:

The time during which territories were occupied by at least one bird per pair was generally high, the mean being 274.15 $\pm$182.70 min/mean observation period in the monospecific colony and 176.43 $\pm$153.14 min/mean observation period in the mixed-species colony (U= 67, n_1= 8 and 13, P> .30; Fig. 20a). Desertions were responsible for the large variations within colonies: in the monospecific colony, 2 of the 13

Table 12. Summary of territorial attributes recorded in the monospecific colony (the Point) and in the mixed-species colony (South and East sides).

	COLONIES			
	MONOSPECIFIC	MIXED-SPECIES	ISLAND	SIG.
Number of nests studied				
	58	34	92	
Index of territory size, ITS (m^2)				
mean	33.77 ±32.84	27.43 ±27.77	29.47 ±30.83	P>.50
range	2.79 - 215.72	1.98 - 160.73		
corr.[1]	NONE	NONE	NONE	
Number of neighbours				
mean	5.6 ±1.6	6.6 ±1.8	6.0 ±1.7	P<.01
range	3 - 11	4 - 12		
corr.[1]	clutch size (P<.05)	NONE	no. fledged (P<.025) fledging success (P<.025)	
Number of Great Black-backed Gull neighbours				
mean	3.4 ±1.6	0.5 ±0.8		P<.001
range	1 - 7	0 - 2		
corr.[1]	NONE	NONE		
Number of Herring Gull neighbours				
mean	2.3 ±2.1	6.2 ±2.0		P<.001
range	0 - 9	3 - 12		
corr.[1]	no. fledged (P<.05) fledging success (P<.05)	NONE		

[1] Correlations with clutch size, number of chicks hatched, number of chicks fledged, hatching, nestling and fledging success.

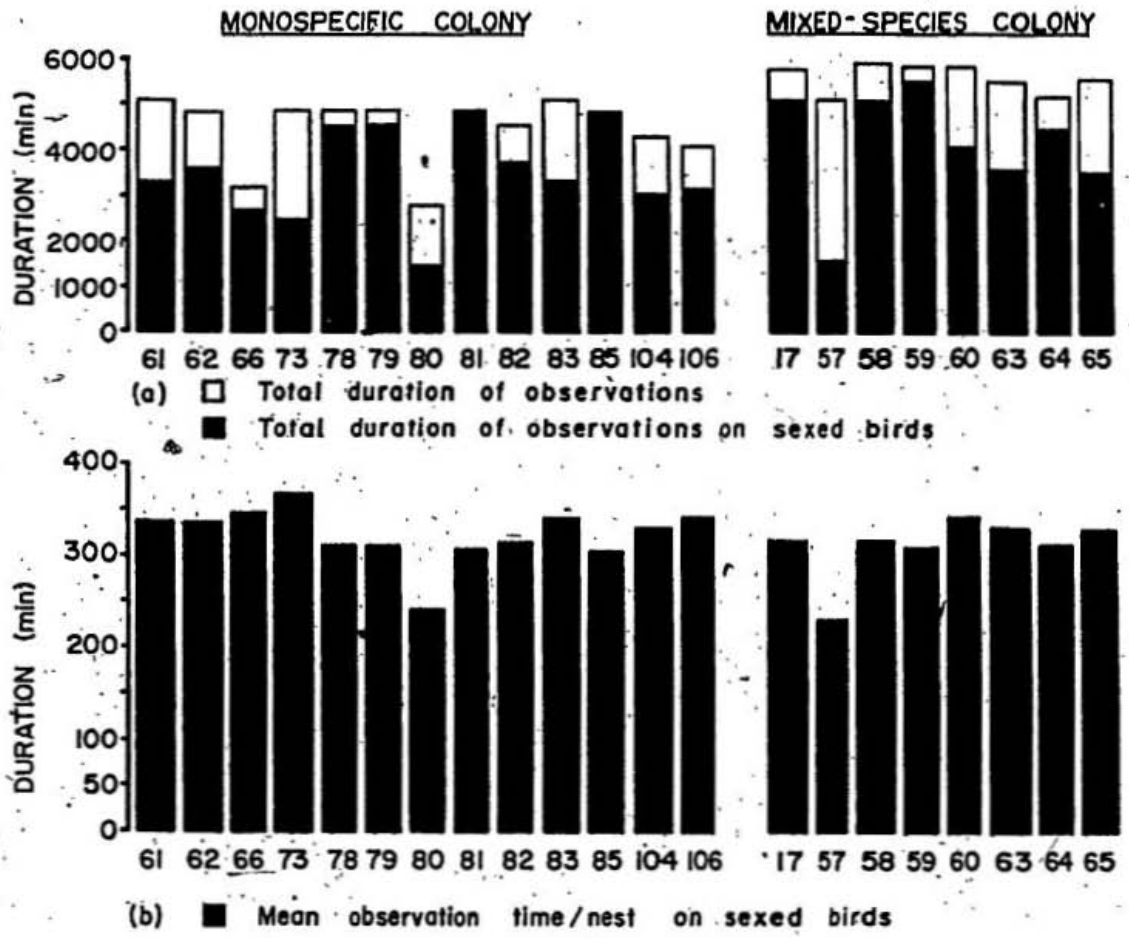

Figure 19. Duration of observations of 13 nests in the monospecific colony and 8 in the mixed-species colony.

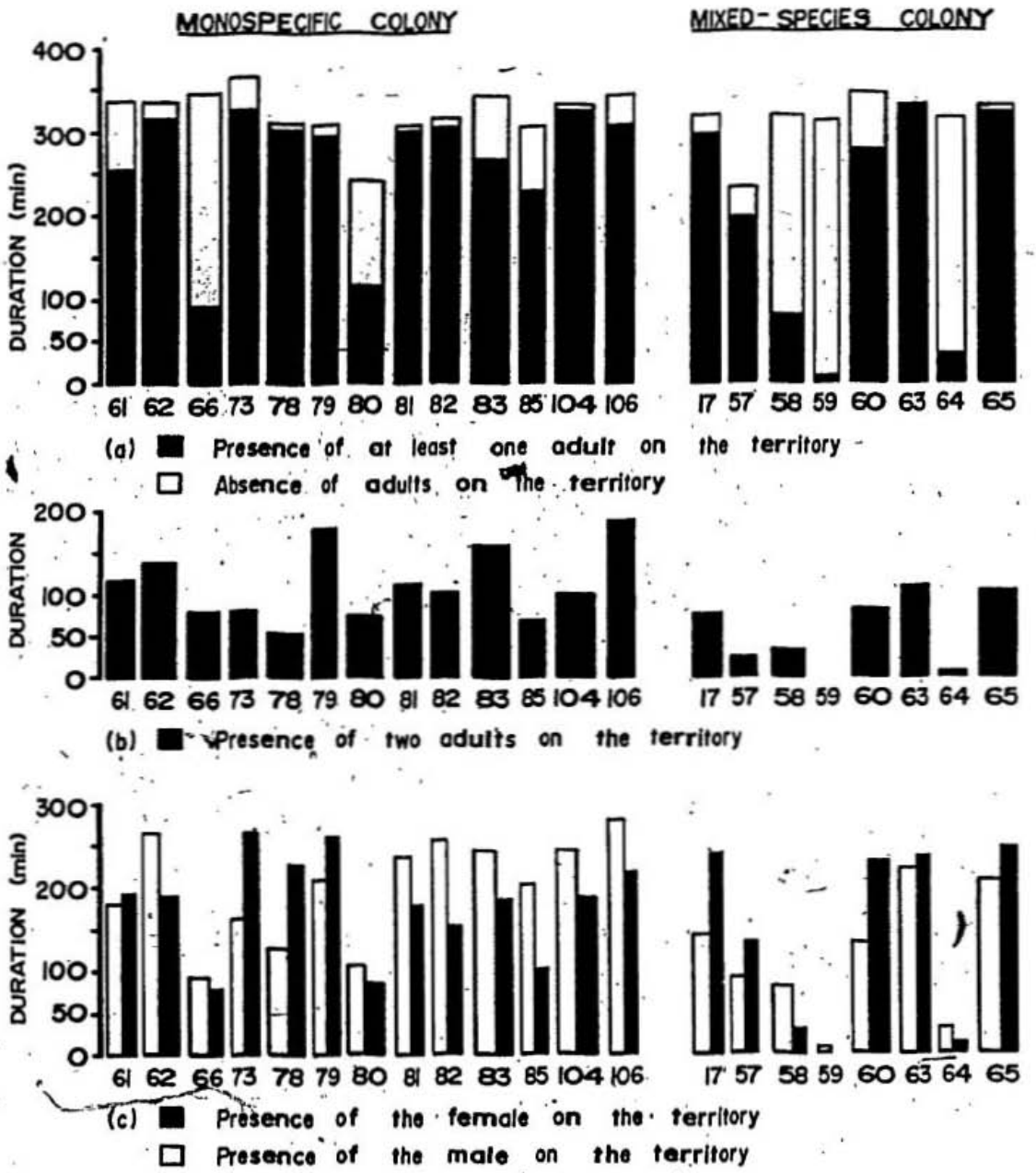

Figure 20. Mean occupancy of territories in the monospecific colony and in the mixed-species colony during mean observation time/nest.

nests observed were abandoned relatively early in the season, causing significant differences in the mean occupancy of territories ($F = 1.884$, $DF = 12$ and 131, $P < .05$). A similar phenomenon was observed in the mixed-species colony ($F = 10.641$, $DF = 7$ and 95, $P < .001$) where 4 of the 8 pairs observed abandoned their nest after their eggs failed to hatch or their chicks succumbed to predators.

