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THE DYNAMICS OF SEABIRD MULTISPECIES FLOCKS IN BARKLEY SOUND, BRITISH COLUMBIA

by

JULIE MARGARET PORTER

A Thesis
submitted to the Faculty of Graduate Studies
in partial fulfillment of the requirements for the
degree of Master of Science

Department of Zoology
Winnipeg, Manitoba

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ABSTRACT

A study concerning the dynamics of seabird multispecies flocks was conducted in Barkley Sound, British Columbia between 10 May and 23 October 1979.

Replicate transects were conducted to determine the chronology of flocking in the Sound; behavioral observations were made on seabird multispecies feeding flocks, experiments were conducted and a time budget analysis carried out in order to describe the dynamics of the multispecies feeding flocks; terrestrial loafing sites were characterized and the chronology of loafing determined, and the frequency and direction of movements of individuals at the loafing sites were described.

The chronology of multispecies feeding flocks was determined to establish the seasonal use of the Sound and provided background for a more detailed examination of the dynamics of feeding flocks. Inter- and intraspecific mechanisms that permitted the birds to feed together were considered. The relationship between terrestrial loafing groups and the seabird multispecies feeding flocks contributed to the interpretation of the function and significance of this feeding phenomenon.

There was a gradual inward movement of seabird multispecies feeding flocks in Barkley Sound over the study season. Thirty-two species were observed in feeding flocks. The most and largest (absolute numbers and biomass) feeding flocks were in August and September corresponding to the post-breeding season for migrants, residents and visitors, alike. Feeding flock locations were related to the overall distribution of birds in the Sound and the bathymetry of the area. California Gulls (80.0%) and Common Murres (67.3%), both visitors, had the highest feeding flock participation and were represented by the largest numbers. California Gulls, Common Murres, Herring Gulls, and Glaucous-winged Gulls had the greatest flocking tendency on the Deer Group Transects. For California and Glaucous-winged gulls, juveniles had the greatest tendency to flock.

Flock initiation and cessation followed a fairly regular pattern. Gulls (adults and subadults) initiated all but three feeding flocks seen being initiated. Both auditory and visual mechanisms appeared to be involved. Juveniles apparently relied on the searching ability of adults. The need for flexibility and versatility in the feeding habits of seabirds was emphasized. Juvenile gulls had a greater flocking tendency, spent more time actively feeding in flocks, spent less time searching, and had lower feeding success rates than did adults.

This implied that the flocks provided inexperienced young with not only an abundant and accessible food supply, but also a dependable and conspicuous means of locating the food.

Terrestrial loafing sites apparently shifted location so as to be centrally located for feeding. California Gulls were seen most often and represented by the greatest numbers at terrestrial loafing sites. Arrivals and departures at terrestrial loafing sites were clumped and directional. Adult gulls had a lower loafing tendency and a greater frequency of departure than juveniles or subadults.

The timing of flock-feeding and post-breeding dispersal of adult and juvenile migrant seabirds to Barkley Sound was consistent. Barkley Sound was not a major nesting area; rather, it was an important post-breeding staging area for these migrants. The role of seabird multispecies feeding flocks as indicated by these findings was interpreted with reference to the manner in which the participants responded to the apparently seasonally abundant and patchy food supply in order to achieve improved post-fledging survival of the inexperienced young.

I. GENERAL INTRODUCTION

Seabirds are the most visible biological component of the marine ecosystem but are still one of the least known, particularly in the north Pacific Ocean and adjacent seas (Bartonek and Nettleship, 1979). This is surprising because this resource is extremely important in terms of species diversity and total numbers of individuals. Sanger (1972) estimated the standing stocks of seabirds in the Subarctic Pacific Region at about eight million in winter and 51 million in summer. These birds consume an estimated 0.6 to 1.2 million tons of food per year from the Region, and void into it an estimated 120,000 to 240,000 tons of feces. Their estimated primary food production was the equivalent of 0.8% of the estimated carnivore production of the Region (Sanger, 1972). Seabirds are important members of marine ecosystems; their ecological roles need to be defined and placed in perspective through studies of their feeding relations.

Seabirds spend most of their time away from land and obtain all or most of their food from the sea while flying, swimming or diving (Ashmole, 1971). Information on the relationship between the distribution and abundance of seabirds and other marine resources is being generated presently. We are beginning to understand the interplay of factors that influence the breeding distribution of species, their patterns of foraging and their dispersion at sea, particularly during the breeding season. There is much less known about their ecology and distribution during the non-breeding season. Seabird distribution and abundance at sea have been studied mainly by opportunistic observations (Kuroda, 1960; Sanger, 1965; Swartz, 1966; Martin and Myres, 1969; King, 1970, 1974; Pocklington, 1979) although some detailed studies have been conducted (Sanger, 1970; Bailey, 1968; Scott, 1973; Nettleship and Gaston, 1978). Belopol'skii (1957), Uspenski (1958), Ashmole and Ashmole (1967), Pearson (1968), Bédard (1969), Sanger (1972), Sealy (1972), Cody (1973), Wiens and Scott (1975), Baltz and Morejohn (1977) and Furness (1978) studied aspects of the ecology of seabird communities, but such investigations, particularly of the birds at sea have been infrequent. This has been due in part to the difficulties and costs incurred during at-sea studies.

Knowledge about non-breeding distribution, the relation between day-to-day distribution of seabirds and the apparently often patchiness of resources upon which they depend are important in establishing their relationships with the marine environment. Because seabirds are highly mobile animals, they may respond quickly to changing environmental conditions, and therefore are potentially good indicator species (Sanger, 1972). Several characteristics that appear to prevail in this group enhance this quality and at the same time endanger them: they are long-lived, reach sexual maturity slowly, and have low reproductive rates, with correspondingly slow recovery rates. These common features of the seabird lifestyle, often combined with wide variations in breeding performances from one year to another, make it difficult to distinguish between changes caused by natural fluctuations in environmental conditions and those induced by human activity.

The present study is an outgrowth of preliminary work by Sealy (1973) from which the formation and ecological significance of multispecific assemblages of seabirds off the coast of British Columbia were described and discussed. Whenever assemblages of birds have been studied, the individual species have been found to overlap in some aspects of the environment they use (see Fisher and Lockley, 1954; Recher, 1966; Ashmole, 1968; Cody, 1968; MacArthur, 1971; Sealy, 1973; Wiens and Scott, 1975; Baltz and Morejohn, 1977; Diamond, 1978). As food is generally considered one of the most important aspects of the habitat, the degree of specialization by a predator in selecting prey and the degree of prey overlap between species are critical elements of the structure of any community. Because of this potential overlap in resource use and the antecedent environmental conditions, marine birds show a variety of adaptations for feeding (Bédard, 1969; Ashmole, 1971; Cody, 1973; Ainley, 1977; Ainley and Sanger, 1979).

The conspicuous multispecies associations of seabirds have been considered by Ashmole and Ashmole (1967), Ashmole (1968), Pearson (1968), King (1970), Scott (1973), Sealy (1973), Gould (1974), Erwin (1977, 1978), Wiens (1976), Baltz and Morejohn (1977), and Diamond (1978). These studies examined the use of foraging space, advantages of group feeding, foraging time and distribution, and the abundance of food in the environment.

The present study was designed to assess quantitatively the relative abundance and distribution of flock-feeding on transects in Barkley Sound, British Columbia and to determine the degree of interdependency among various species of flock-forming seabirds over the breeding season and early part of the post-breeding season in 1979. Patterns exist in species inter-relationships and community organization, but these patterns may be produced by species-specific preadaptations to different resources and varying mixtures of processes such as competition, predation, physical disturbance, or recurrent but unpredictable environmental fluctuations. The dynamics of feeding flocks were studied to determine the degrees and directions of interaction among seabird species. The prey to which individuals in the multispecies flocks responded and subsequently preyed upon was not determined in the present study. This work remains to be carried out in Barkley Sound. The assumption was made that the birds were preying upon surface schools of fish, probably involving a single species and size class in each school (see Sealy,1973; Baltz and Morejohn,1977).

This project is part of an on-going program where the feeding biology of species in Barkley Sound that forage singly and in single or multispecies flocks is being considered on a community level. This thesis involves a description of the seasonal chronology of flocking in the study area, the roles of different species in flock formation and development and an analysis of the members' contribution to the efficiency and performance of the entire system. The occurrence of terrestrial loafing sites in space and time and movements associated with these loafing sites were examined to also facilitate explaining the adaptive significance of this social feeding to the participants.

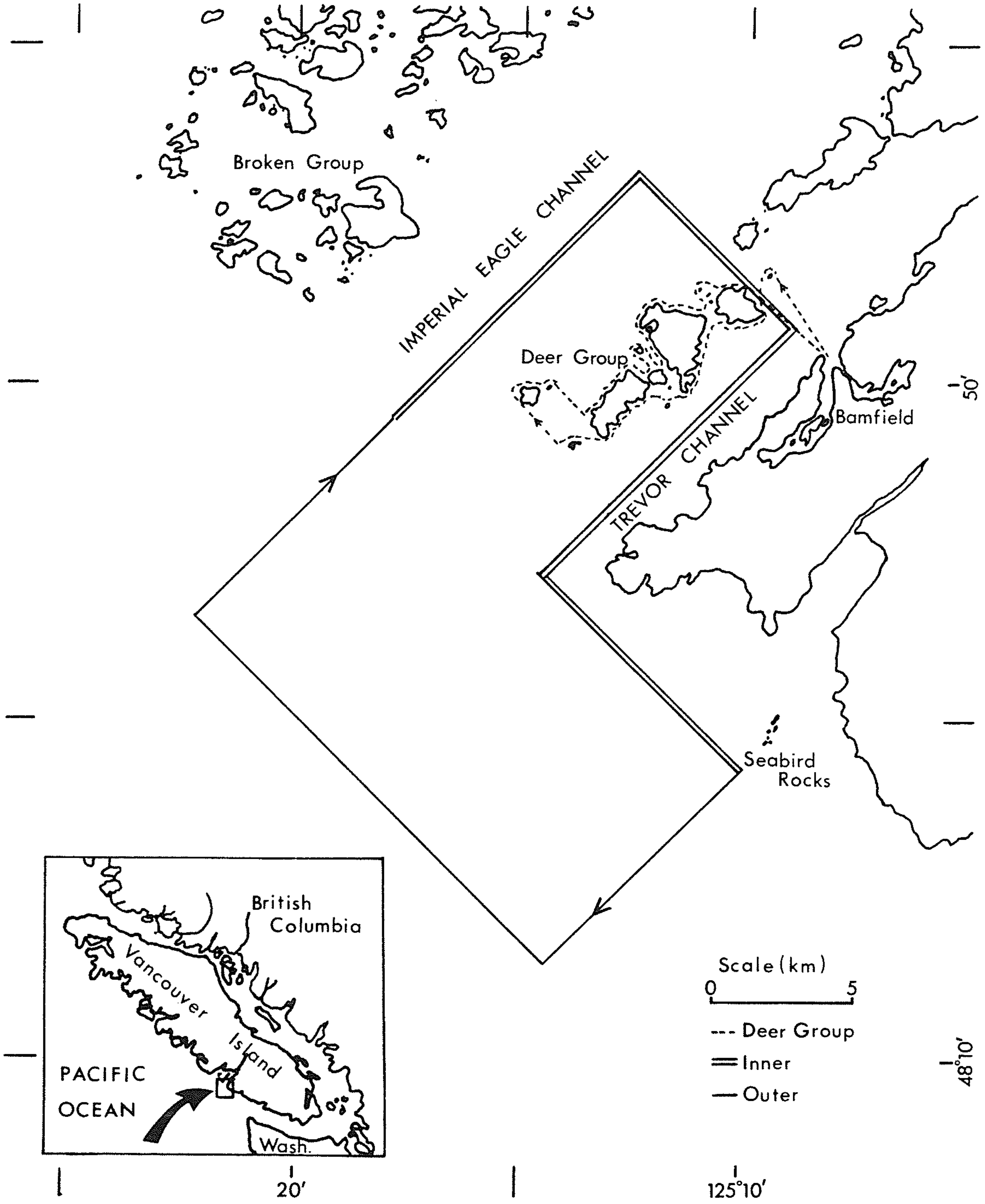
II. STUDY AREA AND METHODS

Barkley Sound is located on the west coast of Vancouver Island on the Pacific Ocean (Figure 1). The study area proper consisted of the waters of Trevor and Imperial Eagle Channels and a 10 km band extending outward from the Sound from mid-Imperial Eagle Channel to Seabird Rocks. Other areas of the Sound and adjacent regions were visited infrequently. The Bamfield Marine Station (48°50'N, 125°08'W) served as a base for operations. Field work was conducted from 10 May to 23 October 1979.

A. Transect data collection

At-sea transects were conducted regularly from 10 May to 17 October 1979, to characterize the marine avifauna in the Sound and offshore waters over one summer. The two routes covered by the replicate transects were classified as follows (see Figure 1): Deer Group Transects - A pneumatic boat with a 15 hp engine was used on transects every seven days, in the evening and the following morning, except in Weeks 1 and 2 when only the evening transects were run, Week 10 when the morning transect was made and Week 17 when no transects were conducted. Inner Transects - These transects were conducted in a converted, 10 m fishing boat at approximately 10 day intervals until

Figure 1. Map of the study area in Barkley Sound, British Columbia. This location is indicated by the inset showing Vancouver Island. The lines indicate the direction and route of the Deer Group, Inner and Outer Transects.


Broken Group
IMPERIAL EAGLE CHANNEL
Deer Group
TREVOR CHANNEL
Bamfield
50'
Seabird Rocks
British Columbia
Vancouver Island
PACIFIC OCEAN
Wash.
Scale (km)
0
5
--- Deer Group
═ Inner
— Outer
48°10'
20'
125°10'

28 September. Outer Transects - These were a continuation of the Inner Transects. The bulk of the data for the analysis of the chronology of both feeding flocks and terrestrial loafing sites was based on the Deer Group Transects. Supplementary information was obtained on the Inner and Outer Transects.

The continuous observations made on these regular transects included the time (P.D.T.) and location of each bird sighting, species, number of individuals per sighting (i.e., group size), and when possible the age, activity (e.g., whether loafing on land or water, flying or feeding), and molt status. Overall, 5,436 sightings of 40,868 individuals were made in 73 hours of observations on the Deer Group Transects. The 41 transects covered 1288 km. The multispecies feeding flocks observed on the 13 Inner and Outer Transects (455 km, each) were used for comparative purposes in the analysis of the chronology of flocking; data for the total number of individuals seen on these transects will be treated elsewhere (Carter, Porter, and Sealy, in prep.).

Records of weather and sea conditions were obtained from Mr. A. Thompson, keeper of the Cape Beale light station at the southwest entrance to Barkley Sound. Sky conditions, visibility, weather, wind speed and direction, and swell and sea conditions were recorded by him eight times daily.

Each boat was run at a nearly constant speed, depending upon the sea and weather conditions during a transect. The position of the boat along the transect route was determined by recording the time when predominant landmarks were passed on the course.

Factors such as wind, chop, wave height and period, fog, glare, and observer alertness varied from transect to transect and may have affected the distance at which different species could be seen (see King, 1970; Sanger, 1970). The effect of as many of these variables as possible were eliminated or minimized. Wind velocity, chop and swell height were minimized by the limited weather conditions under which the transects could be conducted. Glare and possible effects of the time of day on the birds' behavior were minimized by standardizing the initiation time (with respect to sunrise and sunset) of all transects. I made observations on all Deer Group Transects and had the assistance of a boat driver until 1 September. After this time, I drove the boat and made observations simultaneously. On Inner and Outer Transects, there were two observers for the first four of the 13 transects, after which time there was one observer. On these transets the boat driver spotted birds that may not have been seen by the observer(s).

Differences in conspicuousness among the species and the lack of lateral or frontal constraints in the Deer Group Transects made any expression of bird densities on an absolute basis (individuals per unit area) inappropriate. The census data, however, permitted the relative intensity of bird activity to be quantified in different areas and at different times, and was expressed as birds per linear km.

B. Feeding flock dynamics

(1) Behavioral observations of feeding flocks

Over 350 multispecies feeding flocks were observed, in part or in total, during the study period. Most observations were made from the pneumatic boat with the aid of binoculars, as needed. Depending on the circumstances, flock composition and numbers, flock location, position of age classes and species in the flocks, the sequence and timing of flock events, feeding methods, success rates, and interactions among individuals were recorded.

Seventy-six flocks were seen being initiated but most were discovered after feeding had begun. The conspicuousness of the feeding birds aided in locating flocks. Feeding flocks were watched until feeding stopped or until circumstances beyond my control (i.e., a sports fisherman drove through the flock or the pneumatic boat drifted too close to the flocks) terminated the feeding and my observations.

(2) Experiments

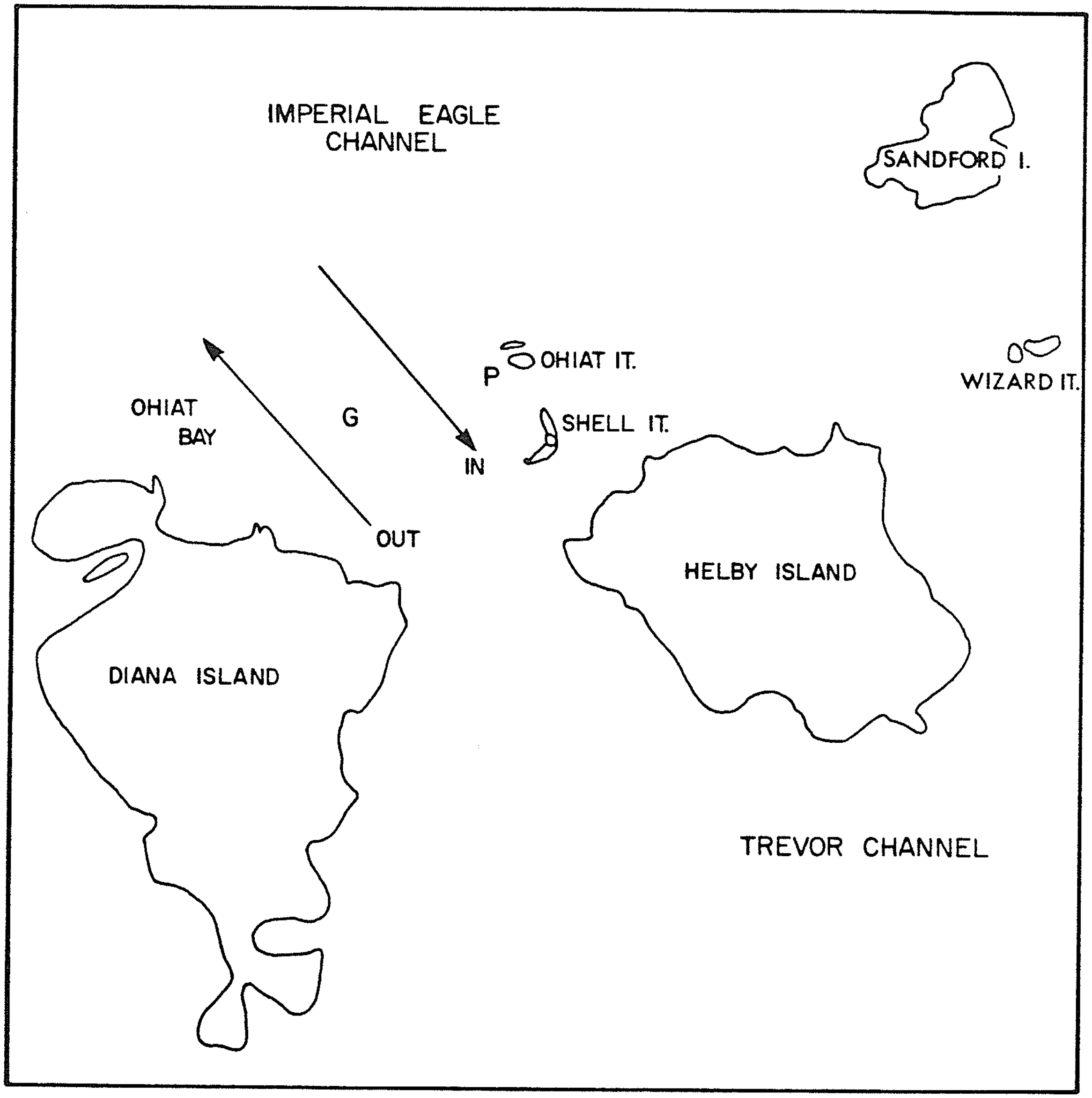
Experiments with adult Glaucous-winged Gull models were conducted to test the attractiveness of a group or a single bird on the water to other individuals. The models were made by carving styrofoam blocks into gull shapes and sizes, each model was hollowed out underneath, filled with cement, and a ring-bolt placed in it. They were painted to match a museum specimen of an adult Glaucous-winged Gull. During the tests, the 23-26 models were connected by a cord through the ring bolts, clumped into a dense group and released in the location as indicated in Figure 2. During control observations the models were placed in the bow of the pneumatic boat and covered with a tarpaulin.

