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COMPARATIVE ECOLOGY OF CALIFORNIA AND RING-BILLED GULLS (LARUS CALIFORNICUS AND L. DELAWARENSIS)

Patricia A. Baird
The University of Montana

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    University of Montana, Ph.D., 1976
    Ecology

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PATRICIA ANN BAIRD

COMPARATIVE ECOLOGY OF

CALIFORNIA AND RING-BILLED GULLS

(Larus californicus and L. delawarensis)

By

Patricia Ann Baird

M.S., California State University, 1970

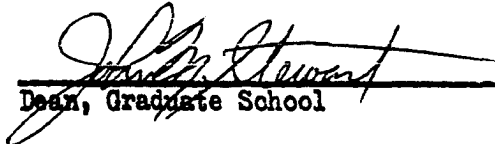Presented in partial fulfillment of the requirements for the degree of
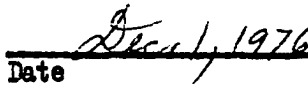
Doctor of Philosophy

UNIVERSITY OF MONTANA

1976

Approved by:

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Chairman, Board of Examiners

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Dean, Graduate School

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Date

Baird, Patricia Ann, Ph.D., December, 1976   Zoology

Comparative Ecology of California and Ring-Billed Gulls (Larus californicus and L. delawarensis) (183 pp.)

Director: Andrew L. Sheldon *AÞ*.

The ecology of mixed and single species colonies of Ring-billed and California Gulls was studied in insular and peninsular locations in Montana. The purpose of this study was to investigate the foraging and nesting niches of these sympatric congeners and to ascertain what enabled them to coexist, what possible differences in lifestyles existed between them, and possible causes of these differences. The adaptive significance of patterns of habitat choice of the 2 species was also investigated with respect to reproductive success. The inter- and intraspecific behavior of the 2 species was described. Vegetation height, cover, volume, and species composition, distance to water of each nest, nest density, and nearest neighbor distances were examined as possible factors influencing nest construction on a particular site. Resource utilization was examined with respect to choice of feeding sites, interspecific interaction at feeding sites, and types of food eaten. Reproductive success of each species with respect to colony type, location in colony, vegetation profile, nearest neighbor distance, and species of nearest neighbor was investigated. Egg and chick success were determined and multivariate regression used to determine what factors influenced mortality.

California Gulls arrive 2 weeks in advance of the Ring-billed Gulls and establish territories in specific areas of the colony. There is little interspecific interaction and although the California Gulls are more aggressive and occasionally predate the Ring-billed chicks, the behavior is usually one of avoidance.

The 2 species segregate the nesting habitat with respect to vegetation characteristics and nest in monospecific subgroups. Both prefer the middle of the colony to the edges. California Gulls nested in the higher denser vegetation. The nearest neighbor distances differed between the 2 species, and for Ring-billed Gulls, this distance is related to species of nearest neighbor. In the monospecific colony of California Gulls, the nesting niche is wider.

California and Ring-billed Gulls segregate the food niche mainly by distance from the colony and by habitat type of the foraging areas, and less by food type. They had a 62% overlap in their diets. California Gulls forage farther from the colony on dryland farmlands and prairie while Ring-billed Gulls forage near the colony in irrigated farmlands.

Chick survival from the egg stage was higher on the mixed species insular than on the peninsular colony, and least on the monospecific colony. Death rates of chicks were positively correlated with nearest neighbor distance and clutch size, and negatively correlated with vegetation cover, in most colonies. There is an indication that an optimal density exists within colonies and that densities above or below this cause a higher chick death rate.

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CHAPTER I

INTRODUCTION

Different species solve the problems of niche segregation or sympatric association in different ways. It is important to study many diverse species representing different trophic levels, reproductive strategies, and geographic locations in order to more fully understand evolutionary and comparative ecology. I chose Ring-billed (Larus delawarensis) and California (Larus californicus) Gulls as subjects for this study in comparative ecology. These 2 gulls are good subjects for such a study. They are unique among ground-nesting gulls in that they are the only white-headed gulls in the contiguous United States to nest inland. Ring-billed Gulls have a more extensive breeding range from east to west than do California Gulls. Their range extends from northeastern California to northern Saskatchewan and from Newfoundland to northern New York (Figure 1-1). The range of California Gulls is south from the north central Mackenzie River to northeastern California and west from east central North Dakota to northwestern Wyoming (AOU 1957). The 2 species are sympatric over approximately 70% of their range, although locally, the breeding populations can be either mixed or single species. No other closely related species interacts on the breeding ground with these 2 gulls (Moynihan 1959) thus simplifying the study. Franklin's (Larus pipixcans) Gull, a black-hooded gull, nests in the same area, but has a completely different ecology from that of California and Ring-billed

1

King-billed gull

California gull

(from Vermeer)

Figure 1-1

Main winter range
Breeding range
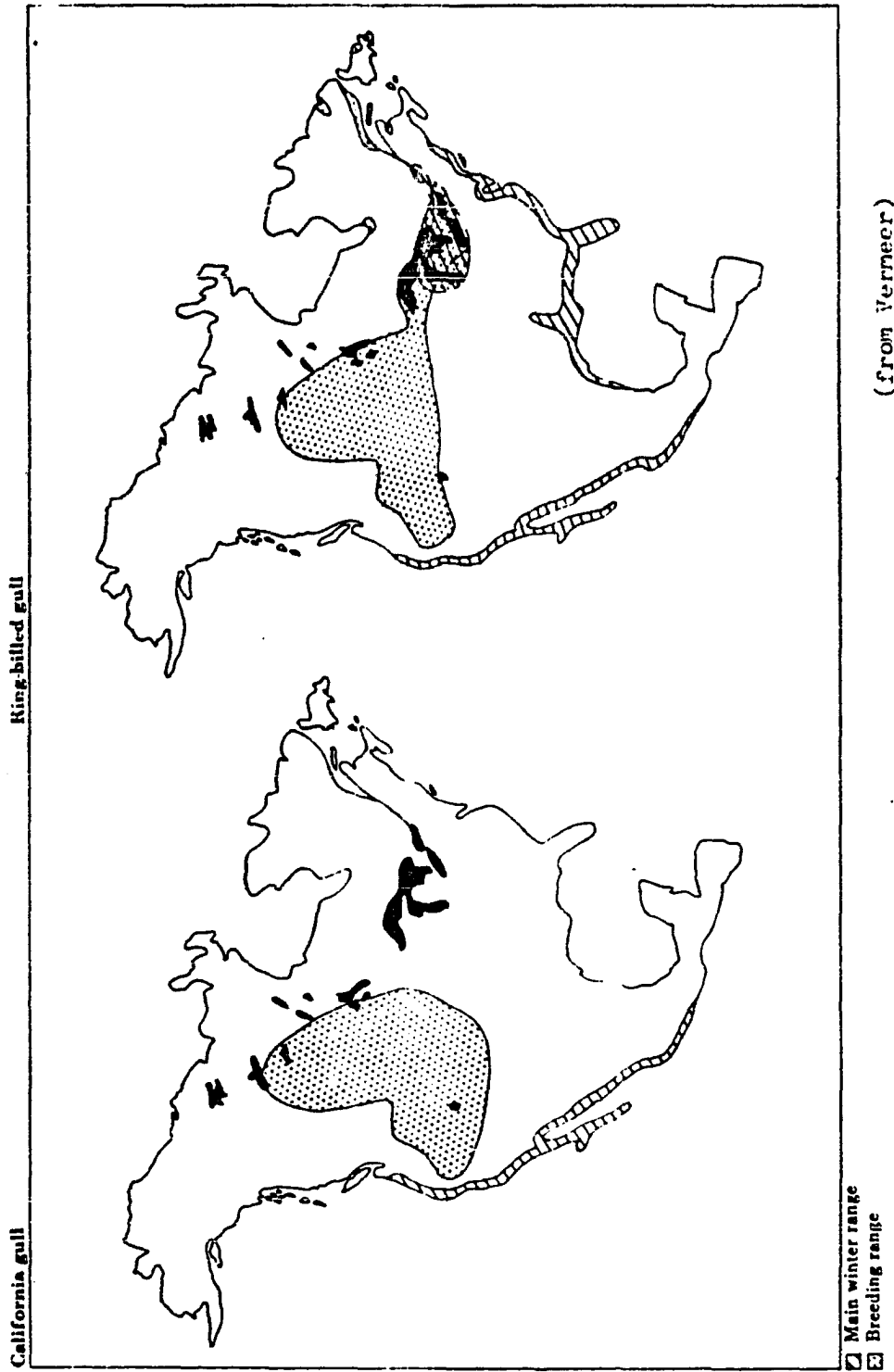
Gulls (Burger 1974). These gulls are readily available research animals because they occur in great numbers, are easily observed, and the colonies are quickly censused (Brown 1967b, Moynihan 1959, Patterson 1965, Paynter 1949, Tinbergen 1953, Vermeer 1963,1970). Likewise, both the mixed and single species colonies are found near each other and this obviates the necessity to take into account differences in population parameters caused by latitude, altitude or gross habitat variation (Figure 1-2).

The sample areas in this study—Arod and Freezeout Lakes—are ideal sites for the following reasons. On each lake there is a mixed breeding colony, on the one it is an island, on the other it is a peninsula. Also at Freezeout Lake there is an island with a colony of only California Gulls. The gull populations in these colonies can all be contrasted with respect to possible differences in nesting patterns, breeding biology, reproductive success, and variation in the feeding niche.

Much of the past research in comparative ecology has been mainly descriptive until ecologists like Cole (1949,1954), Lack (1933,1944, 1945,1946) and MacArthur (1957) investigated causal and functional relationships between species with respect to the environment or the niche. Before their studies, most of the comparisons between species were an enumeration of the 2 species' characters. Then came a collection of "competition"-oriented research where many of the co-existing species were studied to determine if they were competing. These latter investigations sometimes simply demonstrated differences between the 2 species involved.

MONTANA

KALISPELL

FREEZEOUT LAKE

AROD LAKE

MISSOULA

BUTTE

GREAT FALLS

X X

BOWDOIN LAKE

MALTA X X

BILLINGS

SAMPLE AREAS
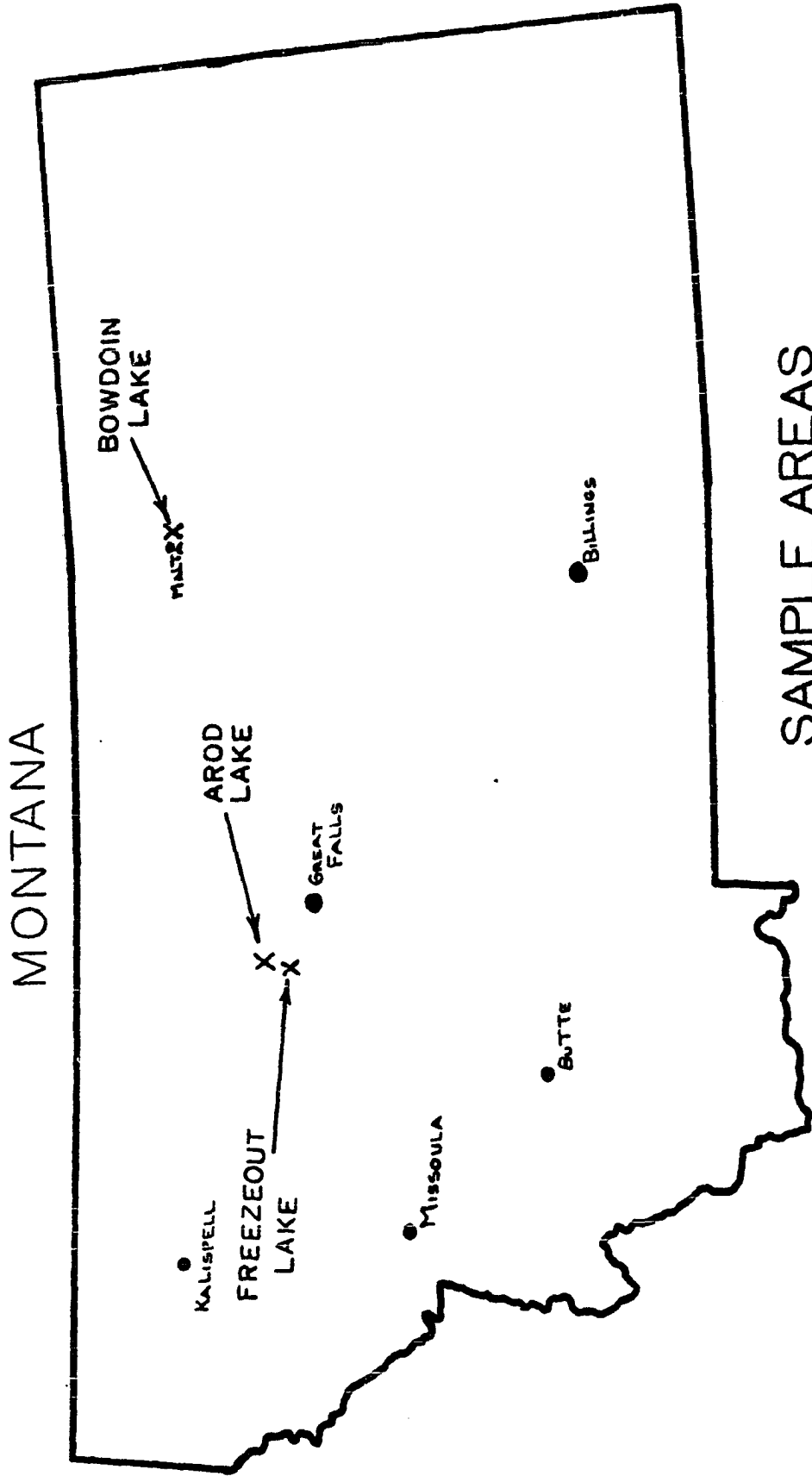
Figure 1-2

Competition, often defined as the utilization by 2 species of common resources of which the supply is limited (Birch 1957, Milne 1961) or the effect of one species on the other (Miller 1954), has been divided more clearly into 2 categories, exploitation and interference (Park 1962). Both types of competition can be avoided by 2 species by physical separation or in the way they divide up the space. If they utilize no common resources, then 1 cannot exploit the common resource. Likewise, if they are separated physically, 1 cannot interfere with the other. Physical separation and division of resources, however, can be the result of competition. As is often the case, when 2 species are not physically isolated from one another, they may avoid competition by dividing up the resources in the habitat.

There is a limit to the similarity of species if the 2 are to coexist (MacArthur and Levins 1967). There must be a certain amount of difference in lifestyles between 2 species to prevent them from occupying the same niche (Hutchinson 1957). These differences are shown in food types, preference of the foraging habitat, morphological differences, nesting habitat choice and by behavior. All these factors together may be considered a certain "strategy" for that species in a certain environment. In a study of comparative ecology, one must look more deeply into not only how the 2 species actually divide up the habitat so that they can coexist, but also how the proximity of 1 species might influence the reproductive success of another. Only by comparison and analysis of sympatric and allopatric situations can we

begin to determine what qualities affect the productivity or survival of the 2 species and how they may influence one another (Elton and Miller 1954).

An investigation of the breeding ecology of Ring-billed and California Gulls may give a clearer understanding as to how these 2 species coexist during the breeding season. The nest site resources are extremely limited because the preferred breeding ground is on islands in lakes. This site preference may produce possible severe inter- and intraspecific competition for nest sites. There must of necessity be an upper limit to the abundance of each species on the colonies unless 1 or both undergoes a radical niche shift and either decreases size of nest territories or nests in another habitat. These gulls are also examples of different kinds of breeding strategies because they represent a "breed, eat and get out fast" strategy. Their sojourn inland on the breeding ground is relatively short although many remain inland until early fall. The adults leave the colony soon after the chicks fledge in late July. Due to the inland nature of the breeding sites, these gulls are also exposed to harsher weather than gulls that breed near the ocean. When the gulls arrive in the spring, ice is usually present on the lakes surrounding the islands or peninsulas on which they nest. It can snow as late as June and as early as September in these areas.

The mechanisms behind the settling factors, factors which attract the birds to breed in a certain area, on these locally mixed or single species colonies are not known. In fact, it is not known how these breeding colonies are set up. Many species of _Larus_ gulls nest near a

congener and it is interesting to note that the courtship behavior of all of them is very similar although most do not interbreed even though they are closely related (Moynihan 1959). There may be a dominance interaction at the outset in the creation of the nest territories, or the 2 species may differ enough in the preferred habitat types that this is not necessary.

The gulls' breeding habits also represent a different strategy from other groups that have been studied in that the adults do not usually feed where they nest. They exhibit the Type 4 territory category of Nice (1941). Other colonial groups such as terns and cormorants likewise show this pattern (Nice, 1941). Most available space on the islands is used for nest sites. Thus, the gulls must make frequent trips from the colony to the feeding grounds.

Gulls are likewise unique in that they coexist well with humans (Hunt 1972, Moynihan 1959, Vermeer 1970). Their feeding grounds are disturbed areas such as dumps or cultivated fields. Association with humans has actually improved breeding success in some cases because of the proximity of garbage dumps.

Thus, gulls, as a taxon, are representative of certain breeding and feeding strategies. However, most work has been conducted on Old World gulls and has concentrated on their behavior (Beer 1965, Brown 1967a b, Lack 1968, Patterson 1965, Paynter 1949, Tinbergen 1953). The comparative studies on New World gulls have concentrated on behavioral and ecological descriptions (Beer 1965, Brown 1967a b c, Brown, et al. 1967, Coulson 1963, Coulson and White 1961, Cullen 1957, Drury and Smith 1968, Harris 1964,1965, Maunder 1972, Moynihan 1955,1956,1958a b,1959,

Paynter 1949, Smith 1966,1967, Schreiber 1970, Snow and Snow 1968,

Threfall 1968); or on censusing of the breeding colonies only (Johnston

and Foster 1954, Moos 1968, Vermeer 1963,1970).

Because of the copious amount of data to be gleaned from the

colonies, much can be learned about niche preference, niche overlap,

nest-site competition or species dominance, and especially any beneficial

or detrimental influence on reproductive success in a mixed species situa-

tion.

DIVISION OF SPACE

For most species of animals, space and food are items which are

at a premium (Paine 1966). For gulls, space on the breeding ground is

decidedly limited due to the scarcity of suitable islands or peninsulas

and their physically limiting space. In other studies of other birds,

space has been found to influence productivity or population size (Brown

1967a b, Chapman 1966, Lack 1945, Patterson 1965). Chapman (1966) states

that regardless of the food supply, there is usually a minimal space re-

quirement for animals and this puts upper limits on the density. The

same may be true for gulls. It is important to discover what factors may

influence nest spacing, and if nest distribution and density vary among

the colonies. If they do vary, is this variance related to the interac-

tion between the 2 species? In other bird species, the presence of a

congener has often altered nesting patterns (Brewer 1963, Catchpole 1972,

Crowell 1968, Dixon 1954, Legg and Pitelka 1956). This alteration may or

may not affect reproductive success. If dense nesting insures that a

predator is more likely to be noticed, resulting in less nest destruction,

then a change towards denser nesting would be beneficial. However, if the inter- and intraspecific aggression increases with denser nesting, then this might be detrimental to the reproductive success of 1 or both species.

There have been many studies on various species describing preferences of nest site with respect to habitat parameters (Brown 1967a b, Colquhoun and Morley 1943, Hawksley 1956, Horn 1970, Johnson 1966, Klopfer 1963, Lanyon 1956, Legg and Pitelka 1956, MacArthur 1957,1964, MacArthur and MacArthur 1961, MacArthur, et al. 1966, Newton 1967, Raitt and Hardy 1970, Root 1964,1967, Selander and Giller 1959,1961, Wiens 1965). Most of these studies, however, have been on passerine birds in habitats with definite vertical components. The conclusions about habitat preference reached in some of these studies are that birds distribute themselves in a habitat in part according to the height or volume and not the species, of the foliage and that each vertical zone has its own dominant species. There can also be vertical horizontal and temporal components of habitat preference (MacArthur 1964). On the gulleries, factors other than, or in addition to, height-influenced settling factors may be operating because there is little height variation of vegetation on the breeding grounds. Some colonies are almost devoid of vegetation, and in fact, no vegetation was found higher than 120 cm on the colonies used in this study.

The gulls may be attracted to the small differences in height of vegetation, or perhaps the bushiness of the plants, the distance to water, or even to other birds when they land on the breeding colony to court and build their nests. In colonial breeders, the presence of a

conspecific may be enough to promote settling (Nelson 1966, Patterson 1965). Niche shifts in habitat selection, even into a marginal habitat, are another way that similar species have avoided "competitive elimination" (Cody 1968a, Crowell 1968, Dilger 1956, Dixon 1954, Wiens 1965).

FOOD, FEEDING GROUNDS, AND FORAGING BEHAVIOR

On the breeding grounds of many bird species, competition for food for the young is severe (Ashmole 1968a, Dorward 1962, Lack 1969). The gulls may not have this problem because they are omnivores and scavengers and food always should be abundant. Yet, they may be omnivorous because food is scarce. Paynter (1949) believes that abundance of food is of no importance to Herring (Larus argentatus) Gull survival. He states that the gulls have practically unlimited food in a normal year. Willis (1966) believes that for birds, superabundance of food may be the rule rather than the exception. However there may be some limitation of food resources near the colonies. Gulls may share food resources by dividing up the actual foods eaten, the places where the 2 species feed, and/or by varying feeding or foraging behavior.

Food

For the moment, if we think of food as the only important component in a gull's lifestyle, the 2 species may be able to coexist providing that every habitat they utilize has enough heterogeneity and the right species or size of prey. However, it must be kept in mind that the analysis of the food niche is very subjective. "From a bird's viewpoint, a caterpillar and a berry may be closer together on some hypothetical

food axis than a seed and a berry—that is, the hardness may be a more important criterion than the chemistry or phylogeny . . ." (Soulé and Stewart 1970).

Feeding Grounds

The birds may also divide up the habitat according to where in the habitat they forage, the vegetation types in which they forage and the height at which they forage or even the specific part of the plant they forage in. Many other studies have demonstrated that if 2 species are searching for a particular habitat type and not just specific types or sizes of prey, they may segregate the habitat physically (e.g. Austin and Smith 1972, Brewer 1963, Carpenter 1952, Cody 1968a, Colquhoun and Morley 1943, Crowell 1961, Dilger 1956b, Gibb 1960, Hamilton 1958, Hartley 1953). In some species, even the sexes occupy different habitats (Kilham 1965, Ligon 1968, Selander 1966).

Where gulls feed, therefore, might be more important than the type or size of prey species especially since gulls are omnivorous. If this is true, then the different feeding sites may be important in lessening or even eliminating any possible competition between them. This can be brought about by passive circumstance, a bird's simply avoiding an unsuitable habitat, or active avoidance when a member of the other species is present—both examples of competitive exclusion. Likewise, the gulls may forage in different types of habitats where their foraging ranges overlap. When these ranges do not overlap, the gulls may choose similar foraging habitats. Lack of divergence in ways of exploiting the environment may mean: 1) that there has been insufficient evolutionary

time for the birds to shift, 2) the environment imposes some limitation preventing evolution of different foraging niches, 3) the other species, by its behavior, prevents divergence in certain directions, or 4) divergence is not advantageous because there is a resource surplus.

Foraging Behavior

The third way 2 similar species may divide up the habitat is simply by dominance at the foraging site (Austin and Smith 1972, Birch 1957, Dixon 1954, Dorward 1962, Drury and Smith 1968, Gibb 1960, Kilham 1965, Ligon 1968). If 1 species is dominant on the feeding grounds then the other species may simply avoid feeding in the same area. If it does feed there when the other is present, it may keep at a distance and restrict itself to the marginal habitat. This avoidance may be simply a change in feeding behavior patterns in the presence of another species (Wiens 1965). On the feeding ground, dominance or a reduction in interspecific contact, a result of a behavior change, has been shown in various species and is 1 method of resource segregation (Austin and Smith 1972, Dixon 1954, Selander and Giller 1959, Willis 1966).

Another possibility is that the 2 species may actually feed in different ways like many other similar species when they feed sympatrically (Austin and Smith 1972, Ashmole 1970, Holmes and Pitelka 1968, Newton 1967, Orians and Horn 1969, Root 1967, Selander 1966). If the method of foraging they use differs and if they subsequently catch different food items, it may preclude or reduce any competition (Catchpole 1972).

TEMPORAL SEGREGATION

Another way many species avoid competition or divide up the hab-
itat resources is by a difference in timing of breeding (Brown 1967a,
Catchpole 1972, Dane 1966, Maher 1962, Nelson 1966, Patterson 1965,
Rickleffs 1966, Root 1967, Koyama 1966, Wiens 1965).

Previous studies and also observations on 5 Montana colonies show
that the gulls' first hatching and fledging dates at these altitudes are
close to each other (Smith personal communication, Vermeer 1963,1970).
For gulls, the interesting questions about temporal segregation are: Which
species arrives first on the breeding grounds? Does this first species
get displaced by the later arriving species or does it decrease the size
of its territories, and does the peak energy demand by the chicks occur
at the same time? A few other studies have reports of dominance displace-
ment in birds (Orians and Willson 1964, Pitelka 1951, Wiens 1965).

BEHAVIOR ON THE BREEDING AREA

Behavior, especially aggressive behavior, between the 2 species
may account for any difference in reproductive success between the mixed
and single species colonies which is not explained by nest placement,
food habits, or timing. Too often in ecological studies the behavioral
interactions at the nest site between the 2 species are excluded or
simply overlooked and these may be some of the more important factors
affecting productivity.

It is important to know just what sorts of interactions occur be-
tween the 2 species in setting up their territories because the setting

up of territories in a preferred habitat may ultimately determine the re-
productive success of the birds on the colonies. A bird nesting in a less
preferred habitat, perhaps a peninsula as in this study, may not fledge as
many young as a bird nesting in its preferred habitat. Observations on
these interspecific interactions tell us much about the influence 1 species
has on the other and its benefit or detriment to reproductive success.
From this we can possibly hypothesize why the mixed and single species
breeding population endure.

Gulls are known to be predatory on gull chicks and eggs (Moyni-
han 1956, Smith personal communication, Tinbergen 1953, Vermeer 1963,
1970). At times they are even cannibalistic. Larger gulls tend to be
predatory on smaller gulls nesting nearby (Moynihan 1956, Vermeer 1963,
1970). Immature gulls that do not breed but inhabit the breeding colony
are often predatory (Kennedy 1973, Smith personal communication).
Chicks in a crowded situation with potential predators nesting nearby
might suffer a greater mortality than chicks in an uncrowded situation
with no predator nesting nearby. Likewise, the presence of another
species might elicit a greater (or lesser) intraspecific aggression,
thus indirectly influencing productivity. Predation by other gulls and
cannibalism are the major mortality factors on gull colonies (Paynter
1949, Vermeer 1963,1970). Cody (1968a) is even stronger in his wording:
"Predation is the single greatest cause of reproductive failure in
birds." In the above studies, an average of 48% of the eggs were ob-
served to fledge. Reproductive success likewise is influenced by the
predation on chicks by other species and by gulls (Paynter 1949, Vermeer
1963,1970). Also, like all ground-nesting species, the gulls are

continuously threatened by other predators of all sorts—coyotes, weasels, snakes, and humans. Just the presence of a predator on the colony disturbs the gulls and increases mortality (Hunt 1972, Pratt 1970, Vermeer 1963,1970).

In other comparative studies on various species, interspecific aggression has not always been an important factor in the behavior repertoire (Carpenter 1952, Drury 1961, Jaeger 1972, Morse 1970, Orians and Collier 1963, Root 1964, Selander and Giller 1959, Smith 1967). The explanation for this may be that either the 2 species do not elicit aggression in each other because their behaviors are so different or because they partition the environment so well and are segregated spatially or temporally.

Where aggression is shown, it can be for a variety of reasons. The 1 species may be recognized as a predator and evoke a typical antipredator reaction. The aggression also simply may be a response to a competitor especially if the habitat is not well segregated. Also each species may look so similar to the other that they elicit similar intraspecific responses (Brown 1966, Catchpole 1972, Dixon 1954, Legg and Pitelka 1956, Ligon 1968, Minock 1972, Orians and Collier 1963, Rohwer 1973, Wiens 1965). Interspecific territoriality is expected with an absence of sufficient ecological divergence (Orians and Collier 1963). If the 2 species are compatible, selection should eliminate interspecific aggression (Orians and Collier 1963). Interspecific territoriality is a useless expenditure of energy according to Orians and Horn (1969).

The relative abundance of each species also may influence interspecific aggression. However, Patterson (1965) believes that aggression

itself can influence the spacing instead of the spacing influencing the aggression. In fact, often the aggression of 1 species is so great that it completely excludes the other from breeding in that area (Pitelka 1951).

REPRODUCTIVE SUCCESS

One of the more important outcomes of a study such as this is a comparison of productivity of each of the colonies. From this comparison can be obtained a measure of what influences each species has on the reproductive success of the other. Other studies have determined fairly accurately the causal factors of reproductive success from the data gathered on spatial and temporal distribution, vegetation cover, food and foraging habits, and interspecific interactions of various species (Crowell 1968, Jaeger 1972, Legg and Pitelka 1956, Maher 1962).

Brown (1967b), in a comparative breeding biology study on Herring and Lesser Black-backed (Larus argentatus and L. fuscus) Gulls, noted that breeding success was positively correlated with vegetation cover. Burger (1967) found that there was greater nesting density with more vegetation cover. Spacing, density, and colony placement in the habitat likewise influence productivity in many other species (Legg and Pitelka 1956, Patterson 1965, Tenaza 1971).

The date of nesting is an important factor in successful breeding (Brown 1967b, Maher 1962, Patterson 1949) as is previous breeding experience (Coulson and White 1961). For many species, clutch size is smallest and breeding success is least if eggs are laid at the end of the nesting period. Early eggs have a greater chance of fledging than

late eggs in most of these studies, but less chance than eggs laid in the middle of the breeding cycle. Weather is another factor influencing productivity (Nelson 1966, Pratt 1970, Seel 1969). Emlen (1976) states that for colonial birds, synchrony in nesting is probably more important than actual date of laying.

In summary, this study describes the breeding biology, timing of reproductive activities, and behavior of California and Ring-billed Gulls. It compares their feeding and nesting niches, and analyzes any differences in reproductive success of the 2 species on several colonies.

CHAPTER II

BREEDING BIOLOGY AND BEHAVIOR

INTRODUCTION

No general description has been made of the breeding biology and behavior of California and Ring-billed Gulls in Montana. Many of the studies of the breeding biology of gulls have involved Old World gulls (Beer 1965, Brown 1967a b, Lack 1968, Patterson 1965, Paynter 1949, Tinbergen 1953). The majority of the research on New World gulls has involved the coastal breeding gulls only (e.g. Brown, et al. 1967, Cullen 1957, Maunder 1972, Snow and Snow 1968, Threfall 1968). None of these studies elaborates on the way the 2 species divide up the habitat at the onset of the breeding season upon arrival on the colony.

MATERIALS AND METHODS

I observed the birds from a 10-foot tower on the Freezeout Lake Peninsula, from a blind on the Arod Lake Island, or from a canoe at the Freezeout Lake Island and at Arod Lake Island. In 1973 I obtained preliminary observations from a blind at Freezeout Peninsula and Arod Island, intermittently, from 20 April until 13 May, and recorded data for approximately 4 hours a day. Later in the season, from 14 June until 8 August, I obtained data on behavior and breeding biology mainly from the Freezeout Peninsula colony during 10-12 hour observation sessions in the blind each day. Total observation days were 28 at Freezeout and 6 at Arod.

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In 1974 I observed gulls on and sometimes away from the colonies from 21 March through 3 August. I observed them from 2 to 8 (average = 4) hours per day. In 1975 I primarily observed the colony at Arod from 28 March through 1 June. Four days of this time period I spent at Freezeout Peninsula and Freezeout Island. The observation sessions averaged 4 hours each. Types of data recorded during all the observation sessions were: times of arrival, nest construction, egg laying, chick hatching and fledging. In addition, I recorded descriptive data on all agonistic encounters (inter- and intraspecific) during all phases of the breeding cycle.

CHRONOLOGY OF BREEDING BIOLOGY

Gulls of the same species arrive on the Montana colonies within a day of each other (Table 2-1). The various stages of their reproductive sequence also are similar in time. The factor that influences the timing of the cycle is the date of arrival. It is not known what influences this, but weather may be an important factor. Arrival times on the colony differ from year to year. They can vary over approximately a 2-week period from one year to the next. Once the breeding sequence has been started on the colonies it can be delayed, set back, or even entirely disrupted or terminated by storms or by severe disturbance (usually human) on the colony.

The California Gulls arrive on the average 2 weeks (range: 11-17 days) earlier than do the Ring-billed Gulls. This is true for each colony studied. Similar results for both species have been obtained in Idaho and Canada (Trost personal communication, Vermeer 1970).

20

Table 2-1

Chronology of Breeding Biology

Colony and Date	First Arrival on Colony		First Nest		First Egg		First Chick		Comments
	Larus californicus	Larus delawarensis	Larus californicus	Larus delawarensis	Larus californicus	Larus delawarensis	Larus californicus	Larus delawarensis	
1975 Ared Island	21-III	30-III 31-III	7-IV 10-IV	21-IV 27-IV	ice left 30-IV	3-V	4-V	30-V	1-VI	Human disturbance 14-V, 15-VI. Some L. californicus leave nests. Some L. delawarensis still eggs as of 30-V. Population 2-V.
1974 Ared Island	9-III	26-III		30-IV	14-V		19-V	
Present Peninsula	9-III	ice left 25-II		16-IV 1-V	25-V		16-V	
1973 Ared Island	4-III		16-III		27-IV	27-IV		
Present Peninsula		18-III		26-IV	26-IV			
Bendela				25-IV	25-IV			
1972 Bendela (Chronicler)		First Gull 16-III						
1959 Present Peninsula (Rothmuller)	~12-III	26-III						
1958 Present Peninsula (Rothmuller)	~7-III							

= Stern

California Gulls construct the first nests approximately 5 weeks after arrival while the Ring-billed Gulls construct their nests a little over 3 weeks after arrival. For both species, the first eggs are laid a week after the nests are begun. Depending, perhaps, on the first arrival time of the gulls, the period between arrival time and egg laying can be shortened. For California Gulls this period is 6-8 weeks; for Ring-billed Gulls it is 4-6 weeks.

The incubation time is 26-27 days for both species. The first California Gull chicks hatch 10-11 weeks after the first gulls arrive on the colony, while the first Ring-billed chicks hatch approximately 8 weeks after the arrival of the first adults.

Thus, even though the Ring-billed Gulls arrive later than the California Gulls, they come into breeding synchrony with the latter by decreasing the time between time of arrival and construction of the first nest. This decrease in time may be due to: 1) the fact that they are already in physiological synchrony with the California Gulls and are at the same breeding stage when they arrive 2 weeks later, or 2) the advanced breeding state of the California Gulls may somehow stimulate or facilitate the reproductive cycle of the Ring-billed Gulls and accelerate it so that they become synchronous, or 3) the nest building may be triggered by the same environmental clues for both species.

BEHAVIOR DESCRIPTIONS

In order to understand the behavioral aspects of comparative ecology, I found it necessary to study postures of the gulls. This enabled me to distinguish between agonistic, sexual, and other sorts of

behaviors of the gulls. The agonistic and sexual behaviors are the important behaviors to study for intra- and interspecific comparisons with respect to niche segregation. I made observations, described the postures myself and then reviewed Tinbergen's description of postures of other species of gulls. The following descriptions are mine with some modification from Tinbergen (1953,1958).

There are 10 postures both California and Ring-billed Gulls assume in agonistic and sexual encounters with other adults. Both species also exhibit four attack-chases. These behaviors are described below. They are the same for both species except when otherwise noted.

Forward

The Forward is accompanied by 1 sharp vocalization, the typical gull Long Call. The display's movement is directed straight ahead and the gull has the neck elongated and the beak open, with the body inclined towards the horizontal but not nearly as much as in the Black-headed (Larus ridibundus) Gull, for instance (Tinbergen 1958). The Forward is one of the low-threat displays. Conspecifics to whom the Forward is directed are not within 1 to 2 meters of the California Gull or within approximately 2 meters of the Ring-billed Gull. The Forward is directed either at a potential territory trespasser or at a territory holder. The Forward is sometimes followed by threat displays of greater intensity. Tinbergen (1958) describes this low-threat display as one that stops the accidental intruder.