In both colonies the presence of at least one adult on the territory was positively correlated with the number of chicks hatched (monospecific: $r = .648$, $F = 7.82$, $DF = 1$ and 11, $P < .02$; mixed-species: $r = .739$, $F = 7.20$, $DF = 1$ and 6, $P < .05$) and with hatching success (monospecific: $r = .815$, $F = 19.76$, $DF = 1$ and 10, $P < .002$; mixed-species: $r = .908$, $F = 37.69$, $DF = 1$ and 6, $P < .002$).

Similarly, even though there was no difference between colonies in the time territories were left unattended ($U = 64$, $n_1 = 8$ and 13, $P > .40$), there were significant differences among nests within colonies (monospecific: $\bar{X} = 46.06 \pm 89.70$ min, $F = 5.47$, $DF = 12$ and 131, $P < .001$; mixed-species: $\bar{X} = 144.83 \pm 137.06$ min, $F = 12.77$, $DF = 7$ and 95, $P < .001$; Fig. 20a). Great Black-backed Gulls did not usually leave their progeny without surveillance until at least 3 weeks after hatching. No difference in territorial occupancy was observed between successful and unsuccessful pairs during incubation (1 or 2 adult(s): $U = 24.5$, $n_1 = 6$ and 8, $P > .20$; 0 adult: $U = 25.5$, $n_1 = 6$ and 8, $P > .20$) or very early in the nestling

period (1 or 2 adult(s): U= 48, n_1= 6 and 10, P>.05; 0 adult: U= 38, n_1= 6 and 10, P>.20). Successful pairs did not leave their progeny for more than a few minutes at a time there afterwards. This behaviour contrasted with that of unsuccessful pairs who abandonned their territories or visited them irregularly after the loss of their progeny (1 or 2 adult(s): U= 58, n_1= 6 and 10, P= .001; 0 adult: U= 55, n_1= 6 and 10, P= .005). As discussed earlier, chick mortality usually occured early in the nestling season and was probably caused by human disturbance. Although it was not always possible to determine the causes for the complete loss of broods, both inter- and intraspecific predation were observed during visits to the colonies.

The absence of adults from their nesting site was negatively correlated with the number of chicks hatched (monospecific: r= -.674, F= 9.13, DF= 1 and 11, P<.02; mixed-species: r= -.824, F= 12.66, DF= 1 and 6, P<.02) and with hatching success (monospecific: r= -.786, F= 16.12, DF= 1 and 10, P<.005; mixed-species: r= -.944, F= 48.80, DF= 1 and 6, P<.001) in both colonies. It was also related to nestling success in the monospecific colony (r= -.668, F= 6.44, DF= 1 and 8, P<.05).

The simultaneous presence of two adults on territories lasted generally longer in the monospecific colony than in the mixed-species colony (U= 80, n_1= 8 and 13, P= .05; Fig. 20b) but differences were observed among nests in both col-

onies (monospecific: $\bar{X}$= 109.36 ±84.84 min, F= 2.99, DF= 12 and 131, P= .001; mixed-species: $\bar{X}$= 47.74 ±50.32 min, F= 9.28, DF= 7 and 95, P<.001). It was positively correlated with hatching success in the mixed-species colony (r= .753, F= 7.86, DF= 1 and 6, P<.05).

Even though the division of labours between sexes was apparently characteristic of each pair, males and females generally spent equal time on their territories (monospecific: U= 104, n_1= 13 and 13, P>.20; mixed-species: U= 39, n_1= 8 and 8, P>.20; Fig. 20c). Furthermore, males generally spent more time on their territories in the monospecific colony than in the mixed-species colony (U= 85, n_1= 8 and 13, P<.02) but there were significant differences among nests within each colonies (monospecific: $\bar{X}$= 204.08 ±137.46 min, F= 1.88, DF= 12 and 131, P<.05; mixed-species: $\bar{X}$= 100.99 ±86.33 min, F= 10.64, DF= 7 and 95, P<.001). In the mixed-species colony, hatching success was correlated with the presence of males (r= .777, F= 9.14, DF= 1 and 6, P<.025).

The presence of females was not different between colonies (U= 59, n_1= 8 and 13, P>.60) but significant differences were found among nests within each colonies (monospecific: $\bar{X}$= 179.43 ±135.70 min, F= 2.05, DF= 12 and 131, P<.025; mixed-species: $\bar{X}$= 132.18 ±123.34 min, F= 10.92, DF= 7 and 95, P<.001; Fig. 20c). The presence of females seemed to be very important for a successful breeding season, especially

in the monospecific colony where it was correlated with the number of chicks hatched ($r = .630$, $F = 7.24$, $DF = 1$ and 11, $P < .05$), the number of chicks fledged ($r = .556$, $F = 4.93$, $DF = 1$ and 11, $P < .05$), hatching success ($r = .837$, $F = 23.351$, $DF = 1$ and 10, $P < .001$) and fledging success ($r = .624$, $F = 6.39$, $DF = 1$ and 10, $P < .05$). In the mixed-species colony, it was only correlated with the number of chicks hatched ($r = .711$, $F = 6.13$, $DF = 1$ and 6, $P < .05$) and hatching success ($r = .9[illegible]9$, $F = 32.60$, $DF = 1$ and 6, $P < .002$).

3.3.2 - Mating behaviour (MB):

During the summer of 1984 (May 27 to July 26), more time was invested in courtship and mating activities in the monospecific colony than in the mixed-species colony ($U = 91$, $n_1 = 8$ and 13, $P < .005$). Although very low for two pairs, MB was relatively uniform in the monospecific colony ($\bar{X} = 9.88 \pm 12,57$ min, $F = 1.39$, $DF = 12$ and 131, $P > .10$) but significant differences were found among nests in the mixed-species colony ($\bar{X} = 3.40 \pm 6.85$ min, $F = 2.88$, $DF = 7$ and 95, $P < .01$; Fig. 21a).

No correlation between MB and various reproductive parameters was statistically significant in either colony. The reproductive parameters used in the correlations were: clutch size, average egg volume, number of chicks hatched, number of chicks fledged, hatching, nestling and fledging success.