Tests were carried out in September and October, 1979. One test was conducted per day between 1200 and 1600 under similar weather and sea conditions. A test consisted of watching the water between Ohiat Islet and Diana Island (Figure 2) for 15 minutes (control A), then putting the model(s) on the water for 30 minutes (experimental period), and finally removing the models and watching for a further 15 minutes (control B). One test series compared controls with one model and a second series compared controls with

Figure 2. Location of model observations in Ohiat Bay.

G = test area where models were placed

P = position of observer


IMPERIAL EAGLE CHANNEL
SANDFORD I.
OHIAT IT.
P
WIZARD IT.
OHIAT BAY
G
SHELL IT.
IN
OUT
HELBY ISLAND
DIANA ISLAND
TREVOR CHANNEL

a group of 23-26 models. Tests were repeated five times each.

During both the experimental and control periods, the pneumatic boat was anchored on the south side of Ohiat Islet, and records of (1) the number of birds moving directly into the bay, (2) the number of birds moving directly out of the bay, (3) the number of birds moving through the test area (or within 10 m on either side, including times when birds actually altered course to move through the test area) as indicated by "G" in Figure 2, and (4) the number of birds moving to and remaining in the immediate area of the models. A Chi-square analysis compared control and experimental conditions.

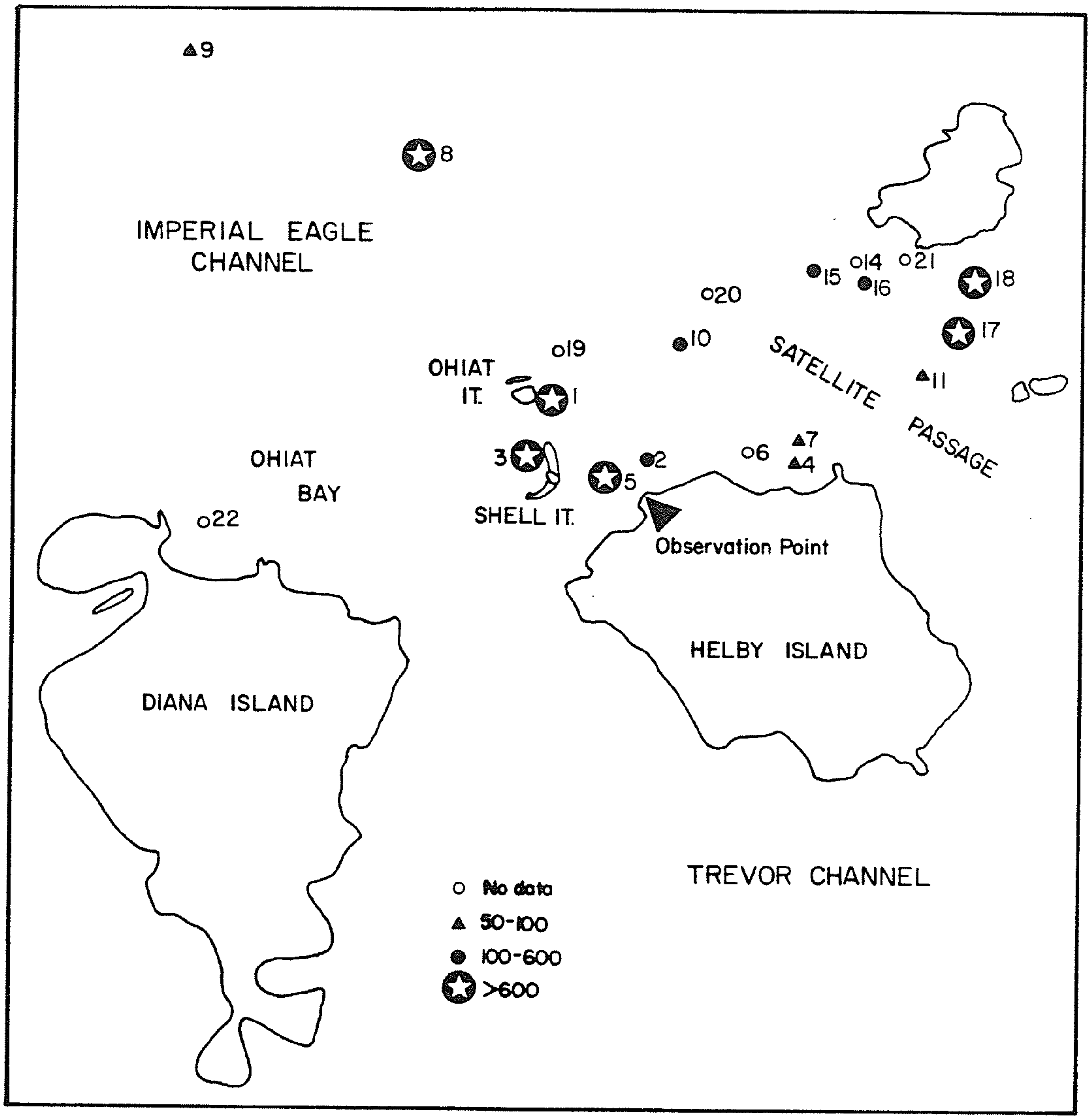
Several experiments involving supplementary food were conducted during the study period. Pieces of fish, popcorn and bread were used to "chum" the birds to form flocks. Again, the timing of the sequence of events, the composition and number of birds and behaviors were recorded. These observations were made from the stern of the marine station research vessel or from the centre of the pneumatic boat. The latter was less appropriate, as the observer was too close to the birds so that they only flew in, picked up food and departed to a "safer" distance.

(3) Time budget analysis

On 17 September from 0730-1930 (P.D.T.) a time budget analysis was conducted from an observation point on Helby Island (Figure 3). All feeding flocks observed over the 12-hour period were noted and species composition and numbers, time and duration of flocks were recorded. In some cases, because of the observation distance, the numbers of individuals per flock could not be determined.

In the analysis, a Kruskal-Wallis Test (Conover, 1971) was used to compare data among four equal portions of the day (0730-1030, 1030-1330, 1330-1630, 1630-1930). Inter-feeding flock distances, inter-feeding flock time intervals and the duration of feeding flocks were tested for clumping by comparing the distribution of intervals to a distribution generated under the hypothesis of randomness. The exponential distribution is the distribution of time intervals or distance intervals of or between successive events (feeding flocks), and is a continuous distribution. The observed intervals were grouped into five minute (duration of feeding flocks and inter-feeding flock time intervals) and 500 m (inter-feeding flock distances) classes for analysis (discretized), so a geometric distribution was appropriate for the theoretical distribution (Johnson and Kotz, 1969; O'Malley, 1980). If Y was the feeding flock duration or inter-feeding flock

Figure 3. Location and size of multispecies feeding flocks observed from Helby Island on 17 September 1979. Numbers indicate the sequence of initiation of the feeding flocks observed (precise location data for flocks 12 and 13 were not obtained).


9
8
IMPERIAL EAGLE CHANNEL
15
14
21
16
18
20
17
10
SATELLITE PASSAGE
19
OHIAT IT.
1
11
3
2
6
7
4
OHIAT BAY
5
SHELL IT.
22
Observation Point
HELBY ISLAND
DIANA ISLAND
TREVOR CHANNEL
○ No data
▲ 50-100
● 100-600
>600

time or distance interval rounded up to five minutes (former two) or 500 m (latter one), then the theoretical distribution of Y under the hypothesis of randomness was:

$$p_i = \Pr (Y = i) = \theta^{i-1} (1 - \theta)$$

where θ was the probability of no feeding flock in any interval, and i was the number of interval classes ($i = 1, 2, 3, \ldots$). If $\bar{x}$ was the mean feeding flock duration, inter-feeding flock time or distance interval (in units of five minutes or 500 m), then the maximum likelihood estimate of θ was $\hat{\theta} = 1 - (1/\bar{x})$. The expected distribution was obtained by multiplying the p_i by N, the total number of intervals (see Appendix A).

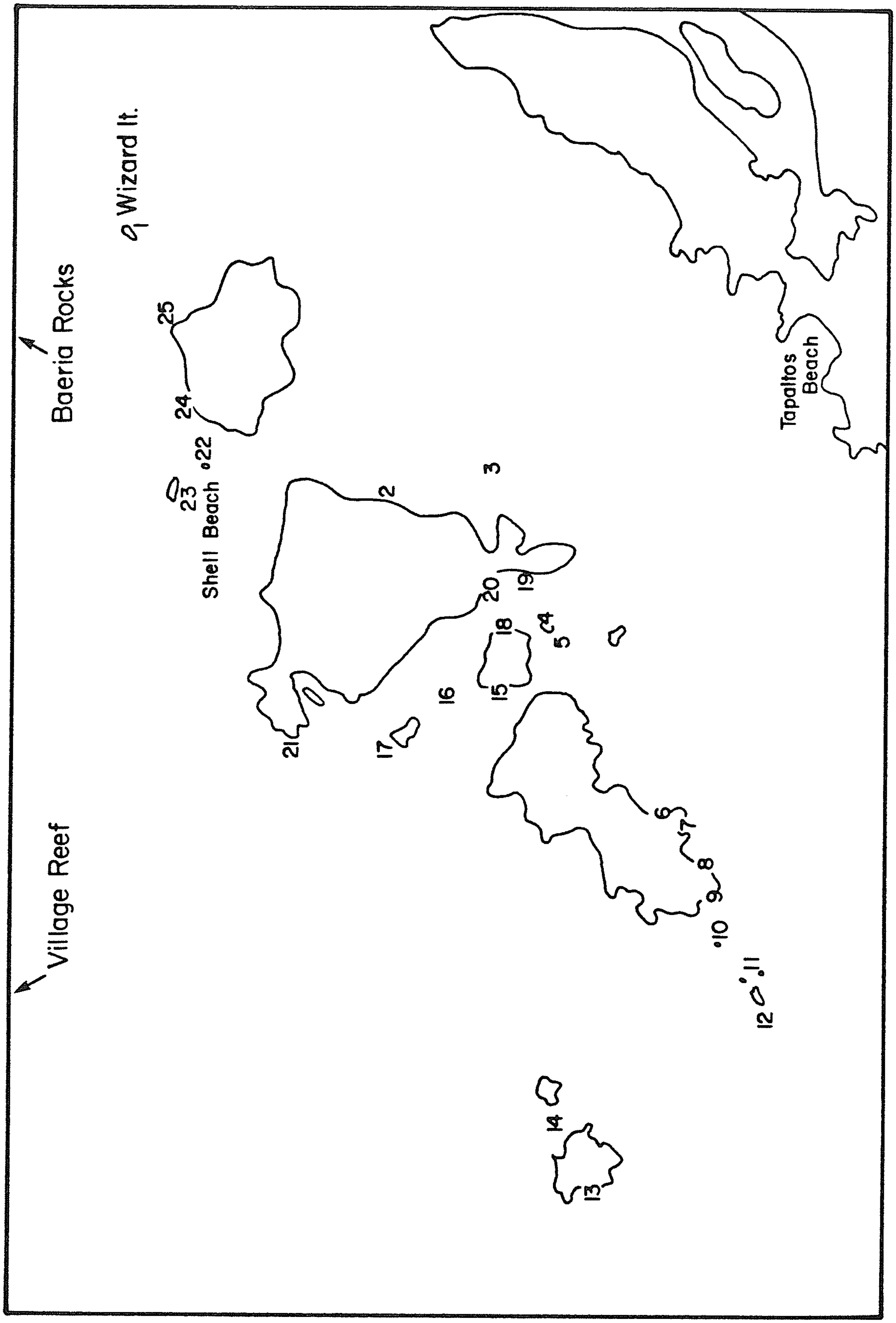
C. Observations of loafing birds

Terrestrial loafing site abundance, distribution and composition data were obtained from the Deer Group Transects as described in II.A. The 25 land loafing sites were located as indicated in Figure 4. Qualitative observations of the behavior and structure of the loafing birds were also made during the transects.

The movements of birds to and from various loafing sites were studied. Twenty-nine and a half hours of observation were made at five of the major terrestrial loafing sites: Wizard Islet, Shell Beach in the Deer Group Islands; Tapaltos Beach on the east side of Trevor

Figure 4. Locations of terrestrial loafing sites on the Deer Group Transects.

1. Wizard It.
2. East Diana I.
3. Cia Rock
4. Haines Point
5. Inside Taylor It.
6. Cormorant Cave
7. Cliff 1
8. Cliff 2
9. South Edward King I.
10. Mid-Bordelais Its.
11. North Bordelais Its.
12. Outside Bordelais Its.
13. Folger I.
14. Folger-Leach
15. West Haines I.
16. Inside Seppings I.
17. Outside Seppings I.
18. Haines Beach
19. Diana Rock
20. Diana Beach
21. Kirby Point
22. Shell It.
23. Ohiat It.
24. West Helby I.
25. North Helby Rock


Village Reef
Baeria Rocks
Wizard It.
Shell Beach
Tapaltos Beach
1
2
3
4
5
6
7
8
9
10
11
12
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14
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Channel; and North and South Baeria Rocks at the northwest end of Imperial Eagle Channel (Figure 4). All sites were considered in the quantitative analysis of movements.

Observation bouts at loafing sites of 60 or 90 minutes were conducted periodically from 29 July to 23 September. The pneumatic boat was anchored about 50 m from the loafing site and the flight direction and time for all arrivals and departures of all species and age classes of species, where such were identifiable, were recorded. Prior to observations, compass directions were taken from a Canadian Hydrographic Service chart (No. 3671).

The arrivals and departures per minute were tested for clumping by comparing the distribution of intervals to a distribution generated under the hypothesis of random arrivals and departures. The Poisson distribution is a discrete frequency distribution of the number of times an event occurs (Sokal and Rohlf, 1969). To say that arrivals and departures were randomly dispersed over time is to say they follow a Poisson distribution. If x was the number of movements per one minute interval, then the theoretical distribution of x under the hypothesis of randomness was:

$$p_i = \Pr(x = i) = \frac{\bar{x}^i \cdot e^{-\bar{x}}}{i!}$$

where $\overline{x}$ was the mean number of movements per minute, and i was the number of individuals per minute ($i = 0, 1, 2, \ldots$). The expected distribution was obtained as in II.B.(3) (see Appendix B).

Common and scientific names of the species mentioned in the text appear in Appendix C. Additional methods were presented where appropriate.

III. DEFINITION OF TERMS

A. Terms that describe the status of species in Barkley Sound:

<u>resident</u> - species that are present all year (permanent resident) or during the nesting season (summer resident), and that nest on islands within, or coasts peripheral to Barkley Sound (adapted from King, 1970; Sanger, 1972);

<u>visitor</u> - species that nest outside Barkley Sound, but spend part of their lives in the study area (adapted from Sanger, 1972);

<u>migrant</u> - species present only during passages to land masses or to oceanic areas distant from the study area (Sanger, 1972).

B. Terms that describe the birds' activities:

<u>feeding flock (of seabirds)</u> - a group of two or more seabirds feeding on the water in a confined area (over a presumed prey concentration), whose formation depends upon positive responses by individuals to other foraging birds (see Morse, 1970). These flocks may be of one or more species;

<u>loafing area</u> - a site where birds engage in non-feeding and non-nesting activities, either on land or water.

C. Terms that describe the stage of the birds' life cycles:

nesting period - that time when birds establish nesting sites, lay eggs, incubate, and care for young in the nest;

post-fledging period - dispersal or migration periods or a portion thereof.

D. Terms that describe age designations of the birds:

adult - one which has attained complete adult plumage (see Dwight, 1925 for gulls);

juvenile - a bird in its first calendar year of life, can also be referred to as a young-of-the-year or a hatching year (HY) bird;

subadult - a bird in at least its second calendar year of life, can also be referred to as a second year (SY) or third year (TY) bird, as appropriate.

E. Terms used in the analysis of feeding flocks (King, 1970):

flock composition - number of flocking individuals of one species/number of flocking individuals of all species;

flock participation - number of flocks in which seen/ total number of flocks;

flocking tendency - number of individuals seen in flocks/number of individuals seen on transects.

F. Terms that describe the feeding methods of birds (adapted from Ashmole, 1971; Ainley, 1977):

<u>diving</u> - bird submerges from a water surface position to pursue and capture prey underwater propelled by either wings or feet;

<u>surface seizing</u> - includes surface filtering and scavenging, and entails taking prey from the sea's surface or from just beneath it while the bird swims or floats on the surface;

<u>surface plunging</u> - bird sits on the water, jumps into the air and plunges into the water to become partially or totally submerged, but thereafter only the momentum of the fall, is used to reach the prey;

<u>aerial plunging</u> - involves plummeting from the air to become totally submerged, but thereafter only the momentum of the fall is used to reach the prey;

<u>pursuit plunging</u> - involves plummeting from the air to become submerged and thereafter pursuing the prey short distances underwater propelled by the wings;

<u>dipping</u> - involves taking prey on the surface, or from just beneath it, while remaining airborne or while halting flight for just a fraction of a second (contact dipping and shallow plunging);

<u>kleptoparasitism</u> - one bird secures food from another.

IV. CHRONOLOGY OF THE MULTISPECIES FEEDING FLOCKS IN BARKLEY SOUND

A. Introduction

The different patterns of distribution at sea, habitat use and foraging by seabird species reveal an intricate and complex relationship between them and the marine environment. Very important is the availability of adequate food. Each species, therefore, has timed its breeding, molded by natural selection, so that it (or part of it) coincides with maximum availability of food. A critical point in a species' annual cycle occurs immediately after young have fledged, when population densities are their highest and a large percentage of individuals are the inexperienced young (see Pearson, 1968; Immelmann, 1971).

These seasonal distributions and the attendant changes in the environment pose a variety of stimulating ecological problems. Obvious questions arise about interspecific partitioning of resources such as colony sites, seasonal food sources and(or) roosting and loafing areas.

Knowledge of the seasonal occurrence of seabirds in the waters along the west coast of Vancouver Island is fragmentary. Several species have received some attention (see Martin and Myres, 1969; Sanger, 1970; Hatler *et al.*, 1978) although the studies were generally qualitative and were obtained from scattered locations and(or) at irregular intervals. The west coast of Vancouver Island is not noted for supporting numerous, large breeding colonies compared to areas such as the Queen Charlotte Islands that border the region (see Drent and Guiguet, 1961; Guiguet, 1971; Campbell, 1976). Barkley Sound has Glaucous-winged Gull colonies, several Pelagic Cormorant breeding sites and areas where Marbled Murrelets apparently breed, but potentially suitable nest sites remain vacant (Myres, 1979). On the other hand, large numbers of birds that do not breed in the area are there for a portion of the year during their migration or post-breeding dispersal. This phenomenon has been attributed to the variable and unpredictable oceanographic conditions characteristic of the study area (see Martin and Myres, 1969; Sanger, 1970; Myres, 1979).

The occurrence of the seabird multispecies feeding flocks in Barkley Sound was related to the overall distribution and abundance of the avifauna. Information on the seasonal use of the Sound provided background for a more detailed examination of the dynamics of the feeding flocks.

B. Results

The following analysis of 58 multispecies feeding flocks, observed on the regular transects in Barkley Sound, deals with the frequency, spatial and temporal distribution, and species composition of the flocks. A monthly summary of the species composition on the Deer Group Transects appears in Appendices D, E, F, and G.

(1) Feeding flock abundance

Table 1 shows the number of multispecies feeding flocks seen on the Deer Group Transects in 1979. On these transects, birds in flocks accounted for 12.7% of the total birds observed. The four months which fell substantially below this percentage--May, June, July, and October--were months when relatively few birds were present in the study area. In other words, as the total number of individuals increased, the relative proportions of those occurring in flocks also increased. June and July were periods of nestling care for resident species and migrants had not yet begun to arrive. Indeed, the lowest number of birds per transect was recorded in June. As the number of individuals of species that appeared in flocks increased, so did the number of

Table 1. Abundance of individuals on the Deer Group Transects and in multispecies feeding flocks.

Month (No.) transects)		Individuals/ transect	Sightings/ transect	Individuals/ sighting	No. feeding flocks	Individuals/ feeding flock	Percent of individuals in flocks
May	(4)	229.3	103.0	2.2	1	68.0	7.4
Jun	(8)	140.3	58.6	2.4	0	0	0
Jul	(7)	156.4	64.0	2.4	1	64.0	5.8
Aug	(8)	1107.6	127.4	8.7	8 (7)[1]	119.7	9.5
Sep	(8)	2983.5	243.1	12.3	13 (11)[1]	358.7	16.5
Oct	(6)	834.2	190.5	4.4	1	273.0	5.5
Total	(41)	996.8	132.6	7.5	24	247.1	12.7

[1] Numbers in parentheses are the number of feeding flocks where the individuals were counted, if two numbers are presented.

individuals per sighting on the Deer Group Transects; there was a tendency for larger sightings in August and September. Flock size decreased again in October as fall migrants began to move out of the Sound. At the same time, the mean number of birds per sighting was 4.4, less than that of August or September.