Oblique

In the Oblique, the body and head of the gull are at a 45° angle to the ground. The beak is open and a Long Call is given. This is a threat display of higher intensity than the Forward because it is often followed by a high-threat Down-Up display or by a fight. Likewise it is used more often when a conspecific is close to the gull issuing the Oblique. The Oblique also can follow a Down-Up or a fight. It is more common in californicus than in delawarensis and is not part of the Down-Up sequence as in Herring (Larus argentatus) Gulls (Tinbergen 1953). The Oblique more often is directed initially at a potential territory trespasser than at a territory holder.

Head Toss

The Head Toss is primarily a sexual display by the 1 of a pair towards its mate. Before copulation, the female circles the male tossing her head back three to four times with the beak closed. The male in later stages of the mating cycle repeats this. The female's Head Toss in this sequence is followed by aggression from the male, chest pecking by the female, Head Toss by either sex, or copulation. In the early part of the season there is more aggression by the male. Some researchers call the Head Toss an appeasement display because the female bird usually looks away from the male and does not utter a call (Tinbergen 1953). Avoidance of eye contact is a classical appeasement gesture (Marler and Hamilton 1966). Gulls display the Head Toss outside of the mating situation also. It sometimes occurs after an "Anxiety Upright" posture (Tinbergen 1958); and in this context, I believe it is an anxiety display, neither

aggressive nor appeasing. The Head Toss often occurs when another gull is just outside the territory or even after an aggressive exchange.

Down-Up

The Down-Up can be broken into two components consisting of a Head Toss with the beak open and a Long Call, and a Choking-Mew component with the head tucked to the chest or even between the legs. The Down-Up differs in form between Ring-billed and California Gulls.

Head Toss (Throwback—Tinbergen).

The Head Toss component of the Down-Up is similar to that described previously. However, the Long Call does occur. The Ring-billed Gull form of this display is similar to the sexual or anxiety Head Toss in that the toss is repeated up to 6 times with a separate Long Call vocalization at each toss. In between tosses, the head is placed in its normal horizontal position. The California Gull's Head Toss differs in that the head remains in the back extended position with up to 6 Long Calls emanated at this position and then a return to the normal position. A separate toss is not initiated for each vocalization.

Choking-Mew.

The "down" segment of the Down-Up is similar to the Mew described by Tinbergen (1958). In the mild Choking-Mew, the head is thrown down on the chest with the beak open, neck straight, and "mew" vocalizations are emitted. In the intense Mew the head is thrown down almost to the ground, often between the legs, the beak is open, the neck is arched and up to 8 mew vocalizations are emitted.

The Down-Up is a display of high threat and intensity. It is emitted by territory owners or by offensive, not accidental, territory intruders. It is a display of "readiness to attack" and is often followed by attack from the bird who emitted it. The Down-Up also occurs after fights or chases and seems in this sense to be a reaffirmation of territorial ownership. Intense Down-Up displays occur as distances between 2 adjacent birds decrease, and as aggressive displays by other birds increase.

Pre-Attack

The Pre-Attack display is an extension of the intense Mew and does not always lead to attack by the gull emitting it. It is a display of high threat. The head is lower than the body, horizontal, and facing towards the opponent. The wings are either spread or the carpals are positioned forward. These are both described by Tinbergen (1953) as wing positions of high threat. Either the active intruder or the territorial gull can display the Pre-Attack posture.

Jabbing

Jabbing is not a posture but rather an active threatening movement. The jabbing by Ring-billed and California Gulls is similar to Jabbing in other species of gulls (Moynihan 1955a,1958a,1962, Tinbergen 1953,1958). Jabbing occurs when 2 birds are within pecking distance of each other. It is the last intense display used before an actual attack, but is not necessary for an attack to occur. A Jabbing display is similar to the Pre-Attack display with respect to position of the head, neck, and wings of the bird. The main difference is that Jabbing is a

moving display while Pre-Attack is stationary. Jabbing sometimes follows a Pre-Attack display. The bird producing the Jabbing display snaps its beak open and shut in a pecking-like motion but does not touch its opponent. The reaction of the opponent is usually a Jabbing display in return.

After a series of jabbings (1 to 5 spars), the confrontation will either escalate or dissipate. Usually, and especially if the gulls are on their nests, it dissipates. Probably due to the energy used and the intensity and high threat of the Jabbing, the bird cannot remain stationary. Jabbing is seen more often in Ring-billed Gulls than in California Gulls. This may stem in part from the greater nesting density of the former, because the majority of the Jabbing I observed occurred while 2 adjacent gulls were sitting on their nests.

Usually 2 gulls in the colony will never get within Jabbing distance of each other. Likewise, Jabbing is usually an intraspecific display. This may be due to the fact that it is often more than a threat; it is a statement of purpose. Tinbergen (1958) puts it more succinctly: ". . . don't attack—if he is attacked he will fight back." A fight between a California and a Ring-billed Gull is not a balanced match. The California Gull will always win because of its size. If a californicus invades or gets too close to a delawarensis' territory, the latter instead of Jabbing will usually Grass-Pull, a far less threatening gesture. Tinbergen (1958) describes a display of less threat: ". . . he is ready to attack." The opposite situation, that of a Ring-billed Gull's invading a California Gull's territory, never or rarely happens. Ring-billed Gulls avoid all California Gull territories and

nest in their own tight subcolonies, never walking in the area of the

California Gull subcolony. The only possible violation of <u>californicus'</u>

territories by <u>delawarensis</u> occur on the outlying California Gull terri-

tories where they are positioned in the areas that contain nests of Ring-

billed Gulls.

Grass-Pulling

Grass-Pulling is a display of low threat. It occurs when a gull

is within 1 to 2 meters of another gull's territory. This display in-

dicates that the gull is ready to attack but often the encounter termin-

ates at this point. If the intruder trespasses near or onto the Grass-

Pulling gull's territory, the latter will attack. Grass-Pulling is self-

explanatory. The gull, while standing, reaches down with its neck

straight and pulls out growing vegetation with its beak. Two gulls in

adjacent territories often face each other and Grass-Pull. Tinbergen

(1958) describes Grass-Pulling as a display that is combined with actual

attack movements and that displacement activity is superimposed on these

attack movements.

The highest aggression was manifested in chases and fights.

These are not displays, but actual contact movements, unlike the other

behaviors I have described. There were 3 levels of "chase" and 2 main

kinds of fights. Chases and fights are usually initiated by the terri-

torial gull in defense of the territory. The territorial male will

chase or fight other gulls; territorial females will chase or fight

other females.

Run-Chase

The Run-Chase is the chase movement with the lowest aggression of the chase sequences. The gull which is Run-Chasing may lunge towards another in an Oblique posture or it may run a distance of up to approximately 10 meters. Most chased gulls subsequently ran or flew away from the area that the aggressor was defending.

Run-Fly-Chase

The Run-Fly-Chase is the middle level of aggression of the chase sequences. The gull will start to run after the trespassing gull but near the end of the chase, its feet leave the ground and the gull flies low (1 meter above the ground) at the intruder.

Fly-Chase

In the Fly-Chase posture, the territorial gull flies at the trespasser immediately, pecking at it, less often hitting it with the feet. This is the chase of highest aggression.

Ground Fights

A fight occurs when a trespassing gull does not leave the disputed area after numerous threats by the territorial gull. These fights can be mild with the intruder's leaving after a few pecks, or can be long and violent. Much pecking occurs and 1 gull usually attempts to grasp the other's beak or sometimes a wing. At this point, neighboring gulls often get into the fight and peck at the body or grab onto the tail of the gull that is the intruder. Gulls sometimes hit each other with their wings during these fights.

Aerial Fights

The airspace approximately 2 meters above a territory is also defended. When a gull violates this airspace, the territory owner flies up and chases or else fights the intruder. The aerial fights usually consist of hitting with the wings. Gulls are sometimes pecked while in the air and occasionally are knocked down to the ground. Aerial fights mainly take place during the very onset of territorial behavior. Once territories were firmly established and nests were built, I rarely observed this behavior.

From my observations I learned that the above postures were not as important as I had thought in interspecific interactions. Because of the facts that the Ring-billed Gulls avoid California Gulls and that the 2 segregate themselves from their congeners in their own subcolonies, the postures were not significant in the spatial segregation of the nesting grounds.

BEHAVIORAL PROGRESSION: ARRIVAL ON THE COLONY THROUGH THE CHICK STAGE

Arrival on the Colony and Territory
Construction

The following descriptions are from observations at Arod Lake on the mixed-species colony. However, the behaviors are the same as for other mixed-species colonies.

The first birds to arrive are the California Gulls which fly back and forth over the colony and then land on the frozen lake or on the insular colony itself. If they land on the island, they take flight again

immediately, and either fly back and forth or land on the frozen lake
where they congregate in groups of 10 to 50 birds.

Two weeks after the first birds arrive, the majority of the
California Gulls that will nest at Arod have arrived and the first of the
Ring-billed Gulls are arriving. The Ring-billed Gulls also fly over the
colony upon arrival, landing only occasionally on the island and also
grouping on the ice.

When the gulls land on the colony, they remain segregated by
species on the areas of the colony where they have been known to nest
before. These preferred areas for each species are approximately in the
same location from year to year. The 2 species areas are at opposite
ends of the island from each other (Figures 2-1 through 2-9). A 40-meter
plateau with little vegetation separates the 2 areas.

The majority of gulls alight on the distal parts of each of the
subcolony areas. Few descend near the plateau and if they do, they leave
quickly. As the breeding season progresses, gulls begin to arrive in
greater numbers and also begin to remain on sites a longer time. Perhaps
as a result of these factors which bring about a more permanent crowding,
the gulls begin to exhibit agonistic behavior towards each other. Dis-
plays of low threat, like Forwards and Obliques, typical territorial be-
havior, occur at this time. The onset of territorial behavior, therefore,
commences approximately 2 to 3 weeks after the California Gulls arrive.

Ring-billed and California Gulls are still separated by a great
distance (approximately 60 meters) at the onset of the setting up of
territories. Yet the gulls are not as crowded at this time as they will
be later on in the season. They distribute themselves in a density

AROD ISLAND 1975

DENSITY
OF
NESTS/M²
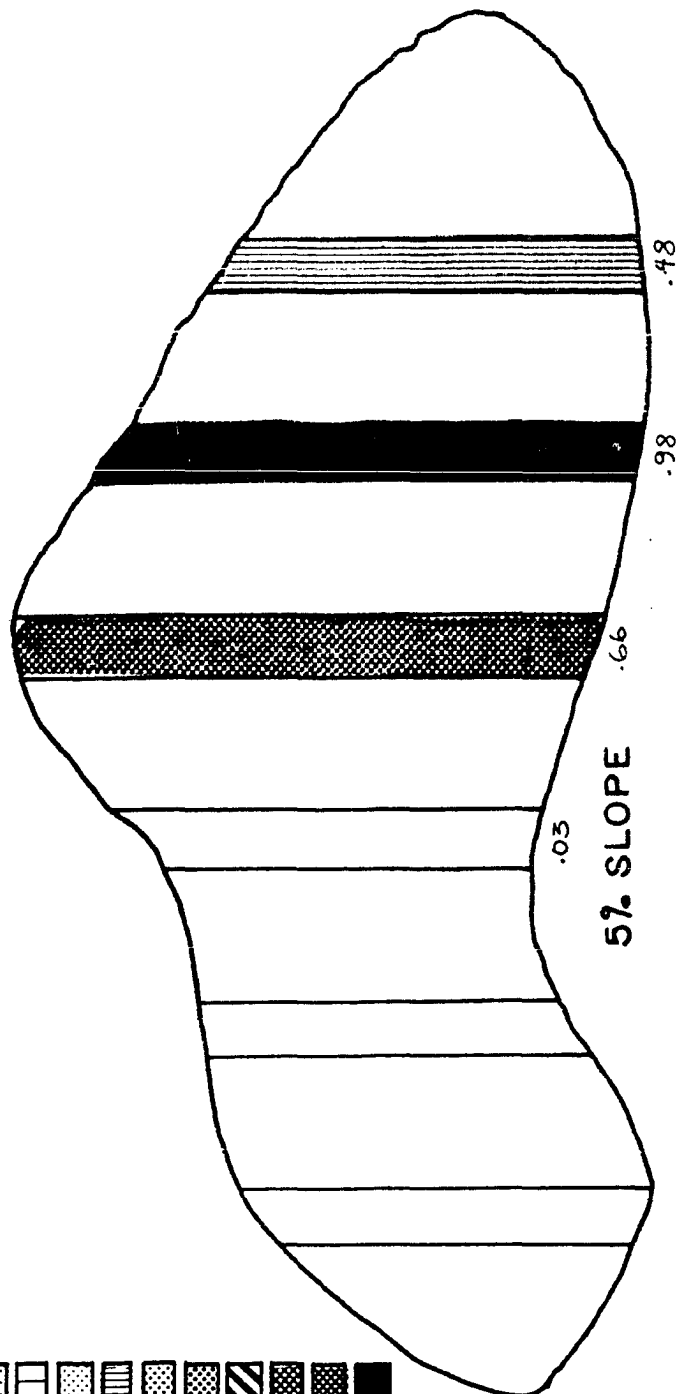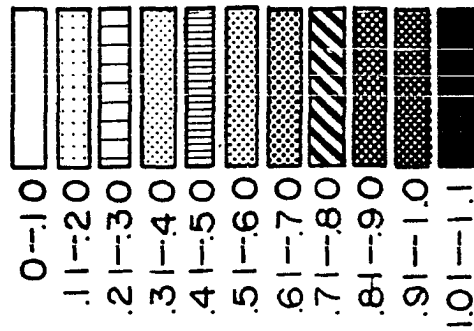
0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE

Figure 2—1

Larus delawarensis May 11

AROD ISLAND 1975

DENSITY
OF
NESTS/M²

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE

Figure 2-2

Larus delawarensis May 17

32

AROD ISLAND 1975

DENSITY
OF
NESTS/M²

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

E
10°

.05

.72

.82

.66

5% SLOPE

Figure 2-3

Larus delawarensis May 25

33

AROD ISLAND 1975

DENSITY OF NESTS/M²

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE

.08   .88   1.1   .80

Figure 2-4

Larus delawarensis June 1

AROD ISLAND 1975

DENSITY OF NESTS/M^2

0—.10
.1—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE

.04

.05

.18

.23

.30

Figure 2-5

Larus californicus May 11

E 10°

AROD ISLAND 1975

DENSITY
OF
NESTS/M^2

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE

Figure 2-6

Larus californicus May 17

E

AROD ISLAND 1975

DENSITY
OF
NESTS/M^2

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

.02

.15

.16

.22

.25

5% SLOPE
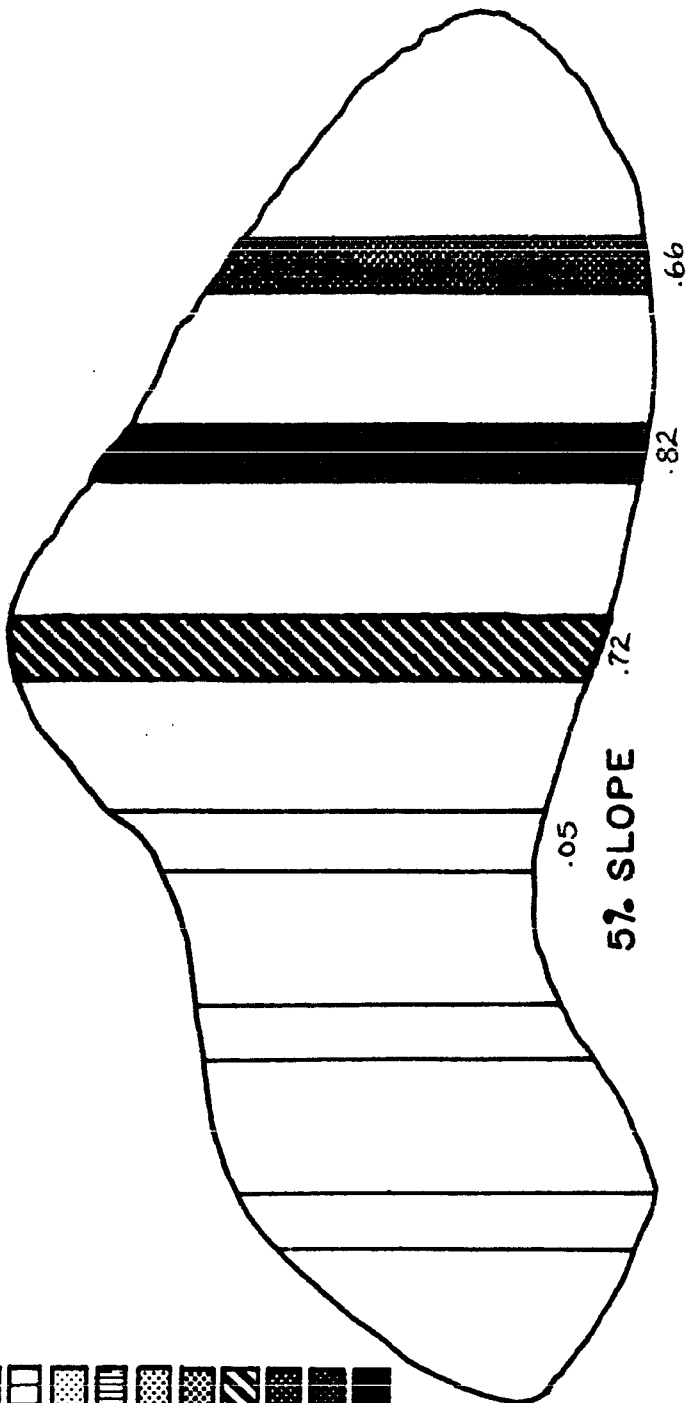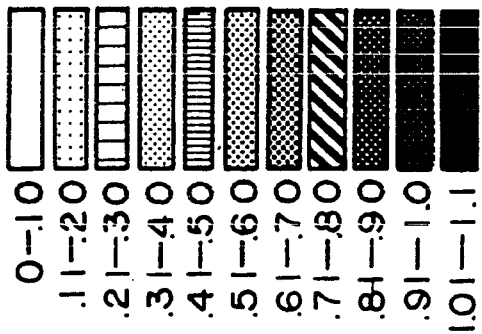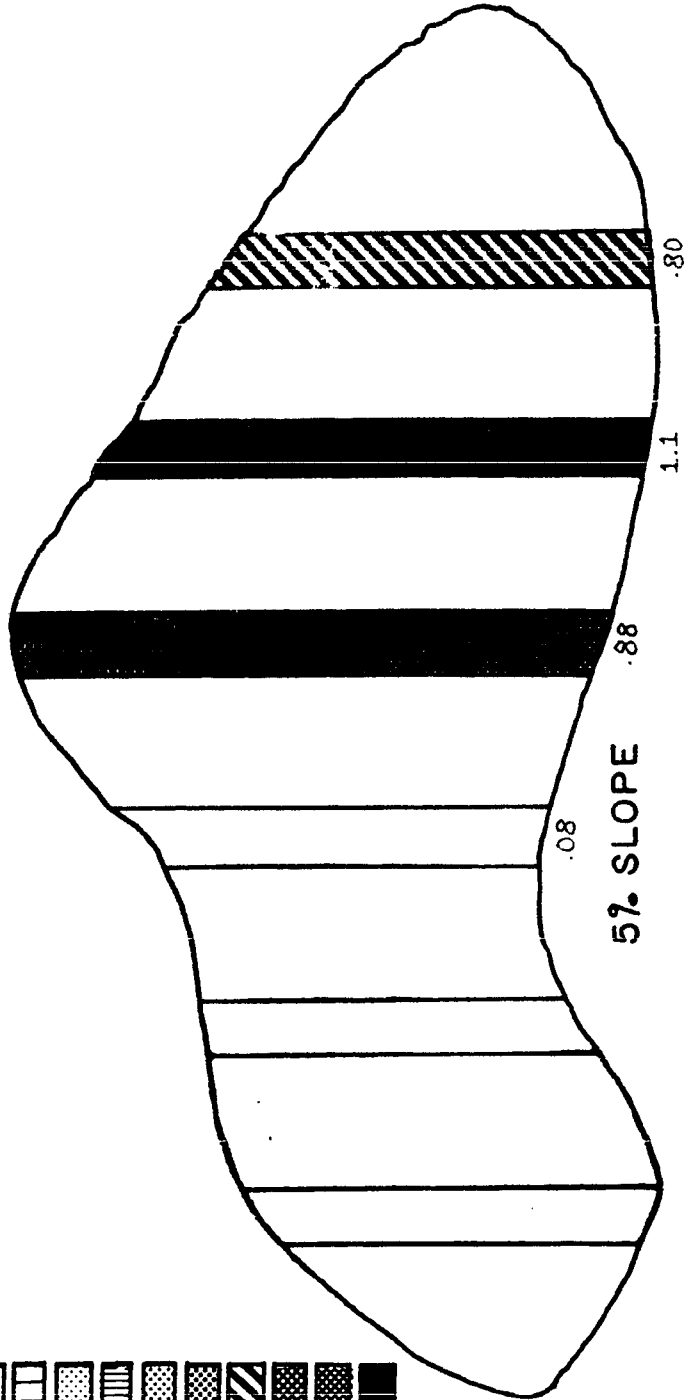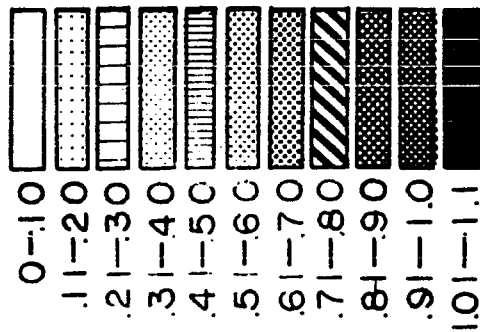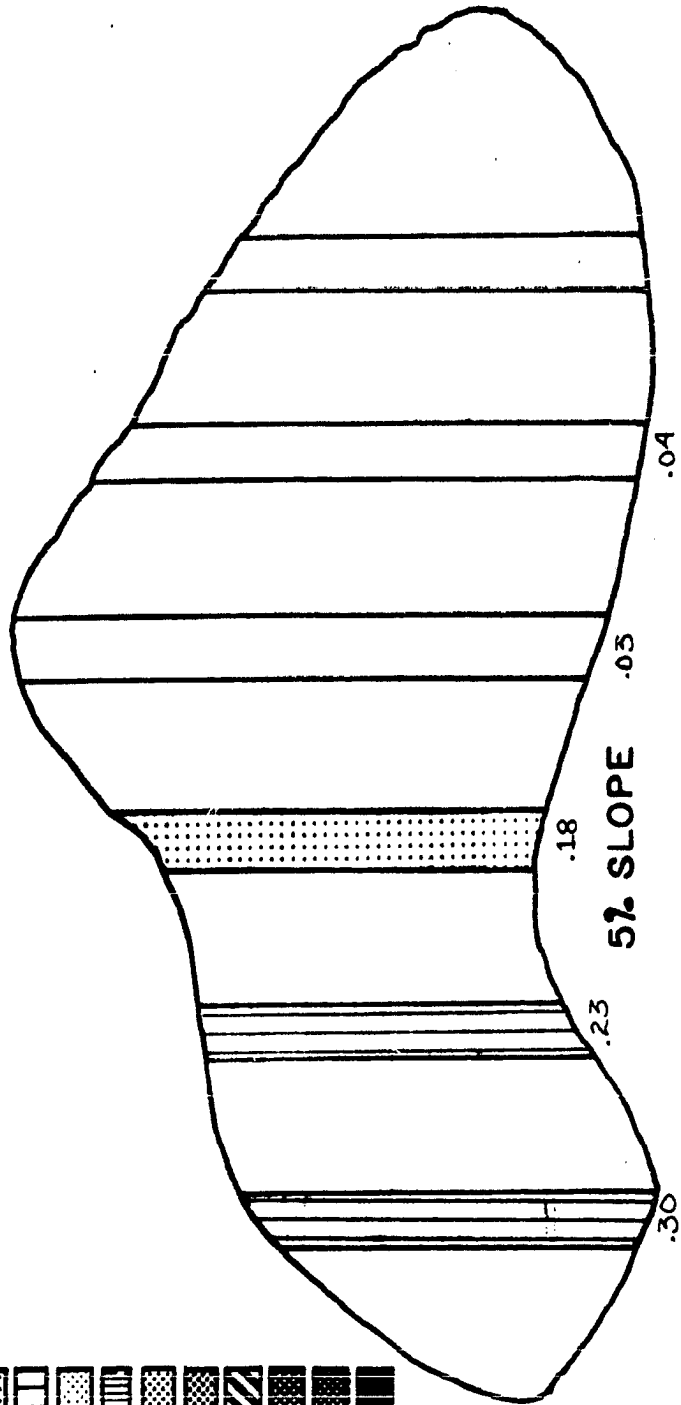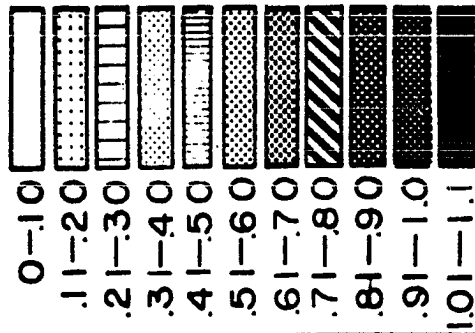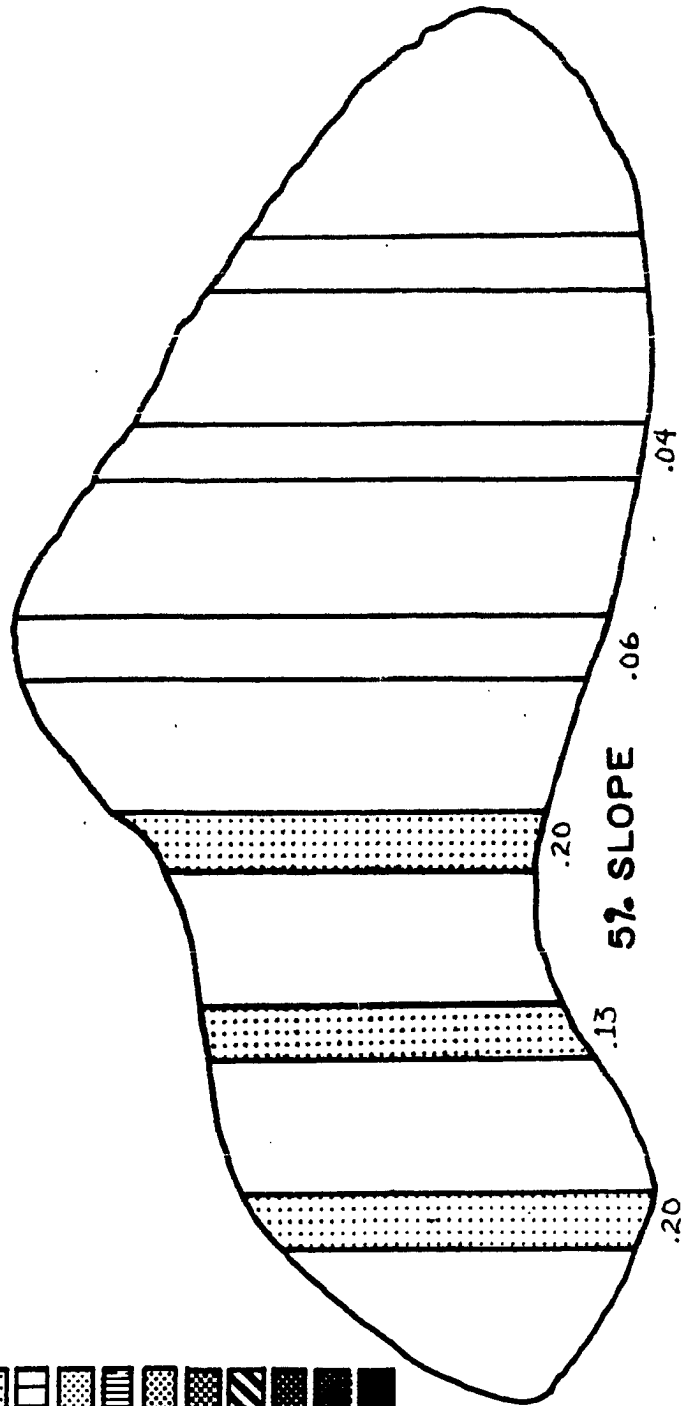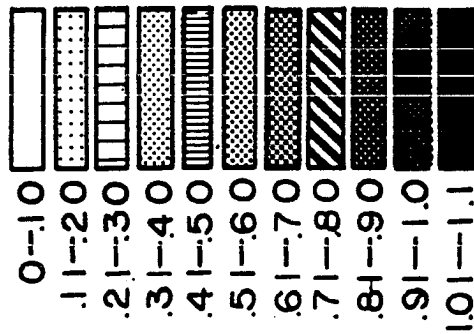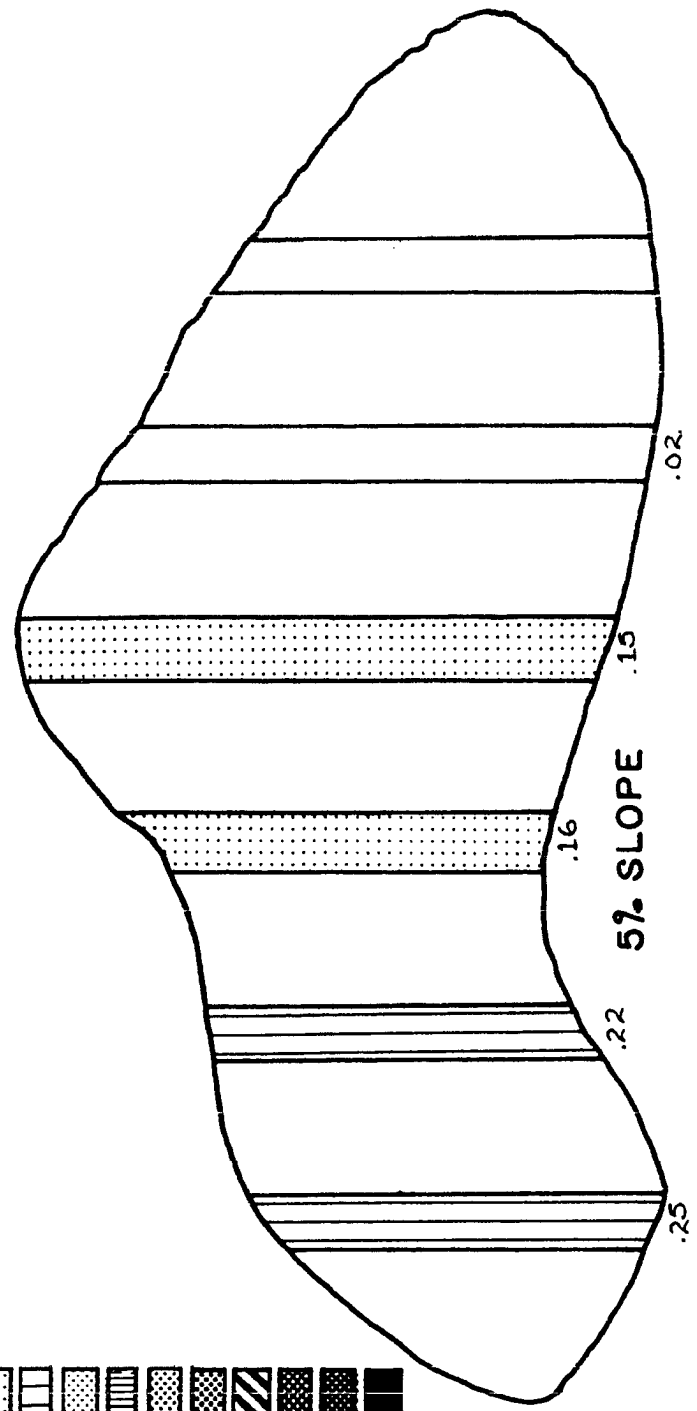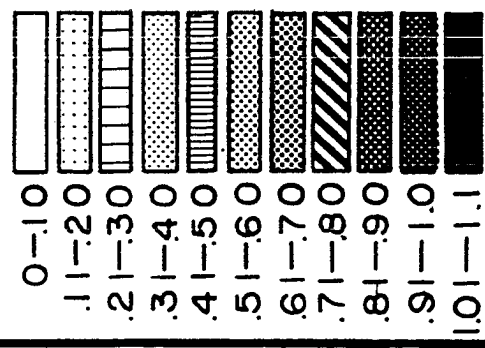
Figure 2—7

Larus californicus May 25

E
10°

AROD ISLAND 1975

DENSITY
OF
NESTS/M²

0—.10
.11—.20
.21—.30
.31—.40
.41—.50
.51—.60
.61—.70
.71—.80
.81—.90
.91—1.0
1.01—1.1

5% SLOPE
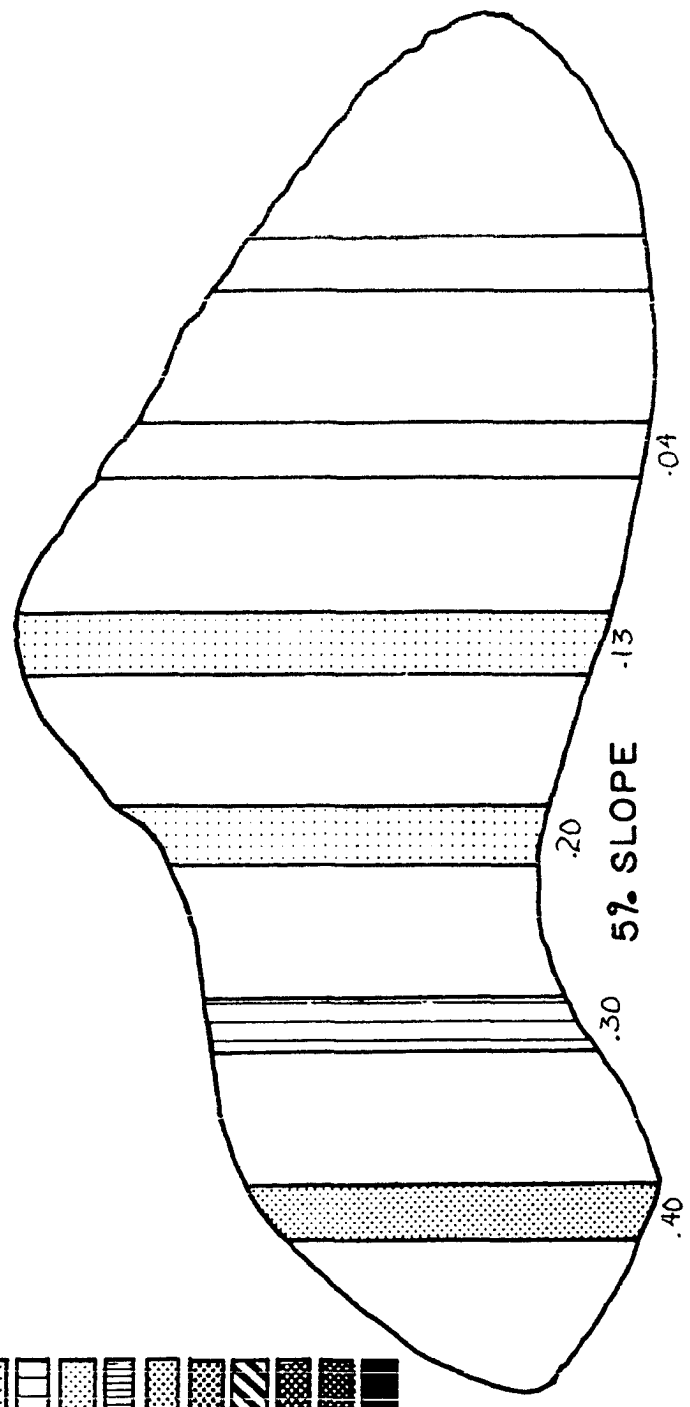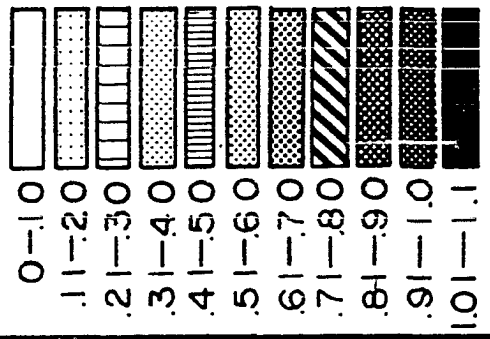
Figure 2–8

Larus californicus June 1
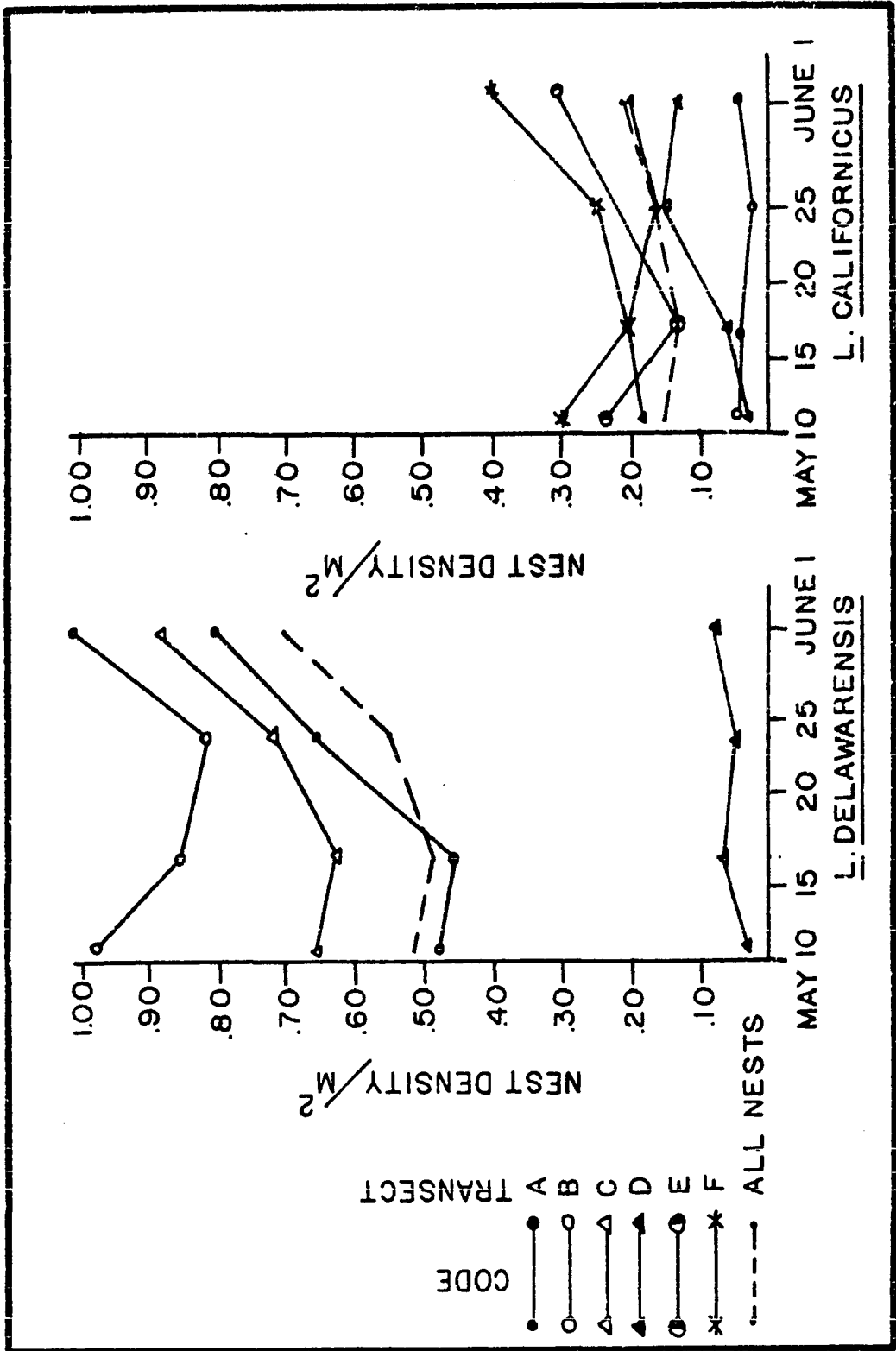
Figure 2-9

gradient with the densest areas being those approximately 15 meters from the water but on the extreme ends of the island. This gradient arrangement suggests that there is intraspecific attraction and/or avoidance of the other species. Yet there is also intraspecific competition dispersing them. Otherwise the densities in the preferred areas would be high from the outset.