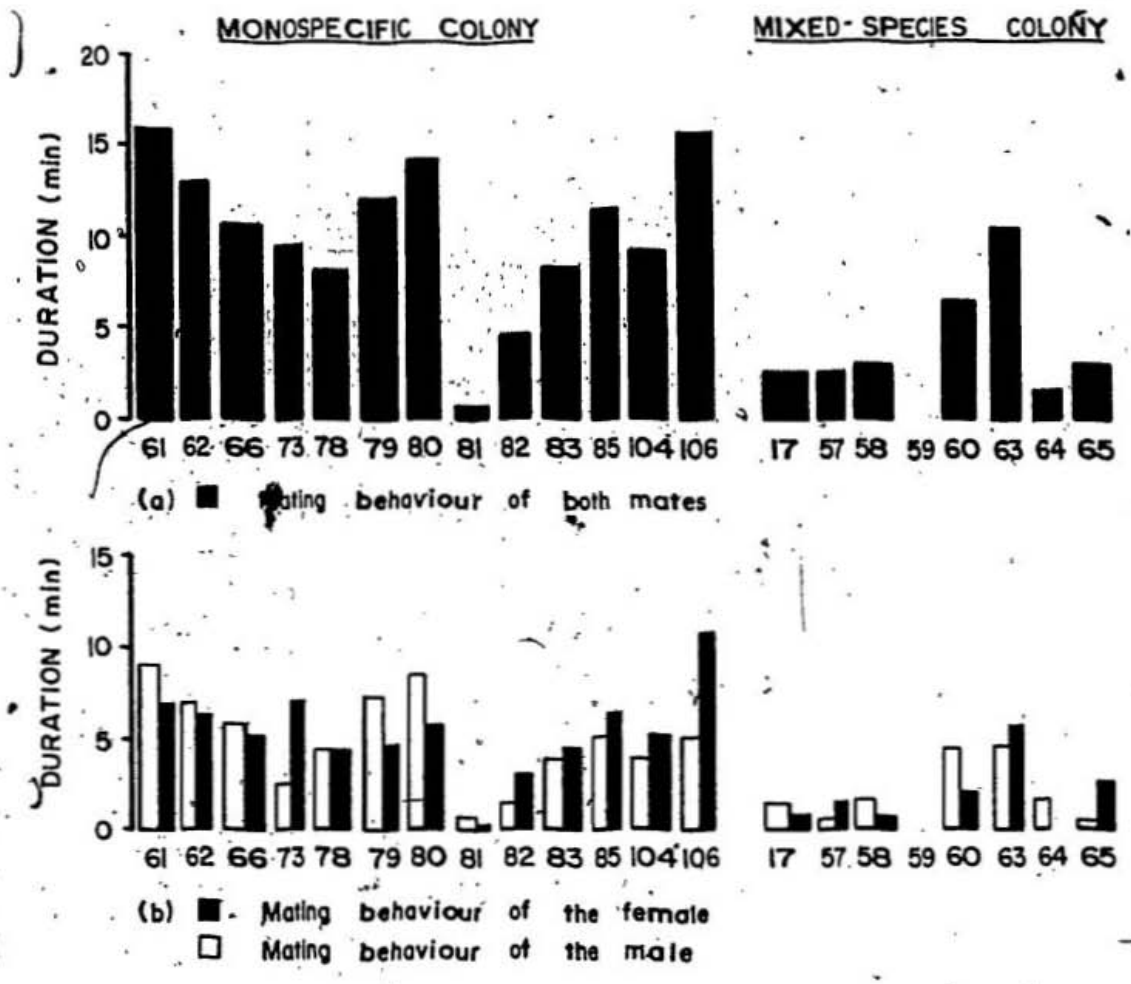

Figure 21. Mean mating behaviour in the monospecific colony and in the mixed-species colony during mean observation time/nest.

Comparisons between sexes within each colony revealed no difference in average MB (monospecific: $U = 96.5$, $n_1 = 13$ and 13, $P > .20$; mixed-species: $U = 33$, $n_1 = 8$ and 8, $P > .20$; Fig. 21b). Male MB was not different among nests in the monospecific colony ($\bar{X} = 4.81 \pm 6.93$ min, $F = 1.42$, $DF = 12$ and 131, $P > .10$) or among nests in the mixed-species colony ($\bar{X} = 1.84 \pm 4.39$ min, $F = 1.82$, $DF = 7$ and 95, $P > .05$) but males invested more time in MB in the monospecific colony than in the mixed-species colony ($U = 87$, $n_1 = 8$ and 13, $P = .01$). No correlation was found between male MB and the various reproductive parameters listed above.

Females also invested more time in MB in the monospecific colony than in the mixed-species colony ($U = 91$, $n_1 = 8$ and 13, $P < .005$). The time spent in MB was not statistically different among females in the monospecific colony ($\bar{X} = 5.07 \pm 7.68$ min, $F = 1.22$, $DF = 12$ and 131, $P > .25$) but there were differences in the behaviour of females in the mixed-species colony ($\bar{X} = 1.55 \pm 3.98$ min, $F = 2.81$, $DF = 7$ and 95, $P < .02$; Fig. 21c). Female MB was also not correlated with the various reproductive parameters listed earlier except for clutch size, in the monospecific colony ($r = -.676$, $F = 9.27$, $DF = 1$ and 11, $P < .02$). In this case, the relationship between the two variables was negative and females that laid few eggs engaged more often in mating activities during the summer than those who laid full 3-egg clutches.

3.3.3 - Parental behaviour (PB):

The mean time spent incubating and caring for young was similar between the two colonies ($U = 70$, $n_1 = 8$ and 13, $P > .20$). However, significant differences in PB were observed among nests in the monospecific colony ($\bar{X} = 38.52 \pm 79.93$ min, $F = 2.81$, $DF = 12$ and 131, $P < .002$) and among nests in the mixed-species colony ($\bar{X} = 9.00 \pm 17.56$ min, $F = 3.72$, $DF = 7$ and 95, $P < .002$; Fig. 22a).

No correlation between PB and the various reproductive parameters listed in section 3.3.2 was statistically significant in the monospecific colony. In the mixed-species colony, PB was positively correlated with the number of chicks hatched ($r = .815$, $F = 11.85$, $DF = 1$ and 6, $P < .02$) and hatching success ($r = .787$, $F = 9.79$, $DF = 1$ and 6, $P < .05$).

Comparisons between sexes within each colony revealed no significant differences in average PB (monospecific: $U = 84.5$, $n_1 = 13$ and 13, $P > .20$; mixed-species: $U = 39$, $n_1 = 8$ and 8, $P > .20$; Fig. 22b). However, male PB was different among nests in the monospecific colony ($\bar{X} = 17.85 \pm 47.89$ min, $F = 3.56$, $DF = 12$ and 131, $P < .001$) and among nests in the mixed-species colony ($\bar{X} = 3.69 \pm 10.44$ min, $F = 3.08$, $DF = 7$ and 95, $P < .01$) but not between colonies ($U = 70$, $n_1 = 8$ and 13, $P > .20$). No correlation between male PB and the various reproductive parameters listed earlier was statistically significant in both colonies.