A comparison of Deer Group, Inner and Outer Transect areas revealed that, in general, most feeding flocks occurred in August and September (Table 2, Figure 5). On all three transects, flocks were largest and contained the greatest biomass of birds, in September. On the Deer Group Transects, there were more flocks per transect in September (1.63), while on the Inner and Outer Transects, there were more flocks per transect in August (5.0 and 1.5, respectively). A Kruskal-Wallis Test indicated that the numbers of individuals per feeding flock were similar in all three transect locations ($T = 0.94$, d.f. = 2, $p > 0.10$). That is, none of the areas promoted the formation of larger feeding flocks. There were more feeding flocks in the Inner area, than in the Deer Group or the Outer areas ($\chi^2 = 27.6$, d.f. = 2, $p < 0.005$), but there was no difference between the latter two ($\chi^2 = 0.5$, d.f. = 1, $p > 0.50$).

(2) Spatial distribution of feeding flocks

Throughout the study season there were five centres with particularly high numbers of feeding flocks: Shell

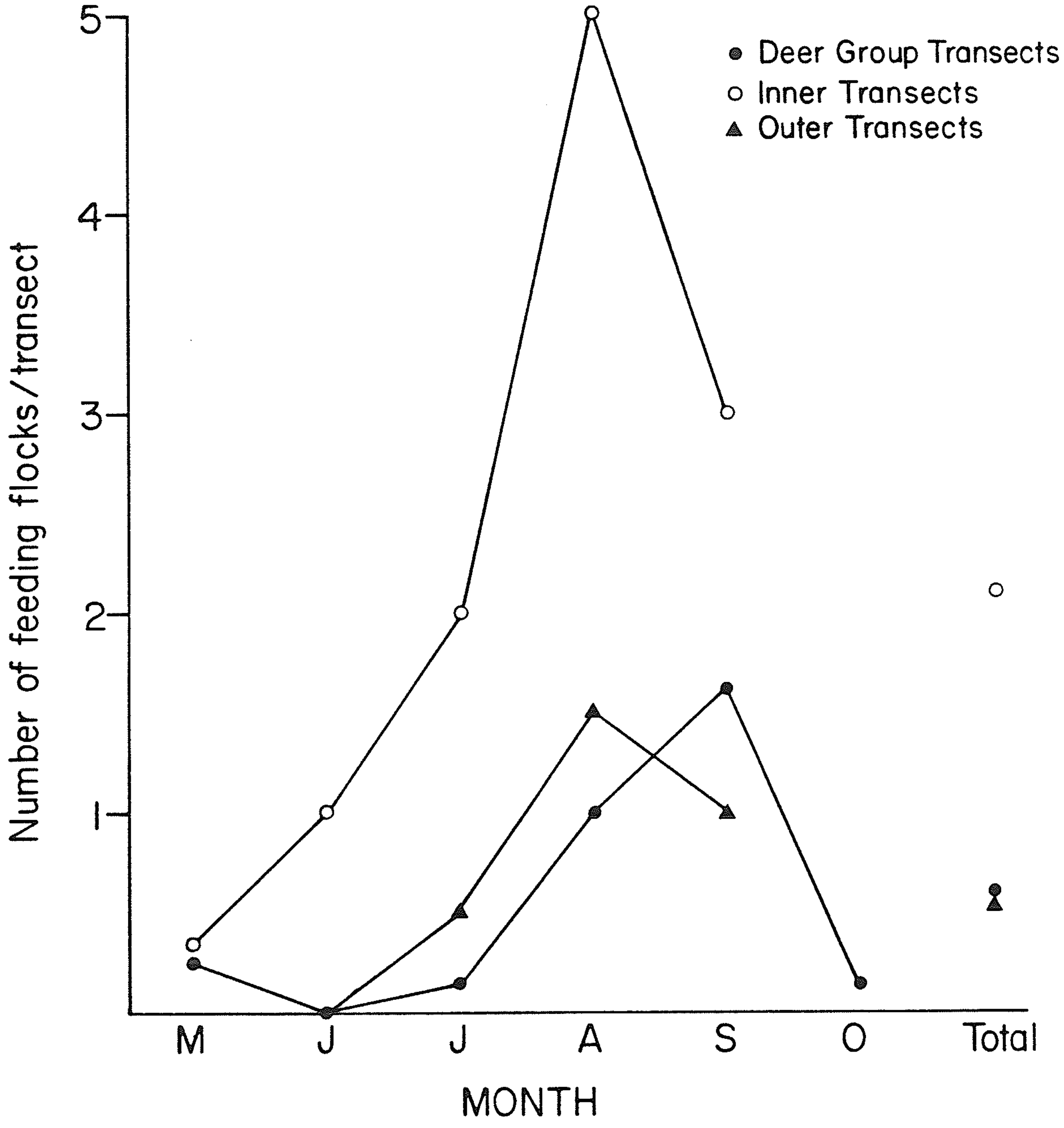
Table 2. Abundance and biomass of individuals in multispecies feeding flocks on the Deer Group, Inner and Outer Transects.

Transect	Month						Total
	May	Jun	Jul	Aug	Sep	Oct	
Deer Group							
No. transects	4	8	7	8	8	6	41
No. feeding flocks	1	0	1	8	13	1	24
Feeding flocks/transect	0.25	0	0.14	1.0	1.63	0.17	0.59
Individuals/feeding flock	68	0	64	119.7±113.9[2]	358.7±260.3	273.0	247.1±231.6
Biomass/feeding flock (kg)[1]	115.0	0	48.9	98.4	316.6	264.4	219.0
Inner							
No. transects	3	3	2	2	3	0	13
No. feeding flocks	1	3	4	10	9	-	27
Feeding flocks/transect	0.3	1.0	2.0	5.0	3.0	-	2.1
Individuals/feeding flock	261	88.3±82.8	23.0±13.7	152.1±147.2	403.8±310.7	-	213.8±243.3
Biomass/feeding flock (kg)[1]	285.2	78.7	16.6	122.7	355.7	-	185.8
Outer							
No. transects	3	3	2	2	3	0	13
No. feeding flocks	0	0	1	3	3	-	7
Feeding flocks/transect	0	0	0.5	1.5	1.0	-	0.54
Individuals/feeding flock	0	0	71	74.3± 41.2	155.3± 52.7	-	112.9± 62.5
Biomass/feeding flock (kg)[1]	0	0	56.5	61.1	129.1	-	89.6

[1] Biomass per feeding flock; body weights of individuals of each species in Appendix E.

[2] Mean±SE.

Figure 5. Number of multispecies feeding flocks per transect on the Deer Group, Inner and Outer Transects.


Number of feeding flocks/transect
5
4
3
2
1
● Deer Group Transects
○ Inner Transects
▲ Outer Transects
M
J
J
A
S
O
Total
MONTH

Beach, Folger-Leach, Cape Beale, Seapool Rocks, and Seabird Rocks (Figure 6).

The density centres near Cape Beale and Seapool Rocks were present from June onwards (Figure 6), thus corresponding to the occurrence of feeding flocks on the Inner Transects (see Figure 5). Folger-Leach and Shell Beach centres were active primarily in August and September. Flocking occurred by Seabird Rocks also from August through September around the time most Glaucous-winged Gull chicks from that colony fledged.

The five centres of feeding flock density shared similar features (Table 3, Figure 6). They usually were only one km or less from land and in areas where the water was not very deep (contours from 25-40 m), but more importantly, where the bathymetry was complex. In all locations land or islands close by facilitated the formation of eddies and currents (Figure 6).

(3) Feeding flock composition

Gulls, murres and shearwaters, in that order, were the predominant species groups in feeding flocks in the study areas (Tables 4, 5 and 6). Gulls, primarily California and Glaucous-winged, dominated the composition in the Deer Group (79.4%) and the Inner (73.5%) areas covered by the transects, while Sooty Shearwaters made up 65% of the individuals in the Outer area. In both the Inner and the Deer Group areas, Common Murres were

Figure 6. Location and size of multispecies feeding flocks on the Deer Group, Inner and Outer Transects. M = May, J = June, J' = July, A = August, S = September, O = October.

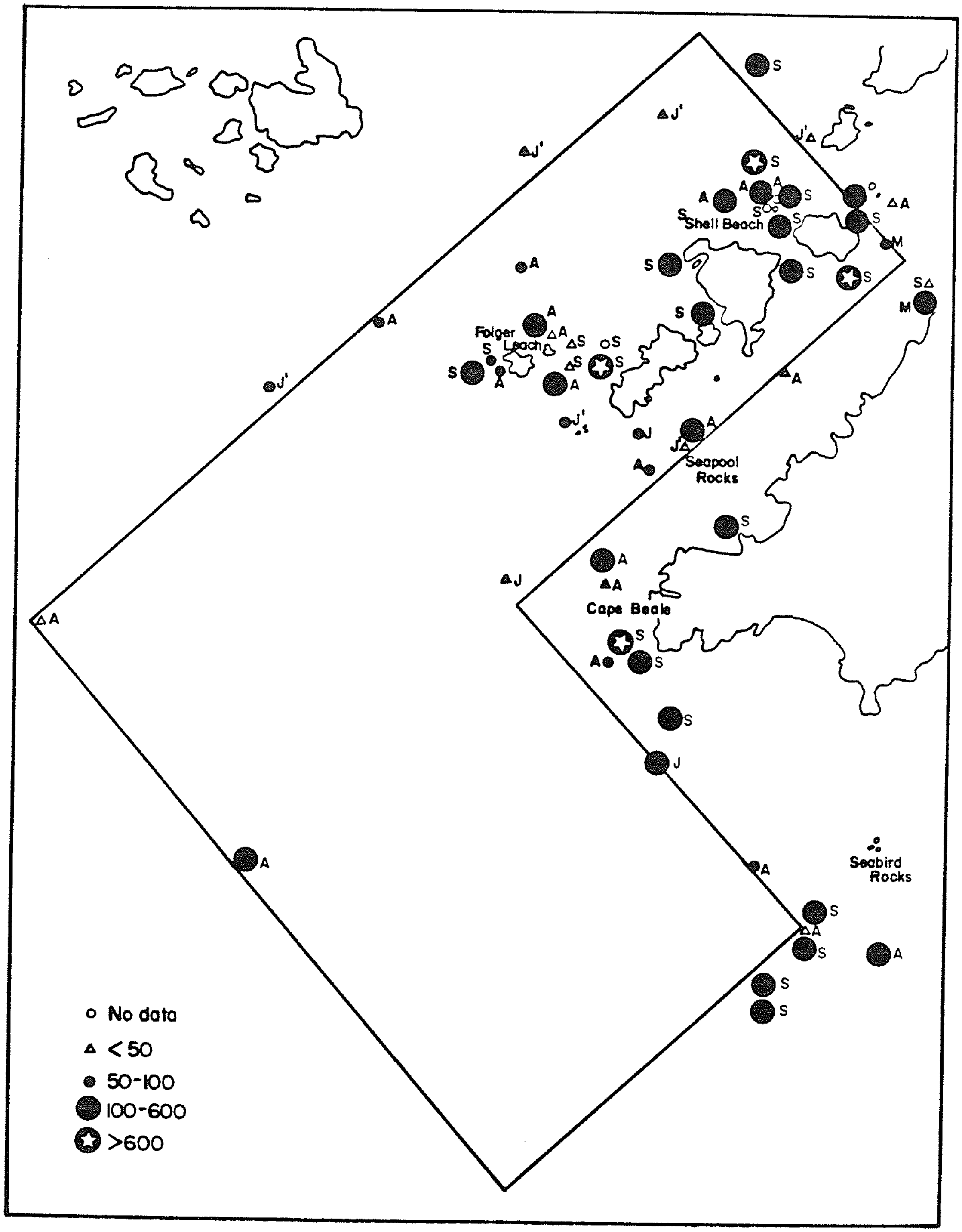

Shell Beach
Folger
Leach
Seapool
Rocks
Cape Beale
Seabird
Rocks
○ No data
▲ <50
● 50-100
● 100-600
✪ >600

Table 3. Bathymetric features[1] of the centres of multispecies feeding flock density.[2]

Centre of flocking density	Distance from land (km)	Water depth (m)	
		Mean	Range
Shell Beach	0.49	25	10-50
Folger-Leach	0.62	40	5-110
Cape Beale	0.86	30	5-40
Seapool Rocks	1.00	25	5-30
Seabird Rocks	2.59, 4.81[3]	35	5-45

[1] Estimated from Canadian Hydrographic Service marine charts 3627 (1977) and 3671 (1979).

[2] Centres of feeding flock density as in Figure 6.

[3] First number indicates distance from Seabird Rocks, the second indicates the distance from Vancouver Island.

Table 4. Species composition of multispecies feeding flocks on the Deer Group Transects.

Species	Percentage of all flocking birds/month (n)						
	May (68)	Jun (0)	Jul (64)	Aug (839)	Sep (3946)	Oct (273)	Total (5190)
Arctic Loon	2.9	0	0	0	0	0	*
Western Grebe	0	0	0	0	0	0.4	*
Brandt's Cormorant	0	0	0	0	*	0	*
Pelagic Cormorant	58.8	0	0	0	0	0	0.8
Glaucous-winged Gull	36.8	0	3.1	0	3.4	0	3.1
Herring Gull	0	0	1.6	0	0.3	0	0.2
California Gull	0	0	79.6	28.6	7.1	0	11.1
Herrmann's Gull	0	0	0	0	0.1	0	0.1
Gull spp.[1]	36.8	0	96.8	92.1	82.1	7.3	79.4
Common Murre	1.5	0	1.6	7.8	17.8	91.6	19.6
Marbled Murrelet	0	0	0	0	0	0.7	*
Rhinoceros Auklet	0	0	1.6	0.1	0.1	0	0.1

[1] Gull spp. includes all of the birds in the previous four rows, plus some unidentified gulls, assumed to be one of those species.

*Less than 0.05%.

Table 5. Species composition of multispecies feeding flocks on the Inner Transects.

Species	Percentage of all flocking birds/month (n)					
	May (261)	Jun (265)	Jul (92)	Aug (1521)	Sep (3634)	Total (5773)
Arctic Loon	0	0	0	0	0.1	0.1
Sooty Shearwater	0	0	0	14.3	1.4	4.6
Brandt's Cormorant	0	0	0	0	0.1	*
Pelagic Cormorant	0	1.1	0	0.1	0.1	0.2
Northern Phalarope	0	0	0	0	0.3	0.2
Glaucous-winged Gull	76.6	12.1	7.6	0.9	0.4	4.7
Herring Gull	0	9.1	3.3	0.3	0.2	0.7
California Gull	0	22.6	38.0	23.6	1.3	9.5
Bonaparte's Gull	23.4	0	0	0	0.3	1.2
Gull spp.[1]	100	61.5	72.8	70.5	71.5	73.5
Common Murre	0	21.1	5.4	10.7	24.1	19.1
Pigeon Guillemot	0	0.4	0	0	0	*
Marbled Murrelet	0	3.8	19.6	1.9	*	1.0
Cassin's Auklet	0	1.1	1.1	0	0	*
Rhinoceros Auklet	0	1.1	1.1	2.5	0.2	1.3

[1] Gull spp. includes all of the birds in the previous four rows, plus some unidentified gulls, assumed to be one of those species.

*Less than 0.05%.

Table 6. Species composition of multispecies feeding flocks on the Outer Transects.

Species	Percentage of all flocking birds/month (n)					
	May (0)	Jun (0)	Jul (71)	Aug (223)	Sep (496)	Total (790)
Pink-footed Shearwater	0	0	0	2.7	0.4	1.0
Sooty Shearwater	0	0	0	49.3	80.6	64.5
Northern Phalarope	0	0	0	0	0.2	0.1
Glaucous-winged Gull	0	0	4.2	0	0	0.3
California Gull	0	0	67.6	0	4.6	8.9
Gull spp.[1]	0	0	71.8	44.9	16.7	29.6
Common Murre	0	0	22.5	3.1	0.4	3.1
Cassin's Auklet	0	0	0	0	1.6	1.0
Rhinoceros Auklet	0	0	5.6	0	0	0.5

---

[1] Gull spp. includes all of the birds in the previous two rows, plus some unidentified gulls, assumed to be one of those species.

the second most abundant group (about 20%). In the Outer areas, gulls comprised about 30% of the individuals present. An important difference between the Inner and the Deer Group feeding flocks was that the former had about 5% Sooty Shearwaters present, while they were absent in the latter.

Eleven different species were recorded participating in multispecies feeding flocks on the Deer Group Transects, 14 in flocks on the Inner Transects, and eight in flocks on Outer Transects. The number of species per feeding flock ranged from one to eight and did not differ among the three areas (Median Test, Conover, 1971: $T = 0.34$, d.f. = 2, $p > 0.50$).

Arctic Loons, Western Grebes, Pink-footed Shearwaters, Brandt's Cormorants, Pelagic Cormorants, Northern Phalaropes, Herring Gulls, Bonaparte's Gulls, Heermann's Gulls, Pigeon Guillemots, Marbled Murrelets, Cassin's Auklets, and Rhinoceros Auklets were also observed in the multispecies feeding flocks but their numbers comprised less than 3% of the birds seen in the flocks in any area.

(4) Feeding flock participation

Gulls participated in 98.2% of all of the multispecies feeding flocks observed in the three transect areas (Table 7). Of the gulls identified, California Gulls were present in 80% of the flocks and Glaucous-winged

Table 7. Species participation in multispecies feeding flocks on the regular[1] transects.

Species	No. flocks present	Percent participation
Arctic Loon	5	9.1
Western Grebe	1	1.8
Pink-footed Shearwater	3	5.5
Sooty Shearwater	12	2.2
Brandt's Cormorant	4	7.3
Pelagic Cormorant	4	7.3
Northern Phalarope	2	3.6
Glaucous-winged Gull	32 (28)[2]	58.2
Herring Gull	12 (11)	21.8
California Gull	44 (30)	80.0
Bonaparte's Gull	2	3.6
Herrmann's Gull	2 (1)	3.6
Gull spp.[3]	54 (52)	98.2
Common Murre	37 (28)	67.3
Pigeon Guillemot	1	1.8
Marbled Murrelet	8	14.5
Cassin's Auklet	2	3.6
Rhinoceros Auklet	15	27.3

[1] Deer Group plus Inner plus Outer.

[2] Numbers in parentheses are the number of feeding flocks where the individuals were counted, if two numbers are presented.

[3] Gull spp. includes all the birds in the previous five rows, plus some unidentified gulls, assumed to be one of those species.

Gulls in 58.2%. Two alcid species, the Common Murre and the Rhinoceros Auklet participated in 67.3% and 27.3% of all flocks, respectively. No other species participated in more than 25% of all feeding flocks.

When the transect areas were considered separately (Table 8), the relative participation by species in feeding flocks differed slightly. Gulls were a part of all Deer Group feeding flocks, with California (90.5%) and Glaucous-winged (61.9%) gulls predominating. Murres participated in 76.2% of the Deer Group flocks. In the Inner Transect areas the same trend persisted. The main differences between these two areas were a high incidence of Marbled Murrelets and the presence of Northern Phalaropes, Pigeon Guillemots and Sooty Shearwaters in the Inner Transect flocks. The flocks in the Outer areas, on the other hand, had very different participants. Sooty Shearwaters were in 85.7% of these flocks, gulls in 71.4% and murres in 51.7%. Cormorants were not present in the Outer Transect flocks. The most important gull species was the California Gull, while the Glaucous-winged Gull was present in only one of the seven Outer Transect flocks.

Regardless of transect location, California Gulls and Common Murres were present in most feeding flocks and were represented by large numbers. The resident Glaucous-winged Gull was an important flock member in the

Table 8. Species participation in multispecies feeding flocks on the Deer Group, Inner and Outer Transects.