Ring-billed Gulls never flew over or walked onto the California Gull area. California Gulls often flew low over the Ring-billed Gulls nearest to the plateau. A few California Gulls alighted on the Ring-billed side of the plateau. At first, these journeys were similar to the arrivals of a few weeks before in their own subcolony. They landed, stayed no longer than approximately 2 minutes, and flew off again.

The only interactions I observed between the 2 species were on the border between the 2 subcolonies. The inter- and intraspecific behavior patterns differed in intensities. It has been stated before that California Gulls are more aggressive than the Ring-billed Gulls (Moos personal communication, Vermeer 1970), and this was evident at the border area. The behavior of the Ring-billed Gulls towards California Gulls is one of avoidance. They faced away when California Gulls approached. If the California Gulls approached too closely, the Ring-billed Gulls walked away from them. The behavior of the California Gulls, however, could be described as dominance rather than as overt aggression. They did not actively seek out and pursue Ring-billed Gulls. Yet, if one approached too closely or showed agonistic behavior, the California Gulls responded aggressively, first with displays, then with attacks. The aggression by the California Gulls directed to the Ring-billed Gulls was

not as intense as that directed towards conspecifics because of the avoid-
ance behavior of the Ring-billed Gulls. There was absence of any counter-
aggressive behavior. A conspecific on the other hand would at least give
a display of low threat in response to overt agonistic behavior.

In the Ring-billed subcolony, agonistic displays by conspecifics
were met with agonistic displays. Thus, it is not always the nature of
the Ring-billed Gull to avoid possible aggressive encounters. This avoid-
ance only occurs in response to agonistic behavior of the California
Gulls. This cannot be explained by a failure to recognize the congener's
behavior as agonistic because the behaviors of the 2 are very similar,
as in all gulls, and the message cannot be mistaken.

A series of severe storms $2\frac{1}{2}$ weeks after the arrival of the first
gulls interfered with the smooth transition from initial territory con-
struction to mating. The gulls, which had already established territories,
vacated the colony during the 2 weeks of storms. When they returned,
the territories were not all the same as they had been previous to the
storm, and many of the gulls had started copulating. I knew that the
territories were different by the different dispersion pattern of the
birds after the storm and by the different positioning of a few color-
marked gulls.

Incubation and Chick Stage

In both species, both sexes build the nest and incubate the eggs
and brood the chicks. The agonistic displays described previously dim-
inish in intensity and in frequency once the territories are established.
However, both low- and high-threat displays still occur through the chick

stage. The aerial and ground fights found so often during the establishment of territories rarely are present then. During the incubation and the brooding stages, both adults are rarely present together at the nest during the day. They alternate food gathering and incubating or brooding. One of the pair can be absent 20 minutes to 3 hours. The greeting displays of the 2 species when 1 adult arrives back at the nest are similar. The arriving adult calls as it flies and nears the nest. The sitting gull then becomes alert with its neck straight and its head horizontally inclined, evidence that gulls can recognize individuals' calls. Before, or at the time the arriving adult lands, its mate stands up and gives several Down-Ups. Often these are the more intense type. This gull is then joined in its Down-Up display by the returning gull and they often walk around their territory together, giving the Down-Up call. Perhaps, this is a reaffirmation of territory ownership.

When the chicks are 3 days to 1 week old, both parents food gather, leaving the chicks unattended. Upon hearing an alarm call from other gulls, at 1 to 6 days of age the chicks crouch in the nest; from the age of 1 to 2 weeks the chicks run into the nearby vegetation; and from 2 weeks on they either run to the water or remain where they are without crouching.

From 3 days to approximately 3 weeks, the chicks are most vulnerable to predation by other gulls. They have become mobile and readily leave the protection of the nest and its surrounding territory. Even though adults are not attending a nest, another gull will rarely enter that territory unless it is to eat the eggs (if any) present and only when there is a major disturbance in the colony. Other more aggressive

species (Moynihan 1955,1958a, Paludan 1951, Tinbergen 1958) enter occupied territories and snatch chicks off their nests. The chicks from 3 days to 3 weeks, besides being mobile and thus unprotected, are also not large enough to fight back effectively if attacked. Many chicks at this age are killed by adult gulls. From about 3 weeks on the chicks peck or chase adult gulls that begin to attack them, or even that are near their territory.

There is social facilitation in many of the gulls' activities, a common phenomenon for gregarious colonial birds. One socially facilitated behavior that occurs often at the chick stage is chick-killing behavior. Other adult gulls often will seek out a nearby chick that is being attacked and will join in the attack. As illustration, at one point I observed a chick that wandered off its territory and which was chased in a circuitous route by a number of territorial adults. The chick found refuge under a bush away from any gull's territory. Five adult gulls traveled up to 10 meters off their territories to the bush and stood in a ring around it; and when the chick finally emerged, they killed it by pecking it. Young chicks are sometimes eaten whole according to Tinbergen (1953) although I never observed it.

SUMMARY

The California Gulls arrive 2 weeks in advance of the Ring-billed Gulls. They establish territories in one area of the entire colony. The Ring-billed Gulls, upon their arrival, alight in the unfilled areas of the colony, distant from the California Gulls. There are many agonistic interactions which take place intraspecifically and which

function to maintain territories. However, there is little interspecific contact and any that occurs is usually an avoidance by the Ring-billed Gulls. Occasionally agonistic interactions take place between species, but they are of short duration and terminate by avoidance of the California Gull by the Ring-billed Gull.

CHAPTER III

COMPARISONS OF THE FEEDING NICHES

INTRODUCTION

Two congeners that are broadly sympatric over a large area, as
are the California and Ring-billed Gulls, Larus californicus and Larus
delawarensis, often have similar feeding niches. They may forage in
similar ecotopes and choose the same sorts of prey items. Because of
this similarity, the 2 congeners have the potential to compete in limited
forage areas or over limited food items. Most closely related species
avoid active competition and are able to coexist well by segregation of
the feeding niche. This is effected in many ways. They can eat dif-
ferent foods, forage in different habitats, or forage in different ways.

FOOD NICHE

On the breeding grounds of many bird species, competition for
food for the young is severe (Ashmole 1968a, Dorward 1962, Lack 1969).
According to some researchers, however, gulls may not compete for food
because they are omnivores and scavengers and food should always be
abundant (Paynter 1949, Willis 1966). However, because resources are
not inexhaustable, there is some limit to how similar the 2 species can
be and still coexist. How much overlap in the feeding niche will they
tolerate? The measure of the overlap between 2 species with respect to
the feeding niche is often complex. Two individuals in the same

45

environment may find different foods by foraging in different ways, or may obtain the same foods in slightly different environments (Orians and Horn 1969).

Gulls, like most birds, are opportunistic feeders, often feeding in large multispecies groups. They are also extreme generalists, often eating non-biotic things such as a paper and string. Yet, because they are opportunistic and probably are eating food items that are most abundant at the time, there is a potential of ecological overlap and thus competition.

HABITAT NICHE

Another way for 2 closely related species to avoid conflict is to forage in different habitats. They may divide up the foraging habitat according to gross habitat types, vegetation types, foraging heights, or even specific parts of the plants. Many studies have demonstrated that if 2 species are searching for a particular habitat type and not for specific food items, they may segregate their food resources (Austin and Smith 1972, Cody 1968b, MacArthur and Levins 1964, Schoener 1968b, Selander 1966). Numerous other observations on habitat segregation are scattered throughout the ecological and ornithological literature.

Where gulls feed might be more important than the type or size of prey species especially since they are omnivorous. If this is true, then the segregation of the feeding habitat may be important in lessening or even eliminating any possible competition between the 2 species. This segregation can be passive, a bird will simply avoid an unsuitable habitat, or active, an avoidance of a habitat when a member of the other

species is present. Lack of divergence in exploitation of the feeding habitat may simply mean that there has been insufficient time for the birds to shift, the environment is structurally simple and cannot be segregated, some other species, by its behavior prevents divergence in certain directions or that divergence is not advantageous due to some resource surplus (Orians and Willson 1964).

MORPHOLOGY AND BEHAVIOR

Two similar species may forage in the same area but due to different sizes of bills, bodies, or legs, or to different ways of foraging, or to dominance at the foraging site, they may sample completely different sets of the available prey population (Austin and Smith 1972, Birch 1957, Dixon 1954, Dorward 1962, Drury and Smith 1968, Gibb 1960, Kilham 1965, Ligon 1968).

If 1 species is dominant on the feeding grounds, then the other species may be excluded from feeding in the same area. If it does feed when the other is present, it may keep at a distance and restrict itself to marginal habitat. A reduction in interspecific contact, a result of a behavior change, sometimes in response to dominance of the other species, has been demonstrated in various animals and is 1 method of resource segregation (Austin and Smith 1972, Dixon 1954, Selander and Giller 1959, Willis 1966).

Two species may also feed in different ways due to morphological differences in the feeding apparatus (Austin and Smith 1972, Ashmole 1970, Holmes and Pitelka 1968, Newton 1967, Orians and Horn 1969, Root 1967, Selander 1966). Thus, they may experience no overlap at all in

their foraging. Many other studies have shown that morphological dif-
ferences preclude competition and that in some cases these differences re-
sult from character displacement (e.g. Ashmole 1970, Brown and Wilson 1956,
Catchpole 1972, Dilger 1956, Dixon 1954, Ficken, et al. 1968, Keast 1968,
Pitelka 1951, Rickleffs 1966, Soulé and Stewart 1970, Tinkle and Ballinger
1972).

My research offers some concrete evidence which supports the
hypothesis that California and Ring-billed Gulls are not the complete
generalists they seem. In fact, they neatly segregate the feeding hab-
itat and tend to eat different foods which they gather in similar ways.

MATERIALS AND METHODS

There are 2 major gull colonies at Freezeout Lake, 9.66 km north-
west of Fairfield, Montana. One is a mixed-peninsula colony of Ring-
billed and California Gulls; the other is an island colony of California
Gulls. I conducted a census of the feeding habitat of these gulls during
the breeding season of 1974 while the gulls were feeding their chicks.
Since the adult gulls usually do not feed on the colony, and often fly
great distances to forage, I drove in concentric circles 1 km apart (as
roads permitted) around the colonies. I recorded all observed gulls as to:
species, whether flying or feeding, direction of flight, gross habitat where
feeding, feeding behavior, distance from the colony, and time and date ob-
served. The choice of the radius distance I picked to drive along each day
followed no pattern. Every 5 days, however, I covered all distances up to
65 km and all directions equally. I divided the area surrounding the col-
onies into 4 quadrats and each quadrat into 2 distance classes: 0-30 km

and >30 km. Every trip I chose 1 of these 8 areas to census. There were

32 trips with an average distance covered and time elapsed of 69.5 km and

3 hours 4 minutes respectively. The foraging data only uses observations

of gulls on the ground.

RESULTS

Foraging Distance

California and Ring-billed Gulls fed at varying distances from the

colony (Figures 3-1, 3-2; Table 3-1). The values are not continuous be-

cause any gulls feeding between 2 concentric circles were totaled for final

display as being the distance of the further radius from the colony center.

Not all peaks can be related to ecological changes in the habitat. Large

values at 6 km reflect activity at the Fairfield dump, while those at 30

and 31 km reflect presence of gulls on 2 reservoirs. The peak between 9

and 10 km for California Gulls represents feeding in a lake adjacent to

Freezeout. The largest peaks reflect no major ecological change in the

habitat. Gaps in the data may be from lack of roads. I also recorded gulls

overhead as to species, direction flying, where and when seen. These data

are not included in Figures 3-1 and 3-2 nor in Table 3-1 (See Appendix).

There is a significant difference in foraging distance between Cal-

ifornia and Ring-billed Gulls (Mann-Whitney U test, p < 0.001, Table 3-1, and

Appendix). This significance also holds when the distances foraged are

compared by habitat type: irrigated farmland, p < 0.069; dryland farm-

ing, p < 0.001. In this comparison, it appears that the Ring-billed

Gulls feed at a greater mean distance in the irrigated farmland than

do the California Gulls. Of the total number of all California Gulls

FREEZEOUT LAKE 1974

L. CALIFORNICUS

$\overline{X} = 17.40$
S.D.=8.6

NUMBER OF GULLS FEEDING

KM. FROM COLONY CENTER
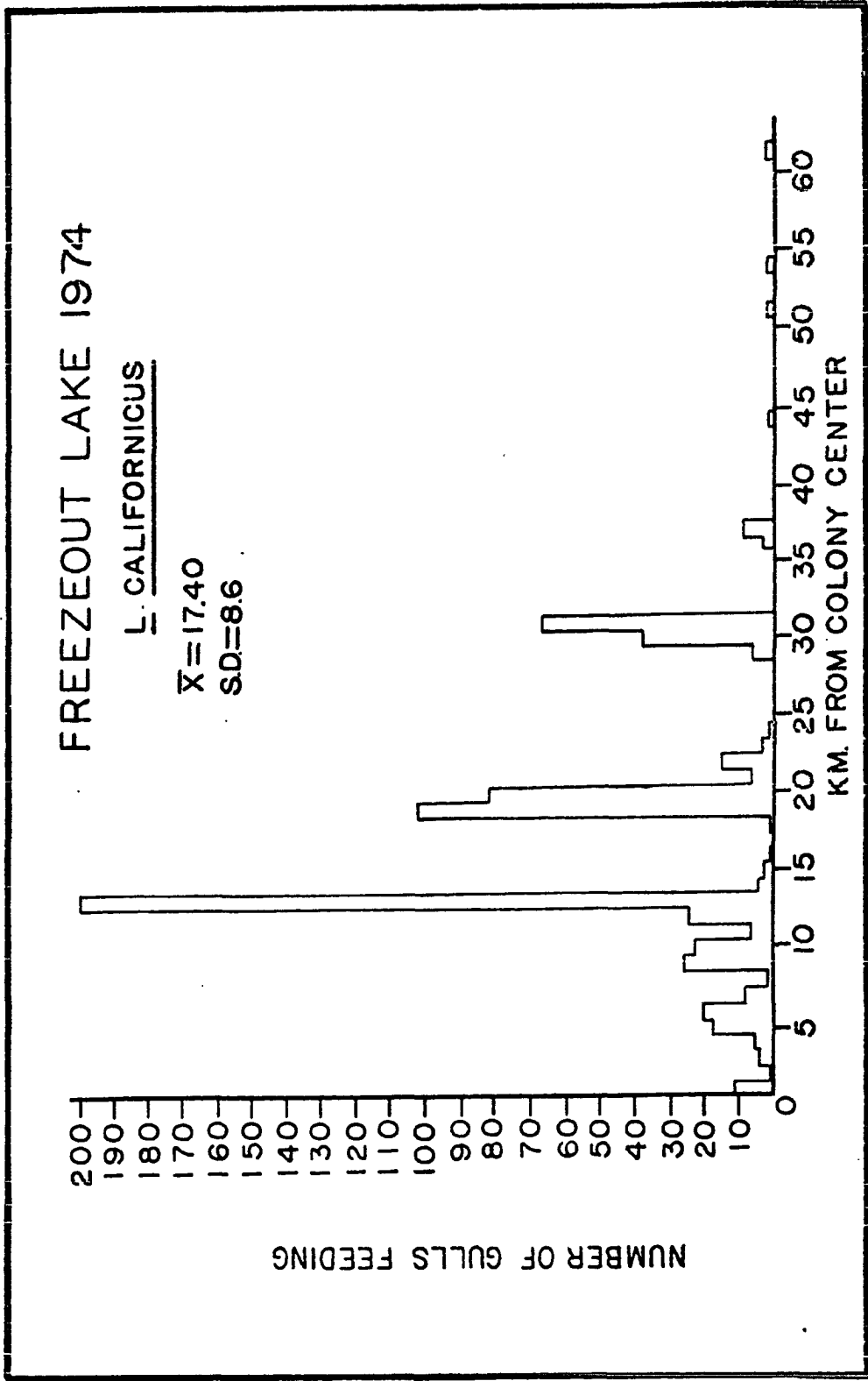
Figure 3-1

FREEZEOUT LAKE 1974
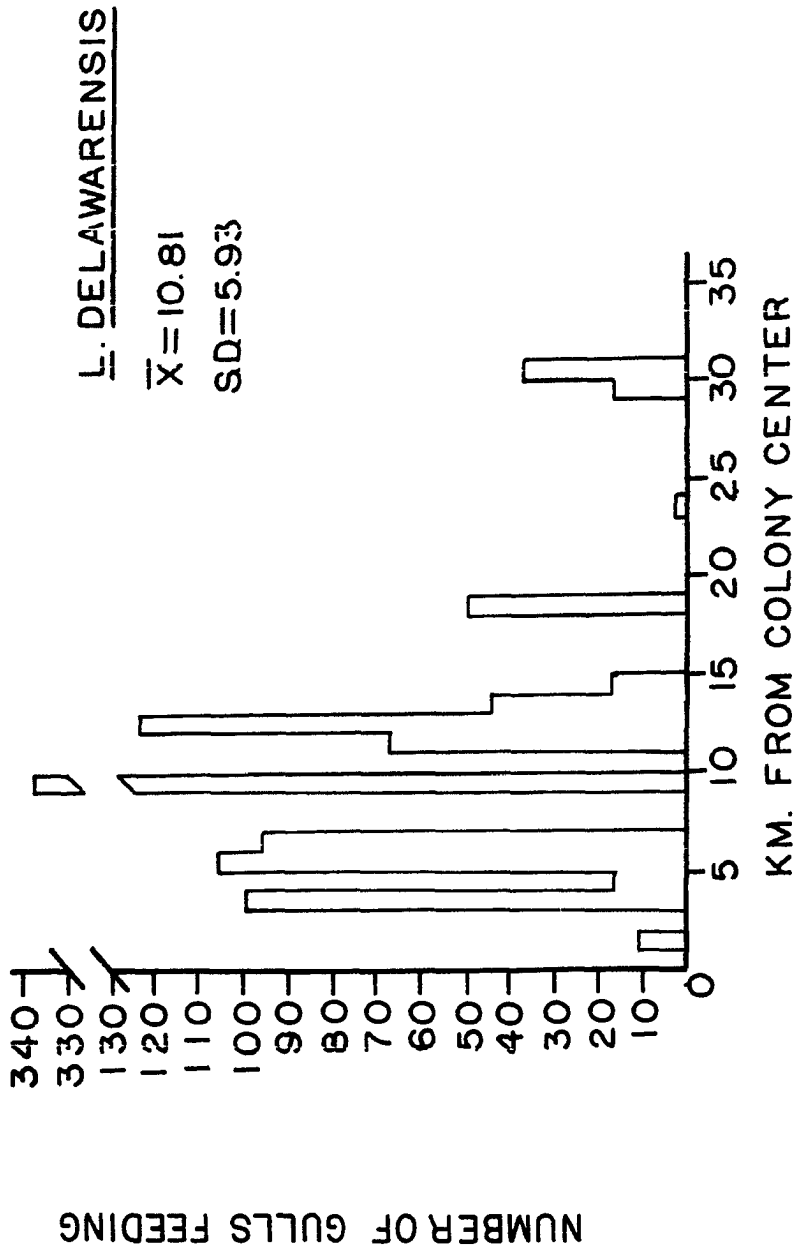
L. DELAWARENSIS

$\bar{X} = 10.81$

S.D.=5.93

NUMBER OF GULLS FEEDING

KM. FROM COLONY CENTER

Figure 3-2

TABLE 3-1

Numbers of Gulls Feeding at Different Distances
From the Colony and in Different Types of Farmland

Kilometers from Colony Center	Larus californicus			Larus delawarensis		
	Irrigated	Dryland	Total	Irrigated	Dryland	Total
1	11	—	11	—	—	—
2	—	1	1	11	—	11
3	4	—	4	—	—	—
4	5	—	5	100	—	100
5	18	—	18	16	—	16
6	3	18	21	116	37	153
7	3	5	8	53	—	53
8	—	1	1	—	—	—
9	1	25	26	—	—	—
10	13	10	23	338	—	338
11	7		7	—	—	—
12	—	25	25	—	68	68
13	12	188	200	113	11	124
14	4	—	4	45	—	45
15	—	3	3	8	9	17
16	—	1	1	—	—	—
18	—	1	1	—	—	—
19	8	95	103	50	—	50
20	—	82	82	—	—	—
21	3	1	4	—	—	—
22	—	15	15	—	—	—
23	—	3	3	—	—	—
24	—	—	—	—	1	1
29	—	6	6	—	—	—
30	—	38	38	—	16	16
31	—	67	67	—	37	37
36	—	3	3	—	—	—
37	—	9	9	—	—	—
44	—	1	1	—	—	—
51	—	1	1	—	—	—
53	—	1	1	—	—	—
54	—	1	1	—	—	—
61	—	1	1	—	—	—
Totals	92	602	694	850	179	1029

sighted, 49% were on the ground feeding; of the total number of all Ring-billed Gulls sighted, 87% were on the ground feeding.

Foraging Direction

California and Ring-billed Gulls feed in different habitats. If the area surrounding the colonies is divided into 4 quadrats with magnetic north on the vertical axis, and the colony center as the origin, an interesting distribution develops. Each species has its own pattern of distribution (Figures 3-3A, 3-3B, 3-4A, 3-4B, 3-5). Most California Gulls feed in the southwestern area from the colony while most Ring-billed Gulls feed in the area northeast of the colony. Both of these distribution patterns were significantly different from an equal distribution with $p < 0.001$ (df = 3) and $p < 0.001$ (df = 3) respectively. A contingency x^2 test among the 4 quadrats and between the 2 species yielded a x^2 of 1000.3, $p < 0.001$ (df = 3). The gulls included in this comparison were only gulls that were feeding. This is important to note because a gull seen flying in the southwest quadrat, for instance, 3 kilometers from the colony center, may actually be making a big circle and end up feeding in the southeast quadrat.

Habitat Segregation

The habitat around Freezeout Lake can be grossly divided into irrigated and dryland farming areas (Table 3-2, Figures 3-6, 3-7). When this farming pattern is laid over the array of gull feeding areas, a strong correlation between species and farming method becomes evident. Ring-billed Gulls mainly choose irrigated farming areas in which to feed;

FREEZEOUT LAKE L. CALIFORNICUS
1974
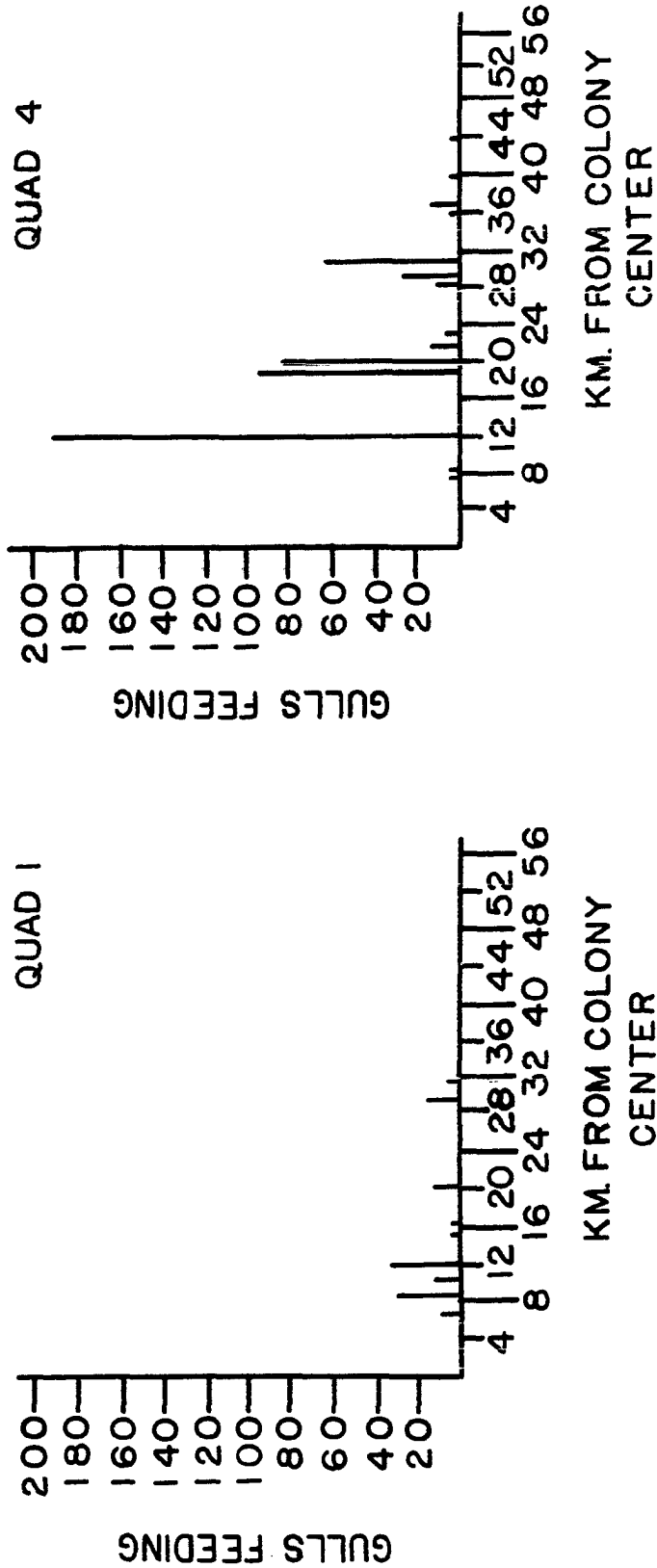
QUAD 1

QUAD 4

Figure 3-3A

FREEZEOUT LAKE L.CALIFORNICUS 1974

QUAD 2

GULLS FEEDING
200 180 160 140 120 100 80 60 40 20

KM. FROM COLONY CENTER
4 8 12 16 20 24 28 32 36 40 44 48 52 56

QUAD 3

GULLS FEEDING
200 180 160 140 120 100 80 60 40 20

KM. FROM COLONY CENTER
4 8 12 16 20 24 28 32 36 40 44 48 52 56
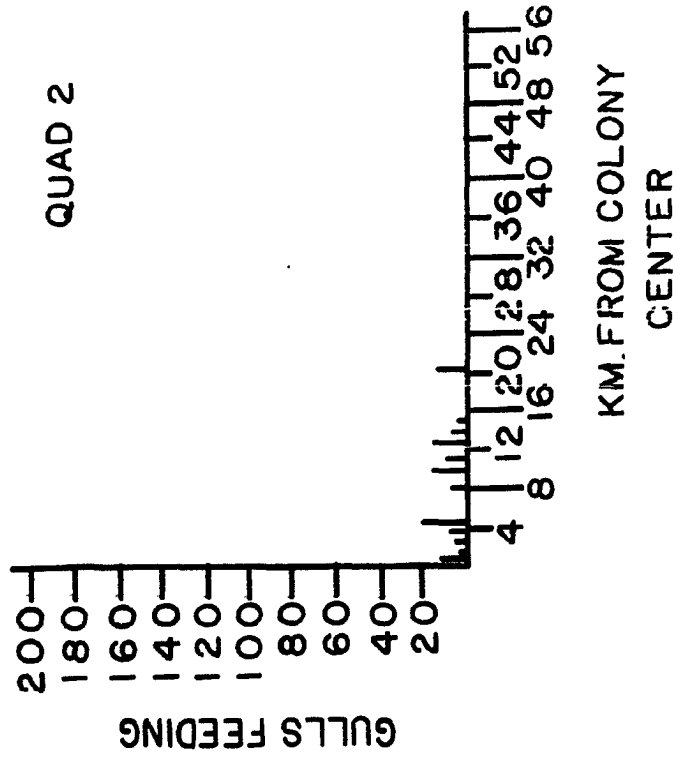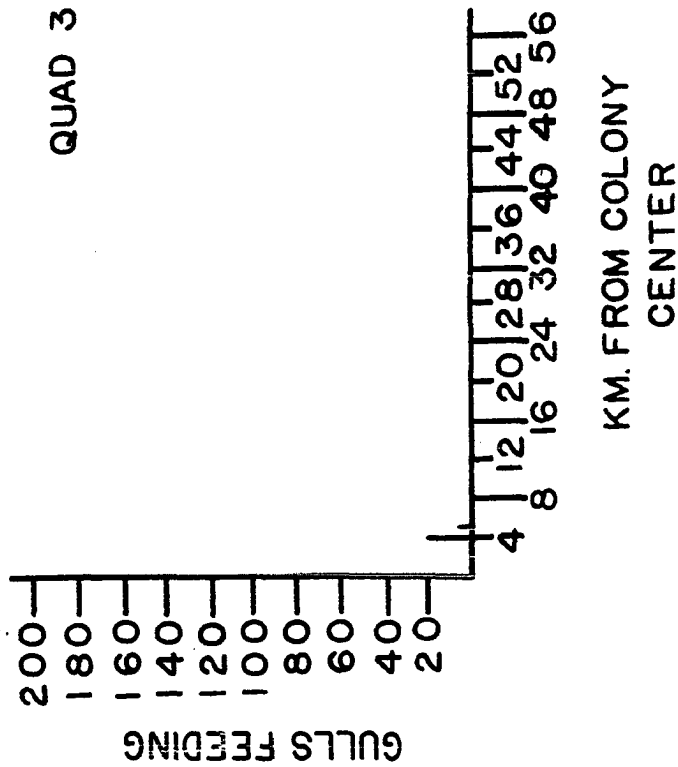
Figure 3-3B

L. DELAWARENSIS, FREEZEOUT LAKE 1974
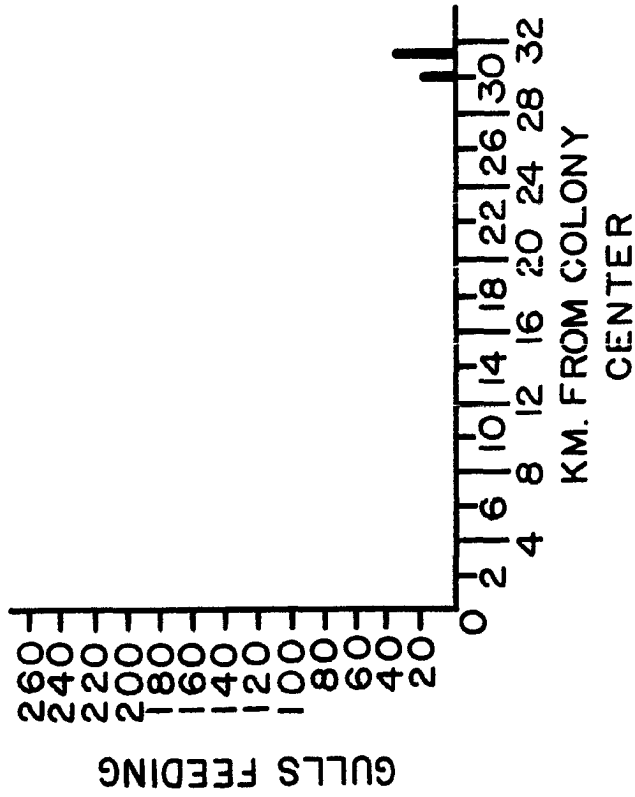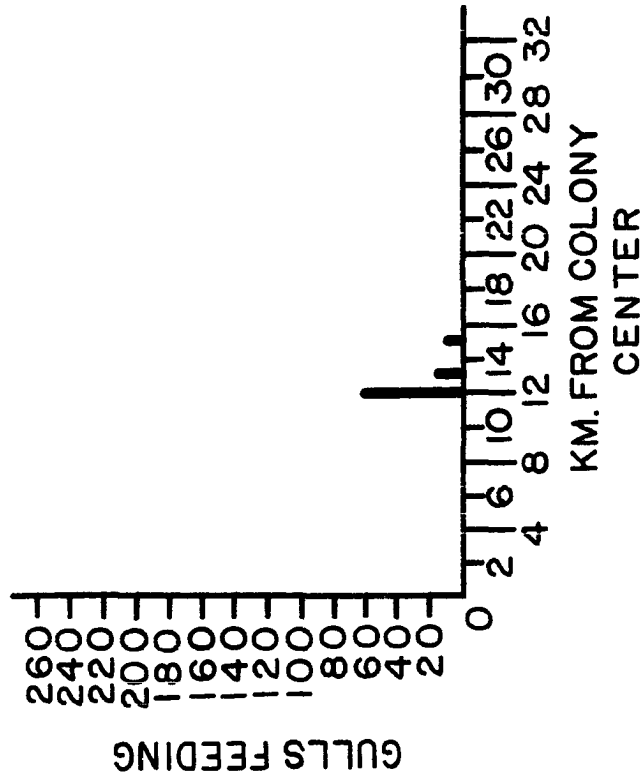
Figure 3—4A