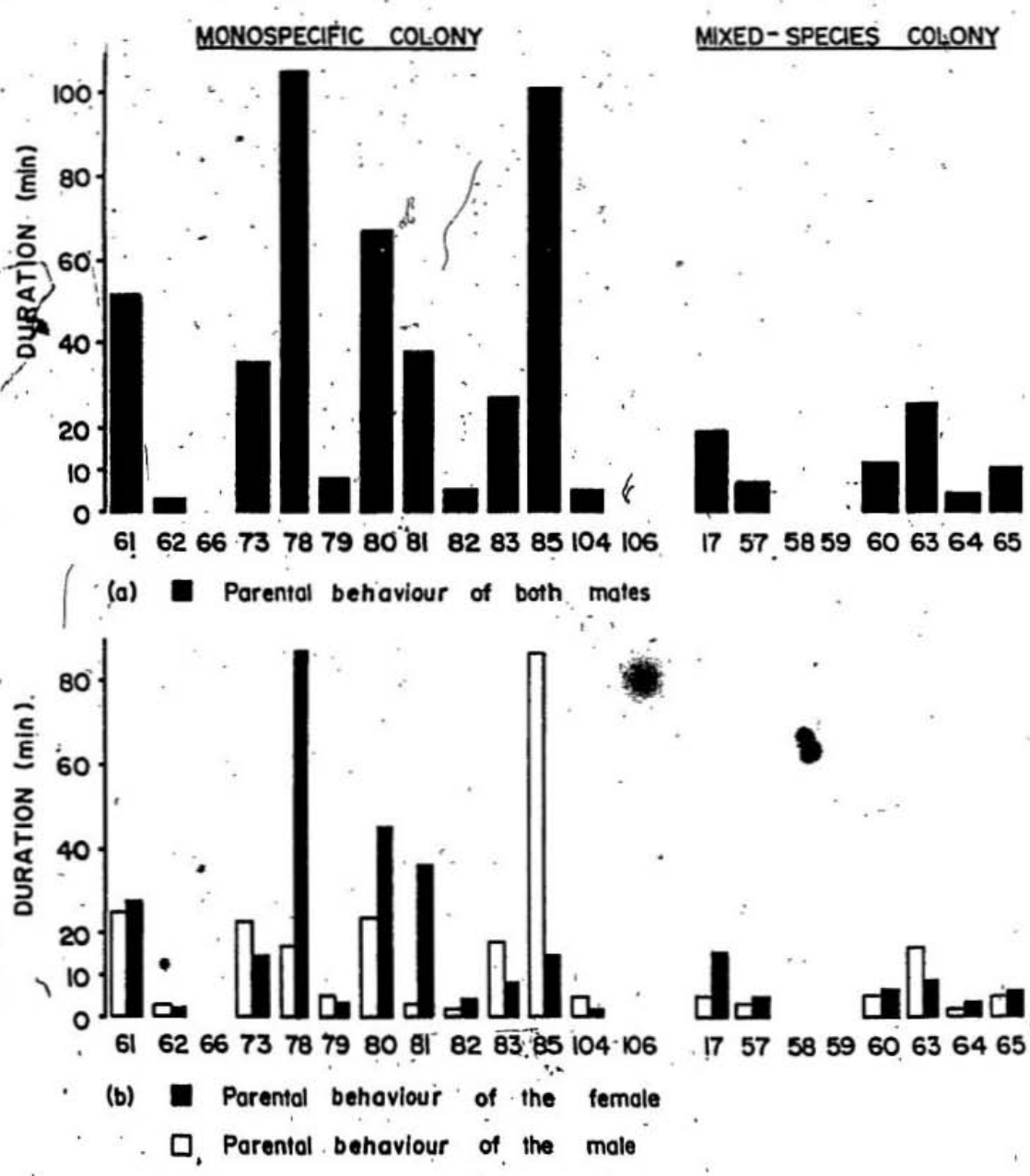

Figure 22. Mean parental behaviour in the monospecific colony and in the mixed-species colony during mean observation time / nest.

Female PB was different among nests in the monospecific colony ($\bar{X}$= 20.68 ±5.53 min, F= 2.72, DF= 12 and 131, P< .005) and among nests in the mixed-species colony ($\bar{X}$= 5.32 ±12.52 min, F= 2.73, DF= 7 and 95, P< .02) but not between colonies (U= 64, n_1= 8 and 13, P> .40). Female PB in the mixed-species colony, although very low, was positively correlated with the number of chicks hatched (r= .765, F= 8.48, DF= 1 and 6, P< .05) and the number of chicks fledged (r= .880, F= 20.52, DF= 1 and 6, P< .005) as well as with hatching success (r= .755, F= 7.94, DF= 1 and 6, P< .05), fledging success (r= 850, F= 15.68, DF= 1 and 6, P< .005) and nestling success (r= .812, F= 7.77, DF= 1 and 4, P< .05). The parental behaviour of females thus seemed to be an important determinant of breeding success in the mixed-species colony, influencing the development of embryos and the survival of nestlings. Similar relationships were not observed on the Point.

3.3.4 - Territorial defence (TD):

The average time spent in territorial defence was greater in the monospecific colony than in the mixed-species colony (U= 86, n_1= 8 and 13, P< .02). Significant differences were also observed among nests in the monospecific colony ($\bar{X}$= 66.56 ±65.09 min, F= 5.30, DF= 12 and 131, P< .001) and among nests in the mixed-species colony ($\bar{X}$= 23.47 ±26.73 min, F= 13.11, DF= 7 and 95, P< .001; Fig. 23a).

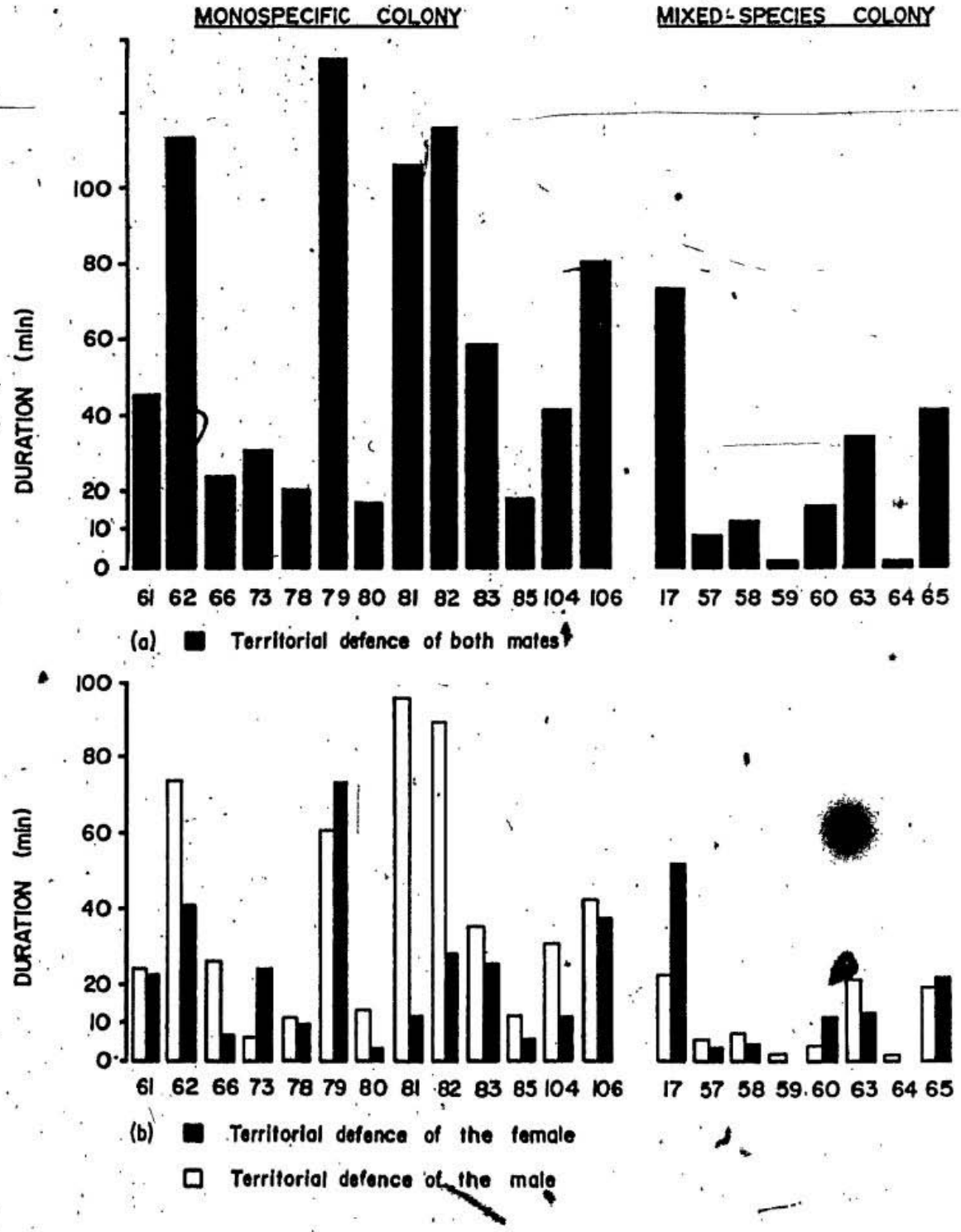

Figure 23. Mean territorial defence in the monospecific colony and in the mixed-species colony during mean observation time/nest.

In the mixed-species colony, TD was positively correlated with the number of chicks fledged ($r = .911$, $F = 29.39$, $DF = 1$ and 6, $P < .002$), with nestling success ($r = .925$, $F = 23.80$, $DF = 1$ and 4, $P < .01$) and with fledging success ($r = .933$, $F = 40.12$, $DF = 1$ and 6, $P < .001$). Similar correlations were not observed in the monospecific colony.

There were no significant differences in average TD between sexes (monospecific: $U = 112$, $n_1 = 13$ and 13, $P > .20$; mixed-species: $U = 34$, $n_1 = 8$ and 8, $P > .20$) but large variations were observed within colonies. Male TD was different among nests in the monospecific colony ($\bar{X} = 42.60 \pm 43.39$ min, $F = 6.26$, $DF = 12$ and 131, $P < .001$) and among nests in the mixed-species colony ($\bar{X} = 9.85 \pm 14.24$ min, $F = 5.59$, $DF = 7$ and 95, $P < .001$) as well as between colonies ($U = 88$, $n_1 = 8$ and 13, $P < .01$; Fig. 23b); males from the monospecific colony being more frequently involved into agonistic encounters.