Species	Deer Group Transect (n = 21)			Inner Transect (n = 27)			Outer Transect (n = 7)		
	No. flocks present	Percent partici- tion	No./flock in which present	No. flocks present	Percent partici- tion	No./flock in which present	No. flocks present	Percent partici- tion	No./flock in which present
Arctic Loon	1	4.8	2	4	14.8	1	0	0	0
Western Grebe	1	4.8	1	0	0	0	0	0	0
Pink-footed Shearwater	0	0	0	0	0	0	3	42.9	2.7
Sooty Shearwater	0	0	0	6	22.2	44.5	6	85.7	85.0
Brandt's Cormorant	1	4.8	1	1	3.7	2	0	0	0
Pelagic Cormorant	1	4.8	40	3	11.1	3.3	0	0	0
Northern Phalarope	0	0	0	1	3.7	10	1	11.1	1
Glaucous-winged Gull	13 (15)	61.9	32.4	18 (12)	66.7	22.4	1	11.1	3
Herring Gull	3 (2)	14.3	5.5	9	33.3	4.3	0	0	0
California Gull	19 (10)	90.5	57.4	22 (17)	81.5	32.1	3	42.9	23.7
Bonaparte's Gull	0	0	0	2	7.4	35.5	0	0	0
Heermann's Gull	2 (1)	9.5	5	0	0	0	0	0	0
Gull spp.[2]	22 (21)	100	224.5	27	100	157.2	5 (4)	71.4	58.5
Common Murre	16 (11)	76.2	92.6	17 (13)	63.0	84.6	4	57.1	6.3
Pigeon Guillemot	0	0	0	1	3.7	1	0	0	0
Marbled Murrelet	1	4.8	2	7	25.9	8.3	0	0	0
Cassin's Auklet	0	0	0	1	3.7	1	1	14.3	8
Rhinoceros Auklet	5	23.8	1	9	33.3	8.4	1	14.3	4

[1] Numbers in parentheses are the number of feeding flocks where the individuals were counted, if two numbers are presented.

[2] Gull spp. includes all the birds in the previous five rows, plus some unidentified gulls, assumed to be one of those species.

Deer Group and Inner areas, but was less so in the Outer regions not close to land.

(5) Flocking tendency

Only the Deer Group feeding flocks are considered in this section as the data for the total number of birds seen on the Inner and Outer Transects were not analysed (see II.A.). Among species observed on transects, California Gulls, Glaucous-winged Gulls, Herring Gulls, and Common Murres had the greatest tendency to flock, that is, the proportion of individuals seen on transects that was in multispecies feeding flocks was highest for these groups. All gulls and murres observed feeding during the transects, did so in feeding flocks. At other times gulls were observed feeding in the intertidal or scavenging on offal. Murres may have been feeding as singles or in monospecific groups, but this was not discerned, as they consumed their food under water. The low flocking tendencies in Table 9 indicate that birds spent much of their time engaging in other activities (e.g., flying, loafing on land or water). The Marbled Murrelet had the lowest flocking tendency (0.2%) of the birds seen participating in multispecies feeding flocks. On the other hand, there were 15 species that occurred on the Deer Group Transects that potentially could have joined such flocks to feed, but did not (see Appendix D). Their flocking tendency was zero.

Table 9. Flocking tendency by species on the Deer Group Transects.

Species	Total individuals on transects	Individuals in feeding flocks	Percent flocking tendency
Arctic Loon	155	2	1.3
Western Grebe	12	1	8.3
Brandt's Cormorant	260	1	0.4
Pelagic Cormorant	2923	40	1.4
Glaucous-winged Gull	3577	162	4.5
Herring Gull	101	11	10.9
California Gull	9528	574	16.0
Heermann's Gull	208	5	2.4
Gull spp.[1]	27811	4119	14.8
Common Murre	6819	1019	14.9
Marbled Murrelet	962	2	0.2
Rhinoceros Auklet	65	5	7.7

[1] Gull spp. includes all of the birds in the previous four rows, plus some unidentified gulls, assumed to be one of those species.

Table 10. Frequency of age classes of Glaucous-winged and California gulls in multispecies feeding flocks on the Deer Group Transects.

Age categories	Individuals on Deer Group Transects		Total	Percent in feeding flocks	G value[1]	
	Present in feeding flocks	Absent in feeding flocks				
Glaucous-winged Gull						
Adult	67	2286	2353	2.9	104.7	472.2
Subadult	1	159	160	0.6	21.1	
Juvenile	69	670	739	10.3		
Totals	137	3115	3252	4.4		56.3
California Gull						
Adult	189	3801	3990	4.7	17.4	164.4
Subadult	79	746	816	8.6	18.7	
Juvenile	315	1891	2206	14.3		
Totals	574	6438	7012	8.2		164.5

[1] G-test of independence (Sokal and Rohlf, 1969); all $p < 0.005$.

It should be noted that for the Glaucous-winged and California gulls, flock-feeding was dependent on age (Table 10; G = 56.25, 164.5, respectively; d.f. = 2; $p < 0.005$) with juveniles having the highest percentages relative to their abundance in both species (10.3% and 14.3%, respectively). For the migrant California Gull, subadults had the next greatest proportions in flocks (8.6%). The reverse was true for the resident Glaucous-winged Gull.

When the relative abundance of species groups found in feeding flocks was compared to that on the transects, certain trends emerged. In both cases, alcids comprised just over 20% of the total individuals recorded. The proportion of gulls was higher in the feeding flocks than for all birds seen. Cormorants were barely represented in the feeding flocks, although they were recorded on transects. The abundance of individuals of species groups (alcids, gulls, cormorants, others) in the feeding flocks differed from that expected, based on relative frequencies of species groups recorded on the transects as a whole ($\chi^2 > 100$, d.f.= 3, $p < 0.005$). This indicated that particular groups of species had a greater tendency to feed in flocks.

C. Discussion

Barkley Sound is not a major nesting area, rather it appeared to be an important post-breeding staging area for certain migrant species. From May until mid-July very few birds were observed in the study area (see Appendices D, E and F). The species present were resident, and most of those individuals dropped from sight in June and July, which corresponded to their major nesting times. August brought with it a large influx of migrant birds, particularly California Gulls and Common Murres. The number of individuals per km of transect increased dramatically from July to August. September had the greatest number of birds, while October showed a decline in numbers. California Gulls started on the southward portion of their migration (Baltz and Morejohn, 1977; Houston, 1977; Southern, 1980); Glaucous-winged Gull juveniles continued their post-fledging dispersal (Butler *et al.*, 1980; Southern, 1980); Common Murre numbers decreased; while resident Glaucous-winged Gull adults and Pelagic Cormorants remained in the study area.

This seasonal and temporary increase in bird density coincided with the presence and abundance of seabird multispecies feeding flocks. The most and largest feeding flocks occurred in August and September. In September, the number of species observed per transect and per feeding flock was highest. This supported Cody's (1974) claim, based on observations from Destruction Island, Washington, that these local and sporadic areas of food abundance in inshore waters attracted large numbers of individuals of many species that might not ordinarily be found feeding adjacent to each other.

Although the arrival of birds and the attendant flock-feeding happened very suddenly, initially, there was a gradation in the location of flocks. There was a gradual, inward movement of flocks during August and September. At the same time, flocks were larger and contained more species in September than in August. On the other hand, regardless of transect location, Common Murres and California Gulls dominated the composition of flocks throughout the flocking period. It has been suggested that the timing and route of migration for California Gulls was an evolutionary response to food and competition pressures at the nest area (see Weseloh, 1975). For California Gulls, as for Common Murres, large numbers of adults and juveniles arrived simultaneously. Extended postfledging care is not expected in California Gulls (see Burger, 1980). On the other hand, juvenile murres were still under parental care when they arrived in Barkley Sound and had to be provisioned with food and protected by the accompanying adult. As stated in the Introduction, the period of initial independence in birds is probably the time of greatest mortality and thus a concurrent accessible, conspicuous and abundant food resource should be important. Apparently, in 1979, Barkley Sound provided this attribute at the appropriate time (cf. off

Senegal, Brown, 1979) and was able to support a portion of the population for a short, but critical period.

Flock-feeding on this patchy and superabundant food supply appeared to provide the vulnerable juveniles with an easy access to food. Proportionately more juvenile gulls were found in feeding flocks than either adults or immatures, suggesting that these aided in counteracting their less skillful foraging and searching powers (see later sections). Although adult Glaucous-winged Gulls were seen on transects throughout the season, peak numbers and feeding flock activity occurred during the post-breeding dispersal of the young (early September).

This distribution data implies that the chronology of seabird flocking was timed such that inexperienced young were provided with an abundant and accessible food supply at a (the) most critical time in their lives. If Barkley Sound had not had this superabundant food resource at that time, migrants and residents would not have remained long in the area, but continued on their dispersal and migration routes. I suggest Barkley Sound was an important post-breeding area for these birds. Given this, in the sections to follow I shall elaborate and speculate on the mechanisms of these multispecies feeding flocks, both physical and behavioral, and what proximate and(or) ultimate functions they served to the participants.

V. DYNAMICS OF THE MULTISPECIES FEEDING FLOCKS IN BARKLEY SOUND

A. Introduction

Two major hypotheses have been proposed to account for the existence of heterospecific groups (and single species ones, as well): enhanced feeding capabilities and(or) improved predator evasion (see Morse, 1977). Feeding advantages include: beating for insects and other active prey (Morse, 1970; Charnov *et al.*, 1976); minimizing duplication of effort (Cody, 1971); facilitation of food-finding (Krebs *et al.*, 1972; Ward and Zahavi, 1973; Krebs, 1974); capturing food items unavailable to single individuals (Barlow, 1974). Predator avoidance advantages include: increased awareness of predators (Goss-Custard, 1970; Page and Whitacre, 1975) and the "confusion effect" (Morse, 1970); cover-seeking (Williams, 1964; Hamilton, 1971); discouraging predators (Moynihan, 1962); and statistical probability of discovery (Morse, 1977; *c.f.* Treisman, 1975). These multispecies feeding flocks presumably formed over, and ultimately in response to a clumped food resource (see below) and advantages (if they existed) were probably related to feeding.

If the numbers of seabirds are regulated by the availability of food, as the evidence suggests

(Lack, 1966, 1968; Ashmole and Ashmole, 1967; Nelson, 1970, 1978; Ashmole, 1971), species which live together in the same area must have evolved means of reducing interspecific competition for food (Cody, 1973). They might find it in different places, in different ways, or feed on different prey; any two species may differ in more than one of these ways. How these separations are brought about may be difficult to determine because they may be manifested only when food is in short supply--the species overlapping in almost all respects when food is plentiful (Harris, 1977).

Seabirds can exploit only a fraction of their potential prey; most seabirds can only feed at or near the surface. For a variety of physical and biological reasons, foraging seabirds must rely on situations in which their prey is concentrated close to the surface. Such local concentrations are important not only for their accessibility, but also for the reduced costs associated with the density of prey (see Brown, 1980).

As the distribution and therefore availability of food becomes increasingly non-uniform, finding these localized concentrations at any particular time becomes a problem (Orians, 1971). This type of food distribution decreases the defensibility of the food resource and decreases the disadvantages of having another individual within easily observable range. Greater resource abundance permits more species to exploit a resource whereas low abundance precipitates the exclusion from that resource of species that are more poorly adapted (Cody, 1974). The present study was an example of the relation between the predictability of a food supply and the orderliness with which it was subdivided among species to which it provided support.

Seabird exploitation of shoals of fish is well known--Atlantic Mackeral (*Scomber scombrus*), Atlantic Herring (*Clupea harengus*) and Capelin (*Mallotus villosus*) by Northern Gannets (Nelson, 1978; Montevecchi and Porter, 1980); Pilchards (*Sardina pilchardus*) by Manx Shearwaters (Lockley, 1953); sticklebacks (Gasterosteidae) by Common and Arctic terns (Lemmetyin, 1973); and Sandlance (*Ammodytes* spp.), Capelin and Arctic Cod (*Boreogadus saida*) by the seabird communities of the North Sea, Newfoundland and the eastern Canadian Arctic, respectively (Tuck, 1961; Pearson, 1968; Brown, 1980). Invertebrate shoals, especially of euphausids (Euphausiidae) and other large crustaceans, are also very important (Komaki, 1967). Euphasids and Market Squid (*Loligo opalescens*), along with Northern Anchovies (*Engraulis mordax*) and Sandlance were found to be the staple foods of seabirds along much of the Pacific coast between California and British Columbia (Sealy, 1973, 1975a; Wiens and Scott, 1975; Baltz and Morejohn, 1977). In the absence of diet analyses in the present study, the nature of the prey was not determined. Based on these previous studies and casual observations of fish rippling the water's surface at feeding flock sites, it is assumed that the seabirds were feeding on highly clumped food resources. The local areas of prey concentration attracted large numbers of many species which may not ordinarily have been feeding adjacent to each other. It is unlikely that any species would ignore potential prey if it could catch it, so ecological separation is probably a combination of both physical and behavioral adaptations.

Most seabirds defer breeding for a few to several years (Amadon, 1964; Lack, 1967, 1968; Burger, 1980). This deferred maturity is believed to permit the young to learn to forage successfully before they themselves attempt to feed offspring. Studies with Brown Pelicans (Orians, 1969), Olivaceous Cormorants (Morrison *et al.*, 1978), Glaucous-winged, Herring and Laughing gulls (Moyle, 1966; Barash *et al.*, 1975; Verbeek, 1977a,b; Ingolfsson and Estrella, 1978; Searcy, 1978; Burger, 1980), and Sandwich and Royal terns (Dunn, 1972; Buckley and Buckley, 1974) all have indicated that young were less successful using most foraging methods when compared to adults. Failure to locate food sources, lower attempt rates and lower success rates appeared to be factors contributing to their lower success. Presumably, this delayed maturity provides young with sufficient time to learn or discover foraging areas and to perfect hunting techniques (Amadon, 1964).

By examining the dynamics of seabird multispecies feeding flocks in Barkley Sound, it was hoped that some of these inter- and intraspecific mechanisms that allowed the birds to feed together would be determined. Interpretation was aided by a consideration of the relationship between feeding adaptations and life history strategies.

B. Results

(1) Feeding flock structure: initiation, duration and cessation

The multispecies feeding flocks were comprised of usually less than 1000 individuals. They began with the discovery of what was assumed to be surface shoals of food and ended when the prey descended or dispersed beyond contact of the birds. Once a feeding flock had formed it developed following a fairly regular pattern. Gulls flew in at 10 to 15 m altitude. In wind, they swung downwind to join the flock, but in calm air they approached the flock from all directions. Alcids swam or flew to flocks and pursuit dove or landed and dove, usually at the boundaries of the flocks. Shearwaters flew to the centre and pursuit plunged. Cormorants flew directly into the centre of the flocks and plunged, presumably in pursuit of prey.

Typically, a single individual or a small group of birds located the prey and began feeding. Gulls initiated all but three of the 74 feeding flocks seen being initiated (Table 11). California Gulls initiated 67.5% of the flocks where initiators were identified and Glaucous-winged Gulls 14.8%. California Gulls were dominant nuclear species in July through September, when their numbers were highest in the study area (see Appendix E). Glaucous-winged Gulls initiated the only flocks seen in May and June. As the proportions of adult Glaucous-winged Gulls rose in October (see Appendix G) so did their tendency to initiate the feeding flocks. Heermann's and Bonaparte's gulls, late arrivals in the Sound, initiated four flocks each in October. No juvenile gulls were seen initiating flocks and adults had a much higher frequency than did subadults.

A Sooty Shearwater was observed initiating one flock. It detected the prey, flew directly to the area of rippling water and plunged into the centre. It was followed within 10 seconds by several gulls. A Common Murre and a Marbled Murrelet, were each recorded as flock initiators. Each dived and surface seized repeatedly in an area where there were fish on the surface. A single California Gull was attracted in each case and began feeding. This

Table 11. Species involvement in multispecies feeding flock initiations in Barkley Sound.

Species	Age	Month						Total	Percent of Total
		May	Jun	Jul	Aug	Sep	Oct		
Sooty Shearwater		0	0	0	1	0	0	1	1.4
Glaucous-winged Gull	adult	0	1	0	1	1	4	7	9.4
	unid[1]	3	0	0	0	0	1	4	5.4
	total	3	1	0	1	1	5	11	14.8
California Gull	adult	0	0	5	10	0	4	19	25.7
	subadult	0	0	2[2]	0	0	1	3	4.0
	unid	0	0	8	9	11	0	28	37.8
	total	0	0	15	19	11	5	50	67.5
Mew Gull	adult	0	0	0	0	0	1	1	1.4
Bonaparte's Gull	unid	0	0	0	0	0	4	4	5.4
Heermann's Gull	adult	0	0	1	0	0	4	5	6.7
Common Murre	adult	0	0	0	1	0	0	1	1.4
Marbled Murrelet	unid	0	0	0	0	0	1	1	1.4
Total		3	1	16	22	12	20	74	

[1] unid = unidentified age class.

[2] Both flocks before 10 July 1979.

attracted other birds to the feeding area and intense feeding began.

On numerous occasions during the study, large numbers of gulls and a few cormorants were observed flying in a specific direction. I followed their direction of flight and invariably found a multispecies feeding flock already well developed and birds actively feeding at the water's surface, presumably on bait fish. Multispecies feeding flocks could be detected with the unaided eye, while sitting in the pneumatic boat from as far as 7.5 km away. The dipping behavior of the gulls and the flashing white of their wings made the aerial component of the flock very conspicuous. The feeding calls (see Smith, 1977) of both gulls and murres could be heard from long distances on calm days. Flocks were often heard before they were seen.

Experiments with adult Glaucous-winged Gull models were designed to test the attractiveness of a group or a single bird on the water. Results of the tests (Table 12) indicated that the large group of models was not more attractive than the single model in terms of birds moving into ($\chi^2 = 0.05$, d.f. = 1, $p > 0.5$) or out of ($\chi^2 = 0.01$, d.f. = 1, $p > 0.9$) Ohiat Bay, or through the test area ($\chi^2 = 0.08$, d.f. = 1, $p > 0.5$) so controls versus models were compared in the analyses. On the other hand, the number of birds that were attracted

Table 12. Results of experiments in which model Glaucous-winged Gulls were put in Ohiat Bay.

	No. moving in bay	χ^2	No. moving out bay	χ^2	No. moving through test area	χ^2	No. remaining at model site
Control A	45	1.25	13	4.76	16	9.60*	0
1 Model	35		4		39		3
Control B	41	2.45	68	43.13*	35	12.80*	0
23-26 Models	28		10		72		36
1 Model *vs.* 23-26**		0.05		0.01		0.08	
Control *vs.* Model***		3.60		47.80*		22.20*	

*$p < 0.01$.

**Control A, 1 Model *vs.* control B, 23-26 models; 2 x 2 contingency table.

***Controls A and B combined, 1 model and 23-26 models combined.

to the model site and remained there differed in the two situations. In control situations, no birds approached the model site and remained there. During the trials, three birds approached and remained by the one model and 36 birds by the 23-26 models. Thus, the larger group appeared to be more attractive in this instance.

Tests showed that the attractiveness of the area as measured by the number of birds that moved through the test area and the number that remained in the vicinity of the model release site was directly related to the presence of gull models ($\chi^2 = 22.2$, d.f. = 1, $p < 0.005$), while the number of birds moving out of the bay was inversely related to the presence of the gull models ($\chi^2 = 47.3$, d.f. = 1, $p < 0.005$). The number of birds moving into the bay was independent of the presence of models ($\chi^2 = 3.6$, d.f. = 1, $p > 0.05$).

The fact that in the presence of models, more birds moved through the test area and moved to and remained at the model site, combined with the finding that fewer birds moved out of the bay, suggested that birds were attracted to the models. Since birds moving into the bay were not attracted, I speculate that these birds were satiated while the others were searching for food. One model had the same effect as the group, but the latter provided a greater stimulus to remain in the model site, suggesting that birds might find good (better) feeding potential (including searching power) in an area with many birds.

Of the birds that moved to the model site and remained there, 62.2% were juvenile Common Murres, 18.9% adult Glaucous-winged Gulls, 13.5% juvenile Glaucous-winged Gulls, and 2.7% of each of juvenile California Gulls and Rhinoceros Auklets.

These results suggest that the presence of models on the water attracted the attention of individuals that were searching (for feeding areas?) and young, particularly, were apt to remain in the test area if a large group of models was present.

Five of the six feeding flocks resulting from experiments involving supplementary food were initiated by adult California Gulls. The one flock started adjacent to the Glaucous-winged Gull colony on Baeria Rocks was initiated by an adult Glaucous-winged Gull.