L. DELAWARENSIS, FREEZEOUT LAKE 1974

QUAD 3

QUAD 2

GULLS FEEDING

KM. FROM COLONY CENTER
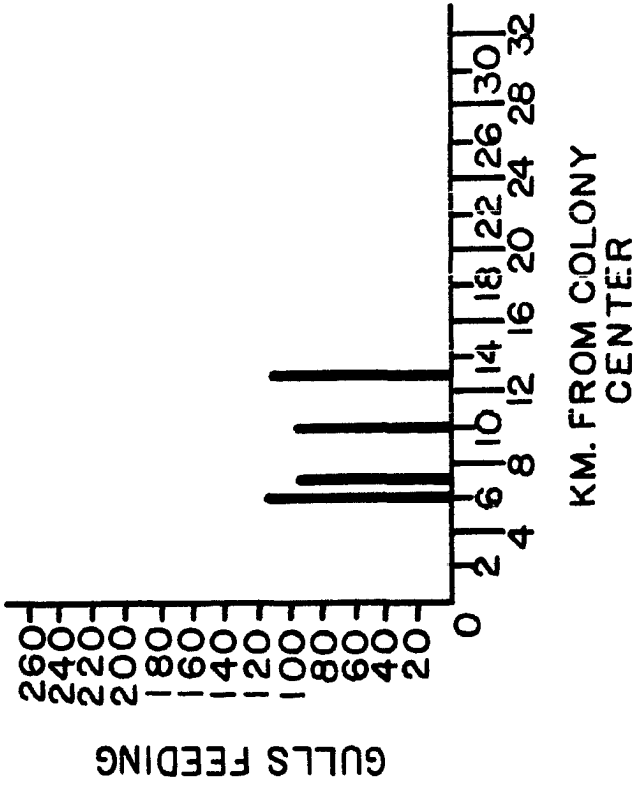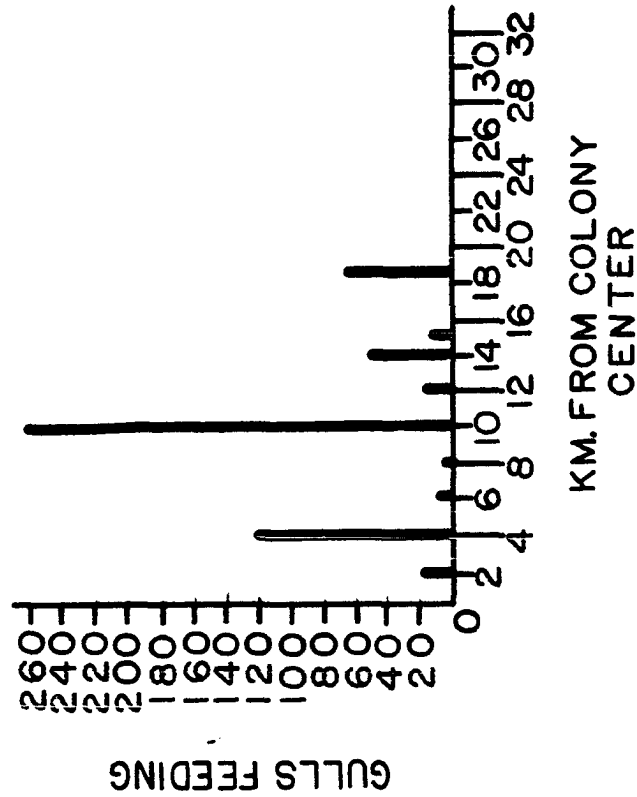
Figure 3-4B

FREEZEOUT LAKE 1974
NUMBER OF GULLS FEEDING

71 | 78

526 | 19
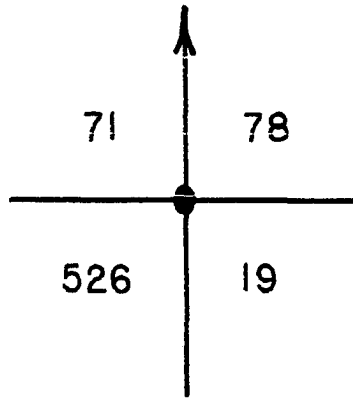
L. CALIFORNICUS

● = COLONY CENTER

↑ = MAGNETIC NORTH

79 | 747

54 | 149
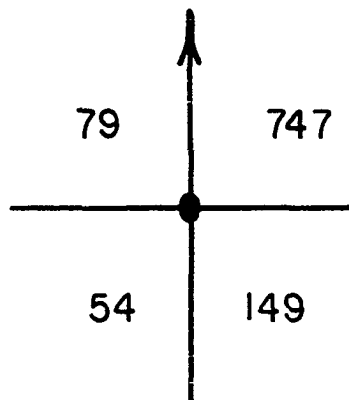
L. DELAWARENSIS

Figure 3-5

Figure 3-6

Larus californicus, 1974

Figure 3-7

IRRIGATED FARMLANDS
Larus delawarensis, 1974

- 1-10 GULLS
- 11-20
- 21-40
- 41-70
- >70
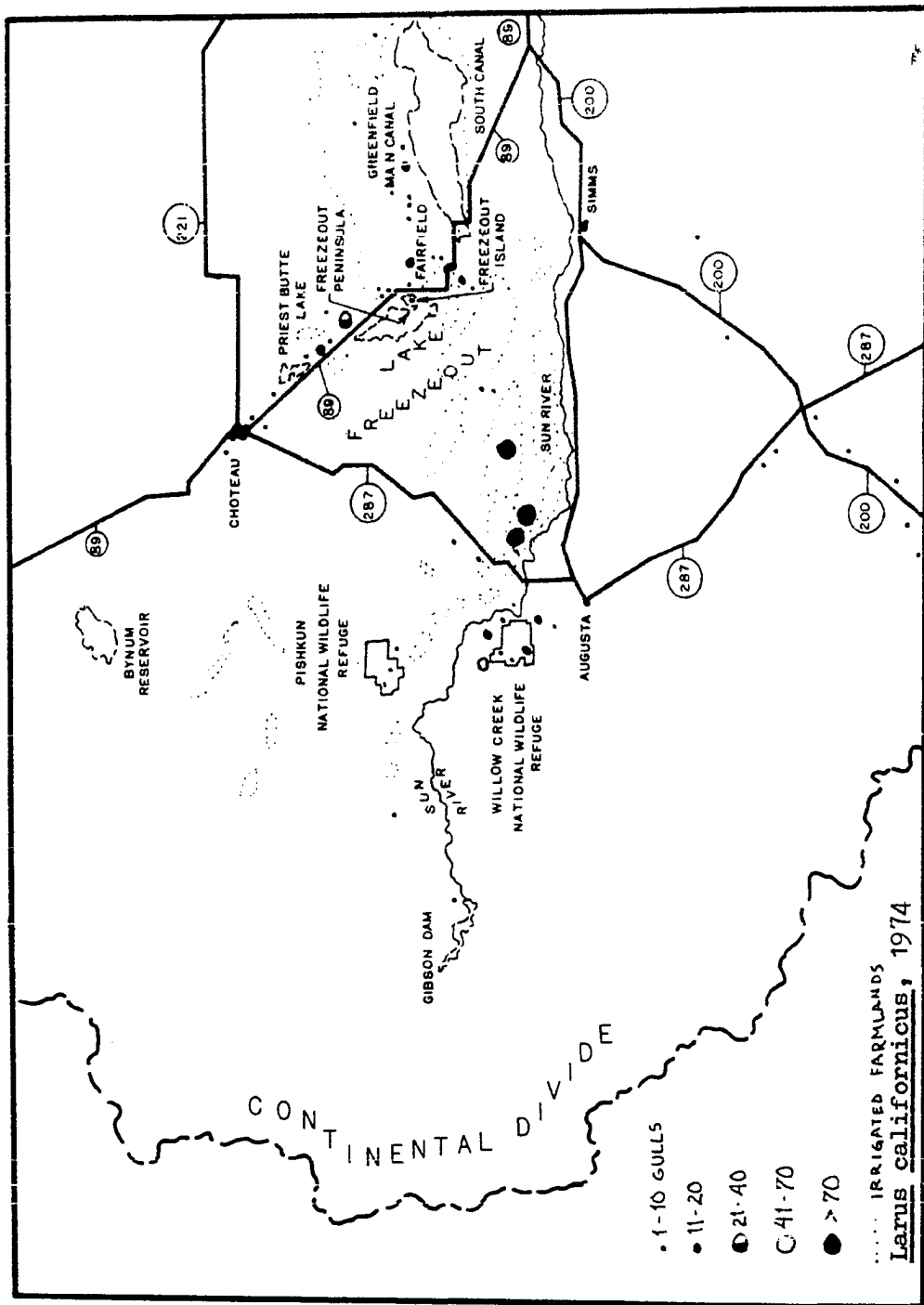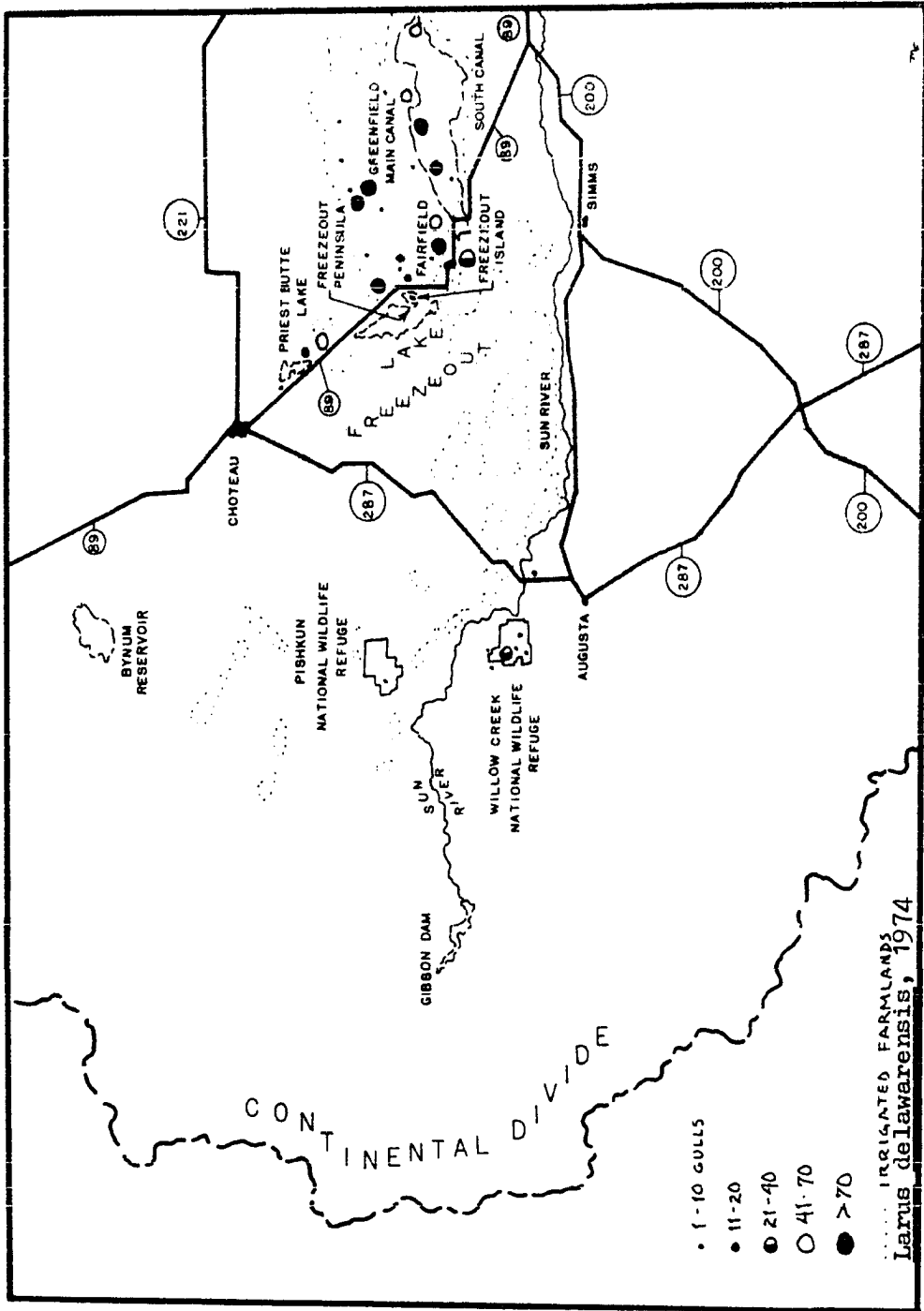
TABLE 3-2

Cross Habitat Segregation,
Larus californicus and Larus delawarensis
Freezeout Lake, 1974

Species	Contingency Table Irrigated	Dryland	Total
Larus californicus	92	602	694
Larus delawarensis	850	179	1029
Total	942	781	1723

$X^2 = 804.31$ $\qquad$ $p < 0.001$

TABLE 3-4

Association Table:
Number of Food Items in Common

	Larus delawarensis +	Larus delawarensis −	Total
Larus californicus +	15	10	25
Larus californicus −	3	0	3
Total	18	10	28

TABLE 3-3

Stomach Contents of 71 California and 25 Ring-Billed Gulls[a]

Prey Items	Larus californicus		Larus delawarensis	
	Number	Frequency of Occurrence	Number	Frequency of Occurrence
Oligochaeta	3	0.011	8	0.082
Crustacea	1	0.004	1	0.010
Orthoptera				
Gryllidae	6	0.021 } 0.028	1	0.051 } 0.133
Acrididae	2	0.007	8	0.082
Ephemerida	1	0.004	0	0
Odonata	4	0.014	0	0
Homoptera	3	0.011	0	0
Hemiptera				
Corixidae	14	0.050 } 0.058	0	0 } 0
Notonectidae	1	0.004	0	0
Gerridae	1	0.004	0	0
Coleoptera				
Carabidae	22	0.078 } 0.142	8	0.082 } 0.204
Elateridae	0	0	1	0.010
Tenebrionidae	2	0.007	3	0.031
Scarabaeidae	12	0.043	2	0.020
Curculionidae	4	0.014	6	0.061
Lepidoptera				
Phalaenidae (larval)	3	0.011	2	0.020
Diptera				
Tabanidae	0	0	2	0.020 } 0.061
Tipulidae	2	0.007 } 0.053	0	0
Chironomidae	6	0.021	0	0
Muscidae	7	0.025	4	0.041
Hymenoptera				
Formicidae	1	0.004	0	0
Amphibia	7	0.025 } 0.146	0	0 } 0.050
Aves	3	0.011	1	0.010
Mammalia	0	0	2	0.020
Unknown Vertebrate	31	0.110	2	0.020
Vegetation[b]	60	0.211	25	0.255
Grit	71	0.251	15	0.153
Debris[c]	15	0.052	3	0.032
Total	282	1.000	98	1.000

[a]Data from R. Rothweiler, unpublished Master's thesis.

[b]Wheat and barley kernels and stems.

[c]Garbage: meat, chicken fragments; wood; sticks; fruit pits; paper; cloth.

California Gulls mainly choose dryland farming areas in which to feed (contingency X^2 = 804.31, p < 0.001).

Food Segregation

I did not collect stomach contents during this project. However, Robert A. Rothweiler collected stomachs of 96 gulls at Freezeout Lake in 1958 and 1959. With his permission, I analyzed the data to see if there were any differences in the types of food the California and Ring-billed Gulls were eating. The data are displayed in Table 3-3 and Table 3-4.

I compared categories with the greatest differences and found that California Gulls consumed more vertebrates, hemiptera and grit than did Ring-billed Gulls whereas the latter consumed more orthoptera, oligochaetes, and coleoptera than did the former.

Behavior

I observed gulls of both species feeding in the same way and side by side. As they walk, they pick up food from the substrate with their beaks. They remain on a feeding area from a few seconds to over an hour. I more often observed gulls in monospecific groups feeding in grossly different habitats, the California Gulls in the dryland areas, the Ring-billed Gulls in the irrigated areas. Even in these widely different areas, they were still feeding in similar ways. The main difference was the amount of time each spent in the area. Although exact times of arrival and departure are not available, from my observations I can say that in the irrigated areas (where there was probably more food) the gulls remained longest. In the dryland areas, the gulls would often

touch down for up to approximately 10 minutes, especially on road kills, and then fly away from that vicinity.

In addition to foraging in similar ways when in the same habitat, the 2 species also showed no inter- or intraspecific aggression while feeding. This was true even when they fed in mixed or monospecific groups, often in large numbers (over 100), and in temporary sources of superabundant food such as behind a plow or at dumps.

DISCUSSION

California and Ring-billed Gulls are omnivores, and are 2 of the few species of gulls which breed inland. They have the potential to come into ecological competition although Willis (1966) and others (Orians and Horn 1969, Paynter 1949) say that food is not limiting to birds during the breeding season. Birds usually breed when the vegetation, emergent insects, and other prey items are also reproducing, and the food at this time is generally abundant. Even if food is not a limiting factor to these gulls, it is necessarily important for chick survival and ultimately for the propagation of the species.

The potential for competition may exist or have existed at some time in the past for these 2 species, or perhaps they never competed because they feed in different areas. They segregate the foraging habitat by ecotope, distance, direction from the colony, and food types. Also, there is little inter- or intraspecific aggression among or within the 2 species at the feeding areas. This seems to be a strong argument against the past or present existence of competition.

Morphological Differences

Other studies have shown that California Gulls are only about
1.14 times larger in length than Ring-billed Gulls of the same sex
(Davis 1925) (Tables 3-5, 3-6). In this same study, Davis found that
males were approximately 1.07 times larger than females of the same
species. He stated that there was much variation among the birds. Be-
cause Davis had already made all the comparative length measurements
between the 2 species, I made no morphological measurements on the gulls
at Freezeout. Many authors attempt to correlate difference in bill
length with ecological segregation of the food niche. It is difficult,
if not impossible, to extrapolate from other data in other geographic
areas, or even in other years for Freezeout because populations vary
over distance and time. Therefore, it would probably not lend much in-
sight into the problem of character differences between the 2 species if
I were to use data from colonies other than Freezeout.

Furthermore, various authors state that too much emphasis has
been placed on beak size differences in ecological comparisons (Hespen-
heide 1971, Schoener 1965), and Lack (1949) stated that the adaptive
significance of beak size differences is hard to determine. The di-
vergence, if any, between these 2 species took place long before the
cultivated land existed in which these birds now feed.

Absolute morphological comparisons among bird species are at
times difficult if not impossible to analyze depending on the niche
widths of the congeners. If the niches are wide as in gulls, there will
often be great morphological variation with respect to bill, tarsus and
body size (Soulé and Stewart 1970). Absence of character displacement

TABLE 3-5

Physical Comparisons of Ring-Billed
and California Gulls[a]

Length of Appendage	Larus delawarensis		Larus californicus	
	n = 13	n = 10	n = 13	n = 10
Wing	347-392 $\bar{X} = 377.1$	335-370 $\bar{X} = 355.0$	383-415 $\bar{X} = 398.8$	368-395 $\bar{X} = 384.2$
Tail	140-162 $\bar{X} = 148.7$	134-149 $\bar{X} = 140.6$	150-162 $\bar{X} = 156.1$	150-155 $\bar{X} = 152.2$
Tarsus	54-62 $\bar{X} = 57.9$	52-58 $\bar{X} = 54.6$	57-63 $\bar{X} = 60.6$	53-60 $\bar{X} = 56.7$
Toe (w/o claw)	36-42 $\bar{X} = 39.5$	35-40 $\bar{X} = 37.3$	46-52 $\bar{X} = 49.0$	43-49 $\bar{X} = 45.7$
Culmen	39-46 $\bar{X} = 42.4$	36-43 $\bar{X} = 38.8$	45-56 $\bar{X} = 50.0$	42-49 $\bar{X} = 46.1$
Bill at Base	12-16 $\bar{X} = 13.6$	12-15 $\bar{X} = 12.9$	15-18 $\bar{X} = 16.3$	13-16 $\bar{X} = 14.7$
Bill at Angle	13-16 $\bar{X} = 14.0$	12-14 $\bar{X} = 12.9$	15-20 $\bar{X} = 16.9$	14-17 $\bar{X} = 15.4$

[a]From Davis (1925).

TABLE 3-6

Ratios of Physical Characteristics
Within and Between Species

Length of Appendage	Ratio Male: Female		Ratio California:Ring-Billed Gulls
	Larus delawarensis	Larus californicus	
Wing	1.06	1.04	1.07
Tail	1.06	1.03	1.07
Tarsus	1.06	1.07	1.04
Toe (w/o claw)	1.06	1.07	1.23
Culmen	1.09	1.08	1.18
Bill at Base	1.05	1.11	1.17
Bill at Angle	1.09	1.10	1.20
Overall Mean	1.07	1.07	1.14

in the area of overlap, though, does not necessarily mean the 2 species are not competing (Ashmole 1968b).

Behavior

Some sympatric congeners have developed differences in foraging technique, segregating the food niche and avoiding competition. By obtaining their food in different ways, for example probing versus gleaning, they sample different prey taxa or prey of different sizes without perhaps selecting the prey item per se but rather obtaining different items because these items occur in different microhabitats (Selander 1966, Selander and Giller 1956). There comes a point, however, when it is difficult to say whether the animal is segregating the foraging niche via its behavior or whether it is segregating it via different habitat selection. Newton (1967), for instance, cites behavior of differences of aerial versus ground feeding, what I would call habitat differences.

The most interesting behavior in the foraging niche is that of overt aggression between congeners while feeding. This is an energy-wasting behavior and should have been eliminated from the population in most cases if indeed it had ever been present (Orians and Willson 1964). I never observed this behavior in gulls. Yet, there are some observations for other species of interspecific aggression during foraging (Ashmole 1968a, Selander and Giller 1959). However, this observed aggression is from birds which feed on the nesting territory, quite a different situation from gulls.

Habitat Segregation

By far, the commonest means of ecological isolation between 2 species is by differences in habitats. There are numerous examples of segregation of the foraging habitat among the ecological literature (e.g. Austin and Smith 1972, Cody 1968a, MacArthur 1968, Morse 1972, Sheldon 1972, Snelling 1968). This habitat segregation can even be microhabitat oriented such as lizards in Bimini which choose different size branches (Selander 1966) or warblers which forage in different areas of trees (MacArthur 1958).

Space often is more easily divided up than is food presumably because prey items are so ephemeral or fluctuating (Hespendeide 1971). Some authors suggest comparisons of different direction the birds fly to and from the colonies in order to demonstrate habitat segregation (Brown 1967a, Hopkins 1972). For reasons already mentioned, these methods often provide erroneous data. The physical area where the birds are feeding of course are the important data to compare.

Not only did the Ring-billed and California Gulls divide the areas within 30 kilometers surrounding the colony, they also segregated where they fed by distance to the foraging grounds and by the gross habitat types of foraging areas they frequented. Other species also exhibit habitat segregation, some on a finer level than others (e.g. Hunt 1973, MacArthur 1968, Schoener 1971a).

Gulls fly away from the colony in order to feed. Much of the area surrounding the colonies is an ecologically disturbed area: cultivated fields. However, the gulls do not saturate the area immediately surrounding the colony in their feeding forays. They have been found

feeding as far away as 72.42 kms from the breeding grounds (Rothweiler 1956, Vermeer 1963). This may mean that although gulls are omnivorous and scavengers, the areas in which they feed may not have a high yield of food per unit time effort and thus the gulls may be forced to feed over a wider area (Farner 1968). The preferred food habitats are very patchy. Often gulls are seen following a plow as it turns up the soil, or following mowers as they cut grain, or feeding at dumps.

Of the total number of all California Gulls sighted, 49% were on the ground feeding; of the total of all Ring-billed Gulls sighted, 87% were on the ground feeding. Therefore, a greater percentage of observed californicus were flying than were delawarensis. The aerial California Gulls were probably flying to or from a feeding area. Their feeding areas were more dispersed than those of the Ring-billed Gulls, and thus it follows that I would observe California Gulls in the air more than I would observe Ring-billed Gulls in the air.

The observed separation of the gulls is what I had expected given 2 congeners of different sizes. The California Gull is larger than the Ring-billed Gull and is slower maturing (Davis 1925, Dwight 1925, Vermeer 1970). Cody (1968a) has shown that chicks of seabirds that are slower maturing are not fed as often as those that mature quickly. Pearson (1968) has shown that less time is spent feeding larger chicks than small. However, he did not observe how much the gulls fed the chicks. If California Gulls do not feed their chicks as often as do the Ring-billed Gulls, then they can afford to go on longer feeding forays.

California Gulls are larger, therefore they can consume larger prey than can the Ring-billed Gulls (Pearson 1968). The feeding data from Rothweiler support this. Large prey, i.e. vertebrates, are mainly found farther away from the colony. Cultivated wheat fields surround the colony for many kilometers. The larger vertebrates such as ground squirrels are not as plentiful in these fields as they are in the open prairie. Thus, the California Gulls fly farther, and obtain larger prey. Earthworms and insects are readily found in the cultivated fields around the colony. Probably not many vertebrates live there though, because the major method of irrigation is simply flooding the fields. Eighty-three percent of the Ring-billed Gulls sighted fed in these fields, and 87% of the observed California Gulls fed in the dryland farming areas of prairies.

Segregation of the Food Niche

If closely related sympatric species are to retain sympatry or separate species status they must develop mechanisms to avoid ecological competition. One such mechanism is to feed on different sorts of food. Soulé and Stewart (1970) argue against many investigations involving comparisons of different food types. They thing that such comparisons are anthropocentric because a bird may be segregating food items via a quality like hardness rather than by taxonomic category.

Table 3-3 shows the frequencies of occurrence of 28 different food items in the diet of California and Ring-billed Gulls at Freezeout. In general, California Gulls have a greater number taxonomically, of items than do the Ring-billed Gulls. I used a Shannon-Weiner H diversity index to measure the diversity of food species. This is an

information content index or a measure of uncertainty. It yields $H' = 2.435$ for _californicus_ and $H' = 2.415$ for _delawarensis_, indicating that the diversity of the 2 diets, the niche breadth, is approximately the same.

The methods of overlap analysis I used were Schoener's (1970) and Snelling's (1968). In Schoener's method: c_{ij} = overlap, p_{ij} = proportion of individuals of species i with resource state j; p_{hi} = proportion of species h with resource state j. The formula is $c_{ij} = 1 - \sum_j \frac{|p_{ij} - p_{hi}|}{2}$ and the c_{ij} for Ring-billed and California Gulls with respect to food type is 0.6240. In Snelling's method: c = overlap, a = number of food items of California Gulls, b = number of food items of Ring-billed Gulls, and w = number of food items in common. The formula is $c = \frac{2w}{a+b}$ and c = 0.70 for the 2 species.

These 2 indices of overlap show that the species have 70% (Snelling method) and 62.4% (Schoener method ecological food similarity. A X^2 value from the association table (Table 3-4) is 1.87 ($p > 0.05$) indicating there is essentially no difference between the 2 species. Unlike some other species, these congeners do not differ significantly in their diets yet they still live sympatrically.

The data from Rothweiler are such that these tests cannot be interpreted with much biological meaning. He shot gulls only in one area, on the eastern shore of Freezeout Lake, and made no attempt to determine where they had been feeding. As others have said (Hespenheide 1971, Soulé and Stewart 1970) taxonomic differences in the food an animal eats do not really explain how an animal is segregating the food niche. Birds especially are opportunistic feeders. Caloric values

and especially the frequency that the prey items occur in the environment should also be investigated. These data then are just a brief descriptive summary of niche breadth with respect to food items of the 2 gull species.

Although Rothweiler obtained no prey sample from the environment, I think it is safe to assume that the biotic diversity vegetation is less in the areas of extensive wheat monoculture than it is in the prairies. Perhaps, because of this limit in taxonomic diversity and simple community structure, the overlap in diet is so great. Not much can be said, however, without knowing also the diversity and abundance of the prey species in the environment.

CONCLUSION

California and Ring-billed Gulls segregate the food niche mainly by distance and habitat type of the foraging areas and less by food type. Eighty-seven percent of the observed California Gulls fed on prairie or dryland farming areas, while 83% of the observed Ring-billed Gulls fed on irrigated areas at a mean distance of 17.4 and 10.8 km from the colony, respectively. They had a 62% (minimum) overlap in diet, with California Gulls eating a significantly greater amount of large food items, mainly in the form of vertebrates, than did the Ring-billed Gulls.

CHAPTER IV

COMPARISON OF THE NESTING HABITATS

INTRODUCTION

California and Ring-billed Gulls, like many colonial ground

nesting waterfowl, prefer to nest in restricted environments, on islands

in lakes (Johnston and Foster 1954, Evans 1972). When islands are not

available, the gulls nest successfully on peninsulas. Since these two

species are not so similar morphologically and behaviorally (Moynihan

1955, Vermeer 1970) and since they occupy the same general habitat and

are colonial nesters, a reasonable conclusion is that they have similar

nesting requirements and that there may be keen competition for space on

these nesting sites.

Because of the colonial and insular aspects of the breeding sites,

an actual boundary surrounds the birds with the result that all inferences

made from the investigation of the nesting habitat can be based on an ac-

tual, not an artificially bounded, breeding group.

Brewer (1963) and others state that for 2 distinct populations of

similar species to coexist sympatrically, they must be reproductively

isolated and avoid competition. Habitat segregation is one of the more

common ways for 2 sympatric species to avoid interspecific competition

(Hardin 1959, Hutchinson 1953, Rickleffs 1966).

Closely related species often select similar but distinctly sep-

arate habitats, the preference of which is actually a result of their

74

evolutionary history. They have had different selective pressures operating on them and at a particular moment in time are adapted to the use of different resources in the environment (Lack 1933,1945). In order to coexist they must have developed slightly different habitat choices. The presence of an adjacent species, however, may somewhat modify the actual niche so that the realized niche is a subset of this due directly to interspecific interaction. Sometimes this narrower niche is actually the optimum habitat; sometimes it is the marginal habitat (Svardson 1949). The presence of conspecifics may act as an attractant or a deterrant to nesting (Nelson and Patterson 1965). Thus, absence of a species from an area may be due to lack of proper physical or biotic features or to intra- or interspecific interactions (DeBach 1966).

There are numerous examples of similar species coexisting by means of partitioning the nesting habitat (e.g. Brown 1967a b, Horn 1970, Klopfer 1963, MacArthur 1957). Most of these studies, however, have been on passerine birds in habitats with definite vertical components. The conclusions reached were that birds distribute themselves in a habitat in part according to the height of, and often to the volume of the vegetation.

Gulls are generalists and often congregate in flocks with other species of gulls. One would not expect a bird such as this to have definite preference of nest sites. The available space to nest would be at a premium, but one would not expect the habitat to be divided up in any orderly way. However, there have been some descriptive studies of gulls' dividing up the nesting site habitat and I believed this to be true for the gulls on the Montana colonies (Bent 1921, Johnston and Foster 1954,

Vermeer 1960, Willet 1919). Yet, no complete analysis of the nesting habitat has been done so that little information has been added to the knowledge of competition and coexistence for these birds. None of the previous studies of gulls tried to explain the functions or causal factors behind the choices of habitat or the nesting pattern of the gulls in this habitat. Since there are factors which are responsible for the way 2 congeners divide up the nesting habitat space, an effort should be made to discover them.

This study of the nesting habitat of Ring-billed and California Gulls presents data on and possible accompanying explanations of the differences in nesting patterns and of preferred nesting sites with respect to vegetation height, cover, and species in 3 colonies.

MATERIALS AND METHODS

Description of Study Areas

The major analyses of the nesting habitat compare 3 gull colonies: 2 at Freezeout Lake and 1 at Arod Lake. Some secondary comparisons include data from colonies at Bowdoin Refuge. The mixed colonies for California and Ring-billed Gulls are located at Freezeout Lake and Arod Lake, the former on a peninsula, the latter on an island. There is also a mixed colony on Long Island at Bowdoin Refuge. A monospecific California Gull colony and a monospecific Ring-billed Gull colony occur at Freezeout Lake and at Bowdoin Refuge respectively, both on islands.

Freezeout Lake is in Teton County, Montana, 59 km northwest of Great Falls. The main lake covers approximately 1200 ha (Figure 4-1) and is shallow, averaging 1 m in depth. There are no natural streams into

FREEZEOUT LAKE

GAME MANAGEMENT AREA

U.S. 89

FREEZEOUT
PENINSULA
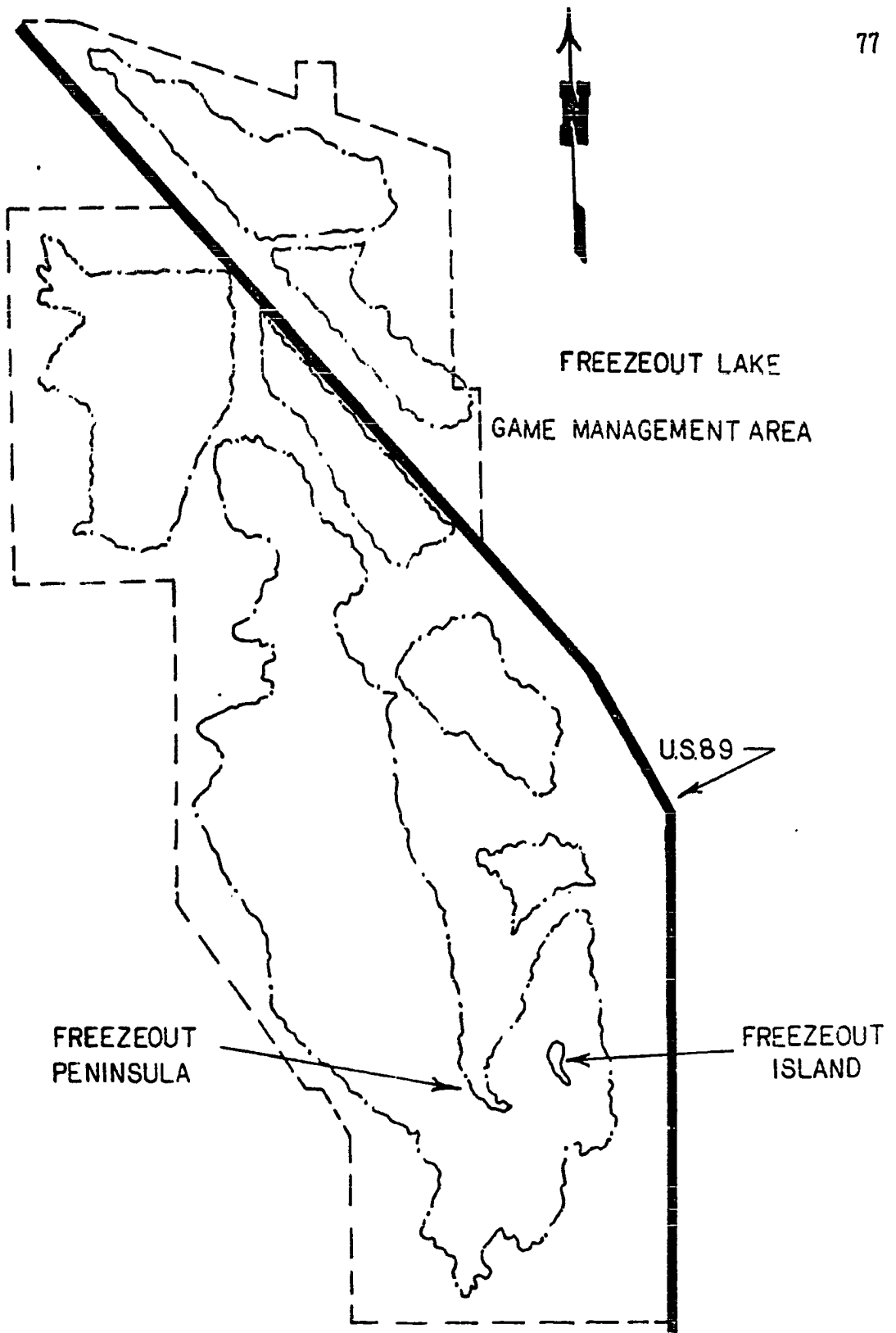
FREEZEOUT
ISLAND

Figure 4-1

or out of the lake. Freezeout was constructed in 1940 to be used in flood
control, and in 1954 an outlet was constructed to control the water level.
The mixed Ring-billed-California Gull colony is located on the peninsula
(Figures 4-2A, 4-2B). The longest axes of the colony are 208 by 116 m
(length x width), and the average width is 71 m. The monospecific Cal-
ifornia Gull colony is located on an island 0.4 km from the peninsula in
the main lake (Figure 4-3). It measures approximately 518 by 122 m and
is more oval than the peninsula.