No significant correlation was found between male TD in the monospecific colony and the various reproductive parameters listed in section 3.3.2 but in the mixed-species colony, male TD was positively correlated with the number of chicks fledged ($r = .772$, $F = 8.81$, $DF = 1$ and 6, $P < .025$) and with fledging success ($r = .817$, $F = 12.19$, $DF = 1$ and 6, $P < .02$).

Female TD was also highly variable among nests in the monospecific colony ($\bar{X} = 23.96 \pm 30.42$ min, $F = 5.42$, $DF = 12$ and 131, $P < .001$) as well as among nests in the mixed-species

colony ($\bar{X}$= 13.62 ±18.16 min, F= 13.83, DF= 7 and 95, P< .001) but not between colonies (U= 73, n_i= 8 and 13, P> .10; Fig. 23b).

No correlation was computed between female TD in the monospecific colony and the various reproductive parameters listed in section 3.3.2 but in the mixed-species colony, female TD was positively correlated with the number of chicks fledged (r= .913, F= 29.88, DF= 1 and 6, P< .002), nestling success (r= .908, F= 18.76, DF= 1 and 4, P< .02) and fledging success (r= .919, F= 32.61, DF= 1 and 6, P< .002).

3.3.5 - Self maintenance (SM):

Self maintenance was not different between colonies (U= 61, n_i= 8 and 13, P> .50). It was not different among nests of the monospecific colony ($\bar{X}$= 268.54 ±215.45 min, F= 1.67, DF= 12 and 131, P> .05) but large variations were observed in the mixed-species colony because some territories were deserted very early in the nesting season ($\bar{X}$= 188.30 ±156.69 min, F= 13.15, DF= 7 and 95, P< .001; Fig. 24a). In both colonies, SM was positively correlated with hatching success (monospecific: r= .815, F= 19.80, DF= 1 and 10, P< .002; mixed-species: r= .881, F= 20.74, DF= 1 and 6, P< .005).

There was no significant difference in average SM between sexes (monospecific: U= 90, n_i= 13 and 13, P> .20; mixed-species: U= 38, n_i= 8 and 8, P> .20) but again, large varia-

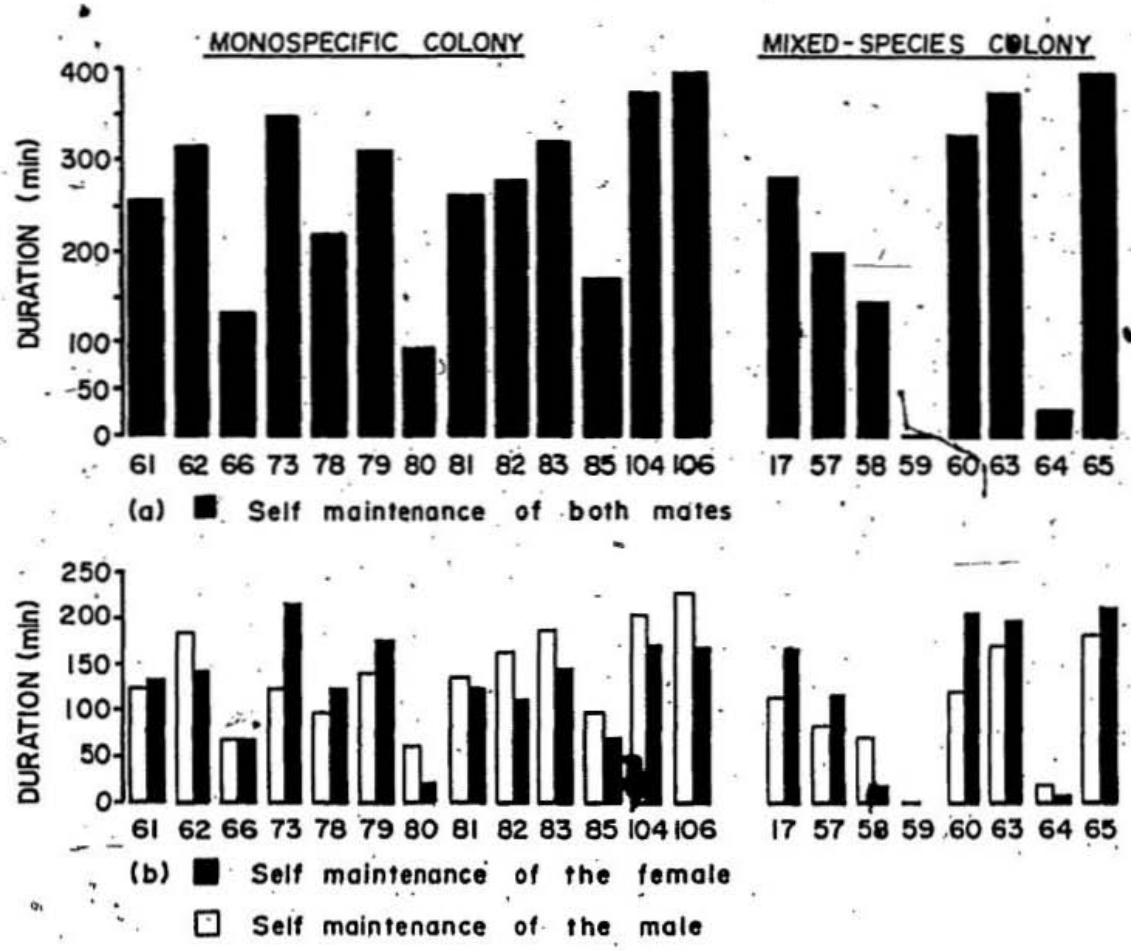

Figure 24. Mean self maintenance in the monospecific colony and in the mixed-species colony during mean observation time/ nest.

tions were observed within colonies. Male SM was different among nests in the monospecific colony ($\bar{X}$= 138.82 ±113.64 min, F= 1.90, DF= 12 and 131, P< .05) and among nests in the mixed-species colony ($\bar{X}$= 85.61 ±76.15 min, F= 9.62, DF= 7 and 95, P< .001) but not between colonies (U= 74, n_1= 8 and 13, P> .10; Fig. 24b). Male SM was positively correlated with hatching success in both colonies (monospecific: r= .692, F= 9.19, DF= 1 and 10, P< .02); mixed-species: r= .782, F= 9.46, DF= 1 and 6, P< .05).

Female SM was not different among nests in the monospecific colony ($\bar{X}$= 129.72 ±125.37 min, F= 1.45, DF= 12 and 131, P> .10) but it differed among nests in the mixed-species colony ($\bar{X}$= 102.69 ±110.76 min, F= 9.57, DF= 7 and 95, P< .001). However, there was no statistical difference between female SM in the monospecific colony and female SM in the mixed-species colony (U= 55, n_1= 8 and 13, P> .80; Fig. 24b). Female SM was positively correlated with hatching success in both colonies (monospecific: r= .785, F= 16.05, DF= 1 and 10, P< .005); mixed-species: r= .922, F= 33.81, DF= 1 and 6, P< .002) and with the number of chicks hatched in the monospecific colony (r= .573, F= 5.38, DF= 1 and 11, P< .05).

3.3.6 - Summary of time-activity budgets:

Since the distributions of clutch size and chicks fledged per nest were similar between the two samples of nests obser-

ved (clutch size: G= 7.340, DF= 3, P>.05; chicks fledged: G= 5.512, DF= 3, P>.10), it was reasonnable to assume that any behavioural differences between gulls nesting in different colonies may have been caused, at least in part, by the type of colony in which the gulls nested. As it has been shown for Kelp Gulls (L. dominicanus L.; Burger and Gochfeld, 1981) where habitat choice relates to predation and cannibalism pressures, nest site selection of Great Black-backed Gulls may have been influenced by the nature and the behaviour of their competitors.

Even though the mean duration of the observation periods was not significantly different between colonies, territorial occupancy and mean time invested in the four behavioural categories (MB, PB, TD, SM) was either longer in the monospecific colony than in the mixed-species colony or of equal duration (Table 13).

Furthermore, behaviours did not necessarily have the same effect(s) on breeding success in each colony (Table 14). For example, no behavioural correlates were found for the number of chicks fledged in the monospecific colony but fledging was related to PB and TD in the mixed-species colony. The number of chicks fledged depended on territorial occupancy in the monospecific colony. Table 14 also shows that:

- MB was correlated with clutch size in the monospecific colony but no significant correlation was found in the mixed-species colony.