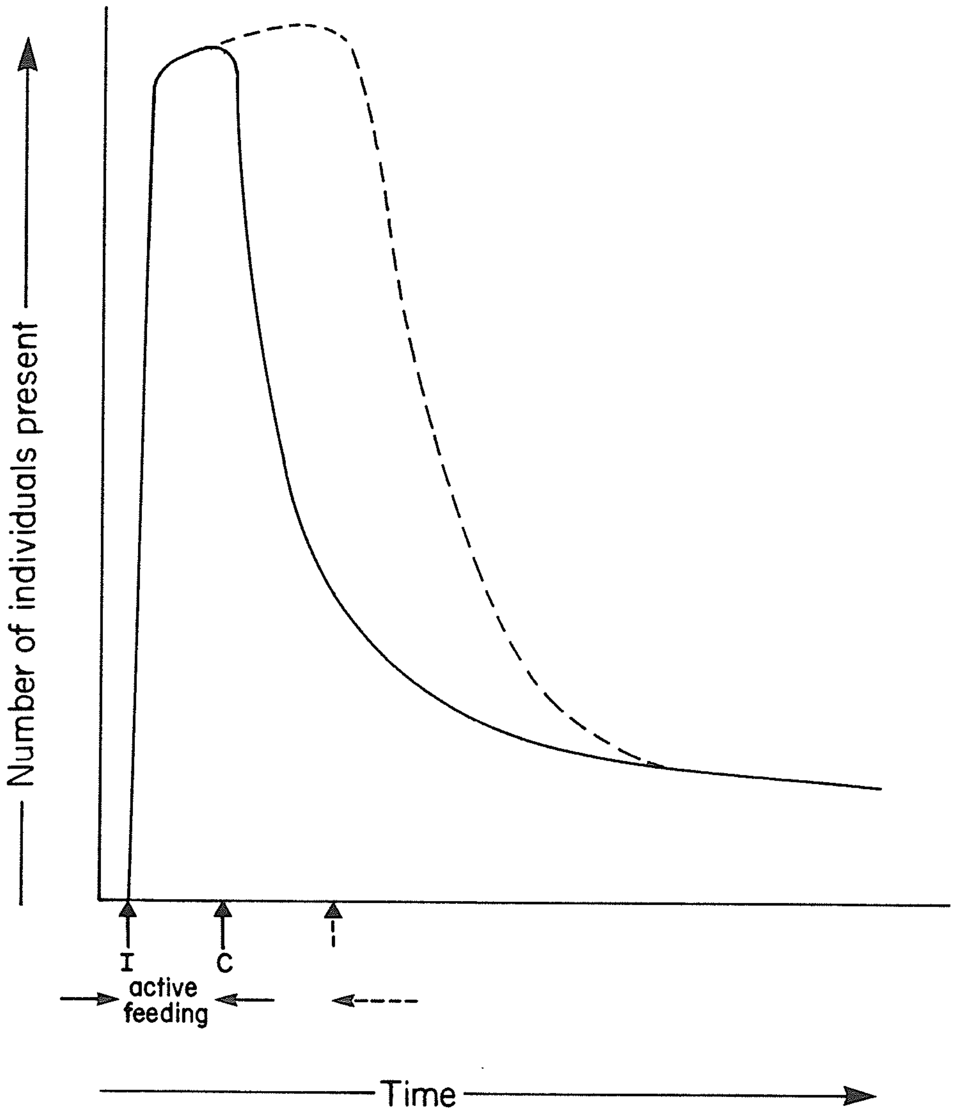
At Village Reef, food was distributed 0.5 km and 0.2 km from the terrestrial loafing site. The active feeding at the second locality, where food was discovered first, lasted about three minutes. After that time, birds went to the first (0.5 km) feeding area, and finally flew back to the 0.2 km feeding area. Although adult California Gulls discovered the food, more adults than juveniles remained at the original feeding site. Juveniles were the first to leave a site if another flock started in a nearby area. On the other hand, if only one feeding flock occurred, more juvenile gulls remained after 15 minutes (seven juveniles to one adult). Adults then usually dispersed or flew back to loafing sites. In early August, 14 feeding flocks were observed in quick succession (spatial and temporal). By the fifth feeding flock, 200 adult gulls sat on the edge of the flock while the juveniles actively dipped in the centre where the food was. In the 10th feeding flock, only juveniles were dipping and in the 13th feeding flock there were 50 juvenile California Gulls and five adult Glaucous-winged Gulls dipping in the centre, and 80 juvenile and four adult California Gulls and four Common Murres sitting on the periphery. Adult gulls were loafing on the water or on nearby rocks.

Figure 7 shows a schematic representation of the initiation, duration and cessation of feeding flocks. Feeding in the flocks lasted for less than one minute up to many hours. In all cases, the flocks conformed to a similar formation pattern. Following initiation there was a rapid increase in numbers. The peak number of individuals in the flocks occurred during the feeding; numbers often reached a plateau during this period (see the dotted line in Figure 7). Once feeding stopped,

Figure 7. Schematic representation of the initiation, formation and cessation of multispecies feeding flocks (see text for explanation).

I = initiation

C = cessation


Number of individuals present
I
C
active
feeding
Time

there was a steep drop in numbers as individuals moved out of the area. Some individuals remained in the foraging site and departed intermittently.

Gulls appeared to lose contact with the prey first and gradually dispersed outward. Adult California Gulls generally were the first to leave flocks. They may have been searching for feeding areas (recall their high flock initiation) or returning to loafing sites. Glaucous-winged Gulls, when present, remained in the feeding area for a prolonged period, unless another feeding flock commenced at another location. In this case they flew to the new feeding flock. Murres also dispersed, soon after the dipping of the gulls stopped. They swam-dove in various directions although they usually maintained themselves in fairly large groups. Juvenile gulls generally left the feeding flock site last, unless another flock had started nearby, in which case they invariably joined.

(2) Feeding methods and success rates of the participants

The feeding methods used by the participants in feeding flocks in Barkley Sound are summarized in Table 13. The gulls comprised the greatest above-surface portion of the feeding flocks and exploited prey on or near the surface of the water. In calm air gulls usually gathered into fairly circular groups, but in wind the flocks were

Table 13. Feeding methods[1] of seabirds in multispecies feeding flocks in Barkley Sound.

Species	Feeding method[2]						
	Diving	Surface seizing	Surface plunging	Aerial plunging	Pursuit plunging	Dipping	Klepto-parasitism
Common Loon	o						
Arctic Loon	o						
Red-necked Grebe	o						
Horned Grebe	o						
Western Grebe	o						
Pink-footed Shearwater		x	x	x		o	
Sooty Shearwater		o	o	o		o	
Double-crested Cormorant	o				x		
Brandt's Cormorant	o				x		
Pelagic Cormorant	o				o		
Harlequin Duck	o						
White-winged Scoter	o						
Red-breasted Merganser	o						
Bald Eagle						o	x
Northern Phalarope		o					
Glaucous-winged Gull		o	o			o	x
Western Gull		x	x			o	x
Herring Gull		o	o			o	x
California Gull		o	o			o	o
Ring-billed Gull		x	x			o	x
Mew Gull		o	o	o		o	
Bonaparte's Gull		o	o	o		o	
Heermann's Gull		o	o	o		o	o
Black-legged Kittiwake		x	x	x		o	
Sabine's Gull		x	x	x		o	
Arctic Tern						o	
Common Murre	o	o			o		
Pigeon Guillemot	o						
Marbled Murrelet	o	o					
Cassin's Auklet	o						
Rhinoceros Auklet	o						
Tufted Puffin	o						

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[1] See III.F.

[2] o = observed feeding method; x = presumed feeding method.

elongated along the axis of the waves. Birds were probably responding to the dispersion of the prey which appeared to be related to the wind and currents.

Juvenile California Gulls spent more time actively feeding (Table 14) in the centre of flocks than did adults. Adults often fed (dipping or surface plunging) for a short while in the centre of the flock and then flew to the periphery and sat there without feeding. The adult California Gulls plunged and dipped from higher in the air and less frequently than did juveniles. Adult Glaucous-winged Gulls flew directly into the centre of activity, dipping or surface plunging. For both species, only adults were seen surface seizing, although dipping and surface plunging were the usual feeding methods in the flocks. The gulls often dipped for fish, caught one (or more), and then flew to the periphery to swallow it.

The smaller gulls--Heermann's, Mew and Bonaparte's--all were observed aerial plunging in the flocks. The latter two appeared to use this method more often than dipping. These smaller species were more highly manoeuverable and acrobatic than the larger Glaucous-winged and California gulls.

Few feeding flocks in which shearwaters participated were observed in detail, partly because they occurred farther from shore, in areas less accessible in the

Table 14. Comparisons of foraging parameters among adult, subadult and juvenile California Gulls.[1]

Foraging parameter	Adult	Subadult	Juvenile	No. feeding flocks
Percent success (n = 256)	95.3	76.2	25.9	33
Flocking tendency[2]	4.7	8.6	14.3	21
Relative frequency in feeding flocks[2]	56.9	11.6	31.5	21
Relative frequency of active feeding in feeding flocks (n = 702)	19.4	2.8	77.8	59

[1] All parameters are significant among age classes (G-test: $p < 0.05$).

[2] Refer to IV.B.(5).

pneumatic boat, and partly because most feeding flocks were located within five km of shore where few shearwaters were found. Shearwaters fed mostly in the centre of the flocks by either aerial or surface plunging. Twice a Sooty Shearwater was seen surface seizing in a feeding flock. In the one flock a Sooty Shearwater initiated (V.B.(1)), the bird flew directly to the area where prey shoaled on the surface and plunged into the centre.

The lower dimensions of the prey source were exploited by divers. Diving birds, with the exception of cormorants were most often seen on the edges of flocks. All loons, grebes and ducks seen, participated at the edges of flocks, usually on the upwind end. Tufted Puffins were seen in feeding flocks four times and each time they were only seen diving and surfacing on the edges. Of 23 observations of Rhinoceros Auklets in feeding flocks, only one juvenile was recorded feeding in the centre while the others fed on the flock periphery.

Common Murres usually occurred on the periphery of the flocks, surrounding the focus of gull dipping and surface plunging. Occasionally, they dove and surfaced in the centre. From the time of their arrival in the study area in early August until young became independent (see Appendices D and F), adult murres had to feed their young. The young generally remained on the edges of the flock or were slightly removed from the flock. Adults dove for fish, retained the fish either longitudinally or cross-wise in their bills and swam back to the edge to feed the chick. Only once was the complete sequence observed; when the adult got to the edge, a juvenile, calling loudly, approached it, and was fed. By mid-September, most murres had completed their prebasic molt and many of the flocking birds were young (discerned by the distinct call of the juvenile murre; see Tschanz, 1968). At that time, there was a greater proportion of murres in the centre of flocks. When a murre surfaced in the centre it generally dove again immediately. Twice a murre was observed surface seizing for fish that were shoaling on the surface. One of those times, the murre was the flock initiator.

Cormorants usually were in the centre of flocks. Only once did I observe more than nine cormorants in a flock; in a May feeding flock there were about 40 Pelagic Cormorants. Generally, cormorants dove and surfaced in the centre of flocks. They swallowed their food beneath the surface of the water.

Six instances of successful kleptoparasitism were observed in feeding flocks. All were by adult gulls, three California and three Heermann's. In one case a subadult California Gull carrying a fish landed near the centre of the flock and an adult California Gull stole the fish from it. On three occasions, an adult chased a juvenile or a subadult to the edge of the flock, the victim dropped the food, and the adult ate it. Surface piracy was recorded once. An adult California Gull chased a Common Murre that had just surfaced with a fish crosswise in its bill. The gull did not steal the fish, and the murre swam to the periphery of the flock and fed a young. The incidence of kleptoparasitism was not high; kleptoparasites were generally medium-sized gulls and the victims were juvenile or subadult gulls.

Feeding success rates were difficult to obtain as it was hard to follow one individual in a feeding flock and the diving species apparently consumed their prey underwater. All juvenile gulls had a 50% or less feeding success rate in the flocks (Table 15). Only sample sizes for California Gulls were sufficient to compare among all three age classes. Adults had a 95.3% success rate, subadults 76.2% and juveniles 25.9%. All differences were significant (G-test of independence: $p < 0.01$). Also juvenile Glaucous-winged Gulls had lower success rates than did adults. These success rates may have underestimated the overall feeding success rates of adults, as they also caught food by surface seizing. Juveniles were not observed using this foraging technique.

Table 15. Feeding (dipping and surface plunging) success rates in multispecies feeding flocks in Barkley Sound.

Species	Age	No. attempts	No. successes	Percent success	G-value[1]	
Glaucous-winged Gull	adult	62	50	80.6	10.2*	
	subadult	3	0	0		
	juvenile	12	4	33.3		
	total	77	54	70.1		
Herring Gull	juvenile	4	2	50.0		
California Gull	adult	85	81	95.3	12.0*	108.4*
	subadult	63	48	76.2	42.2*	
	juvenile	108	28	25.9		
	total	256	157	61.3		116.6*
Mew Gull	adult	3	3	100.0		
Bonaparte's Gull	subadult	10	6	60.0		
Heermann's Gull	adult	4	4	100.0		

[1] G-test of independence.

* $p < 0.01$.

Table 14 details several foraging parameters for California Gulls. Juveniles had the highest flocking tendency (see IV.B.(5)), the highest foraging activity in the flocks (relative frequency of feeding attempts), but the lowest success rates. There were insufficient data to make this comparison among age classes of the other species, although the same general trend appeared to prevail for Glaucous-winged Gulls; juveniles had a higher flocking tendency than did adults (IV.B.(5)) and lower feeding success rates (Table 15).

(3) Time budget analysis at the Shell Islet loafing site on 17 September 1979

There were 22 multispecies feeding flocks observed in the 12 hour period (Figure 3). Flock-feeding comprised a maximum of 243.5 minutes during the day (33.8%). Although all areas could not be seen from the observation point, there were no other large movements of the birds from the loafing site on Shell Islet that would indicate feeding flocks were being formed elsewhere. All individuals did not feed in all flocks. The flocks averaged (±SE) 524.9±102.5 individuals with a mean of 4.7±0.49 species per flock (Table 16).

There was a gradual increase in the number of feeding flocks over the day (Table 16), although this was not significant among the four time periods ($\chi^2 = 6.14$, d.f. = 3, $p > 0.10$). On the other hand, the six feeding flocks

Table 16. Frequency, size and numbers of species in multispecies feeding flocks on 17 September 1979.

Time (P.D.T.)	No. feeding flocks	No. individuals/ flock±SE	No. species/ flock±SE
0730-1030	2	439.0±239.0	8.5±0.50
1030-1330	4	633.7±308.7	4.3±0.25
1330-1630	6	411.7±213.5	4.8±0.48
1630-1930	10	630.0±120.0	3.3±0.25
Total	22	524.9±102.6	4.7±0.49

in the first half of the day were significantly less than the 16 in the latter half ($\chi^2 = 4.55$, d.f. = 1, $p < 0.05$). The first feeding flock was not recorded until 0916 , 116 minutes after observations began. There did not appear to be a tidal effect; high and low tides were at 1110 and 1650, respectively. A circadian activity in the prey may have been present and could account for the number of flocks near dusk.

The size of the feeding flocks ranged from 50-1400 individuals. The mean size of the feeding flocks (Table 16) among the four periods of the day did not differ (Kruskal-Wallis Test: T= 1.70, d.f. = 3, $p > 0.10$). The duration of feeding flocks ranged from 0.5-66.0 min and averaged (±SE) 11.5±3.13 min (Table 17). The duration of feeding flocks was distributed randomly (see Appendix A.(1)) and did not differ among the four periods of the day (Kruskal-Wallis Test: T = 5.79, d.f. = 3, $p > 0.10$).

The distribution of the inter-feeding flock time intervals was random (see Appendix A.(2)), indicating that the feeding flocks were not clumped in time. The time between successive feeding flocks (Table 17) did not differ among the four periods of the day (Kruskal-Wallis Test: T = 4.36, d.f. = 3, $p > 0.10$).

Table 17. Duration of flocks, and inter-feeding flock time intervals and distances on 17 September 1979.

Time (P.D.T.)	Duration of flocks±SE (min)	Time between flocks±SE (min)	Distance between flocks±SE (m)
0730-1030	24.0± 9.0	46.5± 2.5	380.0±0
1030-1300	6.6± 3.9	22.6± 7.5	532.5±130.7
1330-1630	18.0± 9.7	19.8± 9.4	1590.0±353.9
1630-1930	7.0± 2.4	13.1± 3.8	825.6±279.6
Total	11.5±14.7	20.0±17.6	913.5±176.6

Species participation in the multispecies feeding flocks is shown in Table 18. California Gulls participated in all flocks for which there were data. Glaucous-winged Gulls and Common Murres were in 93% of the flocks and Brandt's Cormorants in 64%. Common Loons, Harlequin Ducks, White-winged Scoters, Herring Gulls, Heermann's Gulls, and Rhinoceros Auklets were also present.

Plots were made to compare the dependence of the duration of flocks *vs.* flock size, inter-feeding flock time intervals and inter-feeding flock distances; the inter-feeding time intervals *vs.* flock size and inter-feeding flock distances; and flock size *vs.* inter-feeding flock distances. No positive or negative relationships were found. These results indicated that the multispecies feeding flocks occurred as independent events in space and time.

C. Discussion

Group foraging generally occurs when food is patchily distributed and locally abundant. Seabirds show two mutually exclusive adaptations for exploiting their marine environment. They may have long wings conferring mobility in the air (e.g., gulls), or they may have short wings with legs set far back suited for swimming (e.g., alcids; Bourne, 1977). The former are birds whose foraging and feeding behaviors are highly

Table 18. Species' participation in multispecies feeding flocks on 17 September 1979.

Species	No. flocks present (n = 14)	Percent participation
Common Loon	3	21.4
Brandt's Cormorant	9	64.3
Harlequin Duck	1	7.1
White-winged Scoter	2	14.3
Glaucous-winged Gull	13	92.9
Herring Gull	8	57.1
California Gull	14	100.0
Heermann's Gull	1	7.1
Common Murre	13	92.9
Rhinoceros Auklet	1	7.1

visible. They were usually the initiators of the feeding flocks observed in this study, and even when contact with food was made by a diver, the arrival of the more conspicuous feeders facilitated rapid flock development. In Barkley Sound feeding flocks, the most important of these were the adult California and Glaucous-winged gulls. They were capable of a slow, highly manoeuverable flight that made them well adapted for aerial searching for prey. In Alaska, the initiators or nuclear species were the Black-legged Kittiwake and Glaucous-winged Gull (W. Hoffman, pers. comm.); off the Queen Charlotte Islands the nuclear species was primarily the Black-legged Kittiwake (Sealy, 1973); and off Destruction Island, the nuclear species was usually the Western Gull (W. Hoffman, pers. comm.). All of these species fed by aerial dipping and plunging, which made them highly visible while feeding. In addition, these gulls had largely white underparts and wing linings. It has been suggested that this coloration evolved for the purpose of attracting birds to food sources (Darwin, 1890; Armstrong, 1946; Simmons, 1972). Smith (1977) maintained that a dark plumage combined with a highly conspicuous and vocal mode of foraging, usually prevailed in intraspecifically gregarious land birds. The drabness presumably reduced aggression. This may have been a contributing factor in the evolution of the dark plumage of young gulls; the need to avoid agonistic encounters counteracted any benefits related to conspicuousness (e.g., reducing visibility to prey (Cowan, 1972) or increasing visibility for feeding).

Feeding methods among ecological groups were not wholly stereotyped as some (e.g., Ashmole, 1971) have implied. Murres were recorded surface seizing and gulls plunge diving. This, coupled with the presumption that all of the members of a flock were exploiting the same prey, emphasized that versatility was evidently a key factor in the feeding biology of the many successful seabird species.

The experiments with models indicated that individuals (gulls in particular) were attracted to a decoy(s) of an adult Glaucous-winged Gull (see also Krebs, 1974). Birds flying out from the loafing areas, presumably in search of food were more attracted to the models than were birds flying back to the loafing site (satiated?). Most interesting was the finding that young birds remained near the models, particularly if there was a large number of models present. Juveniles perhaps were more apt to cue in to other birds (potential food-finders) than actual food. This may confirm less searching skill in young birds and ties in with the finding that adults were the flock initiators.

Burger (1980) reviewed the differences in foraging behaviors of seabirds of different ages. When compared to adults, young were less successful using most foraging methods. This lower success was manifested in their initial failure to locate food sources, lower attempt rates when food was located, and ultimately lower success rates. In this study juvenile gulls spent more time feeding, fed most actively and for the longest periods and had the lowest success rates. This supported Lack's (1967, 1968) premise that delayed maturity in seabirds resulted from the need to perfect hunting and foraging skills before birds attempted to raise young of their own. Subadults had success rates intermediate to those of adults and juveniles.

The actual occurrence of feeding flocks relied on the behavior of the prey. There seemed to be no particular pattern (e.g., diurnal, tidal); the time budget analysis suggested that the feeding flocks occurred as independent events in space and time. On the other hand, as we shall see later, the movements of the individuals associated with loafing sites and feeding areas were also not random. This reinforces the theory that some sort of social facilitation was involved in their feeding.

VI. BEHAVIOR AND MOVEMENTS OF BIRDS AT TERRESTRIAL LOAFING SITES

A. Introduction

Social organization expresses the complex evolutionary response of a species to numerous variables in the environment. Most studies that related spacing behavior and feeding dispersion have dealt with breeding and roosting assemblies of birds (e.g., Crook, 1964, 1965; Lack, 1968; Zahavi, 1971; Ward and Zahavi, 1973; Krebs, 1974). In this portion of the study I examined the location of loafing areas and the use and movements by the individuals and species associated with them. To my knowledge, there have been no studies of non-breeding gulls at communal loafing sites not concerned with feeding on garbage or offal.