Arod Lake is 50 km northeast of Freezeout Lake and 17 km west of
Brady, Montana. Arod, like Freezeout, is a human-made lake although much
deeper with an average depth of 4 m. It covers 200 ha. There is a con-
stant flow of water via a stream into and out of the lake and the outflow
can be regulated. The mixed gull colony is on an island which measures
143 by 68 m on its longest axes. The average width is 52 m (Figures 4-4A,
4-4B).

Bowdoin Refuge is in Phillips County, Montana, 25.5 km east of Malta.
Bowdoin Lake and the nearby ponds were also first constructed for flood
control and later established as a refuge. The colonies at Bowdoin are
both on islands. The mixed colony is on Long Island which measures 195
by 21 m with the average width 18 m. It is 20 m from the nearest shore.
The Ring-billed Gull colony is located on a 67 by 26 m gravel bar island
100 m from the nearest shore in a small pond near the main Bowdoin Lake.
All of the lakes in my study areas are flood and irrigation projects and
the water level in them fluctuates seasonally.

It is not known when these colonies were established. On the 3
main colonies studied, there are no detailed records of nesting prior to

FREEZEOUT PENINSULA
1973

L. CALIFORNICUS
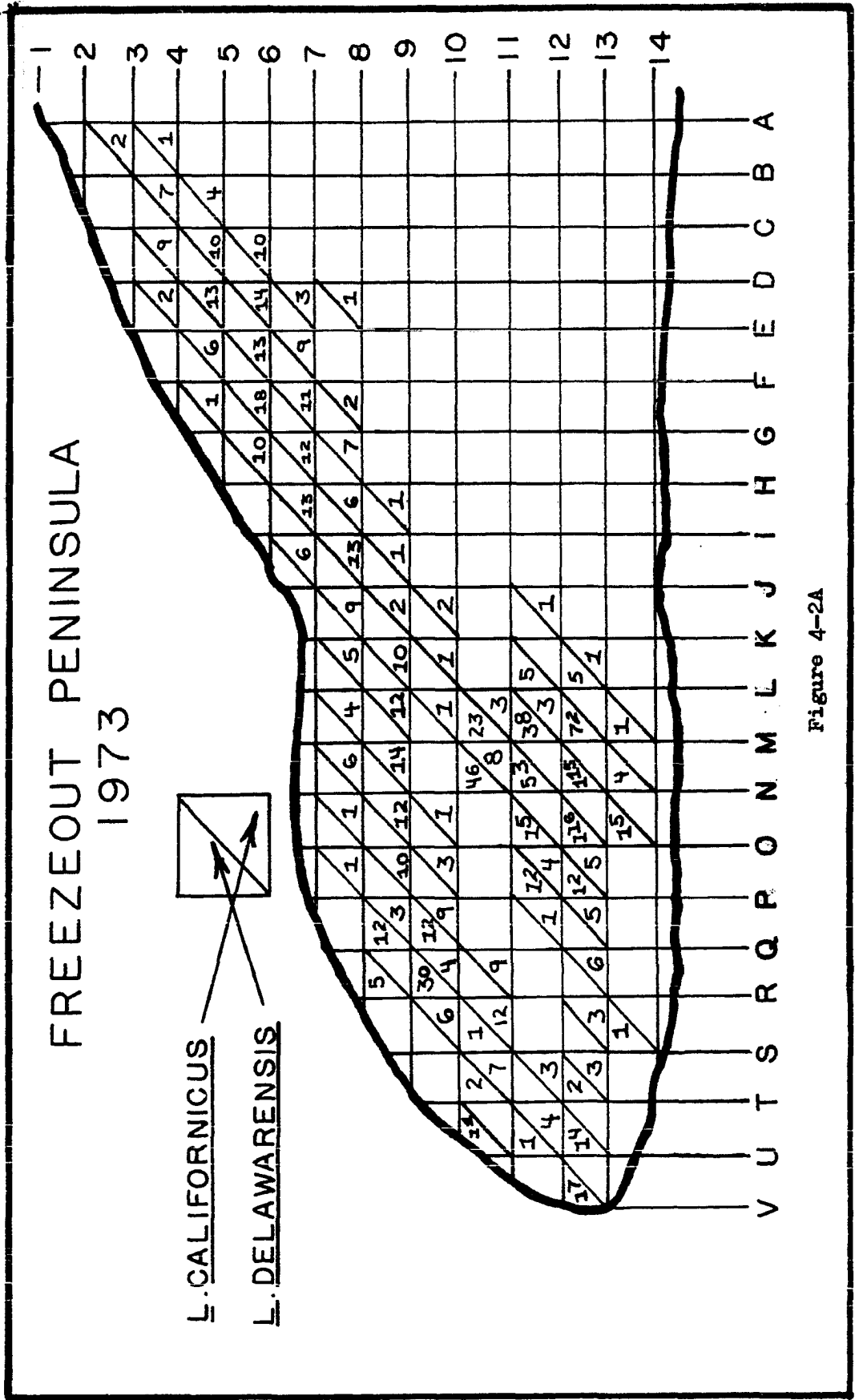
L. DELAWARENSIS

Figure 4-2A

FREEZEOUT PENINSULA
1974
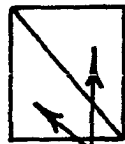
L. CALIFORNICUS

L. DELAWARENSIS
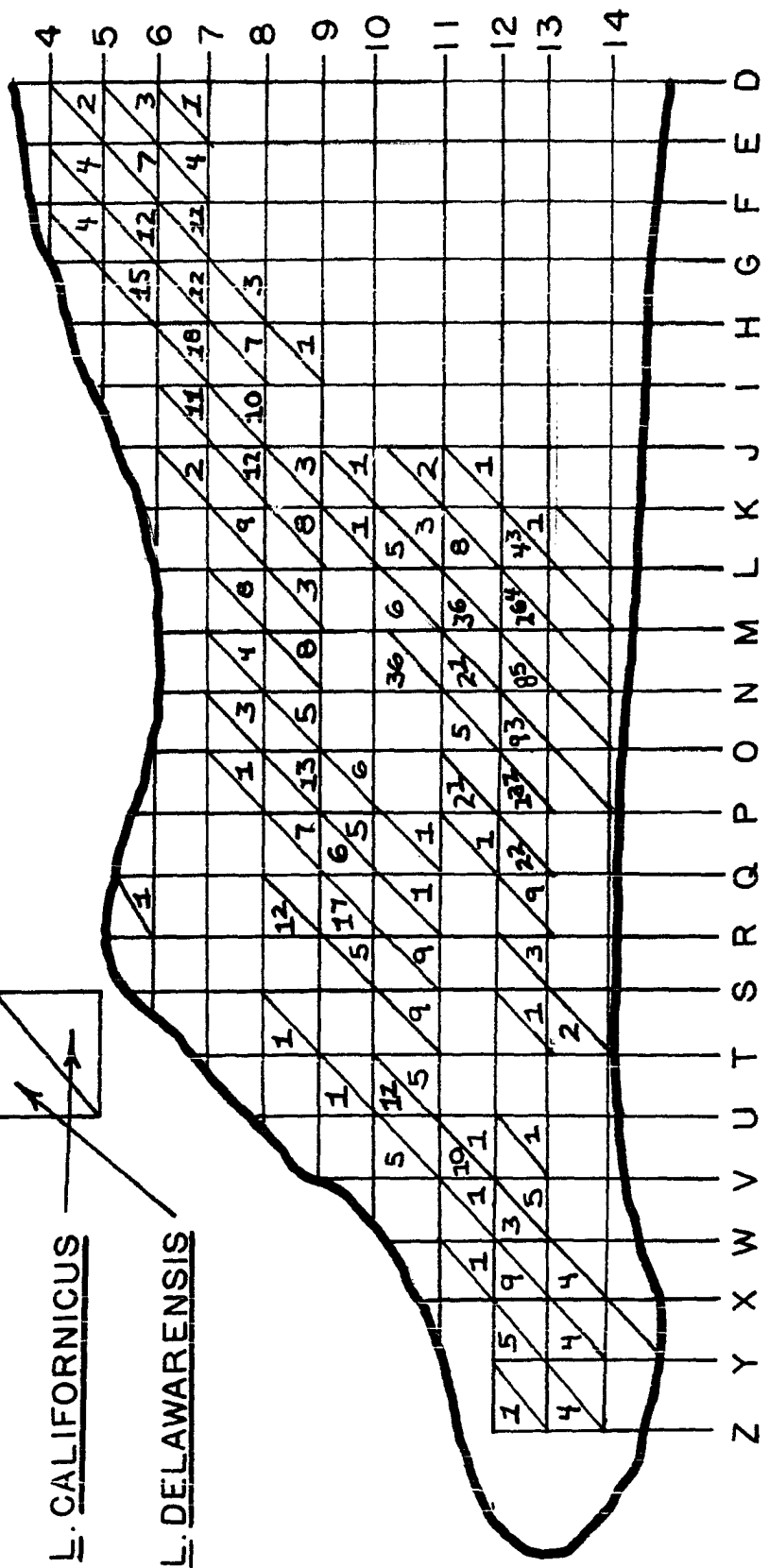
Figure 4-2B

FREEZEOUT ISLAND
1974
LARUS CALIFORNICUS
10 X 270 M TRANSECT

A I — 6
0
13
A 5 — 25
26
40
39
37
A 10 — 29
42
30
41
35
A 15 — 22
2
39
43
34
A 20 — 50
36
36
34
26
A 25 — 27
17
26
10

121.9 M

518.1 M
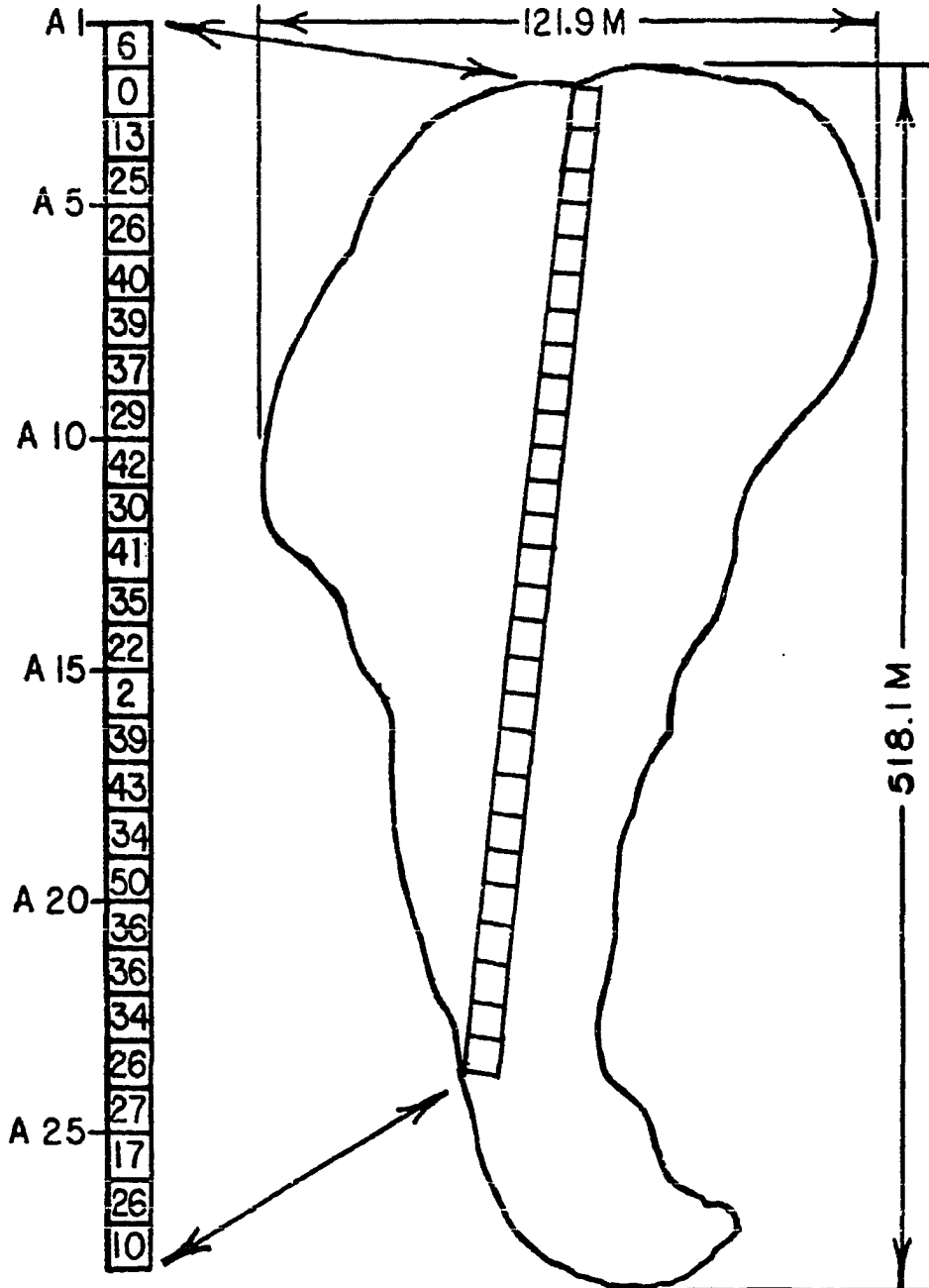
NUMBER OF NESTS PER 10 X 10 M QUADRAT

Figure 4-3

 AROD ISLAND
(TRANSECTS)
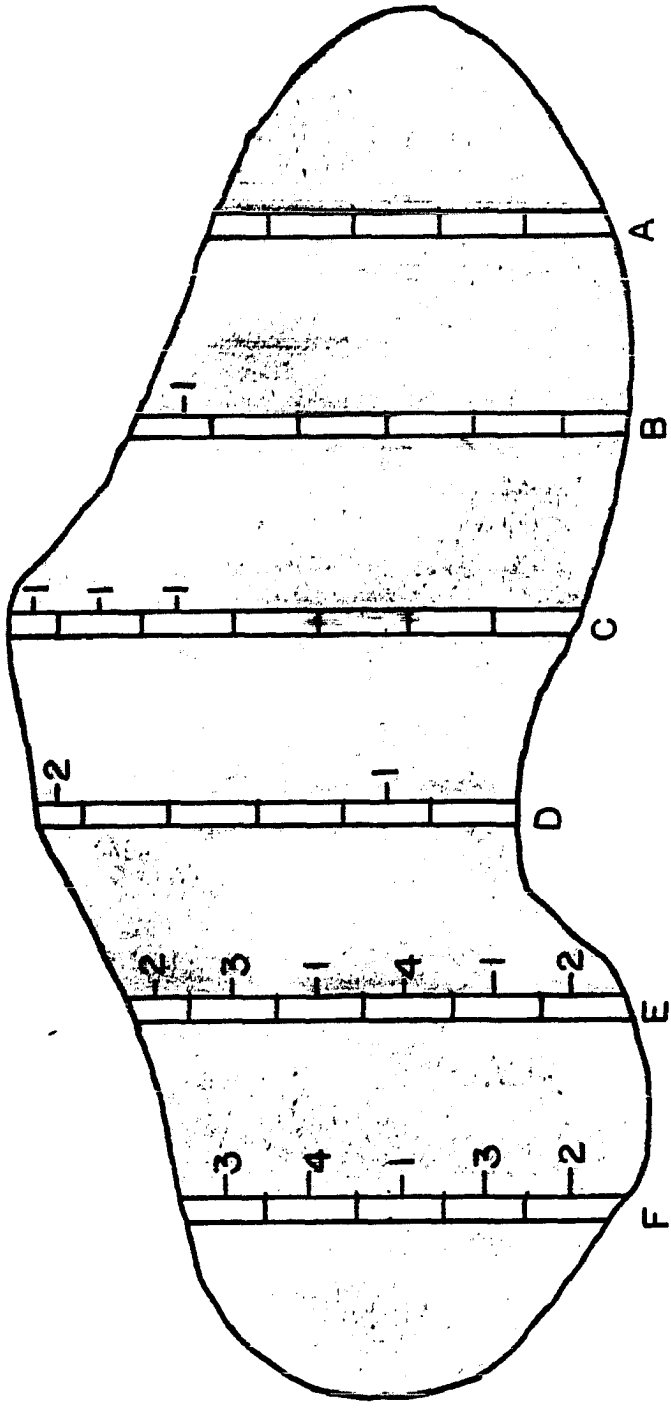
" = 20 METERS
5% SLOPE

Figure 4-4A

L. CALIFORNICUS

AROD ISLAND
(TRANSECTS)
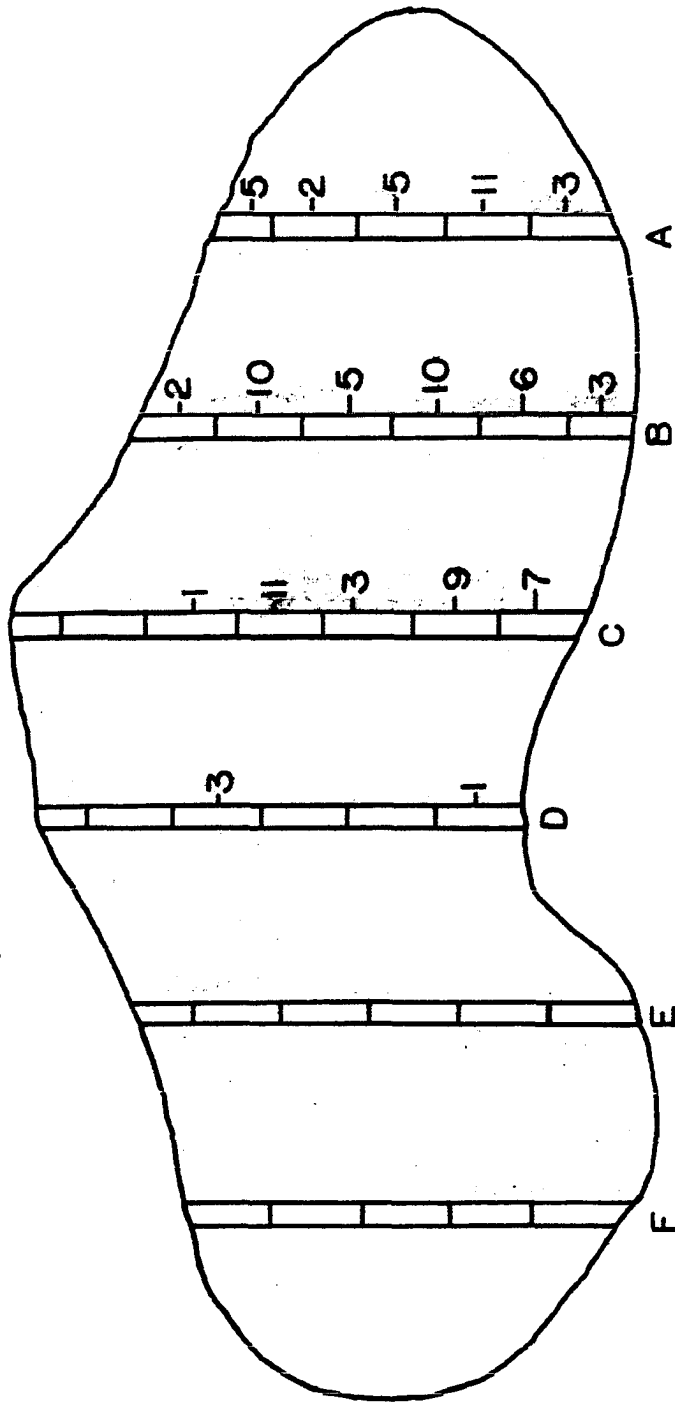
" = 20 METERS
5% SLOPE

Figure 4—4B

L. DELAWARENSIS

this study. At Freezeout Lake, the California and Ring-billed Gulls both occupied the island until 1968 when there was heavy precipitation and the water level rose so as to completely inundate the island. When this happened, the peninsula became the nesting grounds for both California and Ring-billed Gulls. The following season, the island was dry and was used as nesting grounds by California Gulls only (Louis Moos personal communication). The peninsula was used by both California and Ring-billed Gulls that year and has been so ever since. The Ring-billed Gull colony was never re-established on the island. It is not known if the island at Arod flooded during the 1968 season.

Field Methods

During the breeding season of 1973 I censused the entire Freezeout Peninsula colony as follows. I placed a grid of stakes 10 m apart on the colony. I measured the exact location of each nest using rectangular coordinates on each 10 x 10 m quadrat; I measured the height of the highest vegetation, the percent cover of the vegetation, determined the species of the vegetation within a 30 cm radius around each nest, and measured the distance to the nearest vegetation from each nest. From these data I obtained nest densities, exact locations of all nests on the colony, nearest neighbor distances, and vegetation heights on the gull colonies at Bowdoin, Arod Lake and the 2 colonies at Freezeout Lake.

During the 1974 breeding season I sampled the colonies on Freezeout Peninsula, Freezeout Island, and Arod Island by transects 10 m apart, except at Arod where they were 20 m apart. The lengths of the mixed colony transects were the widths of the colonies at the point of the transect;

but on the monospecific colony, Freezeout Island, all transects were 10 m long. The transects were laid across the width of the colonies, and their center lines were the edges of the established quadrats. The transect width was $\frac{1}{2}$ m on either side of this center line. Ever 10 m along the transect was a location stake corresponding to one of the 4 corners of a quadrat (Figure 4-5). I measured placement of each nest within its transect and distance to nearest neighbor. On the Freezeout Peninsula colony I made a count of gulls in each quadrat; and on the Freezeout Island colony, I made a count of gulls in a row of 10 x 10 m quadrats which cut diagonally across the island. On each of the 3 colonies I laid down a Daubenmire plot ever 10 m along the transects to sample the species, height, and percent cover of the vegetation (Daubenmire 1959). From these data I was again able to obtain sample densities and placements of nests within the colonies and average vegetation profile data for the quadrats.

Around 21 June 1974, approximately 7 weeks before the censuses were made, an unknown human intruder(s) disturbed the Freezeout Peninsula colony while I was absent for 2 days. Upon my return I found that many California Gulls had deserted the colony. The vegetation census then involved only the remaining nests and this biased sample may have altered the results for those analyses.

RESULTS

A summary of the nesting habitat is presented for each species. Comparisons are then made within each colony between the 2 species and then among all colonies for each species.
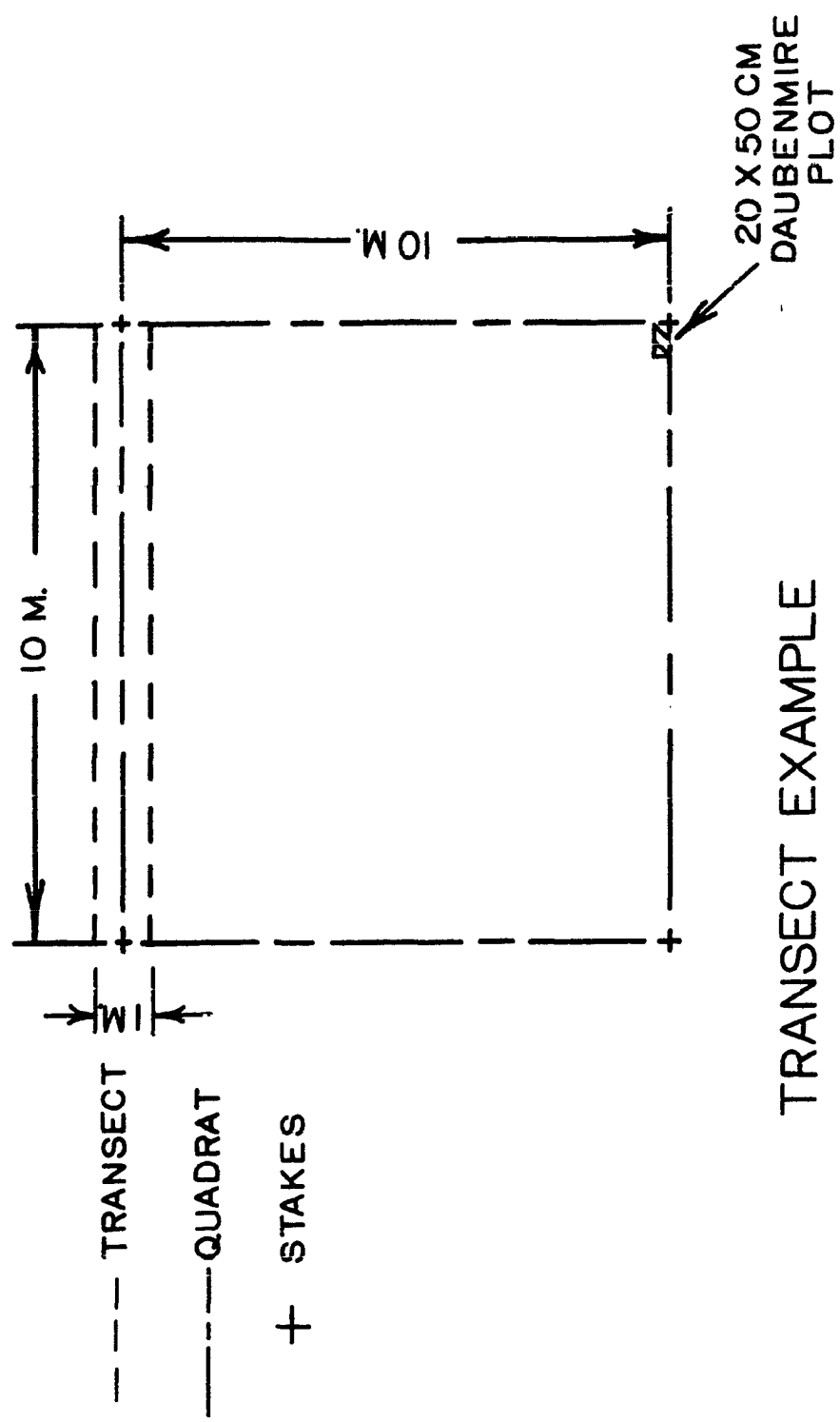
TRANSECT EXAMPLE

Figure 4-5

10 M.

10 M.

1 M

20 x 50 CM
DAUBENMIRE
PLOT

– – – TRANSECT

——— QUADRAT

+ STAKES

Larus californicus—Summary, All Colonies

California Gulls nest next to high, dense vegetation (height means = 40.9-187.7 cm, cover means = 64.02-99.50%) (Figure 4-6, Table 4-1). They perfer the middle of the colony to the edges in the majority of cases (Table 4-2). The nearest neighbor distance and density are not highly correlated with vegetation parameters nor does nearest neighbor distance vary with respect to location of nests within the colony (Tables 4-3, 4-4).

Larus delawarensis—Summary, All Colonies

Ring-billed Gulls nest near low, sparse vegetation (height means = 16.95-135.54, cover means = 59.92-86.44) (Figure 4-6, Table 4-1). They build the majority of their nests in the middle of the colony instead of on the edges. The nearest neighbor distance and density are not highly correlated with vegetation parameters nor does nearest neighbor distance vary with respect to location of nests within the colony in the majority of cases (Tables 4-3, 4-4).

Within Colony, Between Species Comparisons

Within every colony except the Freezeout Peninsula 1974 colony, there are differences between the 2 species with respect to nesting pattern (nearest neighbor distance and density), and nest site preference (vegetation height, vegetation cover, and vegetation species).

Nesting pattern. Consistently, California Gulls have significantly greater nearest neighbor distances and lower densities than do Ring-billed Gulls on all colonies (Tables 4-5, 4-6). The mean nearest neighbor distance is significantly greater for congeners than for

MEANS OF VEGETATION HEIGHT AND COVER
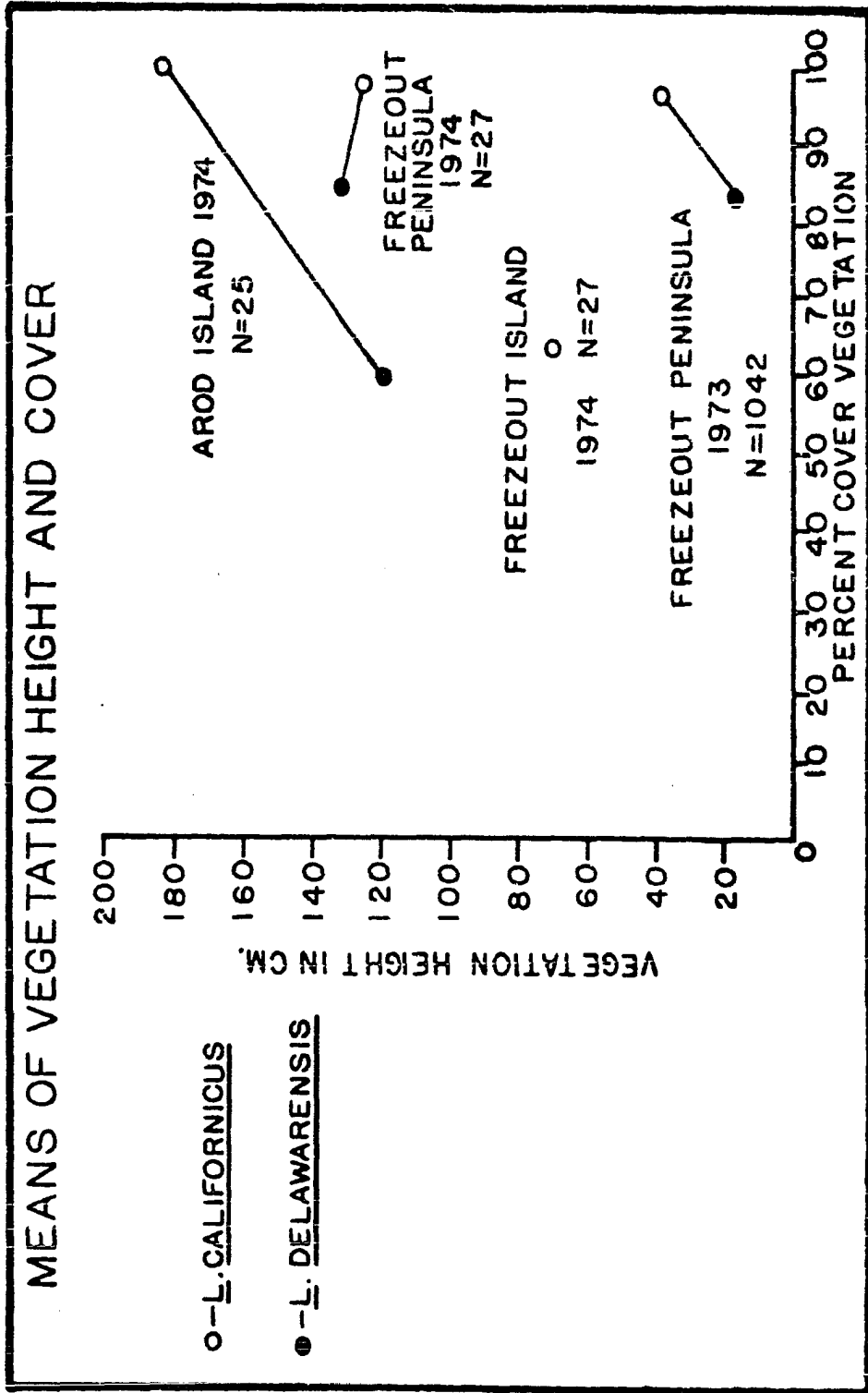
Figure 4-6

TABLE 4-1

Mean Vegetation Height (centimeters), Vegetation Cover (%), and Vegetation Volume (Cover X Height)

Species	Freezeout Peninsula 1973 June	Freezeout Peninsula (transect) 1973 June	Freezeout Peninsula 1974 August	Freezeout Island 1974 August	Arod Island 1974 August
Mean Vegetation Height (cm)*					
Larus californicus	40.89 ± 19.85 N = 396	42.24 ± 15.98 N = 46	127.06 ± 75.49 N = 16	71.80 ± 77.08 N = 27	187.71 ± 84.40 N = 10
Larus delawarensis	16.95 ± 18.32 N = 646	17.99 ± 18.79 N = 75	135.54 ± 112.95 N = 11	——	120.75 ± 81.22 N = 15
Mean Vegetation Cover (%)*					
Larus californicus	97.20 ± 2.94 N = 396	97.03 ± 1.56 N = 46	98.37 ± 6.18 N = 16	64.02 ± 31.25 N = 26	99.50 ± 0.72 N = 14
Larus delawarensis	86.44 ± 3.02 N = 646	85.13 ± 11.69 N = 75	86.34 ± 30.87 N = 12	——	59.42 ± 14.6 N = 17
Mean Vegetation Volume (Cover X Height)*					
Larus californicus	3879.55 ± 1957.27 N = 394	3975.74 ± 1506.98 N = 46	9027.55 ± 6816.76 N = 16	5406.93 ± 6384.38 N = 25	13,720.62 ± 6061.29 N = 12
Larus delawarensis	2686.44 ± 1584.77 N - 638	1746.95 ± 1840.17 N = 75	10,507.23 ± 10,827.07 N = 11	——	7360.31 ± 4807.07 N = 16

*Confidence Interval = 1 S.D.

TABLE 4-2

Numbers of Nests in Different
Locations of the Colony

Colony	Date	Larus californicus			Larus delawarensis		
		Edge of Water	Middle	Landward Edge	Edge of Water	Middle	Landward Edge
Freezeout Peninsula —All	1-VI-73	118	175	119	99	394	146
		$x^2 = 15.50$ $p < 0.005$ 2df			$x^2 = 235.90$ $p < 0.005$ 2df		
Freezeout Peninsula —All	25-V-74	109	82	87	157	573	182
		$x^2 = 4.45$ $p > .05$ 2df			$x^2 = 358.07$ $p < 0.005$ 2df		
Freezeout Peninsula —Transect	20-VI-74	16	4	16	20	40	12
		$x^2 = 7.20$ $p < 0.05$ 2df			$x^2 = 17.33$ $p < 0.005$ 2df		
Arod Island —Transect	20-VI-74	15	18	1	21	72	4
		$x^2 = 12.80$ $p < 0.005$ 2df			$x^2 = 79.12$ $p < 0.005$ 2df		

TABLE 4-3

Correlation Coefficient, r, of Nearest Neighbor and Density on Vegetation Characteristics Freezeout Peninsula, 1973

	Larus californicus		Larus delawarensis	
	r, Nearest Neighbor	r, Density	r, Nearest Neighbor	r, Density
Vegetation Height	0.11	0.36	0.04	−0.12
Vegetation Cover	0.04	0.16	0.05	0.21
Vegetation Volume	0.12	0.35	0.04	−0.09

TABLE 4-4

Mean Nearest Neighbor Distances in Different Parts of the Colonies

Colony and Date	Larus californicus			Larus delawarensis		
	Edge of Water	Middle	Landward Edge	Edge of Water	Middle	Landward Edge
Freezeout Peninsula 1973	$\bar{X} = 1.87$	$\bar{X} = 1.60$	$\bar{X} = 3.12$	$\bar{X} = 1.12$	$\bar{X} = 0.52$	$\bar{X} = 0.78$
	F = 3.06 2df		p > 0.05	F = 0.82 2df		p > 0.10
Freezeout Peninsula 1974	$\bar{X} = 1.43$	$\bar{X} = 1.72$	$\bar{X} = 1.05$	$\bar{X} = 0.52$	$\bar{X} = 0.57$	$\bar{X} = 0.72$
	H = 0.83 2df		p > 0.05	H = 6.24 2df		p < 0.05
Arod Island 1974	$\bar{X} = 1.18$	$\bar{X} = 1.39$	$\bar{X} = 1.58$	$\bar{X} = 0.82$	$\bar{X} = 0.55$	$\bar{X} = 0.58$
	H = 3.97 2df		p > 0.10	H = 6.24 2df		p < 0.05

TABLE 4-5

Nearest Neighbor Mean Distances
(meters)

Colony	Larus californicus			Larus delawarensis		
and Date	All Nests	Conspecific	Congener	All Nests	Conspecific	Congener
Freezeout Peninsula 1973	$\bar{X}$ = 1.64 N = 394	$\bar{X}$ = 1.64 N = 381	$\bar{X}$ = 1.46 N = 13	$\bar{X}$ = 0.56 N = 638	$\bar{X}$ = 0.55 N = 633	$\bar{X}$ = 1.81 N = 5
Freezeout Peninsula 1974	$\bar{X}$ = 1.25 N = 32	—— ——	—— ——	$\bar{X}$ = 0.81 N = 104	—— ——	—— ——
Arod Island 1974	$\bar{X}$ = 1.32 N = 33	—— ——	—— ——	$\bar{X}$ = 0.61 N = 97	$\bar{X}$ = 0.61 N = 96	$\bar{X}$ = 0.89 N = 1
Freezeout Island 1974	$\bar{X}$ = 1.23 N = 81	—— ——	—— ——	—— ——	—— ——	—— ——

TABLE 4-6

Density of Nests

Colony and Date	Larus californicus		Larus delawarensis	
	N	Density/m²	N	Density/m²
Freezeout Peninsula 1973	394[a]	0.059	648[a]	0.246
Freezeout Peninsula 1974	263[a]	0.055	863[a]	0.254
Arod Island 1974	33[b]	0.165	97[b]	0.539
Freezeout Island 1974	729[c]	0.270	—	—

[a]Total nest count.