Table 13. Summary of time-activity budgets: mean time invested in different behavioural classes (in minutes) per mean observation period (±standard deviations) and comparisons between sexes and colonies.

	MONOSPECIFIC COLONY (sig)	COMPARISON (sig)	MIXED-SPECIES COLONY (sig)
Observations	321.21 ±206.66 (P > .99)	= (P > .20)	321.26 ±191.83 (P > .99)
Occupancy			
0 adult	46.06 ± 89.70 (P < .001)	= (P > .40)	144.83 ±137.06 (P < .001)
1-2 adult(s)	274.15 ±182.70 (P < .05)	= (P > .30)	176.43 ±153.14 (P < .001)
2 adults	109.36 ± 84.84 (P = .001)	> (P = .05)	47.74 ± 50.32 (P < .001)
male	204.08 ±137.46 (P < .05)	> (P < .02)	100.99 ± 86.33 (P < .001)
female	179.43 ±135.70 (P < .025)	= (P > .60)	132.18 ±123.34 (P < .001)
m vs f	(P > .20)		(P > .20)
Mating Behaviour			
total	9.88 ± 12.57 (P > .10)	> (P < .005)	3.40 ± 6.85 (P < .01)
male	4.81 ± 6.93 (P > .10)	> (P = .01)	1.84 ± 4.39 (P > .05)
female	5.07 ± 7.68 (P > .25)	> (P < .005)	1.55 ± 3.98 (P < .02)
m vs f	(P > .20)		(P > .20)
Parental behaviour			
total	38.52 ± 79.93 (P < .002)	= (P > .20)	9.00 ± 17.56 (P < .002)
male	17.85 ± 47.89 (P < .001)	= (P > .20)	3.69 ± 10.44 (P < .01)
female	20.68 ± 35.53 (P < .005)	= (P > .40)	5.32 ± 12.52 (P < .02)
m vs f	(P > .20)		(P > .20)
Territorial Defence			
total	66.56 ± 65.09 (P < .001)	> (P < .02)	23.47 ± 26.73 (P < .001)
male	42.60 ± 43.39 (P < .001)	> (P < .01)	9.85 ± 14.24 (P < .001)
female	23.96 ± 30.42 (P < .001)	= (P > .10)	13.62 ± 18.16 (P < .001)
m vs f	(P > .20)		(P > .20)
Self Maintenance			
total	268.54 ±215.45 (P > .05)	= (P > .50)	188.30 ±156.69 (P < .001)
male	138.82 ±113.64 (P < .05)	= (P > .10)	85.61 ± 76.15 (P < .001)
female	129.72 ±125.37 (P > .10)	= (P > .80)	102.69 ±110.76 (P < .001)
m vs f	(P > .20)		(P > .20)

Table 14. Summary of correlations between various reproductive parameters and behavioural classes.

	MONOSPECIFIC COLONY		MIXED-SPECIES COLONY	
Occupancy				
0 adult	no. chicks hatched	(r=-.674, P< .02)	no. chicks hatched	(r=-.824, P<.02)
	hatching success	(r=-.786, P< .005)	hatching success	(r=-.944, P<.001)
	nestling success	(r=-.668, P< .05)		
1-2 adult(s)	no. chicks hatched	(r= .645, P< .02)	no. chicks hatched	(r= .739, P<.05)
	hatching success	(r= .815, P< .002)	hatching success	(r= .908, P<.002)
2 adults	---		hatching success	(r= .753, P<.05)
male	---		hatching success	(r= .777, P<.025)
female	no. chicks hatched	(r= .630, P< .05)	no. chicks hatched	(r= .711, P<.05)
	no. chicks fledged	(r= .556, P< .05)	hatching success	(r= .919, P<.002)
	hatching success	(r= .837, P< .001)		
	fledging success	(r= .624, P< .05)		
Mating Behaviour				
total	---		---	
male	---		---	
female	clutch size	(r=-.676, P< .02)	---	
Parental Behaviour				
total	---		no. chicks hatched	(r= .815, P< .02)
			hatching success	(r= .782, P< .05)
male	---		---	
female	---		no. chicks hatched	(r= .765, P< .05)
			no. chicks fledged	(r= .880, P< .005)
			hatching success	(r= .755, P< .05)
			nestling success	(r= .813, P< .05)
			fledging success	(r= .850, P< .005)
Territorial Defence				
total	---		no. chicks fledged	(r= .911, P< .002)
			nestling success	(r= .925, P< .01)
			fledging success	(r= .933, P< .001)
male	---		no. chicks fledged	(r= .773, P< .05)
			fledging success	(r= .819, P< .02)
female	---		no. chicks fledged	(r= .913, P< .002)
			nestling success	(r= .908, P< .02)
			fledging success	(r= .919, P< .002)
Self Maintenance				
total	hatching success	(r= .815, P< .002)	hatching success	(r= .881, P< .005)
male	hatching success	(r= .692, P< .02)	hatching success	(r= .782, P< .05)
female	no. chicks hatched	(r= .573, P< .05)	hatching success	(r= .922, P< .002)
	hatching success	(r= .785, P< .005)		

- PB was correlated with the number of chicks hatched, hatching, nestling and fledging success in the mixed-species colony but no significant correlation was found in the monospecific colony.

- TD was correlated with the number of chicks fledged, nestling and fledging success in the mixed-species colony but no significant correlation was found in the monospecific colony.

- SM was correlated with the number of chicks hatched in the monospecific colony and with hatching success in both colonies.

- Territorial occupancy was correlated with the number of chicks hatched and with hatching success in both colonies but in the monospecific colony, it was also correlated with the number of chicks fledged, nestling and ledging success.

Furthermore, the behaviour of females, although not statistically different from that of males, might have been more important than that of their mates in determining breeding success in the monospecific colony whereas both sexes shared responsibilities in the mixed-species colony (Table 14).

4.0 - DISCUSSION

In 1984, Great Black-backed Gulls nesting on Gull Island achieved, on average, similar reproductive success and proportionately equal chick production in both colonies. Egg production and mean clutch size were similar, but, the distribution of clutch size, was different: 1- and 2-egg clutches were more common in the mixed-species colony. Furthermore, mean egg volume was also comparable although egg size was more variable in the mixed-species colony.

Many workers have investigated the relationships between clutch size, egg size, age and reproductive success. Young birds generally lay smaller clutches (Coulson, 1966; Skutch, 1976 in Curio, 1983). Egg size is related to the age of females (Richdale, 1955; Coulson, 1963; Davies, 1975; Coulson et al., 1982; Thomas, 1983) as well as to their body size (Verbeek and Richardson, 1982); both older and larger females laying larger eggs. In Herring Gulls, egg size has been shown to increase with decreasing densities (Coulson et al.; 1982) and, in many species, to decrease as the breeding season progresses (Coulson, 1963; Nelson, 1966 in Parsons, 1972; Birkhead and Nettleship, 1982). According to such studies, data collected on Gull Island indicate that females nesting in the monospecific colony are more experienced than those nesting in the mixed-species colony.

In addition, older females generally breed earlier

(Parsons, 1972; Haymes and Blockpoel, 1980) and put more effort in reproduction (Pugesek, 1981). Thus, females nesting in the monospecific colony may have been, on average, older than those nesting in the mixed-species colony since hatching and fledging occurred significantly earlier in the monospecific colony. Furthermore, female MB was correlated with clutch size only in the monospecific colony, indicating that females put more effort in reproduction in this area.

Nevertheless, many similarities in the breeding biology of birds nesting in the two colonies suggest that the average "reproductive quality" (Coulson, 1968) of individuals is comparable. Indeed, there was no difference in fate of eggs, number of chicks hatched, number of chicks fledged, chick growth rates, nestling mortality and age at fledging. Hatching, nestling and fledging success were also comparable.

The occurrence of mortality per age class was also comparable even if it was only observed in the monospecific colony after the age of 35 days. The size of Great Black-backed Gull chicks relative to that of their neighbours (Herring or Great Black-backed Gull) is believed to have played an important role in chick survival after 35 days. In fact, even if very few Herring Gulls nested in the monospecific colony, their presence around Great Black-backed Gull territories was positively correlated with chick production and fledging success. Gull chick survival has also been associated with territory size (Hunt and Hunt, 1976) but

this has not been verified on Gull Island where the ITS were similar in both colonies.