Large groups of gulls and cormorants loafing on islands or beaches were common occurrences in Barkley Sound, particularly from August to October. This prompted a question concerning the function of these land-based loafing sites. Why do so many birds associate in so few areas? As stated in V, groups may form in response to food or predators. An explanation for coloniality in birds, which could also be extended to loafing associations, is the limited supply of suitable nesting sites (Lack, 1968; Nelson, 1978), or in this case, loafing sites. Apparently, the reason most of the birds were in the Sound (especially the visiting Common Murres and California Gulls), was to exploit the food supply (refer to IV; Weseloh, 1975; Houston, 1977; Southern, 1980).

By forming groups, individuals can increase the likelihood that they will find food, for instance if it is locally concentrated but distributed irregularly in space and time (Scott, 1973; Smith, 1977). Ward and Zahavi (1973) proposed an "information centre hypothesis." Flocks of individuals which forage together by day may join other flocks when roosting at night; these communal roosts, according to Ward and Zahavi (1973), act as information centres that give very large numbers of individuals access to each other's information about feeding sites. Birds and flocks that have exhausted sites and failed to find new ones can join the "luckier" ones, following them as they leave in the morning.

Scott (1973) indicated that species which fed on patchily distributed, but locally abundant food types, for example, fish schools, fed by "local enhancement," defined as "an increased tendency to respond to part of the environment as a consequence of the response of another individual to it" (Hinde, 1966 *in* Scott, 1973). This ensures not only a greater area surveyed for food, but also identification of food sources by a significant portion of the population when they are located.

In this section I attempt to illustrate (1) that loafing area abundance and distribution in Barkley Sound was correlated with times of flock-feeding, (2) that the composition at the sites was associated with the composition in flocks, and particularly that this was an age-related phenomenon, and (3) that the movements of birds at these sites were clumped, directional and age-related. Terrestrial loafing areas appeared to be located within visual range of feeding areas. Such loafing site selection was also considered. The relationship between loafing groups and the seabird multispecies feeding flocks contributed to the interpretation of the function and significance of this feeding phenomenon.

B. Results

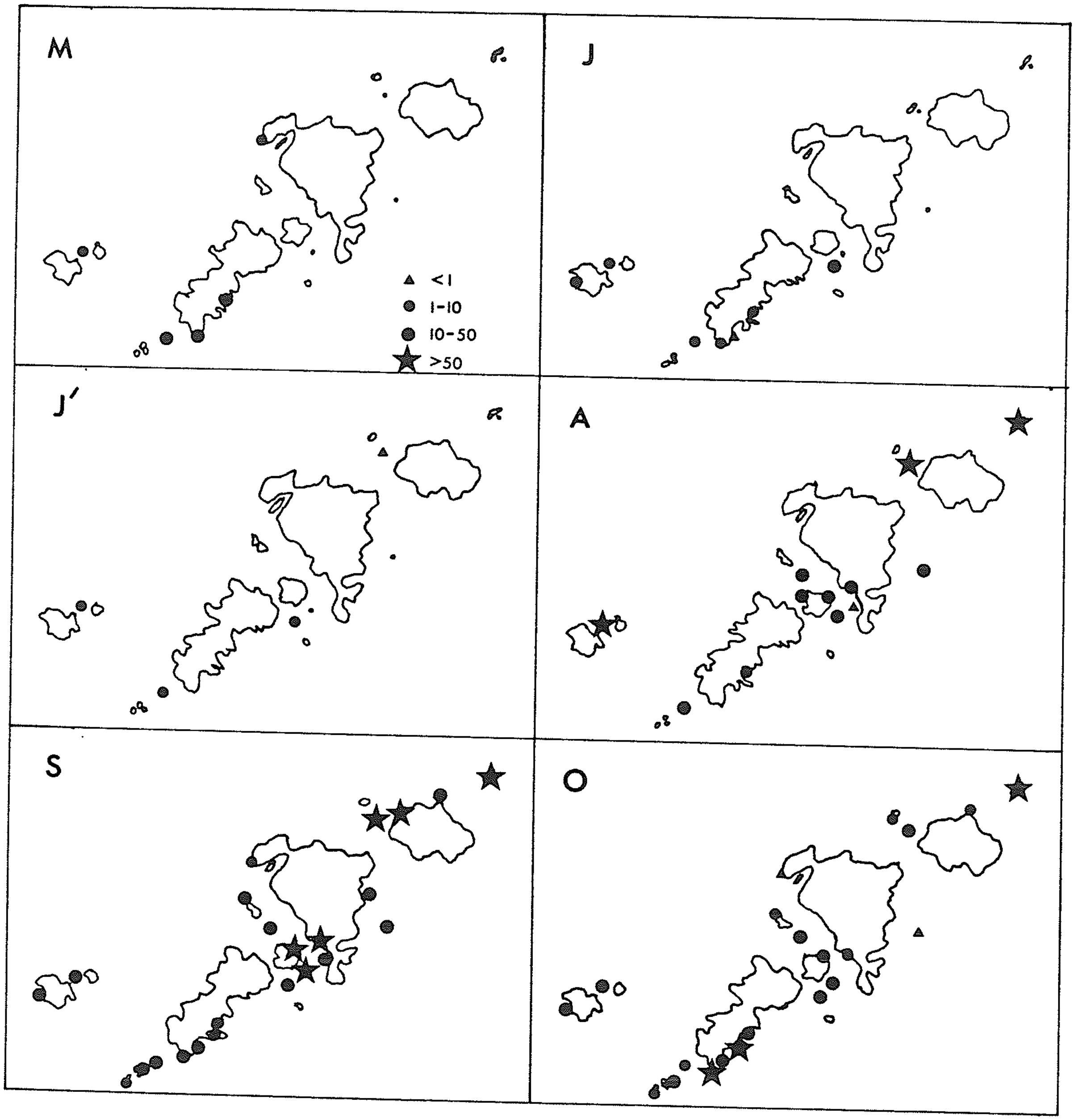
(1) Loafing site use on the Deer Group Transects

Table 19 and Figure 8 show the abundance, size and distribution of loafing areas on the Deer Group Transects (see also Appendix F). On the Deer Group Transects, the

Table 19. Abundance, size and importance of terrestrial loafing sites on the Deer Group Transects.

	Month						Total
	May	Jun	Jul	Aug	Sep	Oct	
% individuals on transects loafing at loafing site	25.3	23.3	4.1	46.9	41.0	47.6	41.3
No. of species per loafing site±SE (min-max)	2.6±0.40 (1-3)	3.6±0.76 (1-6)	2.5±0.65 (1-4)	2.3±0.33 (1-4)	2.8±0.24 (1-5)	2.5±0.34 (1-7)	
No. individuals at loafing sites per transect±SE	65.1±8.4	39.4±27.3	6.7±8.3	585.5±328.3	1189.4±518.6	451.8±215.5	427.8±523.3
No. loafing sites used	5	7	4	12	23	21	25
No. loafing sites used per transect	3.0	2.5	0.86	4.5	11.1	11.3	5.6
Relative importance of loafing sites among months	2.8%	1.7%	0.3%	25.1%	50.8%	19.3%	

Figure 8. Location (see Figure 4) and size (individuals/transect/month) of terrestrial loafing sites on the Deer Group Transects. M = May, J = June, J' = July, A = August, S = September, O = October.


M
J
J′
A
S
O
▲ <1
● 1-10
● 10-50
★ >50

birds at the 25 loafing sites accounted for 41.3% of the birds seen on the transects (Table 19). The numbers during May, June and July were well below this percentage, because there were relatively few birds present in the study area at that time (see Appendix E). As the absolute numbers of gulls and cormorants increased in the area, so did the proportions of these birds observed at the loafing sites.

The average number of birds per transect at the loafing sites was highest in August (585.5 ± 328.3) and September (1189.4 ± 516.6; Table 19), corresponding to the chronology and size of the feeding flocks (IV.B.). The number of areas used by loafing birds per transect was highest in September and October, respectively. In October, there was a greater percentage of birds at the loafing sites (47.6%). This was illustrated best by the resident Pelagic Cormorant and Glaucous-winged Gull (Figure 9). On the other hand, the ratio of loafing to non-loafing California Gulls dropped in October, corresponding to a reduced number of birds in the study area.

Figure 10 shows the relative frequencies of certain activities for the three age classes of Glaucous-winged and California gulls. Most adult Glaucous-winged Gulls were seen flying from May through July, although subadults had a greater tendency to loaf on the land at

Figure 9. Relative frequencies of activities for the Pelagic Cormorant, Glaucous-winged Gull and California Gull.

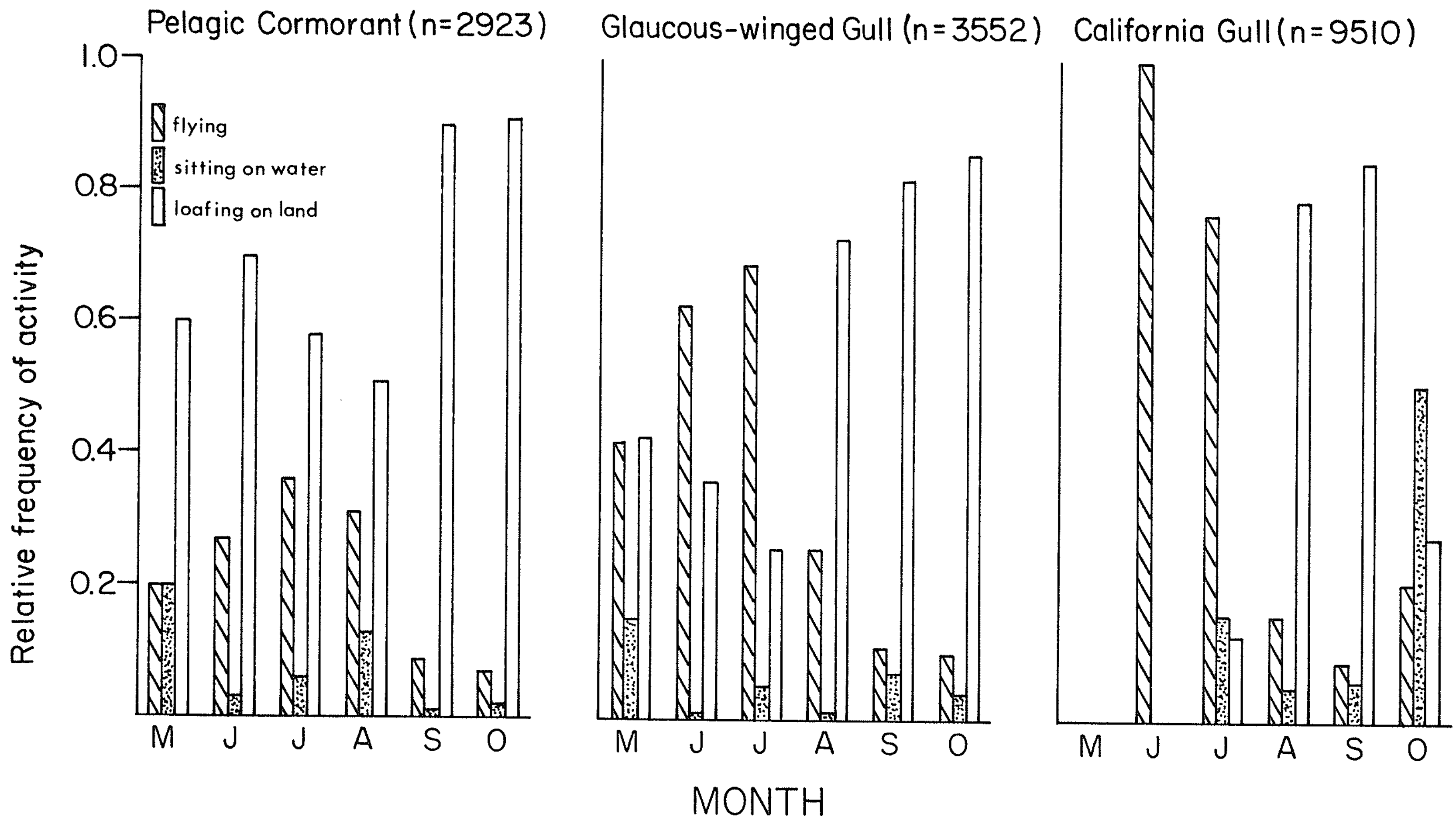
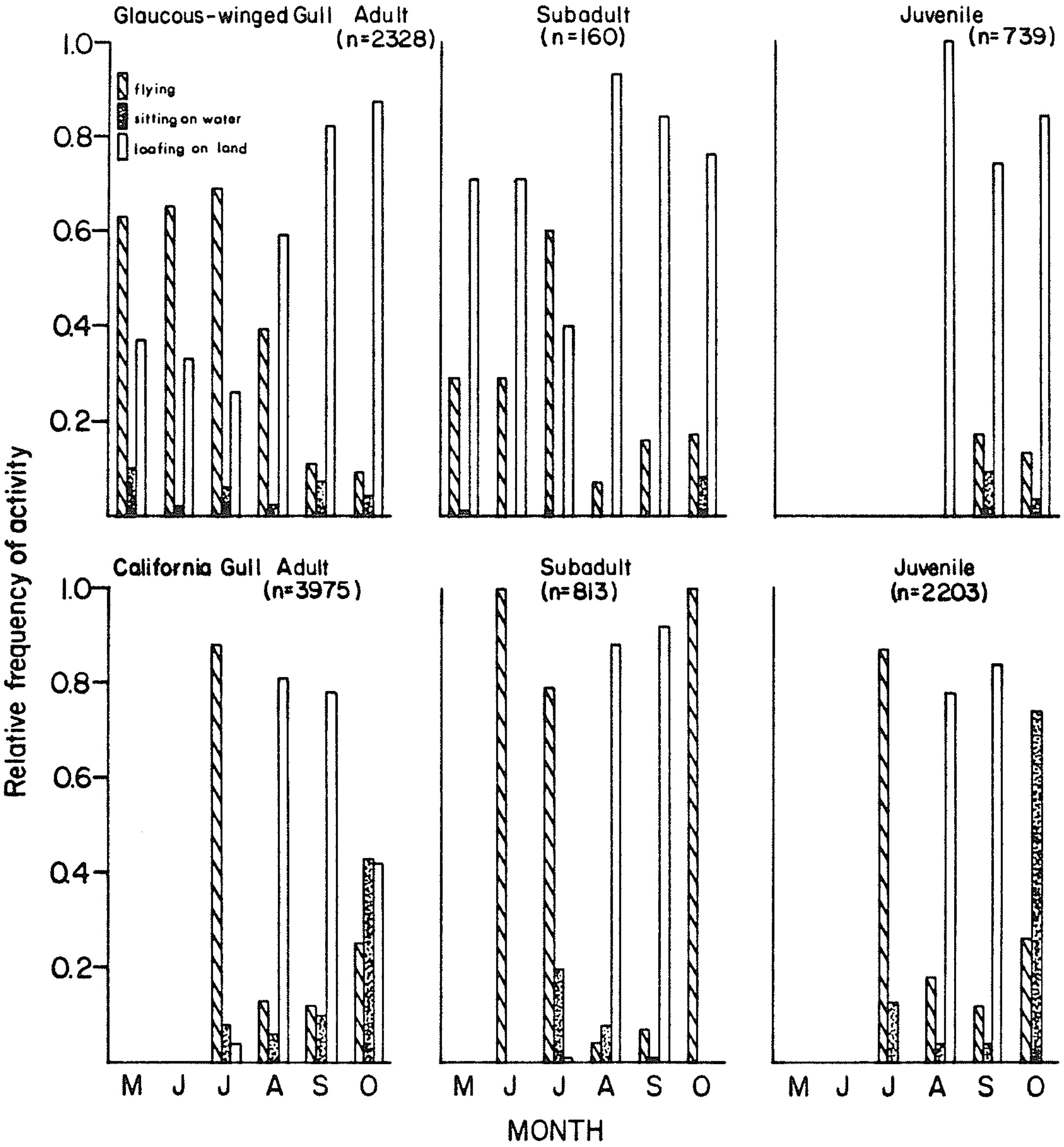

Pelagic Cormorant (n=2923)
Glaucous-winged Gull (n=3552)
California Gull (n=9510)
1.0
0.8
0.6
0.4
0.2
Relative frequency of activity
flying
sitting on water
loafing on land
M
J
J
A
S
O
MONTH

Figure 10. Relative frequencies of activities for adult, subadult and juvenile Glaucous-winged and California gulls.


Glaucous-winged Gull Adult (n=2328)
Subadult (n=160)
Juvenile (n=739)
flying
sitting on water
loafing on land
California Gull Adult (n=3975)
Subadult (n=813)
Juvenile (n=2203)
Relative frequency of activity
1.0
0.8
0.6
0.4
0.2
M J J A S O
MONTH

that time. In August, September and October all three age classes were recorded primarily loafing on land. Until August, most California Gulls were seen flying. After that time, most birds were recorded at the terrestrial loafing sites (about 80%). By October, when their numbers had decreased substantially, most adults were either sitting on the water or loafing on land, while the juveniles had a greater tendency to sit on the water.

Figure 8, showing the distribution of loafing sites over the season, revealed that there were four areas that consistently attracted large numbers of loafing birds. There appeared to be a trend toward an inward movement of loafing site use. The few sites observed from May through July averaged less than 50 birds per transect (see Appendix F). In August, September and October, Wizard and Shell islets (Figure 4) were major loafing sites. Folger-Leach was important, particularly in August. The Dodger Channel group (Inside and Outside Seppings, Haines Beach and Point, Diana Beach and Rock) was an important area in all of these months, particularly September. By October, Wizard Islet was the main terrestrial loafing area used by gulls and Southeast Edward King became a major cormorant loafing site. These four areas corresponded to the density centres associated with the feeding flocks observed on the Deer

Group Transects, when Folger-Leach and Ohiat Islet were areas of importance (IV.B.(2)). The only feeding flock observed in October was west of Wizard Islet, which was the major gull loafing site at that time.

Wizard Islet was the most heavily used loafing site with an average of 164.3 birds recorded there per transect (494.6 birds per transect in September). This location provided a view of both Imperial Eagle and Trevor Channels, probably important for opportunistic foragers like gulls (see VI.B.(3),C).

(2) Loafing site composition and structure on the Deer Group Transects

The average number of species per loafing site per month among months was not different (ANOVA: F = 0.41, d.f. = 5.67, $p < 0.05$). Glaucous-winged Gulls, Pelagic Cormorants and California Gulls were most often seen at the loafing sites. California Gulls (7204 birds), Pelagic Cormorants (2289 birds) and Glaucous-winged Gulls (1733 birds), respectively, were represented by the highest numbers. Herring (14 birds) and Heermann's (111 birds) gulls and Double-crested (75 birds) and Brandt's (136 birds) cormorants were also recorded at the sites during the study season.

Loafing species in May were comprised mostly of Pelagic Cormorants and adult Glaucous-winged Gulls. During June and July, the nesting season for these species, relatively few loafers were recorded. In August and September, California and Glaucous-winged gulls predominated. By October, species composition at loafing sites was similar to that of May with adult Glaucous-winged Gulls and Pelagic Cormorants present in the largest numbers.

An age dependency in gull loafing behavior in August and September on Deer Group Transects was revealed when the frequencies of loafing and non-loafing birds were analysed according to the ages of the individuals (Table 20; $G = 116.43$, d.f. = 2, $p < 0.005$). An STP analysis of homogeneity (Sokal and Rohlf, 1969) showed that the differences between successive age classes were significant: adult *vs.* subadult, $G = 90.66$; adult *vs.* juveniles, $G = 46.7$; subadult *vs.* juveniles, $G = 29.8$ ($p < 0.005$ in all cases). Subadults had the greatest tendency to loaf (82.9%), followed by juveniles (73.9%), and adults (66.0%). There were absolutely more adult gulls on transects or at loafing sites than either of the other classes. In August and September the ratios of adults to subadults to immatures, on the transects as a whole was 6.97 to 1.0 to 3.96, and the loafing on the transects was 5.54 to 1.0 to 3.51. In other words,

Table 20. Frequencies of loafing gulls compared among age classes on the Deer Group Transects in August and September, 1979.

Age	Behavior		Totals	Percent loafing	G value*	
	Loafing	Not loafing				
Adult	3287	1693	4980	66.6	90.6	46.7
Subadult	593	122	715	82.9	29.8	
Juvenile	2079	753	2832	73.4		
Totals	5959	2568	8527	69.9		116.4

*G-test of independence.

adult gulls were present in the greatest numbers, but had the least tendency to loaf on land.

When Glaucous-winged Gulls and California Gulls were seen loafing together, the former were usually farther from the tide level on the loafing island, adults more so than subadults. Cormorants had slightly different loafing habitat preferences, tending to loaf on cliffs and steep rock faces. Among the California Gull age classes, there was no apparent segregation.

When birds arrived at the terrestrial loafing sites they usually flew to an area where there were other birds. The first to arrive, generally landed on a reasonably high point, not exposed to wash from the sea, and on the sunny side of the rock. I suggest that Glaucous-winged Gulls were dominant; they appeared to have larger individual distances, and on the approach of an observer, an adult Glaucous-winged Gull often flew from the group, circled over the boat and returned again. If a large group of birds was already present at the site, arriving birds did not necessarily land in the same general area. This depended much on wind and their arrival direction.