[b]Sample from 6 transects (1 x 70m).

[c]Sample from 27 transects (10 x 10m).

TABLE 4-7

Differences Between Species with Respect to Vegetation Characteristics

	Freezeout Peninsula 1973	Freezeout Peninsula 1974	Arod Island 1974
Vegetation Height	$z = 19.83$ $p < 0.001$	$U = 106$ $p > 0.05$	$U = 81$ $p > 0.05$
Vegetation Cover	$t = 1.88$ $p < 0.05$	$U = 87$ $p > 0.05$	$U = 51$ $p < 0.02$
Vegetation Volume	$t = 18.59$ $p < 0.001$	$U = 97$ $p > 0.05$	$U = 37$ $p < 0.02$

conspecifics in the Ring-billed Gull population but not in the California
Gull population. In Ring-billed Gulls, the mean distance to nearest
neighbor which is a Ring-billed Gull is less than the mean distance to a
nearest neighbor which is a California Gull. In California Gulls, the
mean nearest neighbor distance is not influenced by the species of the
nearest neighbor.

Nest site preference—vegetation profile. The analysis of the
vegetation profile is quite complex when compared among the colonies in
this study. I gathered the vegetation data differently during the 2 field
seasons, and sampled it at different times of the season for 2 years so
that only relative, not actual, measurements can be compared. The species
composition and the physical layout of the vegetation varied markedly from
colony to colony in the same sampling period.

On all mixed colonies, except in the Freezeout Peninsula colony
in 1974, Ring-billed and California Gulls segregated the habitat with re-
spect to height, cover or volume of vegetation (Table 4-7). The actual
values of mean height and mean cover vary for all colonies but the rela-
tive differences between the 2 species are consistent. There is no cor-
relation between vegetation height, cover or volume and nearest neighbor
distance, for either species on all colonies (Table 4-3).

The species and diversity of plants on the nest sites differ be-
tween the 2 species (Table 4-8). The Ring-billed Gulls often nest in the
open; but when they nest near vegetation, the species of plants are dif-
ferent from those of the California Gulls. There is a greater diversity
of plants around the Ring-billed Gull nests than around the California

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TABLE 4-8

Plant Species on the Gull Colonies:
Numbers of Nests with Plant Species Within 30 cm *

| Species | Freezeout Peninsula, 1973 | | Freezeout Peninsula, 1974 | | Freezeout Island, 1974 | Arod Island, 1974 | |
	Larus californicus	Larus delawarensis	Larus californicus	Larus delawarensis	Larus californicus	Larus californicus	Larus delawarensis
Salsola kali	5 (0.01)	386 (0.299)	10 (0.435)	8 (0.571)	20 (0.571)	9 (0.474)	12 (0.444)
Monolepis nutalliana	51 (0.098)	25 (0.019)	4 (0.174)	1 (0.071)	10 (0.286)		
Kochia scaporia			6 (0.261)	1 (0.071)			1 (0.037)
Lactuca serriola	356 (0.682)	339 (0.263)	2 (0.087)	1 (0.071)			
Agrostis spp.				1 (0.071)			
Distichlis stricta	90 (0.172)	276 (0.214)	1 (0.043)				1 (0.037)
Centaurea spp.						5 (0.263)	6 (0.222)
Eurotea lanata							2 (0.074)
Agropyron smithii							1 (0.037)
Discuparia spp.						2 (0.105)	
Cirsium arvense						3 (0.158)	1 (0.037)
Scirpus paludosus	18 (0.034)	191 (0.103)					
Puccinellia nutalliana		1 (0.001)					
Salicornia rubra	2 (0.004)	1 (0.001)					
Myrophyllum paludosus		11 (0.009)					
No Vegetation		60 (0.047)		2 (0.143)	5 (0.143)		3 (0.111)
	= 522	1290	23	14	35	19	27
	H' = 0.4172	H' = 0.6734	H' = 0.5927	H' = 0.5360	H' = 0.4152	H' = 0.5356	H' = 0.7032

*Parentheses = decimal fraction.

Gull nests. The monospecific island has the least diversity. The measure of diversity I used is the Shannon-Wiener diversity (uncertainty) index, H' (Shannon and Weaver 1949). For Freezeout Peninsula 1973, H' Ring-billed Gulls is 0.6738, H' California Gulls is 0.4172; for Freezeout Peninsula 1974, H' Ring-billed Gulls is 0.5860, and H' California Gulls is 0.5927; for Arod Island 1974, H' Ring-billed Gulls is 0.7032 and H' California Gulls is 0.5356; and for Freezeout Island, H' California Gulls is 0.4152.

Nest locations. Ring-billed and California Gulls do not distribute themselves evenly throughout each colony. In every colony each species has a discrete subcolony which is separated from the other subcolony by an area with few or no nests (Figures 4-2A, 4-2B, 4-4A, 4-4B). For analysis of this nesting pattern on the colony I chose the general divisions of nest location as:. within 10 m of water, middle of colony, within 10 m of the landward edge of the colony. Table 4-2 shows the placement of the birds within these subdivisions. It is obvious that both species prefer the middle of the colony because even though there is less "middle," there are more nests there. Ring-billed Gulls in all cases preferred the middle (X^2 test each colony p < 0.005, 2df). California Gulls preferred the middle of the colony the majority of times, yet at the Freezeout Peninsula colony in 1974 they chose the water edge over the landward edge or middle of the colony. A X^2 test for each colony yielded p < 0.005 for Freezeout Peninsula 1973 and Arod 1974; p < 0.05 for the transects on Freezeout Peninsula 1974 (2df). The location of nests on the

colonies did not influence mean nearest neighbor distance, except for the Ring-billed Gull colonies in 1974 (Table 4-4).

Among Colonies Within Species

Nesting pattern. There are no differences in nearest neighbor distance between the 2 colonies of Ring-billed Gulls in 1974 (Freezeout Peninsula and Arod Island), or between Arod 1974 and Freezeout Peninsula 1973 (Mann-Whitney U test p > 0.348, p > 0.10 respectively, Table 4-5). There is a significant difference between Freezeout Peninsula 1974 and Freezeout Peninsula 1973 for nearest neighbor distances of Ring-billed Gulls (p < 0.005). There is no difference in the nearest neighbor distances of California Gulls on the 2 Freezeout colonies, between the 2 mixed colonies in 1974, or between mixed colonies in different years (Mann-Whitney U test p > 0.10 for each). There is a significant difference between the monospecific 1974 colony and that at Arod Lake in 1974 (p < 0.05).

Preference of nest sites—vegetation profile. The preference of the gulls for building nests next to vegetation of a specific height, cover, or volume differed among the colonies but was more a reflection of the differences in available habitat types on these diverse colonies than a shift in general preference (Table 4-9). For each species in the mixed colonies, there was less variation among colonies with respect to vegetation height and cover than there was within each colony between species (Table 4-1). I tested differences between vegetation parameters with a Kruskal-Wallis one-way analysis of variance and then by pairs with a

TABLE 4-9

Non-Parametric Tests—Vegetation Characteristics
1974 Colonies: Within Species

Characteristics	Larus californicus	Larus delawarensis
Vegetation Height	Kruskal-Wallis H = 7.09* p < .05 2df Mann-Whitney U test U = 69 (Freezeout Peninsula and Arod Island) p > .05	Mann-Whitney U test U = 106 p > .05
Vegetation Cover	Kruskal-Wallis H = 7.35* p < .05 2df Mann-Whitney U test U = 78 p > .05	Mann-Whitney U test U = 89 p > .05
Vegetation Volume	Kruskal-Wallis H = 13.38* p < .01 Mann-Whitney U test U = 117* z = 2.22* p < 0.02 (Freezeout Peninsula and Freezeout Island) Mann-Whitney U test U = 47* p < 0.05 (Freezeout Peninsula and Arod Island)	Mann-Whitney U test U = 91 p > .05

*Significant Difference.

Mann-Whitney U test. The California Gulls on Freezeout Peninsula 1974 and
Arod 1974 had a p > 0.05 for height and a p > 0.05 for cover. The Ring-
billed Gulls on these colonies had a p > 0.05 and a p > 0.05 respectively.

On all colonies the Kruskal-Wallis analysis of variance showed
there was no difference in choice of vegetation profile for the Ring-
billed Gulls. Between the mixed colonies for California Gulls there was
a significant difference in choice of vegetation volume (Kruskal-Wallis
p < 0.01). The monospecific gull colony differed significantly from the
other California Gull colonies with respect to all vegetation character-
istics (p < 0.02). On the monospecific colony, the gulls nested next to
plants with a greater variety of volumes, heights, and covers than they
did on the mixed colonies. From colony to colony, they nested next to a
significantly different array of plant species.

Nest location. In all cases, except the Freezeout Peninsula
colony in 1974, the majority of gulls nested in the middle of the colony
rather than along the edge (Table 4-2). I tested this with parametric
and non-parametric analysis of variance. However, this pattern was not
rigid from year to year in that the nests were not built in exactly the
same place. On the same colony but in different years the numbers of
nests in each quadrat were not significantly different for Ring-billed
Gulls (Wilcoxon test p > 0.2546) but were significantly different for the
California Gulls (p < 0.0238) although the same general colony locations
were still chosen (Figures 4-2A, 4-2B).

DISCUSSION

California and Ring-billed Gulls coexist on the nesting grounds
yet they choose different vegetation habitats and have different nesting
patterns from each other. The causes of these differences are probably
due both to the physical environment and to inter- and intraspecific
interactions.

Nesting Pattern

In all cases the California Gulls are more spread out in their
nesting pattern. Their lower density and greater nearest neighbor dis-
tances reflect their size and especially their more aggressive nature.
If the densities were greater they might spend more time in energy-
wasting agonistic encounters. The monospecific California Gull colony
had nearest neighbor distances smaller than but similar to those of Cal-
ifornia Gulls in the mixed colonies, indicating that the presence of
Ring-billed Gulls had no influence on this nesting pattern. However,
when the nearest neighbor to a California Gull is a Ring-billed Gull, the
distance is closer than if it were a conspecific, indicating perhaps a
greater tolerance of Ring-billed than of California Gull proximity by the
California Gulls. This also may be due to the more aggressive and ultim-
ately more cannibalistic nature of the californicus than of the delawar-
ensis to gull chicks (Vermeer 1970). Likewise, the greater nearest neigh-
bor distance for congeners than conspecifics in Ring-billed Gulls re-
flects a possible avoidance of the more aggressive California Gulls by the
Ring-billed Gulls. Perhaps minimal nearest neighbor distances are

determined in part by the size of the California Gull territories. The
preferred nearest neighbor distance is probably the result of a balance
between a mutual intraspecific attraction (for safety and social facilita-
tion) and a deterrent due to social intolerance (intra- and interspecific).

Preference of Nest Site: Vegetation Profile

The same balance between attraction and avoidance may exist for
the 2 gull species with respect to the preference of the nest site.
Choices available for nesting habitats, the potential niche breadth, for
colonial birds, Ring-billed and California Gulls in this case, is quite
limited. The gross preference is a colony on an island, a preference
which probably was dictated evolutionarily by pressure from terrestrial
predators, since these birds are conspicuous ground nesters. With these
limited choices, however, these 2 species segregate the nesting habitat
with respect to vegetation height, cover, or volume.

The pattern of California Gulls' nesting near high, dense vegeta-
tion and the Ring-billed Gulls' nesting near sparse vegetation or in open
areas exists on all mixed colonies censused in Montana: Arod, Freezeout,
and Bowdoin. This pattern does not hold for mixed colonies in other areas
where the situation is reversed (Bent 1921, Johnston and Foster 1954,
Trost personal communication, Willet 1919). However, it seems that where
California and Ring-billed Gulls nest, they will segregate the habitat;
but the actual direction this segregation takes may vary throughout dif-
ferent geographic areas. This may be true in part because each species is
more attracted to nest near its own species than near its congeners.
Thus, habitat segregation by physical location in the colony may be

imposed on these birds. Nevertheless in Montana, the direction this segregation takes is consistent among all mixed colonies.

The Ring-billed Gulls have a smaller mean vegetation height, cover, and volume than do the California Gulls. They also nest in open and in covered areas while the California Gulls nest mainly next to vegetation. Since the Ring-billed Gulls arrive on the average of 2 weeks after the California Gulls, this variation may indicate that they choose whatever habitats remain on the colony after the California Gulls have chosen their preferred nest sites.

High vegetation with much cover could be beneficial to ground nesting birds in that it partially conceals the birds from predators, is good cover for chicks to hide in, and conceals them from gulls nesting nearby which are potential predators also. Perhaps the high, dense vegetation is the preferred nest site for both species, and the California Gulls seek it out and fill it up when they arrive first, and what remains is a variety of different habitats. Two mechanisms could then be working. The Ring-billed Gulls could be more generalized nesters than the California Gulls, preferring a variety of habitats and in their absence would continue to nest in a varied habitat with respect to vegetation characteristics. A lack of preference may have developed over a period of time if they were repeatedly shut out of habitats with a high volume of vegetation, and the birds that successfully fledged chicks were those that nested in the varied habitats. Alternately, the Ring-billed Gulls could actually be in competition with the California Gulls for nest sites near the high, dense vegetation but due in part to their arrival time in addition to their smaller body size and less aggressive nature, they would

not displace the California Gulls. The other alternative of course is that Ring-billed Gulls prefer sites with low vegetation and not much cover.

Perhaps, given a similar but monospecific nesting site, the Ring-billed Gulls would choose the high, dense vegetation. In the latter case, they would be using a switching strategy on the mixed colony, not nesting in their preferred habitat because of the already present California Gulls. They could also nest in as varied a habitat as on the mixed colony, being a general nester in all situations. No comparable monospecific colony was found in Montana to test this theory. This may imply that the normal situation is a mixed colony and that Ring-billed Gulls prefer this to a monospecific colony. If this is the case, the Ring-billed Gulls are balancing detrimental aggression and cannibalism of the California Gulls against some benefit gained when in association with them.

In the absence of a potential competitor, the fundamental niche may sometimes be realized due to ecological release and an increase in intraspecific population pressure. In some respects, this is true of the Freezeout Island California Gull colony. The preferences for vegetation are different from those in the mixed colonies. On Freezeout Island, the nests occur over a more varied habitat with California Gulls often nesting next to low, sparse vegetation or with no vegetation at all near the nest. The explanation for this increase in niche width in the absence of Ring-billed Gulls is not one of competition with the Ring-billed Gulls' forcing the niche of the California Gulls to be narrower in the mixed colony. Rather it is one of gross nest habitat preference and timing. Since California Gulls arrive earlier than do the Ring-billed

Gulls and since the gross preferred habitat is an island, the earlier **California** Gulls fill up this habitat before they settle on the peninsula. An open space on an island probably is preferable to a covered nesting site on a peninsula. However, the covered sites on the peninsula are preferred to open sites and these covered sites are taken next by the California Gulls, leaving the Ring-billed Gulls with whatever remains. Each colony probably has a limited breeding population which returns to it yearly, because even though the California Gulls arrive first on the Arod colony they do not fill it up completely, presumably because there are not enough California Gulls on the Arod colony to fill it up.

The preference of California gulls for high volume vegetation may be in part related to their aggressive and cannibalistic nature, a protection against intraspecific aggression (Burger 1967). The segregation of the habitat between species may be simply to avoid interspecific aggression.

Conclusions

Ring-billed and California Gulls segregate the nesting habitat with respect to vegetation characteristics: vegetation height, cover and volume. They also segregate themselves on the mixed colonies in monospecific subgroups. California Gulls have greater nearest neighbor distances than do Ring-billed Gulls, in part a reflection of their behavior and size. The majority of the time, the gulls build their nests in the middle rather than on the edges of the colony, perhaps because the middle is safer from predators.

The gulls are not so specifically habitat oriented that they are unable to switch to a different nesting habitat given an elimination of the preferred or old habitat. Likewise, in a monospecific California Gull colony, the gulls choose a wider variety of habitats than when in association with the Ring-billed Gulls.

The segregation observed on the mixed colonies may be imposed by a balance between inter- and intraspecific competition.

CHAPTER V

REPRODUCTIVE SUCCESS

INTRODUCTION

In order to discover relationships between 2 co-existing species, one has to investigate various factors that might reveal some of the competitive processes. One of these factors is the reproductive success of a population. The differences in reproductive success of 2 similar species with respect to their locations in the colony, vegetation preference, and nearest neighbor distance preference might give some insight into the adaptive significance of patterns of habitat choice of the 2 species.

Reproductive success in different populations of Ring-billed and California Gulls with respect to the above parameters of species, habitat and placement in colony has not been studied thoroughly. Simple descriptions of habitat choice, of which there are few, do not ask the crucial question of what advantage there might be for the 2 species to segregate themselves and/or choose specific habitats in which to nest. Only by comparison and analysis among and between mixed and single species colonies can the qualities that affect productivity and survival of chicks of the 2 species be determined (Elton and Miller 1954).

In birds, the presence of a congener on the same breeding ground has been reported to alter nesting patterns (Brewer 1963, Catchpole 1972, Crowell 1968, Legg and Pitelka 1956). These alterations often involve a

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switch to a less diverse niche by one of the species. If space is limited, more members of the same species may crowd together, increasing density. Yet, if dense nesting insures that a predator is more likely to be noticed, resulting in less nest destruction, then a change towards denser nesting would be beneficial in either the mixed or single species colony. However, if inter- and intraspecific aggression increases with more closely spaced nests, this might be detrimental to the productivity of 1 or both species, and greater packing together of nests would probably not occur.

Numbers of nests varied with location in the colonies and the distribution of each species was correlated with certain vegetation characteristics. The 2 species distributed themselves quite differently with respect to vegetation height, cover and volume (See Chapter IV). Likewise, there were differences in placement of the nests with respect to the edge and the center of the colony and distance to water. I hypothesized that the analysis of reproductive success of the gulls under these varying conditions might give some insight into the survival value of these factors. Other researchers have analyzed spatial distribution of and vegetation characteristics surrounding the nests to determine the causal factors of productivity (Crowell 1968, Jaeger 1972, Legg and Pitelka 1956, Maher 1962). Brown (1967b) in a comparative study on breeding biology of Herring and Lesser Black-backed Gulls (Larus fuscus), noted that breeding success was positively correlated with vegetation cover. Burger (1967) found that there was greater nest density with more vegetation cover. While this may not have increased productivity per nest, it increased it for the whole colony because more gulls could nest on the colony. Spacing, density, and nest location in the colony

likewise influence reproductive success in many other species (Legg and Pitelka 1956, Patterson 1965, Tenaza 1971).

The date of nesting is an important factor in successful breeding (Brown 1967b, Maher 1962, Patterson 1949). Clutch size is smallest and breeding success is least if eggs are laid at the end of the nesting period. For colonial birds, probably a more important factor is synchrony of nesting (Emlen 1976).

Possible causes of mortality in gull chicks are predation, weather, and starvation. Predation can be divided into predation by other species and predation by a conspecific (cannibalism). In the category of "other species" I place congeners also.

Predation by other gulls and cannibalism are the major mortality factors on gull colonies (Paynter 1949, Vermeer 1963,1970). From 34% to 41% of the eggs were observed to fledge. Paludan (1957) states that Herring Gulls on his study fledged less than 1 chick per nest.

MATERIALS AND METHODS

I obtained both birth data and chick mortality data for all colonies. In 1973 I performed a complete nest census on Freezeout Peninsula, gathering data on the number of chicks and eggs per nest. The values obtained were probably near the maximum clutch size for each nest because, precluding any egg mortality, there was essentially no chick mortality to confound the census since the eggs were just hatching. Likewise, in 1973 I obtained egg ages on 4 colonies from sample nests along transects 10 m apart and 1 m wide.

In 1974 I included in the census of clutch size only nests in transects 10 m apart (20 m apart at Arod) and 1 m wide. I began data gathering a month ahead of expected hatch date and ran 2-3 censuses per colony before the eggs hatched. I did not run censuses after the eggs hatched because of the disturbing factor of the census process, and the resulting chick mortality.

Because censuses disturbed and displaced chicks from their nests, I obtained the mortality data by counts of dead chicks after the breeding season had passed. I inspected each quadrat thoroughly for dead chicks and measured the chicks' tarsi to age them. I could not distinguish Ring-billed Gull from California Gull chicks and thus included for analysis of the dead chicks only monospecific quadrats. Because some chicks were consumed or blown away, not all chicks that died could be accounted for.

I hypothesized that the placement of the nests in the colony, the vegetation profile surrounding each nest, the nearest neighbor distance, density of the nesting and species of gulls would influence mortality rates but not birth rates. I believed that predation on chicks would be the mortality factor most responsible for chick death and that it would be influenced in various ways by the above factors. Subsequently, I analyzed these factors within and between species and within and among colonies with respect to mortality rates and birth rates.

RESULTS

Clutch Size

Using the Kolmogorov-Smirnov test, I found no difference in clutch size for each species among the 3 different 1974 colonies (Figures 5-1, 5-2). There was likewise no difference in clutch size between

the 2 species and among the 3 colonies in proportions of nests in each
category of clutch size (all p > 0.05).

Relationship Between Clutch Size and Various
Measures of Productivity

Figure 5-3 shows the steady decline of numbers of nests with
viable young throughout the early breeding season. This was consistent
for all colonies. Tables 5-1 and 5-2 show the changes in numbers of nests
with viable young and number of nests over time with respect to different
original clutch sizes. The changes in numbers of nests were not cor-
related with the original clutch size.

Tables 5-3A and 5-3B compare the mean age of eggs and the size
of their clutch. The general trend is for smaller clutches to be younger
which is what I expected. A chi square contingency test revealed no in-
fluence of age class on clutch size for Freezeout Peninsula in 1973, for
Larus californicus (p > 0.05), yet there was an influence for Larus
delawarensis (p < 0.05). There was no influence of age on clutch size
for Ring-billed Gulls at the Lakeside Unit Ring-billed Gull colony,
Bowdoin refuge, nor at the mixed Long Island colony at Bowdoin (Table
5-4A). The same was true for Ring-billed Gulls at Arod. The exceptions
were the California Gulls at Long Island and at Arod (p < 0.05).

At Freezeout Peninsula 1974, and Arod Island 1974, for both
species and at Freezeout Island 1974 for California Gulls, the initial
clutch size did not influence hatching success, rate of change of clutch
size, or survival of the eggs (p > 0.05, Table 5-4B).

A Mann-Whitney U test between ages of dead chicks on Freezeout
Peninsula and Arod revealed a significant difference in age of chick

FREEZEOUT PENINSULA:

1973

1974

PERCENT NESTS

CLUTCH SIZE

L. CALIFORNICUS N=393 X=2.61
L. DELAWARENSIS N=647 X=2.63

L. CALIFORNICUS N=22 X=2.27
L. DELAWARENSIS N=43 X=2.07
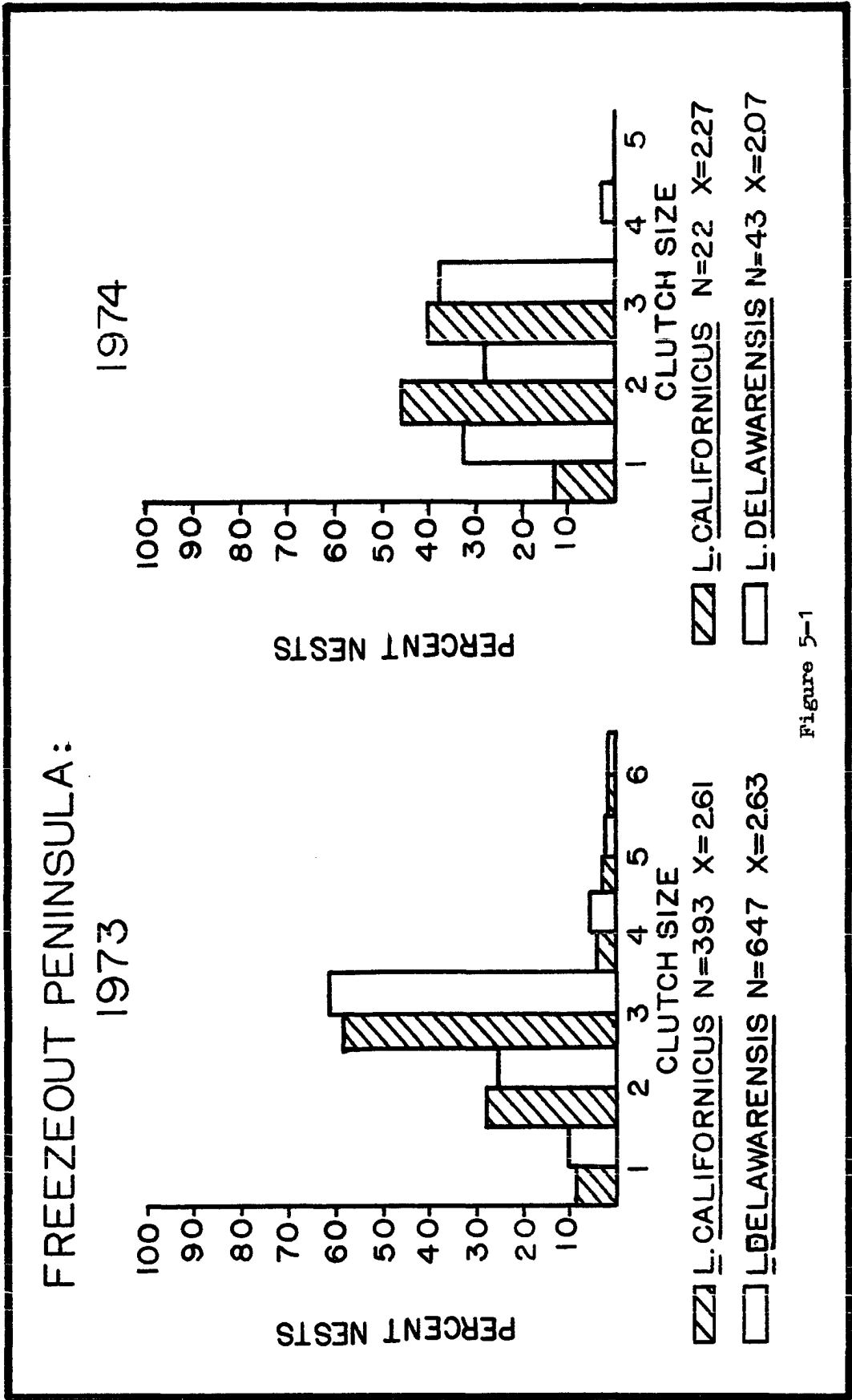
Figure 5—1
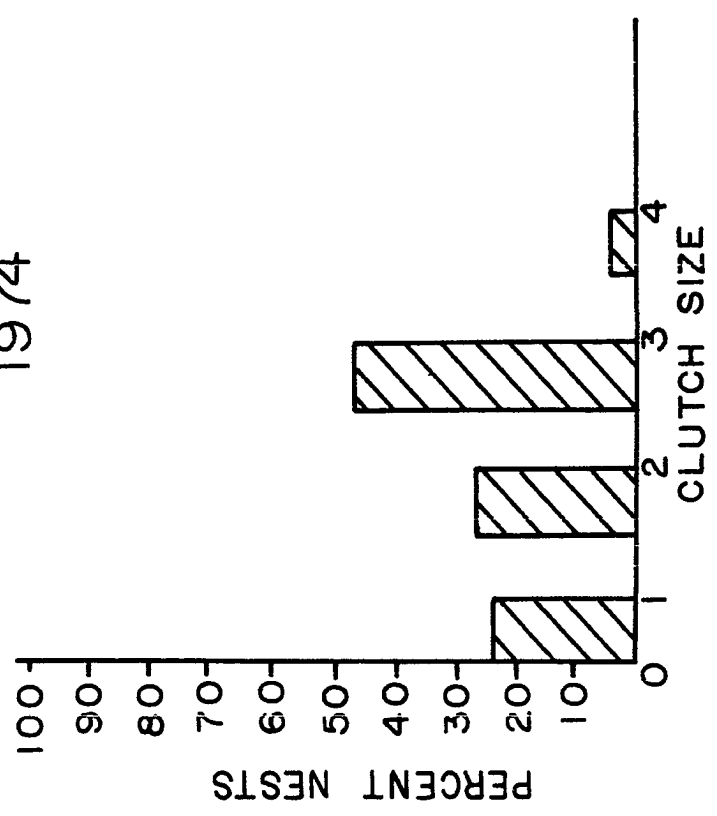
Figure 5-2

Figure 5-3
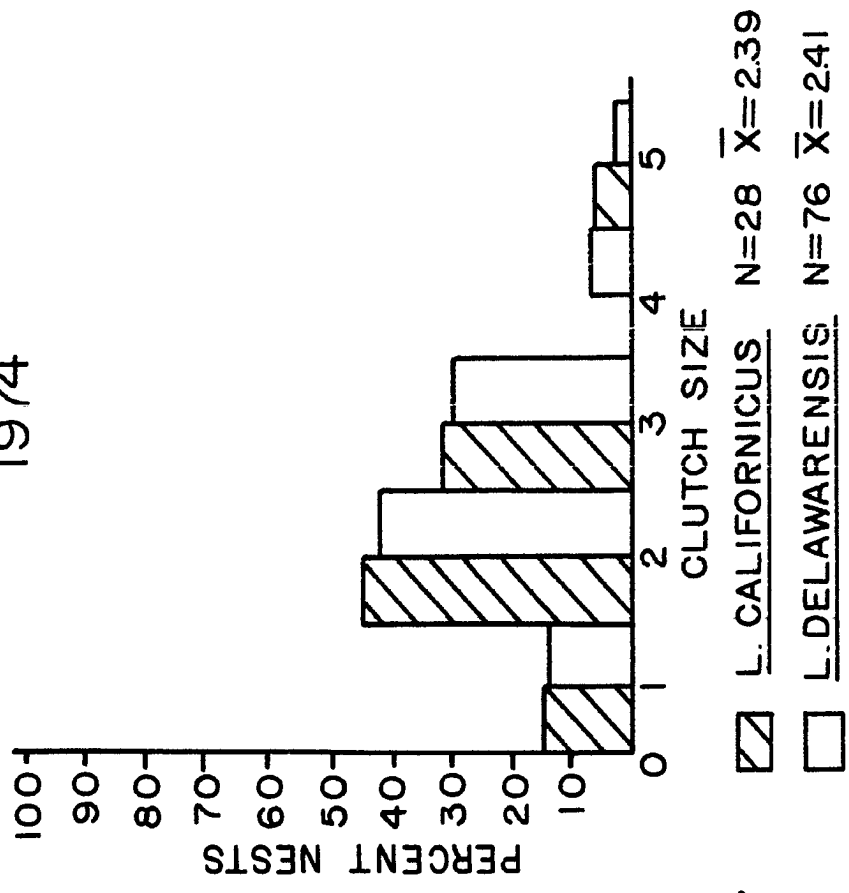
O = L. CALIFORNICUS
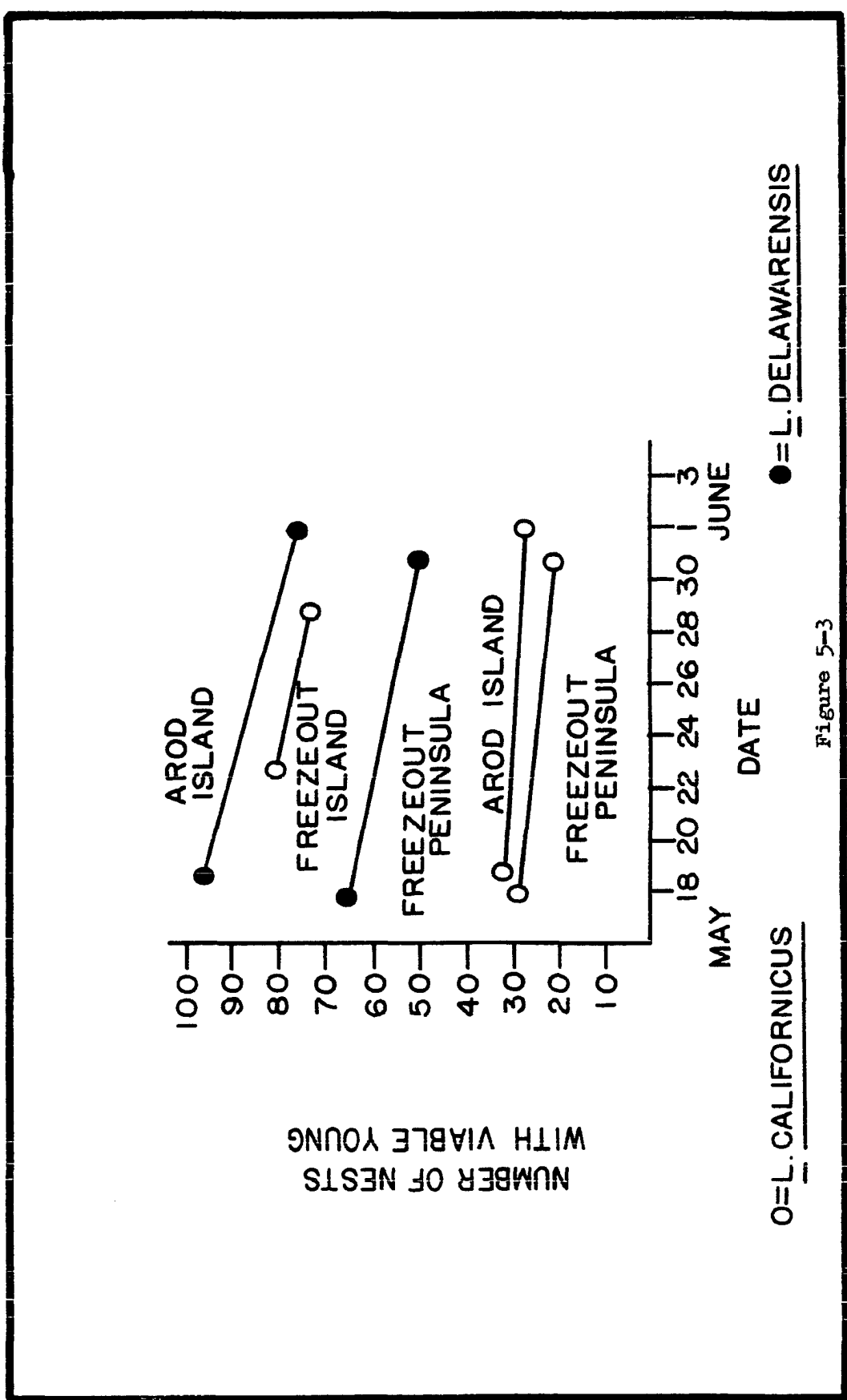
● = L. DELAWARENSIS

TABLE 5-1

Changes in Numbers of Nests with Viable Young

Colony	Larus californicus		Larus delawarensis	
Freezeout Peninsula 1974	18 May 30	31 May 22	18 May 66	31 May 52
Arod Island 1974	19 May 31	1 June 28	12 May 97	1 June 78
Freezeout Island 1974	23 May 81	29 May 75		

TABLE 5-2

Numbers of Nests with Various Clutch Sizes

Colony and Species	Early Spring Census (Post-Laying) Clutch Size						Late Spring Census (Pre-Hatching) Clutch Size					
	5	4	3	2	1	0	5	4	3	2	1	0
Freezeout Island, 1974 Larus californicus	-	1	62	15	3	0	-	3	33	19	19	7
Freezeout Peninsula, 1974 Larus californicus	-	-	6	7	-	1	-	-	6	5	-	3
Larus delawarensis	-	2	50	18	10	3	-	1	23	19	15	25
Arod Island, 1974 Larus californicus	2	-	19	8	2	0	2	-	8	11	5	5
Larus delawarensis	2	-	70	8	2	0	2	-	21	24	12	19

TABLE 5-3A

Mean Age[*] of Eggs in Different-Sized Clutches
10 May 1973

Colony and Species	Clutch Size				Grand Mean
	4	3	2	1	
Bowdoin—Lakeside Unit					
Larus delawarensis	1.25	1.52	1.53	1.50	1.69
Bowdoin—Long Island					
Larus californicus	—	2.5	1.5	—	2.35
Larus delawarensis	1.38	2.03	1.8	1.33	1.99
Arod Island					
Larus californicus	1.75	2.48	2.0	1.5	2.24
Larus delawarensis	1.37	2.2	2.75	2.67	1.93
Freezeout Peninsula					
Larus californicus	—	1.72	2.17	1.0	1.72
Larus delawarensis	—	2.8	1.5	1.5	1.81

[*]Age Code: 3 = 13-15 days old; 2 = 10-12 days old; 1.5 = 7-9 days old;
1.0 = 4-6 days old.