The production of chicks per pair was higher in 3-egg clutches in both colonies. This finding supports Lack's hypothesis (1954) that selection should favour the most productive clutch. However, many studies have shown that the commonnest clutch (uptimal clutch) is in fact smaller than the most productive one (eg. Ward, 1973 in Charnov and Krebs, 1974). In the mixed-species colony, the survival of chicks from 2-egg clutches was almost as high as that of 3-egg clutches. The finding that chick production from different clutches is not the same in the two colonies may give insight in the evolution of optimal clutch size under different environmental constraints but data collected in the present study are not sufficient elucidate this question. Furthermore, the interaction of breeding experience, clutch size and reproductive success may interfere with the testing of this hypothesis.

The theory of "Games" predicts that under stable equilibrium, individuals behaving according to different strategies will achieve, on average, comparable success. Similar breeding success in the two types of colony studied suggests that the existence of such strategies. Perhaps behavioural constraints related to habitat selection play an important role in the spacing system of nesting Great Black-backed

Gulls and determine their breeding success. Many models describing habitat selection of animals and taking into account behavioural constraints have been described and tested (eg. Witham, 1980).

Bent (1963) reported that Great Black-backed Gulls may form monospecific colonies, mixed-species colonies or may nest as single pairs, isolated in remote locations. As it is likely that this species shows site tenacity as do other larids (Southern, 1977), the spacing system of Great Black-backed Gulls is relatively simple, adults returning to the colony and the nesting area (if possible) where they were born. However, considerations about the maximization of lifetime reproductive success may cause Great Black-backed Gulls to compete selfishly for the best nesting territories. If so, their spacing system would be influenced by factors such as past experience, mate selection, competition and habitat characteristics.

Many studies (see Krebs and Davies, 1981) have shown that some individuals in a given population are unable to compete successfully with conspecifics by fighting or by displaying, perhaps because of morphological differences or old age. These poor competitors generally end up with fewer resources and rewards than dominant individuals. The average breeding success of Great Black-backed Gulls in the mixed-species colony may have been equal to that of gulls nesting in the monospecific colony because they found themselves in

a situation of dominance when facing smaller opponents when in the process of acquiring suitable nesting territories and raising young.

If such a phenomenon occurs on the nesting grounds, one would expect to see the largest and strongest individuals invading Herring Gull colonies and concomitantly increasing their reproductive success. Since this did not happen, there must have been other benefits to nesting in the monospecific colony[1] such as increased lifetime fitness by mating with more experienced females.

In larid species, males arrive early on the nesting grounds to secure territories and attract a mate which is not necessarily the same from year to year (Tinbergen, 1953). Thus males are expected to compete fiercely for the best resources. Although experienced gulls generally return to the same site each year, Coulson (1968) observed younger and stronger (but not necessarily inexperienced) males successfully outcompete older birds and establish themselves in the centre of the colony. Since one advantage of living in groups is to attract mates, it is effectively more advantageous to secure territories located in the center of the colony. Accordingly, territorial occupancy, defence and mating behaviour of males lasted significantly longer in the

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[1] On Gull Island, the monospecific colony is considered to be the preferred nesting site because Great Black-backed Gulls have always been observed nesting earlier, in greater numbers and in higher densities in this area (Haycock, 1973; Threlfall, pers. comm.; Roy, present study).

monospecific colony than in the mixed-species colony.

Moreover, experienced and successful females are the first ones to follow males to the gulleries (Parsons, 1972) and are expected to select the most fit partners if they are not already paired. On Gull Island, females' mating behaviour lasted longer in the monospecific colony than in the mixed-species colony.

These considerations about the distribution of Great Black-backed Gulls on Gull Island do not take into account that the area available to nest is physically limited (eg. vegetation cover, obstacles, presence of other breeding seabirds) and that gulls require minimal territory size to reproduce successfully (Tinbergen, 1956). Thus, colony and nest site selection will be influenced by the presence and the behaviour of competitors. As predicted by the Game Theory, whether to nest in the monospecific colony will depend on the costs and benefits associated with reproduction as competition increases.

Although no observation was made in the very early stages of the reproductive season, it appears that Great Black-backed Gulls first selected territories in the monospecific colony. However, the great overlap in hatching and fledking dates suggests that after a while, the costs and benefits of nesting in the monospecific colony were not different from those associated with nesting in the mixed-species colony and thereafter, habitats were filled so that

the reward per individual was the same in both colonies. A similar model of "ideal free distribution" (Fretwell and Lucas, 1970) has also been proposed by Pierotti (1982) to describe habitat selection in Herring Gulls. According to his study, nest site selection in Herring Gulls depends on the nature of the ground cover. In the present study, biophysical parameters such as ground cover, slope and vegetation structure were not measured; efforts being made to assess the behavioural implications of habitat selection. However, Great Black-backed Gulls always nested on grass covered peat and on relatively flat areas.

The model developed above to explain the distribution of Great Black-backed Gulls on Gull Island was based on time budgets and not energy budgets. Although time investment may give a good approximation of the costs of reproduction, there were many parameters that could not be measured.

For example, although territorial defence is a major source of energy expenditure, the costs associated with displaying are certainly less than those involved when fighting. The costs of territorial defence may also vary according to the size of the territory, the number and the nature of the opponents. Other factors such as strength, size, age, experience, sex and species (eg. Great Black-backed versus Herring Gull) of both the intruder and the defender may be important when measuring energy outputs.

Reproductive investment may also vary according to sex, age, experience and various environmental constraints such as availability of food, abundance of predators and competition for nest sites and mates. Other energetic costs that a bird must face are associated with foraging and travelling during the reproductive season. The total energetic demand can be very high for either one or both parents.

In order to increase their reproductive success without reducing their chances of survival, individuals are expected to maximize their energy input and to reduce their costs of reproduction and other activities while increasing their fitness. Costs associated with territorial defence and travelling must be minimized while other activities such as self maintenance and efficient foraging should be maximized. Ideally, time and energy budgets should be optimized according to ecological, biological and environmental factors.

Parental behaviour and territorial defence were correlated with the reproductive success of Great Black-backed Gulls nesting in the mixed-species colony but not in the monospecific colony. Possibly, the levels of parental behaviour and territorial defence were sufficiently high and therefore did not correlate with reproductive success. However, territorial occupancy is in itself indicative of reproductive behaviour and territorial defence and reflects the dependance of breeding success on reproductive effort.

The analysis and interpretation of behavioural data is

limited by two factors. First, the recording of behavioural information at 5 min intervals may have introduced some biass in the time budgets of individuals. Secondly, the assumption that the four behavioural categories are mutually exclusive is simplistic since single behaviours may function in more than one way. For example, self maintenance may serve as territorial defence because the presence of a bird on its territory may be sufficient to reduce intrusion pressure from competitors. There may also be some confusion between territorial defence, mating and parental behaviours: are gulls defending their territories, their mates or their progeny? These limitations have to be taken into account when using time-budgets in behavioural studies and although it may provide useful information on the biology of many species, energetic studies give more reliable descriptions of biological phenomenons. Time-budgets have been used in the present study to speculate on possible nesting strategies based on habitat selection but energetic costs of reproduction are needed to establish the existance of the proposed nesting strategies.

5.0 - SUMMARY

1. A one year study of the breeding biology and behaviour of Great Black-backed Gulls began late in the incubation period in 1984; earlier access to the island was prevented by arctic pack-ice. The purpose of this exploratory study was to determine weather this species shows habitat (colony type) selection and, if so, define a possible mechanism of habitat selection.

2. Egg laying occurred between April 25 and May 26. Mean clutch and egg size were similar in the two colonies. However, the distribution of clutches was not the same: more 1-egg clutches were counted in the mixed-species colony. However, the fate of eggs was similar in the two colonies.

3. Hatching occurred between May 25 and June 24 while fledging started on July 10. Hatching and fledging started significantly earlier in the monospecific colony than in the mixed-species colony. The numbers of chicks hatched and of chicks fledged were similar in the two colonies.

4. Chick growth and chick mortality were similar in the two colonies. The occurrence of mortality per age class (7-day intervals) was also similar in the two colonies: more than 75% of the mortality occurred during the first 14 days after hatching. However, after the age of 35 days, chick mortality was only observed in the monospecific colony. The relative size of young Great Black-backed Gulls compared to neighbours was thought to play an important role in chick survival. Human disturbance was probably the major cause of chick mortality on Gull Island in 1984.