An interesting behavioral response to a potential predator occurred on numerous occasions. When a Bald Eagle flew over a loafing site, the birds all flew up, and either returned to the rock or landed on the water when the eagle had disappeared (observed nine times).

Once I observed this phenomenon when birds were loafing on Haines Beach. They all flew in response to a Great Blue Heron which passed overhead. That was the only time I had observed this behavior in response to anything but an eagle.

(3) Movements of individuals at loafing sites

The observations of movements to and from terrestrial loafing areas suggested that both arrivals and departures were non-random (Figures 11 and 12). More frequency intervals with few observations or a large number of observations were recorded than expected with a random distribution having the same mean number of birds arriving or departing per minute (arrivals: $\bar{x} = 3.49 \pm 6.429$ min, $\chi^2 > 100$, $p < 0.005$; departures: $\bar{x} = 4.96 \pm 24.464$ min, $\chi^2 > 100$, $p < 0.005$). These results indicated the birds were not arriving and departing from loafing sites independently, but tended to be clumped temporally (see Appendix B). On the other hand, there were more departures than arrivals (4017 *vs.* 2828) and the greatest number of birds that arrived per minute was 82, while observations of 110, 117, 300, and 577 birds departing in one minute were recorded. This suggested that groups of departing birds had a tendency to be larger than groups that were arriving.

Qualitative observations also supported this conclusion. Birds were often seen streaming in or out in

Figure 11. Observed and expected frequency distributions of arrivals per one minute interval at terrestrial loafing sites (see Appendix B.(1)).

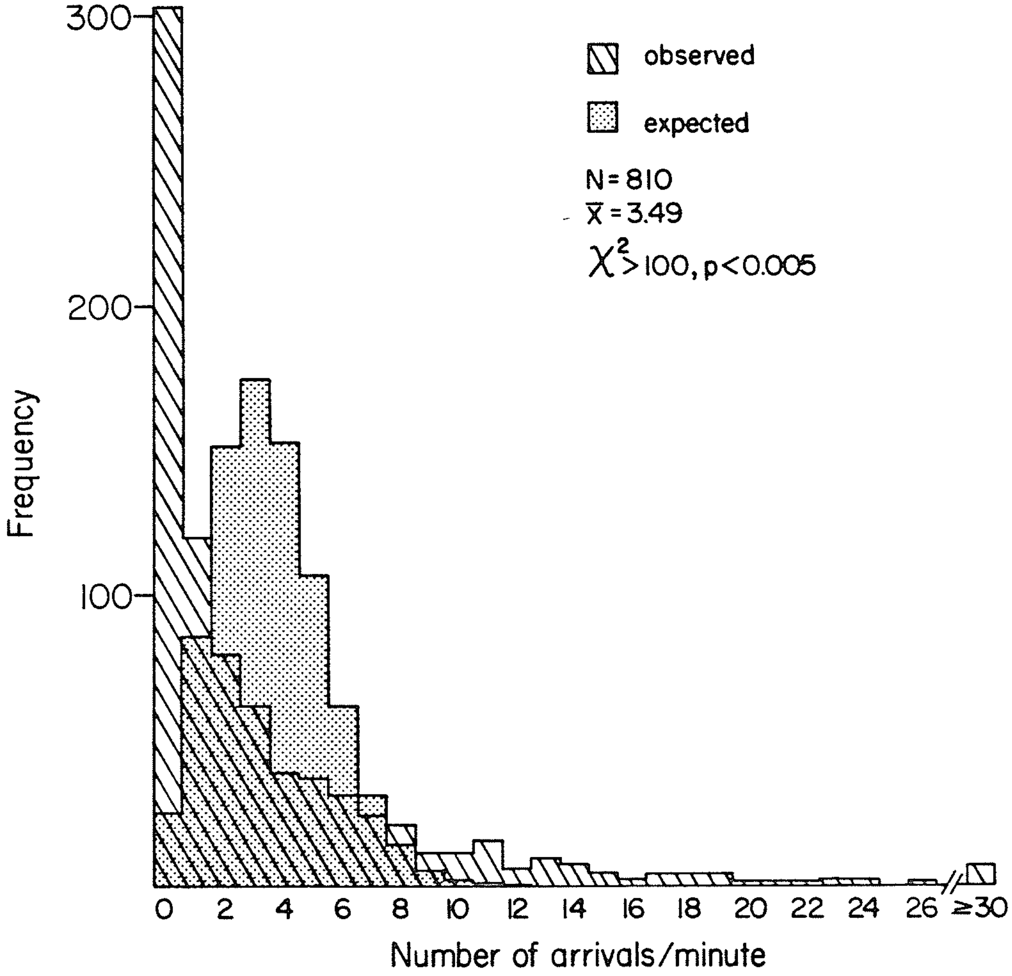
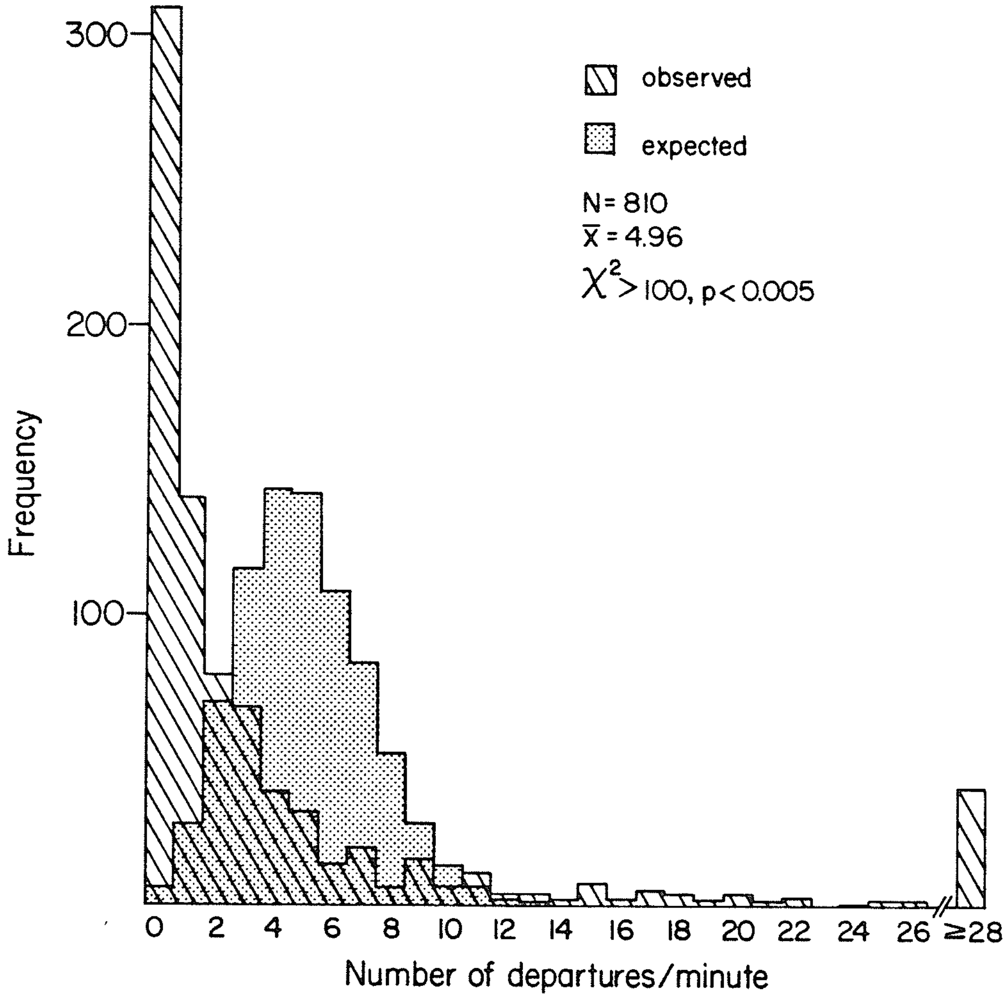

300
200
100
Frequency
observed
expected
N = 810
$\bar{X} = 3.49$
$\chi^2 > 100, p < 0.005$
0
2
4
6
8
10
12
14
16
18
20
22
24
26
≥30
Number of arrivals/minute

Figure 12. Observed and expected frequency distributions of departures per one minute interval at terrestrial loafing sites (see Appendix B.(2)).


300
200
100
Frequency
observed
expected
N= 810
X̄ = 4.96
$\chi^2 > 100$, p< 0.005
0
2
4
6
8
10
12
14
16
18
20
22
24
26
≥28
Number of departures/minute

groups. There were periods, however , when there was little movement to or from the loafing site.

Movements of gulls to and from loafing sites were related to age. The ratio of adults, subadults and juveniles involved in movements at the loafing sites was 8.02 to 1.0 to 3.65, compared to a ratio of 7.59 to 1.0 to 3.85, respectively, for all arriving birds. All differences were significant ($\chi^2 > 100$, d.f. = 2, $p < 0.005$).

The frequency of age classes involved in movements was compared to that at the loafing sites and an age dependency was revealed (Table 21; G = 51.77, d.f. = 2, $p < 0.005$). An STP analysis of homogeneity showed that the differences between adults and subadults or adults and juveniles were significant (G = 19.90, G = 42.0, respectively, d.f. = 1, $p < 0.005$). The frequency of movements and loafing by subadults and juveniles did not differ (G = 0.106, d.f. = 1, $p > 0.5$). Adults had a greater tendency to move at the loafing sites than either subadults or juveniles. When the frequencies of arrivals and departures of gulls were compared among the three age classes (Table 22), an age dependency in arrivals and departures was found (G = 11.85, d.f. = 2, $p < 0.005$). The percentage of juveniles arriving was 68.8, that of subadults was 65.3 and adults was 61.8. The differences between adults and subadults or subadults and juveniles

Table 21. Frequencies of movements and loafing of gulls at terrestrial loafing sites compared among age classes.

Age	Activity		Totals	Percent movement	G value*	
	Movement	Loafing				
Adult	1756	3287	5043	34.8	19.90	42.00
Subadult	219	593	812	27.0	0.10	
Juvenile	800	2079	2879	27.8		
Totals	2775	5959	8734	31.8		51.77

*G-test of independence.

Table 22. Frequencies of arrivals and departures of gulls at terrestrial loafing sites compared among age classes.

Age	Movement		Totals	Percent arrive		G value*
	Arrival	Departure				
Adult	1085	671	1756	61.8	1.02	11.70
Subadult	143	76	219	65.3	0.93	
Juvenile	550	250	800	68.8		
Total	1778	997	2775	61.4		11.85

*G-test of independence.

were not significant, while adults *vs*. juveniles did differ ($G = 11.70$, d.f. = 1, $p < 0.005$). Juveniles were more apt to arrive than adult and subadult gulls, and adults were more apt to depart than juveniles or subadults.

In summary, adults had a greater frequency of movement and departures than subadults or juveniles. This related to the lower frequency of loafing by adults (VI.B.(2)).

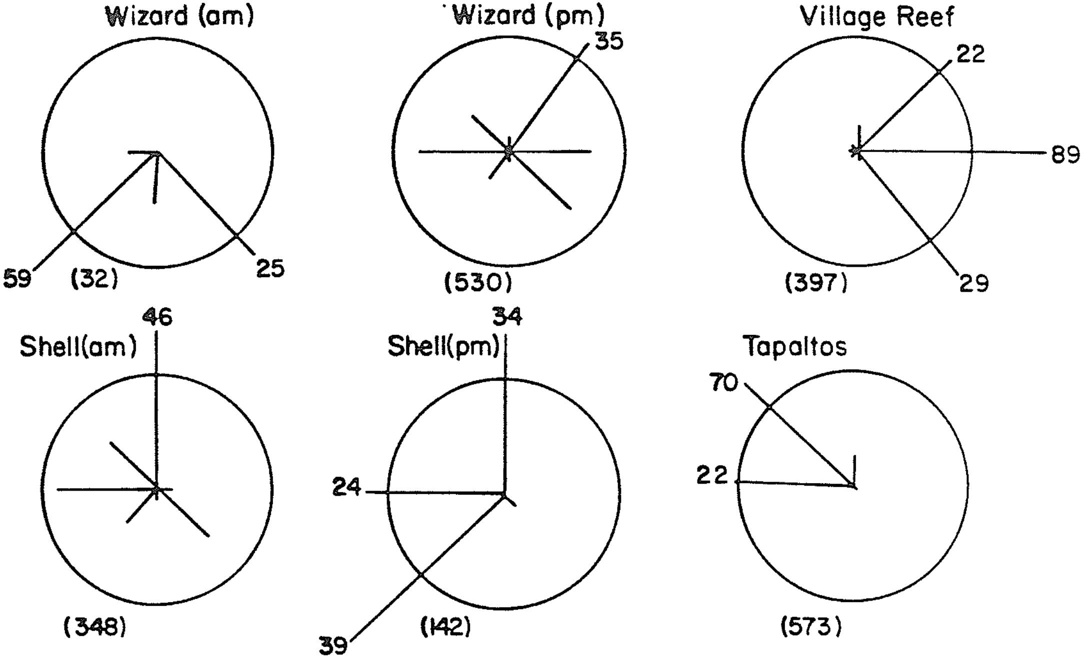
The arrivals and departures at the loafing sites were directional (Figure 13). Although, the number of hours of observation was low, certain trends were revealed. In locations for which there were movement data for both morning and evening (Wizard and Shell) there appeared to be little relationship between successive morning/evening arrivals and departures. This suggested that either there was much movement during the day and night or a large transitory population of birds was involved and hence the same birds were not seen at subsequent observations, or both. The arrival and departure directions as shown in Figure 13 indicated that movements to and from both Trevor and Imperial Eagle Channels were important.

C. Discussion

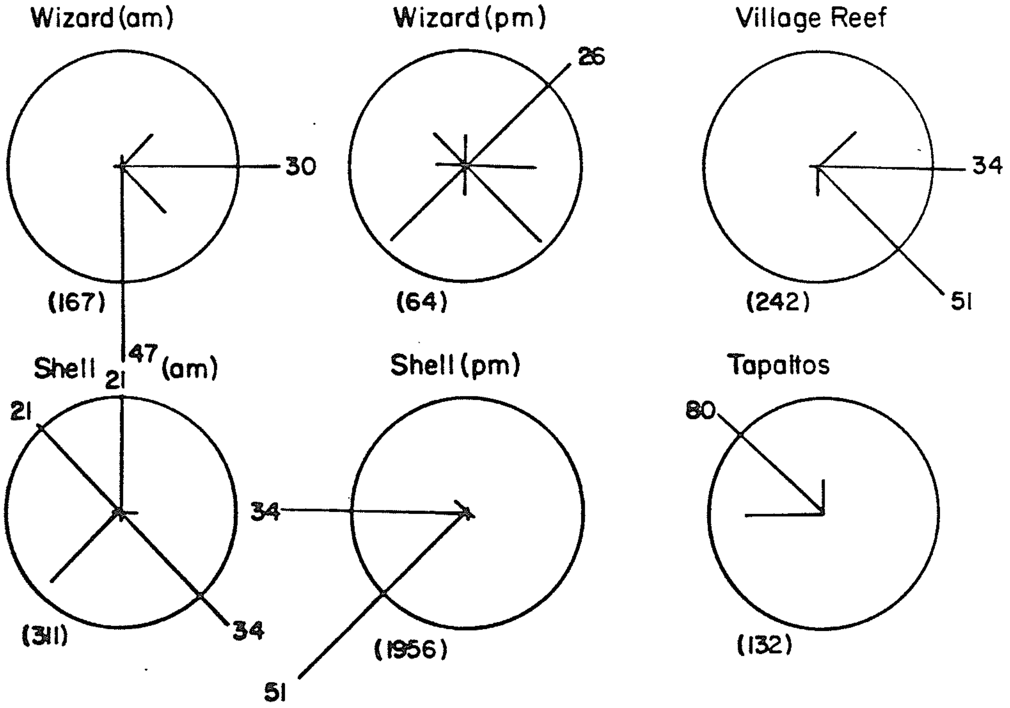
The selection of land loafing areas did not seem to be in response to a predator-free habitat, although this

Figure 13. Percent of seabirds seen arriving and departing in various directions at different terrestrial loafing sites. The outer circle represents 20% of the total. If birds flying in one direction exceed 20%, the bar extends past the circle and the percentage is indicated at the end of the bar. The sample size is given in parentheses under each figure.

ARRIVALS



DEPARTURES



may have been involved to some extent. The gregariousness of individuals was probably not in response to predators either; rather it appeared to be an adaptation for locating food patches by means of locally-enhanced food searching (see Evans, 1980). The terrestrial loafing sites apparently shifted location so as to be in the centre of food patches as suggested by Horn (1968) for Brewer's Blackbirds. This was illustrated by the gradual inward movement of loafing areas and a corresponding movement of centres of feeding flock density. The four major loafing areas, Folger-Leach, Dodger Channel, Shell Islet, and Wizard Islet, all provided vantage of both Trevor and Imperial Eagle Channels, where most feeding flocks occurred (see IV.B.(2)).

The finding that departures from loafing areas were clumped (see also Krebs, 1974; O'Malley, 1980) suggested that individuals were not leaving the loafing sites independently. They were possibly following a leader to a food patch (Krebs, 1974). Most feeding flocks were within sight of loafing areas, and hence loafing areas were visible from defunct feeding areas. It was possible for an individual to sit on the water in Trevor Channel and be aware of a feeding flock out of sight in Imperial Eagle Channel merely by watching the behavior of birds at the loafing sites.

The composition of individuals at terrestrial loafing sites had an age dependence as did the movements of individuals at the sites. Adults had the lowest tendency to loaf, the highest percentage of individuals involved in movements to and from loafing sites, and the lowest relative frequency of arrivals at loafing sites (and therefore the highest proportion of departures). They also had a lower flocking tendency than juveniles. This could indicate that adults spent more time searching for potential foraging patches than did juveniles; the juveniles' strategy may have been to feed in flocks and remain at the flock site or to loaf, and wait for adults to find food, rather than spend time searching. On the other hand, the extra time spent by juveniles feeding may have precluded their searching for food. While this may have been the most energetically beneficial strategy for juveniles, the adults, because they were more successful searchers and feeders, may have had the advantage of experience. This allowed them a greater chance of finding food and possibly being the first individual to locate it. The odds may have been too low for juveniles.

The results indicated that the age-dependent behaviors associated with flocking were related to those at loafing sites. The presence of centrally located loafing sites, combined with the conspicuous mode of foraging probably greatly aided food-finding, particularly in the inexperienced juvenile gulls.

VII. GENERAL DISCUSSION

A. Seabirds in the marine environment: distribution and behavior

Seabirds unquestionably are important components of the complex marine ecosystem. Although most oceanographers ignore or overlook this dimension, and seabird biologists have generally remained on the terra firma, this by no means reduces the impact of the seabird's role in the marine community. Perhaps the difficulty involved in studying these animals can be taken as an indication of the degree of specialization required for their highly adapted mode of life.

Most seabirds come to land only to breed. Delayed maturity in seabirds implies that the non-breeding segment of the population virtually leads a pelagic existence until sexually mature (see Brown, 1980). The result is that millions of individuals consume food from, defecate into and live and die on the ocean. From the standpoint of energetics alone, seabirds are an important cog in the system. On a different level, seabirds are highly visible and may be used as valuable indicators for both the environmental ecologist and the fisherman. Other, less tangible advantages associated with seabirds accrue from the beauty and pleasure they provide to humanity. Seabirds are a resource and must be treated as such. Only by obtaining a more complete understanding of these animals can we accurately assess their vulnerability and implement the proper protective measures.

In 1979, Barkley Sound did not have a large breeding population of seabirds. In fact, only during about two months of the six-month study did the area have a relatively high level of bird activity. This occurred during the post-breeding season for migrants, visitors and residents, alike. At this time, young in their early stages of independence were learning to fend for themselves. There can be no less emphasis placed on the importance of this stage in their life cycle than any other (e.g., the nestling period). Barkley Sound provided a highly conspicuous and abundant food supply at this critical period. It appeared that the multi-species feeding flocks facilitated food-finding for many newly fledged juveniles.

B. Adaptive significance of group foraging

Social foraging is generally regarded as being a response to a clumped and indefensible food supply. Such appeared to be the case in Barkley Sound, in 1979. Many mechanisms may have been involved in flock formation and feeding. Both auditory and visual mechanisms were probably necessary to attract flock members (see Frings *et al.*, 1955). If feeding by locally enhanced search (see Evans, 1980) was the case, and the model seems to fit, then the increased searching power of the group presumably outweighed disadvantages arising from competition or interference. The centrally located terrestrial loafing sites facilitated aerial flockers since they provided a common meeting place and a clear view of both Imperial Eagle and Trevor Channels, and they apparently were free of ground predators. Arrivals and departures at loafing sites were clumped and directional; birds were actually seen streaming from a loafing site directly to a feeding flock.