NOTE: Eggs hatched 31 May - 3 June

TABLE 5-3B

Mean Clutch Size of Different-Aged Eggs
10 May 1973

Colony and Species	Age in Days					Grand Mean
	16-18	13-15	10-12	7-9	4-6	
Bowdoin—Lakeside Unit						
Larus delawarensis	—	2.6	2.8	3.05	2.6	2.83
Bowdoin—Long Island						
Larus californicus	3.0	2.95	2.85	2.55	2.4	2.86
Larus delawarensis	—	2.9	2.75	2.92	2.63	2.82
Arod Island						
Larus californicus	—	2.72	2.95	3.25	2.3	2.76
Larus delawarensis	—	2.85	3.0	3.05	2.75	2.93
Freezeout Peninsula						
Larus californicus	—	2.6	2.95	3.0	2.3	2.71
Larus delawarensis	—	3.0	2.82	2.7	2.5	2.77

NOTE: Eggs hatched 31 May - 3 June.

TABLE 5-4A

Chi Square Contingency Tables:
Numbers of Nests

Colony	Larus californicus				Larus delawarensis			

Freezeout Peninsula 13-V-73

Clutch Size	Age (Coded) of Eggs				Clutch Size	Age (Coded) of Eggs	
	3-2	1½	1			3-2	1½-1
3	23	7	9		3	27	15
2-1	4	0	6		2-1	3	7

$$X^2 = 5.8656 \qquad\qquad X^2 = 3.8919$$
$$p > 0.05 \qquad\qquad\qquad p > 0.05$$

Lakeside Unit 10-V-73

Clutch Size	Age (Coded) of Eggs	
	3-2	1½-1
4-3	20	29
2-1	5	5

$$X^2 = 0.2846$$
$$p > 0.05$$

Long Island 10-V-73

Clutch Size	Age (Coded) of Eggs			Clutch Size	Age (Coded) of Eggs		
	3½-3	2	1½-1		3	2	1½-1
4-3	47	38	7	4-3	21	22	27
2-1	1	5	8	2-1	2	7	8

$$X^2 = 26.3627 \qquad\qquad X^2 = 2.3478$$
$$p < 0.05 \qquad\qquad\qquad p > 0.05$$

Arod Island 12-V-73

Clutch Size	Age (Coded) of Eggs				Clutch Size	Age (Coded) of Eggs	
	3	2	1½	1		3-2	1½-1
4-3	30	17	7	5	4-3	43	33
2-1	10	4	2	10	2-1	3	4

$$X^2 = 11.3868 \qquad\qquad X^2 = 0.489$$
$$p < 0.05 \qquad\qquad\qquad p > 0.05$$

TABLE 5-4B

Hatching Success of Eggs with Respect to Clutch Size

Colony	Larus californicus			Larus delawarensis		
	Clutch Size	# Eggs Laid	# Young Hatched	Clutch Size	# Eggs Laid	# Young Hatched
Freezeout Peninsula 1974	1	1	0	1	9	2
	2	20	5	2	28	12
	3	51	11	3-4	110	36
	Clutch Size	# Eggs Laid	# Young Hatched	Clutch Size	# Eggs Laid	# Young Hatched
Arod Island 1974	1-2	16	4	1	2	3
	3-5	67	23	2	24	10
				3-5	240	97
	Clutch Size	# Eggs Laid	# Young Hatched			
Freezeout Island 1974	1	3	0			
	2	30	12			
	3	183	71			

death on the mixed colonies (p 0.001). Chicks died at a younger age at
Arod than they did at Freezeout. I could not determine from the dead
chicks the date they died.

Relationships Between Clutch Size and
Various Ecological Variables

A Kruskal-Wallis analysis of variance showed no difference in
nearest neighbor distance among nests with different clutch sizes in
either Ring-billed Gulls (p > 0.10) or California Gulls (p > 0.10), all
colonies, both years. I could not compare vegetation parameters for all
colonies in this manner because of the way the data were taken. Likewise,
analyses of variance for the nests on Freezeout Peninsula 1973 for per-
cent cover, height and volume (cover x height) of vegetation showed no
difference among clutch size for the Ring-billed Gulls (all p > 0.10).
However, the California Gulls did exhibit differences in vegetation
cover, height and volume with respect to clutch size (all p < 0.01,
Table 5-5). The cover was greatest with clutches of 5 and 6 and height
of vegetation was greatest with a clutch of 3. However, the differences
in actual measurement were not great: a 13% range in cover and, ex-
cluding 1 nest, a 10 cm range in height.

Table 5-6 compares the r^2 and F values for each set of variables
for both species. There was no correlation between clutch size and any
of the 4 independent variables tested.

On all 1974 colonies, for each species, there is no significant
difference among locations in colony with respect to numbers of young at
last or first census. The locations compared were: 1) within 10 m of
the water, 2) the landward edge of the colony, 3) the middle of the colony.

TABLE 5-5

Mean Vegetation Parameters By Clutch Size
Freezeout Peninsula, 1973*

	Larus californicus Clutch Size						Larus delawarensis Clutch Size					
	1	2	3	4	5	6	1	2	3	4	5	6
Vegetation Height (cm)	39.64 ± 18.31	40.31 ± 20.21	41.58 ± 19.53	39.62 ± 25.61	31.0 ± 25.38	15.0 0	18.8 ± 19.17	14.69 ± 17.42	17.67 ± 18.58	14.42 ± 13.11	23.83 ± 28.61	25.50 ± 30.41
Vegetation Cover (%)	91.3 ± 19.61	90.94 ± 19.48	93.43 ± 9.41	90.43 ± 28.47	94.29 ± 7.33	104.0 0	82.43 ± 30.65	84.98 ± 29.93	84.98 ± 29.93	89.63 ± 28.51	79.97 ± 39.85	60.43 ± 59.38
Vegetation Volume (cover x ht)	3752.87 ±1740.20	3820.81 ±1939.28	3936.8 ±1951.10	3938.47 ±2554.68	3036.7 ±2604.2	1558.35 0	1763.39 ±1790.55	1431.33 ±1764.91	1716.29 ±1829.74	1417.27 ±1253.91	2328.66 ±2689.7	2443.7 ±3351.67

*Confidence Intervals = 1 S.D.

TABLE 5-6

Correlation of Clutch Size and Vegetation Parameters and Nearest Neighbor Distance

Colony and Species	Independent Variable	r^2	F	p >
Freezeout Peninsula, 1974	Percent Cover Vegetation	0.00484	1.8438	0.10
	Height of Vegetation	0.000499	0.2017	0.10
Larus californicus	Cover X Height of Vegetation	0.000184	1.3373	0.10
	Nearest Neighbor Distance	0.00204	0.7861	0.10
	Percent Cover Vegetation	0.000004	0.005	0.10
	Height of Vegetation	0.00051	0.3084	0.10
Larus delawarensis	Cover X Height of Vegetation	0.00085	0.536	0.10
	Nearest Neighbor Distance	0.00091	0.575	0.10

Both the X^2 contingency test, comparing starting and ending numbers of young with location, and the extension of the median test, comparing clutch sizes greater than and less than or equal to the median with respect to location yielded a $p > 0.05$ (Tables 5-7, 5-8).

Mortality of Clutches—Hatching and Pre-Hatching

Total pre-hatching mortality could not be compared accurately among the colonies because the census periods for each colony differed. Therefore, a daily mortality rate was used. This is obtained by the formula $M_d = -\ln\left(\dfrac{N_{t+1}}{N_t}\right)\Big/ d$, where M_d = daily mortality rate, N_{t+1} and N_t are the number of eggs at times t+1 and t respectively, and d = number of days between t+1 and t.

I compared the daily clutch mortality rates in all colonies for both species during the pre-hatching-hatching stage. The average rates per colony are displayed in Table 5-9 and Figure 5-4. Both species at Freezeout Peninsula had a higher average daily mortality rate than they did at Arod and the California Gulls at Freezeout Island had the highest mortality rate for all colonies, both species. A stepwise multiple regression analysis for each colony and species yielded a correlation coefficient that was not significantly different from zero between daily mortality rate and density for the mixed colonies but revealed a significant correlation with density in a curvilinear fashion for the single species colony (Table 5-10). The multiple correlation coefficient for daily mortality rate and density is 0.3168 (F = 4.29). Changes in productivity are displayed in Tables 5-17 through 5-19.

TABLE 5-7

Starting and Ending Numbers of Eggs
with Respect to Location in the Colony

	Location in Colony		
	Edge of Water	Middle	Landward Edge
	Larus delawarensis Freezeout Peninsula, 1974		
First Census	43	21	103
Final Census	18	13	79
	Larus delawarensis Arod Island, 1974		
First Census	55	74	149
Final Census	31	60	93
	Larus californicus Freezeout Peninsula, 1974		
First Census	43	21	103
Final Census	24	13	79
	Larus californicus Arod Island, 1974		
First Census	31	7	47
Final Census	30	6	31

TABLE 5-8

Clutch Size and Location in Colony

Colony		Larus californicus Location of Nest in Colony				Larus delawarensis Location of Nest in Colony		
		Edge of Water / Middle	Landward Edge		Edge of Water Middle		Landward Edge
Arod Island 1974	> Median	7	4	> Median	6	12	16
	≤ Median	9	13	≤ Median	14	15	34
		$x^2 = 1.522$ df = 1 $0.3 > p > 0.2$			$x^2 = 4.029$ df = 2 $0.2 > p > 0.1$		
		Edge of Water Middle /	Landward Edge		Edge of Water Middle		Landward Edge
Freezeout Peninsula 1974	> Median	6	3	> Median	4	1	18
	≤ Median	14	5	≤ Median	15	8	24
		$x^2 = 0.1482$ df = 1 $0.8 > p > 0.7$			$x^2 = 5.035$ df = 2 $0.1 > p > 0.05$		

TABLE 5-9

Reproductive Success
Mortality Rate: Egg Stage

Colony	Larus californicus		Larus delawarensis	
	Daily Mortality Rate	$\bar{X}$ Density	Daily Mortality Rate	$\bar{X}$ Density
Freezeout Peninsula 1974	0.029	0.055	0.031	0.254
Arod Island 1974	0.016	0.165	0.021	0.539
Freezeout Island 1974	0.046	0.270	—	—

Figure 5-4

O = L. CALIFORNICUS
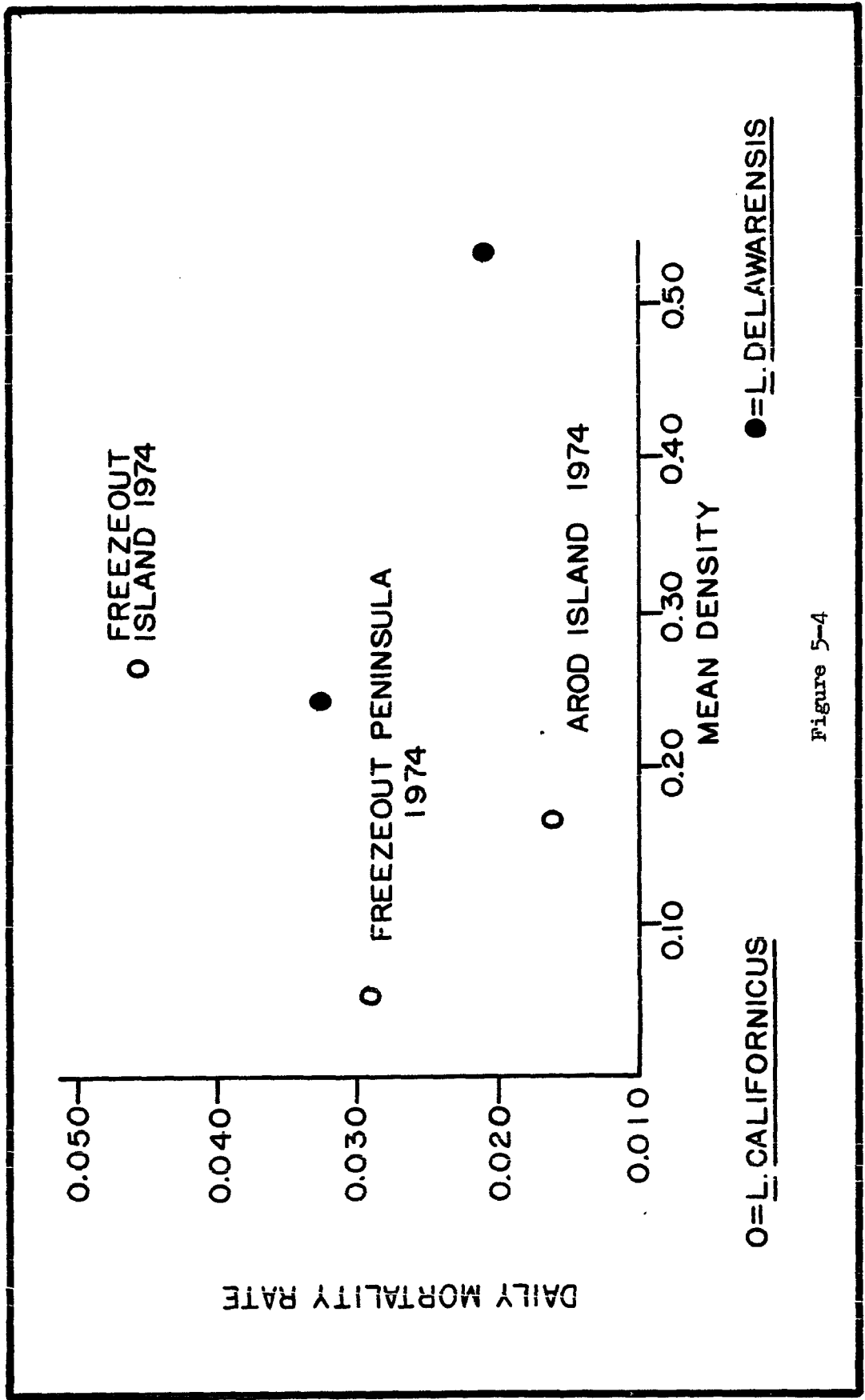
● = L. DELAWARENSIS

TABLE 5-10

Correlation Matrices
Daily Mortality Rate: Clutches

Colony	Larus californicus			Larus delawarensis		
	Mortality Rate	Density	Density^2	Mortality Rate	Density	Density^2
Arod Island 1974 — Mortality Rate	1.0	0.353	0.356	1.0	0.294	0.227
Freezeout Peninsula 1974 — Mortality Rate	1.0	0.147	0.203	1.0	-0.104	-0.138
Freezeout Island 1974 — Mortality Rate	1.0	0.428	0.337			

Descriptions of Mortality

I determined a chick death rate for each quadrat, using the dead chick counts. On each colony, the count of dead chicks revealed no difference in mortality of chicks with respect to location in the colony: water edge, middle, or land edge. All colonies were compared with respect to death rate (#dead/nest per quadrat) first by a Kruskal-Wallis analysis of variance, and then pair-wise by a Mann-Whitney U test. There was a higher mortality rate on Arod in 1974 than on Freezeout Peninsula in 1973 (p < 0.001) or 1974 (p < 0.001). There was a higher rate of chick mortality at Freezeout Peninsula in 1973 than in 1974 (p < 0.009) and there was higher chick mortality on Freezeout Island in 1974 than on the peninsula in 1974 (p < 0.0005).

I compared the mortality in the 3 main areas of the Freezeout Peninsula colony for each species by the Kruskal-Wallis analysis of variance. The location in the colony had no relationship on the mortality for either species (p < 0.05). The mortality rates averaged the same among the 3 areas.

Relationships Between Mortality and
Various Ecological Variables

I tested 3 sample colonies for relationships among mortality rate and density, clutch size, nearest neighbor distance, vegetation parameters, and age of dead chicks. The colonies were: Freezeout Island 1974, Arod Island 1974, and Freezeout Peninsula 1973. I did not use Freezeout Peninsula 1974 in the analyses because it replicates 1973 and there was some unknown human disturbance on this colony in the midst of the chick rearing season, which increased mortality. The test I used

for the above comparisons was a multiple stepwise regression. Table 5-11 compares the summaries for each test and Tables 5-12, 5-13A, 5-13B, 5-14A, and 5-14B give the correlation matrices. Tables 5-15 and 5-16 give the correlation matrices and the summaries for each test respectively for death rate and density only.

Survival of Chicks—Post-Hatching

Ring-billed Gulls on Arod Island and Freezeout Peninsula had mortality rates that were correlated with nearest neighbor distance and clutch size ($p < 0.001$). The greater the nearest neighbor distance, the higher the chicks' mortality for both mixed colonies. However, on Freezeout, the mortality was negatively correlated with clutch size while at Arod it was positively correlated. There was no consistent pattern of correlation for the various California Gulls' mortality rates. On both Freezeout Peninsula and Freezeout Island, mortality was positively correlated with chick age at death ($p < 0.001$). On Freezeout Peninsula, there was high mortality correlated with low cover and on Arod mortality was negatively correlated with density and positively correlated with clutch size ($p < 0.025$).

When all values of mortality and density are combined for each species, all colonies, there is a negative correlation between death rate and density for Ring-billed Gulls ($p < 0.001$) but no correlation for California Gulls. A plot of death rate and density for each species, all colonies combined, suggests a U-shaped and a hyperbolic curve for California and Ring-billed Gulls respectively (Figures 5-5, 5-6).

TABLE 5-11

Stepwise Multiple Regression
Death Rate and Nesting Niche Parameters

Regression Steps and Equation	Multiple r	Multiple F

Freezeout Peninsula, 1973

Larus delawarensis

Step 1—Nearest Neighbor Distance
$r = 0.6278$
$r^2 = 0.3941$
$F = 14.958$
$= 1,29$

Step 2—Clutch Size
$r = 0.6983$
$r^2 = 0.4876$
$F = 4.014$
$= 2,28$

Larus californicus

Step 1—Age of Chicks
$r = 0.5002$
$r^2 = 0.2502$
$F = 17.352$
$= 1,53$

Step 2—Vegetation Cover
$r = 0.5671$
$r^2 = 0.3216$
$F = 5.3685$
$= 2,52$

Arod Island, 1974

Larus delawarensis

Step 1—Nearest Neighbor Distance
$r = 0.8780$
$r^2 = 0.7708$
$F = 50.457$
$= 1,16$

Step 2—Clutch Size
$r = 0.9141$
$r^2 = 0.8357$
$F = 5.522$
$= 2,15$

Larus californicus

Step 1—Clutch Size
$r = 0.6643$
$r^2 = 0.4413$
$F = 8.690$
$= 1,12$

Step 2—Density
$r = 0.7924$
$r^2 = 0.6279$
$F = 5.0128$
$= 2,11$

Freezeout Island, 1974

Larus californicus

Step 1—Tarsal Length
$r = 0.3655$
$r^2 = 0.1336$
$F = 3.393$
$= 1,22$

TABLE 5-12

Correlation Matrices

Death Rate and Nesting Niche Parameters

Freezeout Island, 1974

Species	Density	Clutch Size	Vegetation Height	Vegetation Cover	Vegetation Volume	Nearest Neighbor Distance	Tarsal Length	Death Rate
Density	1.0	-0.516	0.168	-0.078	0.116	-0.693	0.283	0.160
Clutch Size		1.0	-0.149	-0.155	-0.045	0.412	0.006	-0.258
Vegetation Height			1.0	0.674	0.943	-0.012	-0.094	-0.136
Vegetation Cover				1.0	0.769	0.210	-0.007	0.195
Vegetation Volume					1.0	0.045	-0.137	-0.117
Nearest Neighbor Distance						1.0	-0.282	-0.048
Tarsal Length							1.0	0.366
Death Rate								1.0

Larus californicus

TABLE 5-13A

Correlation Matrices
Death Rate and Nesting Niche Parameters
Arod Island, 1974

Species	Density	Clutch Size	Vegetation Height	Vegetation Cover	Vegetation Volume	Nearest Neighbor Distance	Tarsal Length	Death Rate
Density	1.0	-0.118	-0.408	-0.602	-0.391	-0.588	0.323	-0.494
Clutch Size		1.0	-0.014	0.106	-0.183	-0.077	-0.339	0.186
Vegetation Height			1.0	0.499	0.862	0.082	-0.372	0.173
Vegetation Cover				1.0	0.716	-0.028	-0.647	-0.028
Vegetation Volume					1.0	-0.071	-0.561	-0.034
Nearest Neighbor Distance						1.0	0.226	0.878
Tarsal Length							1.0	0.006
Death Rate								1.0

Larus delawarensis

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TABLE 5-13B

Correlation Matrices
Death Rate and Nesting Niche Parameters
Arod Island, 1974

Species	Density	Clutch Size	Vegetation Height	Vegetation Cover	Vegetation Volume	Nearest Neighbor Distance	Tarsal Length	Death Rate
Density	1.0	0.026	0.137	0.539	0.327	-0.486	-0.048	-0.415
Clutch Size		1.0	0.465	0.046	0.237	-0.445	0.170	0.664
Vegetation Height			1.0	0.318	0.911	-0.601	0.332	0.388
Vegetation Cover				1.0	0.617	-0.311	0.125	-0.288
Larus californicus Vegetation Volume					1.0	-0.576	0.363	0.134
Nearest Neighbor Distance						1.0	-0.461	-0.313
Tarsal Length							1.0	0.300
Death Rate								1.0

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TABLE 5-14A

Correlation Matrices

Death Rate and Nesting Niche Parameters

Freezeout Peninsula, 1973

Species	Density	Clutch Size	Vegetation Height	Vegetation Cover	Vegetation Volume	Nearest Neighbor Distance	Tarsal Length	Death Rate
Density	1.0	0.193	-0.116	0.208	-0.093	-0.438	0.021	-0.386
Clutch Size		1.0	-0.324	0.044	-0.277	-0.443	-0.322	-0.552
Vegetation Height			1.0	0.692	0.997	-0.106	0.002	0.163
Vegetation Cover				1.0	0.711	-0.436	-0.152	-0.296
Larus delawarensis Vegetation Volume					1.0	-0.114	-0.026	0.126
Nearest Neighbor Distance						1.0	0.268	0.628
Tarsal Length							1.0	0.395
Death Rate								1.0

TABLE 5-14B

Correlation Matrices
Death Rate and Nesting Niche Parameters
Freezeout Peninsula, 1973

Species	Density	Clutch Size	Vegetation Height	Vegetation Cover	Vegetation Volume	Nearest Neighbor Distance	Tarsal Length	Death Rate
Density	1.0	0.092	0.355	0.156	0.348	-0.495	0.468	0.080
Clutch Size		1.0	0.053	0.241	0.047	0.094	0.187	0.139
Vegetation Height			1.0	0.480	0.985	-0.097	0.387	0.037
Vegetation Cover				1.0	0.507	-0.040	0.072	-0.230
Larus californicus Vegetation Volume					1.0	-0.138	0.372	0.018
Nearest Neighbor Distance						1.0	-0.191	0.030
Tarsal Length							1.0	0.500
Death Rate								1.0

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TABLE 5-15

Correlation Matrices
Log Death Rate: Chicks
All Colonies Combined

	Larus californicus				*Larus delawarensis*		
	Log Death Rate	Density	Density^2		Log Death Rate	Density	Density^2
Log Death Rate	1.0	-0.163	-0.118	Log Death Rate	1.0	-0.311	-0.233

TABLE 5-16

Stepwise Multiple Regression
Log Death Rate and Density + Density^2

Larus californicus
F is not significant

Larus delawarensis		
Regression Step and Equation	Multiple r	Multiple F
Step 1—Density	$r = 0.3114$ $r^2 = 0.0969$	F = 4.938 = 2,50

TABLE 5-17

Changes in Clutches
Freezeout Peninsula, 1974

	Larus californicus		Larus delawarensis	
	Date of Census			
	18 May	31 May	18 May	31 May
Number of Nests	32	32	69	71
Number of Eggs	73	33	167	55
$\bar{X}$ Clutch Size: Eggs	2.28	1.06	2.42	0.77
Number of Chicks	0	17	3	60 (58 live, 2 dead)
Total Potential Young	73	50	170	115 (113 live)
$\bar{X}$ Clutch Size Total	2.28	1.52	2.46	1.59 (live)

TABLE 5-18

Changes in Clutches
Freezeout Island, 1974

	Larus californicus only Date of Census	
	23 May	29 May
Number of Nests	81	81
Number of Eggs	191	99 (98 live, 1 dead)
X̄ Clutch Size Eggs	2.36	1.21 (live)
Number of Chicks	33 (32 live, 1 dead)	87 (71 live, 16 dead)
Total Potential Young	223	169 (live)
X̄ Clutch Size Total	2.75 (live)	2.09 (live)

TABLE 5-19

Changes in Clutches
Arod Island, 1974

	Larus californicus		Larus delawarensis	
	Date of Census			
	12 May	1 June	12 May	1 June
Number of Nests	31	33	97	98
Number of Eggs	83	38	278	74
X̄ Clutch Size Eggs	1.68	1.15	2.87	0.76
Number of Chicks	1	35 (30 live, 5 dead)	0	133 (110 live, 23 dead)
X̄ Clutch Size Total	2.71	2.06	2.87	1.88

DEATH RATE
OF
CHICKS

L.CALIFORNICUS
(ALL COLONIES)

Figure 5-5

DEATH RATE
OF
CHICKS

L. DELAWARENSIS
(ALL COLONIES)

Figure 5-6

DENSITY OF NESTS/METER^2

DEATH RATE OF CHICKS/NEST
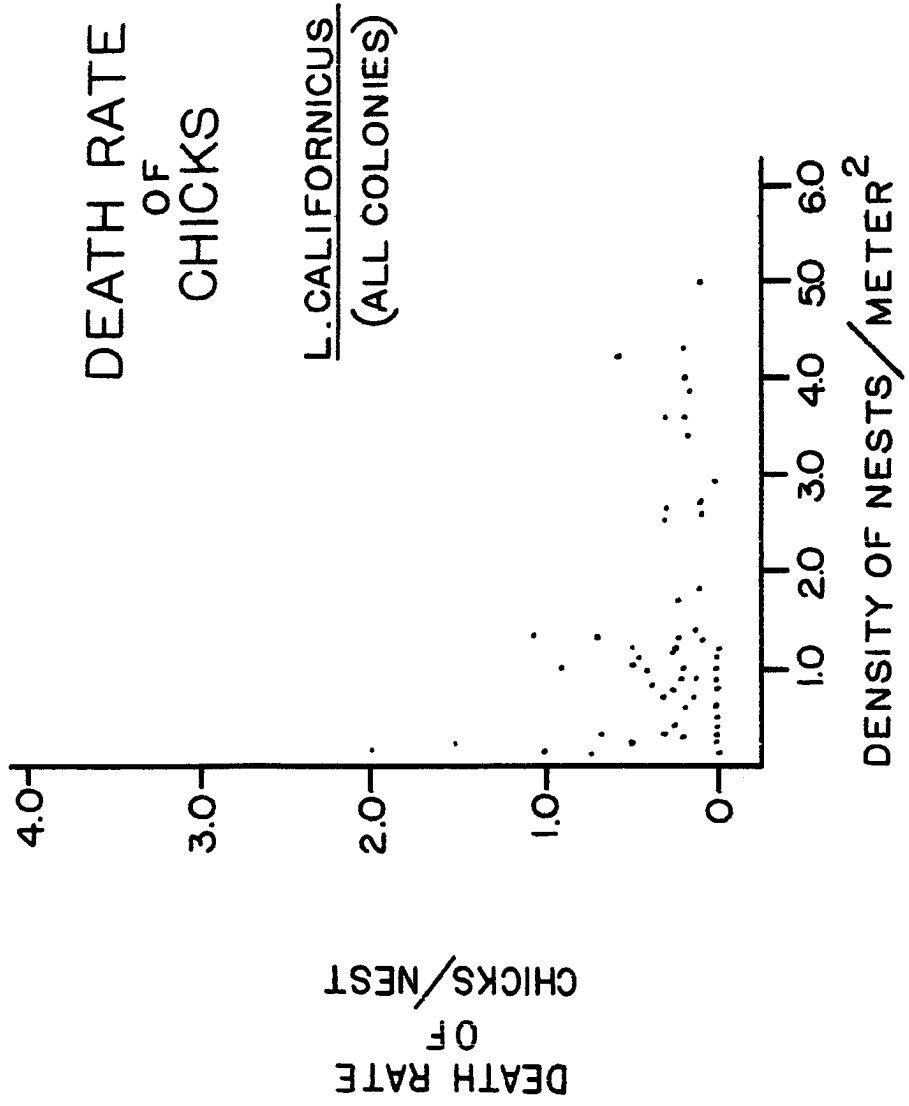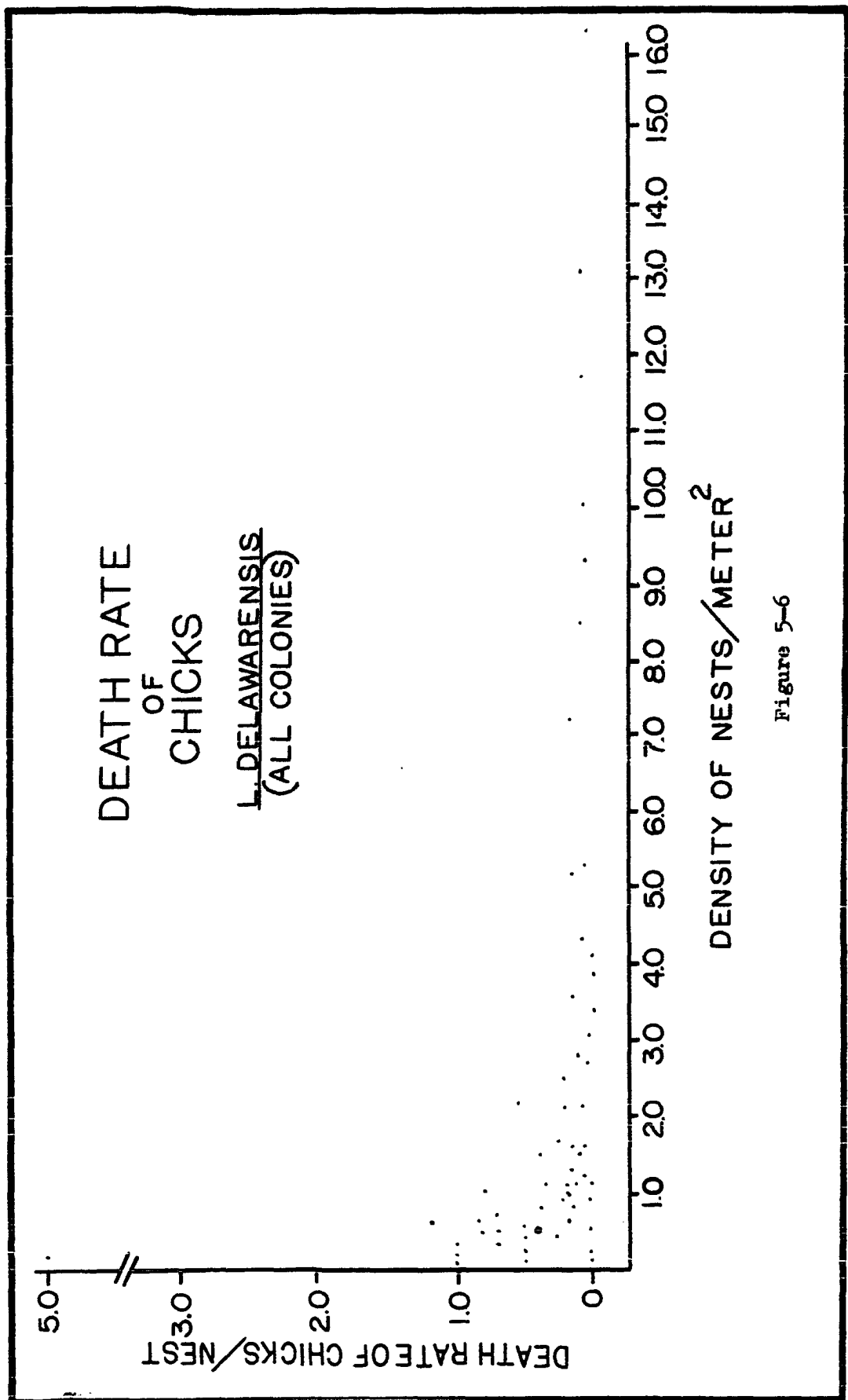
DISCUSSION

All colonies in this study can be compared without bias with re-
spect to productivity because their breeding cycles coincided. This dis-
cussion has 6 major parts: 1) description of clutch size among and
within colonies, 2) comparisons of hatching success and survival of
chicks among and within colonies, 3) relationships between clutch size
and various ecological variables: nearest neighbor distance, vegetation
profile, density, location in colony, date of laying and age at chick
death, 4) influence of clutch size on hatching success, survival, and age
of chick death, 5) mortality description, and 6) correlation of mortality
rates of chicks and variables in the nesting niche.

Description of Clutch Size

Not only were the differences in clutch size among and within the
colonies not significant but also the distribution of nests within clutch
classes was not significantly different. I did not expect any differ-
ences among the colonies for each species because although there are minor
vegetational and topographic differences among the colonies they are near
each other geographically and experience the same **macroclimate** and any
other ecological influences from the environment.

Hatching Success and Survival of Chicks

The hatching success (daily survival rate of eggs) and the chick
survival rates, with the exception of Freezeout Peninsula Ring-billed
Gulls, was what I predicted. For both Ring-billed and California Gulls,
hatching success was less on the peninsula than on the 2 islands. Also,

the total survival of eggs and chicks in the hatching and pre-hatching stages was less on the peninsula with more eggs and chicks unaccounted for there than on any other colony. This is understandable because predators can get to the peninsula colony much more easily than they can to the insular colonies. Terrestrial predators such as the long-tailed weasel, coyotes and snakes were only seen on the peninsula, never on the islands. The low hatching success in 1974 also may have been in part a result of human disturbance early in the season. Some nests were deserted permanently. A greater proportion of Ring-billed Gulls than California Gulls remained on the peninsula after this disturbance. This may have been because the person(s) only trespassed on the California Gull area. The higher survival rate of the Ring-billed Gulls on Freezeout Peninsula may in part have been a result of the release from California Gull predatory pressure.

The high hatching and survival rates on Arod Island for California Gulls may be related to the insular aspects of the colony in conjunction with a higher, denser vegetation and greater nearest neighbor distances. Some authors (Brown 1967b, Burger 1967) have noted a greater breeding success correlated with cover. The greater Ring-billed Gull survival and hatching success may be due to the fact that on Arod they also are nesting at their preferred nearest neighbor distance and near vegetation with the preferred profile. On Arod the Ring-billed Gulls nested near vegetation that was lower and less dense than that at Freezeout. The nearest neighbor distance was closer at Arod for the Ring-billed Gulls than at Freezeout Peninsula. Perhaps this is a spacing pattern to ensure more protection from California Gull predation, hence

the higher chick survival. Also, these may be the preferred conditions under which Ring-billed Gulls have survived for many years and have had the greatest breeding success. The biggest factor, however, may have nothing to do with vegetation, but rather may be the insular nature of the colony.