5. 3-egg clutches were the most productive in both colonies which tends to support Lack's hypothesis that the most common clutch is the most productive. However, in the mixed-species colony, the production of 2-egg clutches was almost as high as that of 3-egg clutches. This suggests that uptimal clutch size may not be the same in the two colonies.

6. An index (ITS) was proposed to give consistant estimates of territory size among all pairs nesting on Gull Island. No significant difference was found in mean ITS between the two colonies but ITS were not randomly distributed within colonies. Both large and small territories were defended in the mixed-species colony.

In the monospecific colony territory tended to be more uniform.

7. More neighbours were present around Great Black-backed Gull nests located in the mixed-species colony. The presence of neighbouring Great Black-backed Gulls did not influence the breeding success of conspecifics in the two colonies but, in the monospecific colony, the occasionnal presence of Herring Gulls around a Great Black-backed Gull territory was positively correlated with fledging success.

8. The behaviour of Great Black-backed Gulls was divided in four categories: mating behaviour, parental investment, territorial defence, and self maintenance. Even if the mean duration of the observation periods was not significantly different between colonies, territorial occupancy and mean time invested in the four behavioural classes was either longer or of equal duration in the monospecific colony than in the mixed-species colony.

9. Females appeared to be more experienced in the monospecific colony; males colonized the monospecific colony first.

10. Based on time-activity budgets and on consideration about costs and benefits (Game theory) associated with each type of coloniality, a spacing system was proposed to explain habitat or colony selection in Great Black-backed Gulls: the "ideal free distribution".

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APPENDIX 1.

List of birds seen on Gull Island from May to August 1983 - 1984.

Red-necked Grebe (Podiceps grisegena (Boddaert))	2,a,O,84
Northern Fulmar (Fulmarus glacialis (Linnaeus))	2,a,O,*
Leach's Storm-Petrel (Oceanodroma leucorhoa (Vieillot))	1,A,*
Northern Gannet (Morus bassanus (Linnaeus))	2,a,sa,C,*
Great Cormorant (Phalacrocorax carbo (Linnaeus))	2,a,R,*
Double-crested Cormorant (P. auritus (Lesson))	2,a,R,*
Black Duck (Anas rubripes Brewster)	2,a,C,*
Common Eider (Somateria mollissima (Linnaeus))	2,m,f,C,83,*
Oldsquaw (Clangula hyemalis (Linnaeus))	2,m,f,C
Golden Eagle (Aquila chrysaetos (Linnaeus))	2,i,O,84
Bald Eagle (Haliaeetus leucocephalus (Linnaeus))	2,a,i,O,84,*
Osprey (Pandion haliaetus (Linnaeus))	2,O
Spotted Sandpipper (Actitis macularia (Linnaeus))	1,C,*
Great Black-backed Gull (Larus marinus Linnaeus)	1,VC,*
Herring Gull (L. argentatus Pontoppidan)	1,A,*
Black-legged Kittiwake (Rissa tridactyla (Linnaeus))	1,A,*
Common Tern (Sterna hirundo Linnaeus)	2,a,O,*
Razorbill (Alca torda Linnaeus)	1,C,*
Common Murre (Uria aalge (Pontoppidan))	1,VC,*
Dovekie (Alle alle (Linnaeus))	2,a,+,84
Black Guillemot (Cepphus grylle (Linnaeus))	1,R,*
Atlantic Puffin (Fratercula arctica (Linnaeus))	1,A,*
Yellow-bellied Flycatcher (Empidonax flaviventris (Baird and Baird))	3,a,O,83,*

Northern Raven (Corvus corax Linnaeus)	2,O,*
American Crow (C. brachyrhynchos Brehm)	3,C,*
Boreal Chickadee (Parus hudsonicus Forster)	1,VC,*
American Robin (Turdus migratorius Linnaeus)	1,R,*
Swainson's Thrush (Hylocichla ustulata (Nuttall))	1,VC,*
Gray-cheeked Thrush (H. minima (Lafresnaye))	1,VC,*
Veery (H. fuscescens (Stephens))	1,C
Ruby-crowned Kinglet (Regulus calendula (Linnaeus))	3,m,O,83,*
Black-and-white Warbler (Mniotilta varia (Linnaeus))	3,a,O,*
Yellow-rumped Warbler (Dendroica coronata (Linnaeus))	1,R,*
Blackpoll Warbler (D. striata (Forster))	3,a,O,*
Northern Waterthrush (Seiurus noveboracensis (Gmelin))	1,VC,*
Mourning Warbler (Oporornis philadelphia (Wilson))	1,R,84,*
American Redstart (Setophaga ruticilla (Linnaeus))	1,R,84,*
Slate-colored Junco (Junco hyemalis (Linnaeus))	1,VC,*
White-throated Sparrow (Zonotrichia albicollis (Gmelin))	2,O,83,*
Fox sparrow (Passerella iliaca (Merrem))	1,VC,*
Lincoln's Sparrow (Melospiza lincolnii (Audubon))	2,O,84

NOTES:

1	Breeder	*	Also reported by Haycock, 1973
2	Non-breeder	+	One specimen found dead
3	Breeding status not established		(winter plumage)
A	Abundant	a	adult
VC	Very common	sa	sub-adult
C	common	i	immature
R	Rare but regular	m	male
O	Occasional	f	female

83, 84 indicated if a species was observed in only one of the two years of observation.

APPENDIX 2.

Data sheet used to record behavioural observations.

Date: Site:
Time: from __:__ to __:__ Observer:
Weather:

TERRITORIAL DEFENCE	MATING BEHAVIOUR	PARENTAL BEHAVIOUR
CC choking	FA face away	I incubation
OG on guard (neck out)	H hunched	B brooding
UTP upright threat posture	BE begging	FC feed chick(s)
GP grass pulling	CF courtship feeding	MC mew call
CG charge (-1m)	♀ copulation	SELF MAINTENANCE
CS chase (+1m)	CC choking	P preening
GB grasp bill	CNM collect nest material	FI feet inspection
GW grasp wing	NB nest building	R rest (neck in)
F fight	NR nest relief	s sit
W winner	MC mew call	S sleep
L looser		
CN call note		
LC long call		
AC alarm call		

A arrival	a adult	✓ on nest
D departure	c chick	X off nest
	e egg	/ absent

nest no.	sex	__:00	05	10	15	20	25	30	35	40	45	50	55
1													
2													
3													
4													

.../ 14 nests.

APPENDIX 3.

Schedule of behavioural observations performed on Gull Island between May 27 and July 26, 1984.

DATE	MONONSPECIFIC COLONY ("the Point") time	no. nests	obs.[1]	MIXED-SPECIES COLONY (East Side) time	no. nests	obs.[1]
27/5	11:30-16:00	8	NAR			
28/5	10:00-14:00	6	NAR	10:00-14:00	6	SBW
01/6	08:00-12:00	11	SBW			
06/6				12:00-14:00	7	SBW
08/6	10:00-14:00	13	SBW			
11/6	14:00-18:00	12	SBW			
12/6				14:00-18:00	7	SBW
13/6	06:00-12:00	11	SBW			
13/6	13:00-18:00	12	NAR			
17/6	06:30-10:30	11	NAR			
18/6				12:00-16:00	8	NAR
25/6				11:00-15:00	7	SBW
26/6				05:00-09:00	8	SBW
27/6				05:00-09:00	8	SBW
29/6				06:00-10:00	8	SBW
30/6	15:00-19:00	13	NAR	15:00-20:00	8	SBW
02/7				10:30-14:30	8	SBW
02/7	18:00-22:00	11	NAR	18:00-21:30	8	SBW
05/7				10:00-20:00	8	NAR
06/7				10:30-15:30	8	NAR
07/7	05:00-09:00	13	NAR			
09/7				12:00-16:00	8	NAR
09/7	18:30-21:30	13	NAR			
11/7	12:00-18:00	12	NAR	12:00-18:00	5	SBW
13/7	11:00-15:00	12	SBW			
13/7	16:00-21:00	12	NAR			
14/7	05:30-21:30	12	NAR	05:00-21:30	8	SBW
19/7				14:00-19:00	8	NAR
20/7				09:00-14:00	8	SBW
25/7	09:00-13:00	11	NAR	09:00-13:00	8	SBW
26/7				10:00-16:00	7	NAR
TOTAL	17 (85.5 h)	13		20 (99.0 h)	8	

[1] Observers: NAR Nicole A. Roy
SBW Stephen B. Will