Freezeout Island has a lower hatching success and chick survival rate than does the mixed colony at Arod. The nearest neighbor distance on this monospecific colony is also lower than it is on Arod and the height and cover of vegetation is much less. These factors perhaps working synergistically may increase the intraspecific predatory pressure and thus account for the lower rates.

In both mixed colonies, more Ring-billed eggs and chicks could not be accounted for than California eggs and chicks. As noted before, California Gulls are predatory not only on their own chicks, but also on Ring-billed Gull chicks. Ring-billed Gull adults do not often trespass onto the California Gull area and therefore are predatory mainly on their own chicks. California Gull adults are also larger and may have a greater ability to eat chicks. Ring-billed Gulls furthermore are not so aggressive nor are they as big as the California Gulls and thus their chick-eating capacity is somewhat limited by size (Vermeer 1970).

The Arod and Freezeout colonies have hatching and chick survival rates comparable to other colonies. The figures may seem low but Lack (1954) states that approximately 25% of ground nesting birds' young survive to fledge. Paludan (1951) found that 20% Herring Gull (_Larus argentatus_) chicks and 5% Lesser Black-backed Gull (_Larus fuscus_) chicks

fledged. The steady decline of nests with viable young (Figure 5-2) was what I expected and is comparable to these other studies.

Relationship Between Clutch Size and Nearest Neighbor Distances, Vegetation Profile, Location in Colony and Date of Laying

There was no significant difference within the Ring-billed Gull clutch sizes at Freezeout Peninsula (1973) in nearest neighbor distance and vegetation profile. However, there was a significant difference for the California Gulls' clutch sizes with respect to the vegetation parameters. However, the actual differences for the California Gulls were not great, a range of 13% cover and 10 cm height.

The comparison of the average nearest neighbor distance with respect to clutch size among and within all 1974 colonies also yielded no significant difference. This is what was expected because clutch size is genetically laid down by years of evolution (Lack 1954,1969). In most bird studies, clutch size is not what is altered to adapt to changing environmental conditions; death rate is and it often has been shown to be density dependent (Lack 1954,1968).

Likewise, the location in the colony had no influence on clutch size. This agrees with what I predicted about clutch size and with the clutch size theories of Lack and others. Location furthermore did not influence egg survival over a three-week period.

A regression analysis yielded no significant correlation between clutch size and the variables: nearest neighbor distances, vegetation profile parameters, and location in colony for all 1974 clutches. There was a general trend for later layers to have smaller clutches. However,

the x^2 test for <u>Larus californicus</u> yielded no influence of age class on clutch size while for <u>Larus delawarensis</u>, clutch size was contingent on date of laying. In the latter case, the clutch sizes had been grouped into just 2 categories for the analysis, so that the results aren't as meaningful as they would have been if, without grouping categories, the test had been significant.

In general, however, the trend is for the mid-season nesters and early nesters to have the largest clutch sizes. This is similar to the Kittiwake (Lack 1969) whose relationship of clutch size and nesting date is related to the availability of food throughout the season. There is probably less food available towards the end of the season. This is un-like the relationship between clutch size and date of laying in many perching birds where the food is most abundant in mid-season. Others have found that the later nesters with smaller clutch size have less breeding success (Kennedy 1973, Lack 1969, Vermeer 1968). However, Emlen (1976) states that synchrony in nesting is more important for colonial birds than is the actual nesting date.

Influence of Clutch Size on Hatching Success, Survival and Age of Chick Death

Clutch size did not influence hatching success, chick survival or rate of change of the size of the clutch over a three-week sampling per-iod. It is Lack's (1954,1958) belief that birds will raise the number of chicks they can feed. There should also be some kind of obvious relation-ship between clutch size and survival of chicks if food is a limiting factor. I found no such relationship on any of the gull colonies. Lack's studies were mainly on passerine birds which are altricial. The colonial

gulls have semi-nidifugous young that are physically and behaviorally be-
tween altricial and precocial young. After the fifth day they leave the
nest for long periods of time and are able to feed themselves although
the parents feed them for at least 6 weeks. This may in part explain why
gulls do not follow the pattern of other birds. The adults and the chicks
are feeding the chicks.

The measurement of the tarsi on chicks is a common and consistent
method of aging them (Behle and Goates 1957). The dead chicks at Arod
were on the average younger than those at Freezeout. This may not be
very significant, however, because a large percentage of the Freezeout
chicks were missing. The smaller and therefore younger chicks are easily
eaten by predators, both by other species and by other gulls. Freezeout
also is less protected from the wind than is Arod because of geography
and vegetation differences and therefore winds could account for a
greater loss of small dead chicks at Freezeout Peninsula than at Arod.
The small chicks are light in weight and could be blown away easily into
the lake by strong winds. Therefore, any interpretation of the results
of the relationship between age at chick death and colony must take into
account these facts.

Mortality: Description

In mortality comparisons among the colonies I measured number of
dead chicks and converted this into a mortality rate by dividing by the
number of nests per quadrat or transect. As I expected, the monospecific
California Gull colony had the highest mortality rate. The intraspecific
pressure was manifested in aggression, fights, and predation on the

chicks. The vegetation volume cover and height were minimal for California Gulls on Freezeout Island and the nearest neighbor distances were closer there for this species than on any other colony sampled.

Freezeout Peninsula in 1973 had a higher mortality rate than did the same peninsula in 1974 perhaps due to the disturbance on the colony early in the breeding season. At this time many eggs would have been present and probably the absence of many dead chicks later on into the season was because they were destroyed in the egg stage. Furthermore, many adult California Gulls deserted nests at that time and therefore removed themselves as predators which contributed to high mortality rates. Arod may have what seems a higher mortality rate than Freezeout Peninsula 1973 because of less wind being present there. The wind at Freezeout could easily blow away any small chicks, thus lowering the count. Likewise, the birds are more crowded at Freezeout and the vegetation is lower and less dense and this may mean that smaller chicks were readily seen and eaten completely, thus artificially depressing the numbers in the count of dead chicks.

Mortality and Location in the Colony

A x^2 test revealed no significant difference for number of chicks dying with respect to location. The numbers of dead chicks found in each of the areas, water edge, middle, and land edge, did not differ significantly from each other. The Kruskal-Wallis test of mortality rate and location in colony likewise revealed no difference. There is, however, a significant difference in every colony between number of nests in the 3 main areas: water edge, land edge, and middle (See Chapter II). This

may be a result of social facilitation of nesting among colonial birds like gulls which other researchers have reported (Lack 1968, Tinbergen 1954, Vermeer 1968). Gulls often settle to nest in the densest part of the colony. The presence of other gulls may help to ensure synchronization of laying and also facilitates breeding behavior (Tinbergen 1954).

Multiple Regression of Various Independent Variables and Mortality Rates

The dependent variable, number of dead chicks per nest per quadrat (mortality rate), was regressed on various independent variables in a stepwise multiple regression equation to find the important variables influencing mortality. The independent variables included measurements of vegetation around the nests: height, cover, and volume; nearest neighbor distance; density; clutch size; date of laying; and age of chicks dying.

For Ring-billed Gulls, as the nearest neighbor distance increased, and density decreased, the mortality rate also increased at Arod and at Freezeout Peninsula. For the California Gulls at Arod, the mortality increased as the density and nearest neighbor distance decreased; while at Freezeout Island, as density increased, mortality increased. These are indications that intraspecific attraction may be an important factor for reproductive success (almost every nearest neighbor for both species was conspecific). Many authors have noted that gulls nest in the already occupied parts of the colony (Brewer 1963, Catchpole 1972, Crowell 1968, Dixon 1954, Hunt and Hunt 1973, Legg and Pitelka 1956).

For both species on Arod Island and for California Gulls at Freezeout Peninsula 1973, the clutch size varied directly with mortality

rate. A high mortality rate for chicks from large clutches may have been caused by the inability of the parents to feed a larger brood. This concurs with Lack's hypotheses (1954,1968). However, for the Ring-billed Gulls at Freezeout Peninsula, the mortality increased with lower clutch sizes.

Some vegetation characteristics influenced mortality rates. High mortality rates of the California and Ring-billed Gulls at Freezeout Peninsula were correlated with low cover of vegetation. This may in part explain their choice of nest sites near vegetation with high cover. The cover, height and volume measurements from the 1974 colonies describe the vegetation over the entire quadrat and were from sample plots that approximated the average vegetation cover and height in each plot. This approximation may not be as accurate as measurements taken 30 cm from the nests as in 1973 (See also Brown 1966b, Maher 1962, Patterson 1965).

California Gulls on all colonies and Ring-billed Gulls at Freezeout Peninsula had high mortality rates correlated with older dead chicks. Although puzzling at first, this becomes clearer when one considers that many chicks are eaten and never show up in the count of dead chicks. My hypothesis is that in quadrats where there are many dead chicks there must be many predatory adults that are big and strong enough to kill larger chicks. These adults are probably large enough to devour whole smaller chicks without leaving a trace and thus the mortality is most likely much higher on these quadrats than is revealed by the count of dead chicks.

When I combined data from all colonies for death rate and density comparisons, I found that the California Gulls showed no correlation between death rate and density, perhaps because these were so variable from colony to colony. The Ring-billed Gulls, though, exhibited a negative correlation between mortality rate and density. This relationship follows from the nature of the tightly compacted Ring-billed Gull subcolonies. Low density areas are on the edges of their subcolony where they are susceptible to predation, especially by adjacent California Gulls.

The graphs comparing density and death rate per quadrat seem to show a trend towards a U shape for California Gulls and towards a hyperbola for Ring-billed Gulls. This would indicate that there is some optimal density or range of densities where death rate of chicks is minimized. This U shape and hyperbola can be explained in part by the colonial behavior of the gulls. The colonies would not have remained cohesive units throughout evolutionary history had there not been some benefit to the individual birds in remaining colonial. For densities less than the optimal colonial density, the death rate increases, presumably from an increase in predation due to the loss of colonial protection, or from some loss in social facilitation of care for the chicks. Perhaps the adults are worse parents when they are removed from the colony or are at least in a less than optimal density. Social facilitation has been shown to play an important part in bird colonial life (Tinbergen 1953). Predators likewise could approach an individual nester more readily than they could approach an entire colony due to the mobbing of the predator by neighboring gulls. A too dense colony on the other hand, especially for California Gulls, would produce an increase in intraspecific and intrageneric

predation and thus also increase the death rate of chicks. Thus, an optimal density, as indicated by the U-shaped and hyperbolic curves in Figures 5-5 and 5-6, would seem the best nesting strategy for the birds to follow. However, more data points are necessary in order to make any definite conclusions about these trends.

CONCLUSION

Chick survival from the egg stage was higher on the mixed species island than on the peninsula. This is probably due to a lack of terrestrial predators on islands. The monospecific colony of California Gulls had a smaller survival rate than did either of the mixed species colonies. On the monospecific colony there was more crowding and probably a greater interspecific competition plus less desirable nesting sites, all which may have contributed to the increased mortality.

Clutch size is not correlated with any vegetation parameters, location in colony, or nearest neighbor distance. Death rate of Ring-billed Gull chicks was positively correlated with nearest neighbor distance for both colonies; and at Arod, positively correlated, and at Freezeout Peninsula, negatively correlated with clutch size. On both the Freezeout colonies, death rate of California Gull chicks was positively correlated with age at chick death. At Arod, there was a positive correlation with clutch size and a negative correlation with density, and at Freezeout Peninsula, a negative correlation with cover. These facts support the theories of other researchers who state that mortality rate not birth rate is what responds to short-term changes in the ecosystem.

There is also an indication that an optimal density exists on the colonies and that densities above or below this tend to have a higher death rate of chicks.

CHAPTER VI

SUMMARY

Much of the current work in ecology investigates the coexistence of two similar species and how this coexistence is effected. Foraging and nesting preferences are of importance in analysis of the ecology of 2 sympatric avian congeners. There is a limit to how similar their lifestyles can be and still allow the 2 species to coexist. The purpose of my study was to investigate the foraging and nesting niches of California and Ring-billed Gulls and to ascertain what enabled these congeners to coexist, what possible differences in lifestyles existed between them, and what may have been the causes behind these differences.

Ring-billed and California Gulls, Larus delawarensis and Larus californicus, migrate inland to breed. They often nest on the same island or peninsula, and nesting space in both these situations is very limited. They create specific subcolonies and they segregate the nesting habitat by height, cover, and volume of vegetation, even with the limited choice of places to nest. Vegetation can be of advantage to the gulls because it helps conceal nests and adults and is a good hiding place for chicks.

The California Gulls arrive 2 weeks ahead of the Ring-billed Gulls and establish nests near vegetation that is higher with more cover. They have greater nearest neighbor distances than do the Ring-billed Gulls, and lower densities. The California Gulls may limit the Ring-billed Gulls' expanding into adjacent nesting areas and may dictate

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the choices in vegetation profile by acquiring what seems to be the better nesting areas in the high dense vegetation, and when the Ring-billed Gulls arrive, they simply take what is left. However, the latter may prefer the low sparse vegetation or may be more generalists in their selection of nest sites. They have a greater range of choices of vegetation profile than do the California Gulls.

The spacing is probably dictated by the size and the behavior of the gulls. The California Gulls are larger and therefore would have larger territories, but they are also more aggressive and more cannibalistic than are the Ring-billed Gulls, and the greater nearest neighbor distances of the California Gulls may also be a result of this aggressive nature of the adults.

The characteristics of the nesting sites of the California Gulls in the monospecific colony differed markedly from those of these gulls in the mixed colonies. The gulls had a broader vegetation profile preference and also had smaller territories. I believe that this was not a case of ecological release but rather a unique packing-in situation resulting from priority preference of an island over a peninsula on which to build nests. In this case, vegetation profile would become a secondary preference. It is notable that no permanent single species Ring-billed Gull colonies were found.

The 2 species segregate the feeding niche by distance to the foraging areas, by what they eat and by habitat type. California Gulls forage farther from the colony and ingest a different array of prey which includes larger prey such as vertebrates. Ring-billed Gulls forage mainly in the irrigated areas and closer to the colony while California

Gulls forage mainly in the dryland farming areas and prairie and farther from the colony. Intraspecific competition for resources decreases with increasing distance from the colony, yet there must be a balance between energy expended traveling to the foraging area, and energy gained by exploiting this area. Perhaps by ingesting larger prey such as ground squirrels the California Gulls gain more energy per foraging trip and are thus able to travel greater distances.

There seems to be little overlap in the feeding or nesting niches of the California and Ring-billed Gulls and also there are few behavioral interactions between them. Ring-billed Gulls never trespass onto the California Gull subcolony, and California Gulls rarely enter the Ring-billed Gull area. When they occasionally do trespass, however, the Ring-billed Gulls respond by avoidance of the California Gulls.

There was no consistently strong trend for all 3 colonies studied with respect to any one parameter influencing reproductive success. However, there were positive correlations in some colonies between large nearest neighbor distance and low chick mortality and high dense vegetation and low chick mortality. There was greater chick mortality for both species on the peninsula than on the islands, which was expected. Island preference for nesting was probably dictated evolutionarily by pressure from terrestrial predators.

Chick and egg mortality is often caused by neighboring gulls, congeners or conspecifics, besides being caused by other predators. Often, congeneric or conspecific predation is a major cause of this mortality. The placement of nests in the colony must be then not only a placement that insures a balance between enhancement of group defense

and predator swamping by clumping and a scattering of nests for crypticity but also a placement that is as close as intraspecific competition will permit and one that is far enough apart to prevent or reduce the possibility of inter- or intraspecific predation. It is interesting to note that density and nearest neighbor distance of the California Gulls are not affected by presence of the Ring-billed Gulls as nearest neighbors, but the nearest neighbor distances of the Ring-billed Gulls are affected by what species the nearest neighbor is.

Instead of a competitive situation so often encountered between congeners, it seems as if there may be a symbiotic relationship between the 2 species. In Montana, the Ring-billed Gulls are almost always found in association with the California Gulls on the nesting grounds. The 1 single species Ring-billed Gull colony I found was at best a temporary one and clearly inferior nesting habitat.

The presence of many conspicuous ground nesters in reproductive synchrony is evolutionarily adaptive. There is mutual warning, they mob predators, and their sheer large numbers may discourage predators. Likewise, synchrony is reproduction which these gulls have has been shown to decrease predation. The smaller, less aggressive Ring-billed Gulls may gain advantage by aligning themselves during the nesting season with the larger California Gulls which have a greater tendency to attack predators. The Ring-billed Gulls may balance detrimental aggression and cannibalism of California Gulls against some benefit gained when in association with them.

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APPENDIX

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Hatching Success By Clutch Size

Freezeout Peninsula 1974

Larus californicus

Clutch Size	# Eggs Laid 18-V-74	# Young Hatched 31-V-74
1	1	0
2	20	5
3	51	11

(N = 27 Nests)

Change in Clutch Size (13 days)

Clutch Size	+	0	-
1	0	0	1
2	1	6	2
3	0	8	9

Larus delawarensis

Clutch Size	# Eggs Laid 18-V-74	# Young Hatched 31-V-74
1	9	2
2	28	12
3	102	35
4	8	1

(N = 59 Nests)

Change in Clutch Size (13 days)

Clutch Size	+	0	-
1	3	3	3
2	2	5	7
3	1	10	23
4	0	0	2

Arod Island 1974

Larus californicus

Clutch Size	# Eggs Laid 19-V-74	# Young Hatched 1-VI-74
1	2	0
2	14	4
3	57	23
5	10	0

(N = 30 Nests)

Change in Clutch Size (13 days)

Clutch Size	+	0	-
1	0	0	2
2	0	6	1
3	0	8	11
5	0	2	0

Larus delawarensis

Clutch Size	# Eggs Laid 12-V-74	# Young Hatched 1-VI-74
1	2	3
2	24	10
3	240	97
5	10	3

(N = 96 Nests)

Change in Clutch Size (20 days)

Clutch Size	+	0	-
1	1	0	1
2	5	6	1
3	4	20	56
5	0	2	0

Freezeout Island 1974

Larus californicus

Clutch Size	# Eggs Laid 23-V-74	# Young Hatched 29-V-74
1	3	0
2	30	12
3	183	62

(N = 79 Nests)

Change in Clutch Size (6 days)

Clutch Size	+	0	-
1	0	2	1
2	1	10	4
3	3	30	27

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Nearest Neighbor Distances in Meters
Freezeout Peninsula, 1973

Clutch Size	$\bar{X}$	S.D.	N
	Larus californicus		
0	2.36	1.91	7
1	1.46	0.91	28
2	1.57	0.85	107
3	1.67	1.41	230
4	1.37	0.85	13
5	1.74	0.92	7
6	2.21	0.0	1
	Larus delawarensis		
0	0.62	0.19	2
1	0.61	0.39	59
2	0.55	0.26	159
3	0.56	0.44	395
4	0.49	0.15	24
5	0.57	0.16	6
6	0.61	0.05	2

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Percent Cover X Height (Volume) of Vegetation
Freezeout Peninsula, 1973

Clutch Size	$\overline{X}$	S.D.	N
	Larus californicus		
0	4,509.7	1,664.55	7
1	3,752.87	1,740.2	28
2	3,820.81	1,939.28	107
3	3,936.8	1,951.1	230
4	3,938.47	2,554.68	13
5	3,036.7	2,604.2	7
6	1,558.35	0.0	1
	Larus delawarensis		
0	225.0	318.2	2
1	1,763.39	1,790.55	59
2	1,431.33	1,764.91	159
3	1,716.29	1,829.74	395
4	1,417.27	1,253.91	24
5	2,328.66	2,689.7	6
6	2,443.75	3,351.67	2

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Percent Cover of Vegetation
Freezeout Peninsula, 1973

Clutch Size	X̄	S.D.	N̄
	Larus californicus		
0	94.22	7.21	7
1	91.31	19.6	28
2	90.94	19.48	107
3	93.95	9.41	230
4	90.43	28.47	13
5	94.29	7.33	7
6	103.89	0.0	1
	Larus delawarensis		
0	90.0	0.0	2
1	82.43	30.65	59
2	84.41	29.56	159
3	84.98	29.93	395
4	89.68	28.51	24
5	79.97	39.85	6
6	60.43	59.38	2

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Height of Vegetation in Centimeters
Freezeout Peninsula, 1973

Clutch Size	$\bar{X}$	S.D.	N
	Larus californicus		
0	47.86	18.04	7
1	39.64	18.31	28
2	40.31	20.21	107
3	41.58	19.53	230
4	39.62	25.61	13
5	31.0	25.38	7
6	15	0.0	1
	Larus delawarensis		
0	2.5	3.54	2
1	18.8	19.17	59
2	14.69	17.42	159
3	17.67	18.58	395
4	14.42	13.11	24
5	23.83	28.61	6
6	25.5	30.41	2

Quadrat Summaries: *Larus californicus* and *Larus delawarensis*
Arod Island, 1974

Total # Nests	Line Transect #		Total Eggs and Chicks (live)	X̄ Clutch Size	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
3d	A2	A3	6	2.0	—	123.21	—	1.36	7	3.5
11d	A3	A4	33	3.0	0	0	0	0.51	4	3.8
5d	A4	A5	14	2.8	251.46	63.44	15,952.62	0.7	3	3.0
2d	A5	A6	6	3.0	139.7	33.21	4,639.44	0.97	2	3.4
5d	A6	A7	14	2.8	203.2	73.41	14,916.91	0.52	2	2.7
3d	B1	B2	9	3.0	203.2	39.23	7,971.54	1.02	3	3.6
6d	B2	B3	18	3.0	198.12	46.24	9,161.07	0.53	7	3.4
10d	B3	B4	30	3.0	162.56	39.23	6,377.23	0.54	2	4.0
5d	B4	B5	14	2.8	152.4	62.02	9,451.85	0.50	4	2.8
10d	B5	B6	30	3.0	142.24	22.79	3,241.65	0.46	8	3.5
4m	B6	B7	9	2.25	152.4	79.58	12,127.99	0.83	2	3.3
—	0	C1	—	—	—	—	—	—	1	—
7d	C1	C2	21	3.0	157.48	71.99	11,336.99	0.54	5	3.6
9	C2	C3	26	2.89	0	0	0	0.55	2	3.2
3d	C3	C4	11	3.67	33.02	90.0	2,977.8	0.51	2	3.7
11d	C4	C5	26	2.36	0	0	0	0.58	2	2.7
2m	C5	C6	5	2.5	83.82	66.86	5,604.21	1.13	1	4.0
2c	C6	C7	5	2.5	—	90.0	—	1.75	3	4.1
1d	D1	D2	3	3.0	134.62	33.21	4,470.73	2.29	5	4.6
1c	D2	D3	1	1.0	15.24	22.79	347.32	1.91	1	3.6
—			—	—	—	—	—	—	1	—
3d	D4	D5	9	3.0	187.96	50.77	9,542.73	0.58	3	2.8
—			—	—	—	—	—	—	0	—
2c	E2	E3	5	2.5	279.4	75.23	18,138.65	0.89	2	3.7
2c	E3	E4	5	2.5	68.58	64.92	3,894.66	1.01	1	3.3
1c	E4	E5	2	2.0	132.08	56.79	10,938.87	2.72	1 Adult	—
4c	E5	E6	11	2.75	68.58	82.82	4,908.27	1.11	2 Eggs	—
1c	E6		3	3.0	68.58	71.57	4,908.27	1.75	1	2.5

Quadrat Summaries: Arod Island, 1974 (continued)

Total # Nests	Line Transect #	Total Eggs and Chicks (live)	X̄ Clutch Size	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
3c	E6 E7	9	3.0	167.64	90.0	15,087.6	1.48	{ 1 Chick, 1 Egg }	5.0
1c	E7 E8	1	1.0	167.64	90.0	15,087.6	1.55	1	3.3
2c	F3 F4	6	3.0	121.92	77.08	9,348.59	1.24	{ 3 Chicks, 1 Adult }	{ 3.2 Chicks }
3c	F4 F5	9	3.0	121.92	71.57	8,725.81	1.16	{ 1 Chick, 1 Adult }	{ 2.6 Chick }
1c	F5 F6	5	5.0	243.84	50.77	12,379.2	0.94	4	3.6
4c	F6 F7	8	2.0	127.0	80.45	10,217.15	1.46	{ 1 Chick, 1 Adult }	{ 2.7 Chick }
3c	F7 0	8	4.0	127.0	80.45	10,217.15	1.82	—	—

c = Larus californicus
d = Larus delawarensis
m = Larus californicus and Larus delawarensis (mixed)

Quadrat Summaries: _Larus californicus_ Freezeout Island, 1974

Total # Nests	Quadrat #	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
6	A1 B2	157.4	90.0	14,166.0	5.94	0	—
—	A2 B3	—	—	—	—	—	—
13	A3 B4	58.34	63.43	3,700.51	2.23	3	4.2
25	A4 B5	48.18	30.0	1,445.4	2.23	8	3.0
26	A5 B6	—	—	—	—	3	3.8
40	A6 B7	0	0	0	0.89	9	3.2
39	A7 B8	132.0	90.0	11,880.0	0.96	4	2.9
37	A8 B9	137.08	90.0	12,337.2	0.95	9	3.7
29	A9 B10	192.96	90.0	17,366.4	1.20	10	3.5
42	A10 B11	0	0	0	1.20	25	3.2
30	A11 B12	73.58	86.35	6,353.63	1.06	17	3.2
41	A12 B13	63.42	63.44	4,023.37	0.80	14	2.7
35	A13 B14	76.12	110.3	8,396.04	0.80	15	4.0
22	A14 B15	—	57.66	—	1.47	9	3.2
2	A15 B16	48.18	81.67	3,934.86	5.54	1	3.5
39	A16 B17	12.62	22.79	287.61	0.97	7	3.4
43	A17 B18	294.56	90.0	26,510.4	0.73	9	3.2
34	A18 B19	228.52	45.0	10,283.4	0.87	8	3.3
50	A19 B20	60.88	26.57	1,617.58	1.26	6	3.2
36	A20 B21	40.56	12.92	524.04	1.05	8	2.9
36	A21 B22	152.32	60.0	9,139.2	1.15	11	4.1
34	A22 B23	43.1	30.0	1,293.0	0.82	6	4.2
26	A23 B24	17.7	15.34	271.52	1.64	8	4.0
27	A24 B25	20.24	9.97	201.79	1.50	3	3.5
17	A25 B26	27.94	33.21	927.89	1.16	4	5.0
26	A26 B27	0	0	0	2.90	3	4.2
10	A27 B28	0	0	0	0.58	1 adult	5.6 adult

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Quadrat Summaries: Larus californicus and Larus delawarensis, Freezeout Peninsula, 1973

Quadrat #	Total # Nests	Total Eggs and Chicks (live)	X̄ Clutch Size	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
1c(w)	2	3	1.5	34.0	90.0	3,060.0	5.5	0	—
2c(l)	1	3	3.0	30.0	90.0	2,700.0	4.5	0	—
3c(w)	7	18	2.57	46.29	92.11	4,250.00	1.84	1	4.0
4c(l)	4	10	2.5	44.5	90.0	4,005.0	1.43	1	4.0
5c(w)	5	16	3.2	44.4	90.0	3,996.0	3.08	3	3.0
6c(m)	10	24	2.4	42.4	91.39	3,856.28	1.72	9	2.8
7c(l)	10	25	2.5	23.1	90.0	2,079.0	1.19	0	—
8c(w)	2	6	3.0	33.0	90.0	2,970.0	1.8	0	—
9c(m)	13	35(1)*	2.69	43.38	90.0	3,904.62	1.41	14	3.9
10c(m)	14	36(18)*	2.57	33.0	90.0	2,970.0	1.49	2	4.0
11c(l)	3	7	2.33	20.0	34.14	2,048.4	1.04	5	4.0
12c(l)	1	3	3.0	43.0	90.0	3,870.0	13.25	0	—
13c(w)	6	18(3)*	3.0	44.33	91.72	4,039.88	1.58	1	2.6
14c(m)	13	33(13)*	2.54	40.62	91.86	3,714.78	1.21	9	4.0
15c(l)	10	25(5)*	2.5	57.0	92.484	5,284.33	1.07	0	—
16c(w)	1	2	2.0	42.0	103.89	4,363.38	2.52	0	—
17c(m)	18	45(10)*	2.5	43.06	91.52	3,944.15	1.16	5	3.2
18c(m)	11	29(8)*	2.64	40.64	92.53	3,733.04	1.64	5	3.2
19c(l)	2	6	3.0	13.5	90.0	1,215.0	1.75	0	—
20c(w)	10	24(3)*	2.4	47.0	91.18	4,296.02	1.19	5	3.4
21c(m)	12	32(8)*	2.67	37.17	94.87	3,541.77	1.07	4	3.4
22c(l)	6	16	2.67	32.33	92.46	2,971.54	2.04	0	—
23c(w)	13	35(2)*	2.69	45.54	90.0	4,098.46	1.25	1	5.7
24c(m)	6	16	2.67	41.5	97.39	4,104.25	2.06	0	—
25c(l)	1	2	2.0	16.0	90.0	1,440.0	3.5	0	—
26c(w)	6	13(5)*	2.17	69.83	90.0	6,285.0	1.28	0	—
27c(m)	13	32	2.46	43.38	94.48	4,122.98	1.65	1	5.7
28c(l)	1	1	1.0	44.0	90.0	3,960.0	4.92	0	—
30c(w)	9	23(3)*	2.56	54.22	93.32	5,035.31	2.12	1	5.7

Quadrat Summaries: Freezeout Peninsula, 1973 (continued)

Quadrat #	Total # Nests	Total Eggs and Chicks (live)	X̄ Clutch Size	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
31c(m)	2	5	2.5	38.0	96.95	3,808.92	3.55	1	4.0
32c(1)	2	5	2.5	18.0	90.0	1,620.0	3.38	0	—
34c(1)	1	3	3.0	15.0	90.0	1,350.0	10.1	0	—
35c(w)	5	8	1.6	34.2	97.38	3,345.27	1.84	0	—
36c(m)	10	26(1)*	2.6	45.1	98.59	4,450.67	1.29	2	2.8
37c(m)	1	3	3.0	39.0	90.0	3,510.0	7.13	1	4.0
39d(1)	5	13(2)*	2.6	35.2	90.0	3,168.0	0.54	2	2.6
40m	6	13(7)*	2.6	37.33	103.13	3,645.47	0.77	3	3.5
42c(w)	4	11(1)*	2.75	45.75	90.0	4,117.5	2.91	1	5.7
43c(m)	12	35(6)*	2.92	40.25	94.58	3,876.21	1.53	1	4.0
44c(1)	1	2	2.0	0	90.0	0	1.58	0	—
45m	27	68(16)*	2.52	3.48	91.71	353.45	0.74	1	2.6
46m	41	112(5)*	2.73	24.78	82.81	2,383.89	0.62	1	4.0
47d(m)	72	192(65)*	2.74	24.15	96.03	2,403.16	0.55	11	3.2
48d(w)	1	1	1.0	45.0	90.0	4,050.0	1.05	0	4.0
49c(w)	6	18	3.0	52.0	99.35	5,053.01	0.45	1	—
50c(1)	13	33(3)*	2.54	45.5	100.42	4,871.42	1.45	7	1.7
51m	52	138(63)*	2.65	13.33	89.30	1,314.73	0.48	2	2.9
52d(m)	53	134(37)*	2.53	4.28	56.43	402.11	0.46	4	2.6
53d(m)	114	305(53)*	2.68	16.8	90.49	1,589.49	0.50	1	2.8
54d(w)	4	5	1.25	33.0	90.0	2,970.0	1.27	0	4.0
55c(w)	1	3	3.0	53.0	104.77	5,552.87	0.88	3	—
56c(m)	12	31	2.58	43.83	102.21	4,463.92	1.44	1	3.5
57c(1)	1	3	3.0	12.0	90.0	1,080.0	2.54	5	4.0
58d(1)	15	40(5)*	2.67	13.47	55.50	1,214.24	0.64	9	2.4
59d(m)	117	295(90)*	2.52	19.43	94.33	1,911.25	0.50	1	3.3
60d(w)	15	44(6)*	2.93	22.87	92.66	2,175.0	0.60	0	4.0
61c(w)	1	3	3.0	22.0	90.0	1,980.0	3.35	4	—
62c(m)	10	27(3)*	2.7	42.9	90.24	3,875.1	1.78	2	3.7
63c(1)	3	5	1.07	46.67	100.01	4,605.54	2.47	2	3.3

Quadrat Summaries: Freezeout Peninsula, 1973 (continued)

Quadrat #	Total # Nests	Total Eggs and Chicks (live)	X̄ Clutch Size	X̄ Vegetation Height (cm)	X̄ Vegetation Cover (%)	X̄ Vegetation Volume (cover x ht)	X̄ Nearest Neighbor (meters)	Total Eggs and Chicks (dead)	X̄ Tarsal Length (dead chicks)
64m	16	35(4)*	2.19	22.13	91.93	2,032.91	1.02	2	4.0
65m	17	39(6)*	2.20	39.88	97.66	3,889.72	8.72	4	3.7
67m	16	46(8)*	2.88	20.38	95.29	2,023.36	0.75	2	1.6
68m	22	61(10)*	2.77	22.27	96.59	2,175.41	0.87	2	4.9
70c(l)	1	3	3.0	56.0	90.0	5,040.0	9.38	1	4.0
71c(w)	4	10(1)*	2.5	48.4	108.77	5,288.04	2.22	1	2.6
72d(w)	5	15(3)*	3.0	30.2	92.78	2,837.45	0.43	0	—
73m	34	100(7)*	2.94	31.5	98.26	3,162.62	0.72	0	—
74c(l)	9	20	2.22	61.89	101.57	6,503.12	1.42	1	5.7
75c(w)	6	17	2.83	49.83	102.42	5,110.01	1.81	1	4.0
76c(w)	6	13	2.17	46.67	90.0	4,200.0	1.58	1	4.0
77c(l)	13	41(3)*	3.15	35.77	102.29	3,719.47	1.59	3	3.2
78c(l)	3	5	1.67	0	0	0	2.45	0	—
79m	9	25(1)*	2.78	20.33	92.61	2,149.97	1.17	0	—
80c(m)	3	9	3.0	23.33	98.56	2,324.5	0.84	0	—
81m	4	13(2)*	3.25	4.50	67.5	405.0	0.98	2	4.0
83d(w)	11	26(4)*	2.36	10.36	68.39	952.84	0.52	2	4.0
84d(l)	1	2	2.0	0	0	0	2.03	1	4.0
85d(w)	11	27	2.45	4.91	57.27	441.82	0.49	0	—
86d(w)	16	45	2.81	0	0	0	0.90	1	4.0

c = Larus californicus
d = Larus delawarensis
m = Larus californicus and Larus delawarensis (mixed)

(w) = Water
(l) = Land
(m) = Middle

* = Number in parentheses is equal to number of chicks.

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Direction Gulls Were Seen Flying
(Based on True North)

Distance From Colony (km)	North	Northeast	East	Southeast	South	Southwest	West	Northwest
			Larus delawarensis					
1	—	—	10	—	—	—	10	—
2	10	—	—	—	—	—	—	—
3	9	10	1	3	5	4	—	—
4	—	—	—	—	—	—	1	—
5	—	—	2	2	—	—	4	7
6	—	—	1	—	—	—	35	2
7	4	—	—	—	2	—	—	—
8	—	—	—	—	—	—	3	—
10	1	—	2	—	1	—	1	—
11	—	—	—	—	—	—	1	—
12	—	—	—	—	—	—	2	—
			Larus californicus					
1	8	—	209	7	4	7	200	3
2	—	16	—	—	—	4	—	—
3	8	4	—	6	1	3	—	6
5	—	—	4	4	2	1	13	1
6	51	—	—	—	32	2	3	1
7	—	—	—	—	2	—	15	—
8	—	—	—	—	—	—	27	—
9	—	—	—	—	9	—	—	—
10	21	—	—	—	4	—	19	—
11	—	—	—	—	—	1	3	—
12	—	2	—	—	7	—	—	—
18	—	—	1	—	—	—	—	—
19	—	—	1	—	—	1	1	—
30	—	—	—	—	—	—	1	—