In addition to the advantages relating to food finding, there may have been benefits associated with the different species' various adaptations for exploiting the food source. The feeding activities of the divers may have aided in maintaining longer contact with the prey and hence allowed all birds to feed for a greater length of time (W. Hoffman, pers. comm.). The conspicuous feeding methods of gulls probably permitted divers to cue into more feeding flocks than they would have otherwise if they searched for prey concentrations on their own.

The need for flexibility and versatility in the feeding habits of the seabird species in order to take advantage of a highly variable food resource, must be emphasized. The birds are highly opportunistic and should adapt themselves in such a way as to make full use of the available resources.

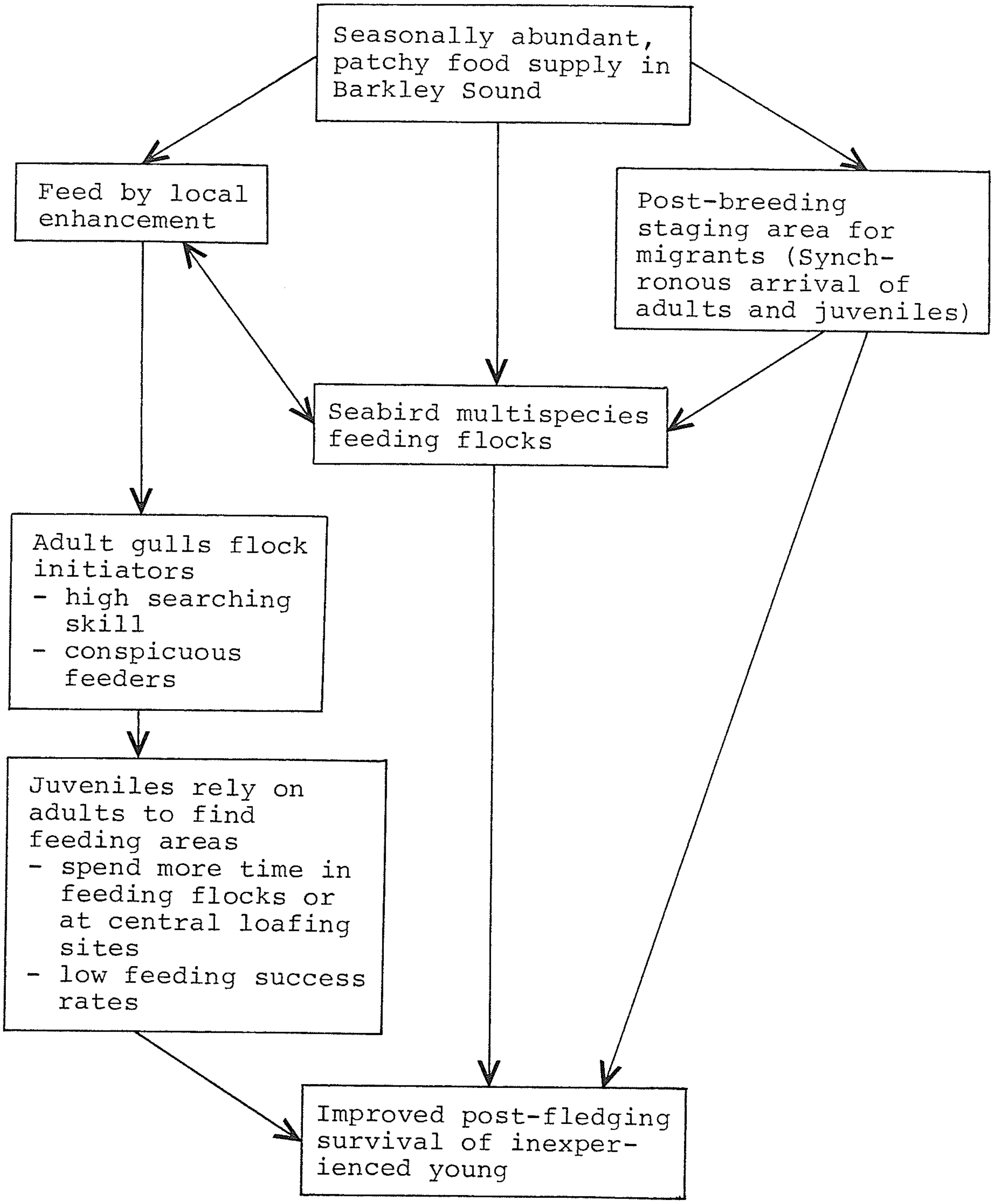
C. The function and significance of seabird multispecies feeding flocks in Barkley Sound, in 1979

Behavior is a mechanism through which adaptations to the environment are forged and maintained. The investigation of this relationship and the survival value accruing from it are useful in interpreting and explaining the many unique features of an organism's life cycle. The seabird multispecies feeding flocks were apparently the most effective means of exploiting the given food resources in Barkley Sound, in 1979. The timing of flock-feeding and the post-breeding dispersal of adult and young-of-the-year migrant seabirds to the Sound was consistent. Barkley Sound was not a major nesting area; rather, it was an important post-breeding staging area for these migrants.

The delayed maturity in seabirds explains why juvenile seabirds were apparently less successful foragers both in locating and catching prey. Juvenile gulls had a greater flocking tendency, spent more time actively feeding in flocks, spent less time searching, and had lower feeding success rates than did adults. This implied that the flocks provided inexperienced young with not only an abundant and accessible food supply, but also a dependable and conspicuous means of locating the food. Other foraging birds were easy to cue in to. This period of initial independence is the time of greatest mortality for fledged young (Southern, 1980) and juveniles benefited from the expertise and skill of the adults. Considering these concepts in an evolutionary framework, we see a complex of behavioral adaptations emerging to enhance survival of these inexperienced young at a critical period in their lives.

The following flow diagram illustrates how improved post-fledging survival may be achieved and places the role of the multispecies feeding flocks in the context of the response of seabirds to their environment during the post-breeding period (Figure 14).

Figure 14. The role of the seabird multispecies feeding flocks in Barkley Sound, in 1979.


Seasonally abundant, patchy food supply in Barkley Sound
Feed by local enhancement
Post-breeding staging area for migrants (Synchronous arrival of adults and juveniles)
Seabird multispecies feeding flocks
Adult gulls flock initiators
- high searching skill
- conspicuous feeders
Juveniles rely on adults to find feeding areas
- spend more time in feeding flocks or at central loafing sites
- low feeding success rates
Improved post-fledging survival of inexperienced young

VIII. SUMMARY

A. This study described the chronology and dynamics of seabird multispecies feeding flocks in Barkley Sound, British Columbia from May to October, 1979.

B. Replicate transects were conducted to determine the chronology of flocking in the Sound; behavioral observations were made on seabird multispecies feeding flocks, experiments were conducted and a time budget analysis was carried out to describe the dynamics of the multispecies feeding flocks; terrestrial loafing sites were characterized and the chronology of loafing was determined; and the frequency and direction of movements of individuals at the loafing sites were described.

C. (1) The most and largest seabird multispecies feeding flocks were in August and September. There was a gradual inward movement of flocks over the season. Feeding flocks on Deer Group, Inner and Outer transects did not differ in the number of species or the number of individuals per feeding flock.

(2) There were five centres of flocking density: Shell Beach, Folger-Leach, Cape Beale, Seapool Rocks, and Seabird Rocks. Locations were related to the overall distribution of birds in the Sound and the bathymetry of the area.

(3) California Gulls, Common Murres and Glaucous-winged Gulls dominated the flock composition in the Deer Group and the Inner feeding flocks; Sooty Shearwaters, California Gulls and Common Murres dominated the flock composition in the Outer feeding flocks.

(4) California Gulls, Common Murres and Glaucous-winged Gulls participated in the most Deer Group feeding flocks; California Gulls, Glaucous-winged Gulls and Common Murres participated in the most Inner feeding flocks; and Sooty Shearwaters and Common Murres participated in the most Outer feeding flocks.

(5) California Gulls, Common Murres, Herring Gulls, and Glaucous-winged Gulls had the greatest flocking tendency. For California and Glaucous-winged gulls, juveniles had the greatest tendency to flock.

D. (1) Gulls initiated all but three feeding flocks seen being initiated. California Gulls initiated 67.5%. Individuals (particularly juveniles) were attracted to a group of gull models on the water. Juveniles left the feeding flock site last unless another flock had started nearby, in which case they invariably joined.

(2) The feeding methods used by flock participants showed versatility. For California Gulls, juveniles had the highest flocking tendency, the highest number of

feeding attempts and the lowest feeding success rates.

(3) Feeding flocks appeared to be random events in space and time.

E. (1) Terrestrial loafing sites apparently shifted location so as to be in the centre of food patches.

(2) California Gulls were seen most often and were represented by the greatest numbers at terrestrial loafing sites. Adults had the lowest loafing tendency.

(3) Arrivals and departures at terrestrial loafing sites were clumped and directional. Adult gulls had a greater frequency of movement and departure than subadults or juveniles.

F. Barkley Sound appeared to be an important post-breeding staging area for migrant seabirds.

The results demonstrated how improved post-fledging survival was achieved for seabird multispecies feeding flock participants. This phenomenon was discussed in terms of the birds' response to the apparently seasonally abundant and patchy food supply.

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APPENDICES

Appendix A. Calculation of expected random distributions of:

(1) feeding flock durations on 17 September 1979,

5 minute interval class	Observed frequency (O_i)		Relative expected frequency (p_i)	Absolute expected frequency (E_i)
1	10		0.578	12.7
2	5		0.244	5.4
3	3	7	0.178	3.9
4	1			
5	0			
6	1			
7	1			
8	0			
9	0			
10	0			
11	0			
12	0			
13	0			
14	1			
Total	22 = N		1.000	22

The mean duration of feeding flocks in units of 5 minutes was calculated as:

$$\overline{x} = \frac{1}{N} \Sigma i(O_i) = 38/22 = 1.73$$

The value of θ was then:

$$1 - 1/\overline{x} = 0.422$$

The values of p_i were then calculated according to the formula:

$$p_i = \Pr(Y = i) = \theta^{i-1}(1 - \theta)$$

$$\chi^2 = 3.06, \text{ d.f.} = 1, p > 0.05.$$

(2) inter-feeding flock time intervals on 17 September 1979 and

5 minute interval class (i)	Observed frequency (O_i)		Relative expected frequency (p_i)		Absolute expected frequency (E_i)	
1	7		0.219		4.6	
2	1		0.171		3.6	
3	1	4	0.133	0.408	2.8	8.6
4	2		0.104		2.2	
5	3		0.081		1.7	
6	1	5	0.064	0.195	1.3	4.1
7	1		0.050		1.1	
8	0		0.039		0.8	
9	3		0.030		0.6	
10	1	5	0.024	0.178	0.5	3.7
≥11	1		0.085		1.8	
Total	21 = N		1.000		21	

$\bar{x} = 4.57$; $\theta = 0.781$; $\chi^2 = 4.367$, d.f. = 2, $p > 0.05$.

(3) inter-feeding flock distances on 17 Setpember 1979.

500 m interval class (i)	Observed frequency (O_i)		Relative expected frequency (p_i)		Absolute expected frequency (E_i)	
1	9		0.444		8.88	
2	6		0.247		4.94	
3	0					
4	3	5		0.309		6.18
5	0					
≥6	2					
Total	20 = N		1.000		20	

$\bar{x} = 2.25$; $\theta = 0.556$; $\chi^2 = 0.454$, d.f. = 1, $p > 0.5$.

Appendix B. Calculation of expected random distributions for the frequency of:

(1) arrivals at terrestrial loafing sites and

Frequency class (i)* - 1 min	Observed frequency (O_i)		Relative expected frequency (p_i)	Absolute expected frequency (E_i)
0	304		0.031	25.1
1	120		0.106	85.9
2	80		0.186	150.7
3	62		0.216	175.0
4	39		0.189	153.1
5	37		0.132	106.9
6	31		0.076	61.6
7	24		0.038	30.8
8	21		0.017	13.8
9	11		0.006	4.7
10	11		0.002	1.6
11	15	70	0.001	0.8
12	6			
13	9			
14	7			
15	4			
16	2			
17	4			
18	4			
19	4			
20	1			
21	1			
22	1			
23	2			
24	2			
25	0			
26	1			
.				
.				
.				
31	1			
33	1			
35	1			
40	1			
47	1			
79	1			
82	1			
Total	810 = n		1.000	810

*No. of minutes with i observations.

The values of p_i were then calculated according to the formula:

$$p_i = \frac{\bar{x}^i \cdot e^{-\bar{x}}}{i!}$$

$\bar{x} = 3.49$; $\chi^2 >> 100$, d.f. = 10, $p << 0.005$.

(2) departures at terrestrial loafing sites.

Frequency class (i)* -1 min	Observed frequency (O_i)	Relative expected frequency (p_i)	Absolute expected frequency (E_i)
0	310	0.007	5.7
1	140	0.035	28.3
2	79	0.086	69.7
3	68	0.143	115.8
4	39	0.177	143.4
5	36	0.175	141.7
6	14	0.145	117.5
7	20	0.103	83.4
8	6	0.064	51.8
9	16	0.035	28.3
10	6	0.017	13.8
11	11	0.008	6.5
12	4 } 65	} 0.005	} 4.1
13	4		
14	2		
15	8		
16	2		
17	5		
18	4		
19	2		
20	4		
21	1		
22	3		
23	0		
24	1		
25	2		
26	2		
27	0		
28	3		
29	1		
30	2		
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.			
.			
32	1		
34	2		
38	1		
42	1		
47	1		
50	2		
62	1		
68	1		
80	1		
110	1		
117	1		
300	1		
577	1		
Total	810 = N	1.000	810

*No. of minutes with i observations.

$\bar{x} = 4.96$; $\chi^2 \gg 100$, d.f. = 11, $p \ll 0.005$.

Appendix C. Common and scientific names and abbreviations of species mentioned in the text, following the A.O.U. checklist (1957) and supplements 1973a,b, 1976).

Common Loon *Gavia immer* (Brunnich)* - COLO[1]

Arctic Loon *Gavia arctica* (Linnaeus)* - ARLO

Red-throated Loon *Gavia stellata* (Pontoppidan) - RTLO

Red-necked Grebe *Podiceps grisegena* (Boddaert)* - RNGR

Horned Grebe *Podiceps auritus* (Linnaeus)* - HOGR

Western Grebe *Aechmophorus occidentalis* (Lawrence)* - WEGR

Pink-footed Shearwater *Puffinus creatopus* Coues* - PFSH

Sooty Shearwater *Puffinus griseus* (Gmelin)* - SOSH

Manx Shearwater *Puffinus puffinus* (Brunnich) - MASH

Brown Pelican *Pelecanus occidentalis* Linnaeus - BRPE

Northern Gannet *Morus bassanus* (Linnaeus) - NOGA

Doubled-crested Cormorant *Phalacrocorax auritus* (Lesson)* - DCCO

Olivaceous Cormorant *Phalacrocorax olivaceus* (Humboldt) - OLCO

Brandt's Cormorant *Phalacrocorax penicillatus* (Brandt)* - BRCO

Pelagic Cormorant *Phalacrocorax pelagicus* Pallas* - PECO

Great Blue Heron *Ardea herodias* Linnaeus - GBHE

Little Blue Heron *Florida caerulea* (Linnaeus) - LBHE

Harlequin Duck *Histrionicus histrionicus* (Linnaeus)* - HADU

White-winged Scoter *Melanitta deglandi* (Bonaparte)* - WWSC

Surf Scoter *Melanitta perspicillata* (Linnaeus) - SUSC

Black Scoter *Melanitta nigra* (Linnaeus) - BLSC

Appendix C (continued)

Red-breasted Merganser *Mergus serrator* Linnaeus* - RBME

Bald Eagle *Haliaeetus leucocephalis* (Linnaeus)* - BAEA

Osprey *Pandion haliaetus* (Linnaeus) - OSPR

Black Oystercatcher *Haematopus bachmani* Audubon - BLOY

Black Turnstone *Arenaria melanocephala* (Vigors) - BLTU

Wandering Tattler *Heteroscelus incanum* (Gmelin) - WATA

Western Sandpiper *Ereunetus mauri* Cabanis - WESA

Northern Phalarope *Lobipes lobatus* (Linnaeus)* - NOPH

Glaucous-winged Gull *Larus glaucescens* Naumann* - GWGU

Western Gull *Larus occidentalis* Audubon* - WEGU

Herring Gull *Larus argentatus* Pontoppidan* - HERG

California Gull *Larus californicus* Lawrence* - CAGU

Ring-billed Gull *Larus delawarensis* Ord* - RBGU

Mew Gull *Larus canus* Linnaeus* - MEGU

Laughing Gull *Larus atricilla* Linnaeus - LAGU

Bonaparte's Gull *Larus philadelphia* (Ord)* - BOGU

Heermann's Gull *Larus heermanni* Cassin* - HEEG

Black-legged Kittiwake *Rissa tridactyla* (Linnaeus)* - BLKI

Sabine's Gull *Xema sabini* (Sabine)* - SAGU

Common Tern *Sterna hirundo* Linnaeus - COTE

Arctic Tern *Sterna paradisaea* Pontoppidan* - ARTE

Royal Tern *Sterna maximus* (Boddaert) - ROTE

Sandwich Tern *Sterna sandvicensis* (Latham) - SATE

Common Murre *Uria aalge* Pontoppidan* - COMU

Appendix C (continued)

Pigeon Guillemot *Cepphus columba* Pallas* - PIGU

Marbled Murrelet *Brachyramphus marmoratus* (Gmelin)* - MAMU

Cassin's Auklet *Ptychoramphus aleuticus* (Pallas)* - CAAU

Rhinoceros Auklet *Cerorhinca monocerata* (Pallas)* - RHAU

Tufted Puffin *Lunda cirrhata* (Pallas)* - TUPU

Brewer's Blackbird *Euphagus cyanocephalus* (Wagler) - BRBB

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[1] Abbreviation.

[*] Species observed in multispecies feeding flocks during the study period.

Appendix D. Monthly summaries of the species composition on the Deer Group Transects.

Five of the 35 species on the Deer Group Transects had a frequency of greater than 0.05 birds per km over the six month period of the study (Appendices E and F). They were also present in the multispecies feeding flocks. Pelagic Cormorants, Glaucous-winged Gulls and Marbled Murrelets, all resident, were present throughout the study period. Most abundant were California Gulls and Common Murres which were visitors. The latter two species were observed primarily in August and September.

In May, adult Glaucous-winged Gulls were the most numerous birds in the study area (Appendices E and G). Pelagic Cormorants and Marbled Murrelets ranked second and third, respectively. Of the 35 species observed between May and October, only 14 species, many of them resident or wintering, were recorded in May. This was the lowest number of species sighted in all months.

Marbled Murrelets were the most abundant species in June, followed by Glaucous-winged Gulls and Pelagic Cormorants. Subadult California Gulls appeared in June, but represented <1% of the total birds observed. There were 21 species recorded and only 4.60 birds seen per transect (Appendix E).

In July, the proportions of California Gulls increased (Appendix G) with the arrival of adult and juvenile birds following their breeding, possibly in Alberta and Saskatchewan colonies (see Weseloh, 1975; Houston, 1977; Southern, 1980). Glaucous-winged Gull and Pelagic Cormorant numbers dropped at that time, corresponding to their early nesting periods.

In August, the numbers of California Gulls increased dramatically with peak numbers mid-month. In early August, juvenile Common Murres accompanied by a presumed parent, arrived in the study area (Appendix F). Young became independent, adults completed their pre-basic molt and plumages became indistinguishable about three weeks later. Juvenile Glaucous-winged Gulls appeared in late August (Appendix F), but the proportion of Glaucous-winged Gulls remained low (Appendix G). Twenty-one species were sighted and 34.51 birds per km. California Gulls and Common Murres still comprised more than 65% of the total birds seen.

September was the month of heaviest use in Barkley Sound. Over 93 birds per km were sighted and 28 species were recorded. Gulls comprised over 70% of these individuals. The proportion of California Gulls dropped in this month, but absolute numbers were probably higher than recorded due to the greater number of unidentified gulls. The proportions and numbers of Glaucous-winged

Gulls increased, corresponding to the fledging of their young and possibly to their initial post-breeding dispersal. Common Murres increased appreciably and comprised nearly 25% of the birds seen.

Many changes occurred in October in the study area due mainly to the departure of many murres and California Gulls. Baltz and Morejohn (1977) reported that California Gulls generally began to arrive in Monterey Bay, California about that time. Southern (1980) also documented this southward movement. The proportions of cormorants and Glaucous-winged Gulls increased, making the relative contributions of cormorants, alcids and gulls similar to those in May, although absolute numbers were higher. By 17 October, adult Glaucous-winged Gulls outnumbered juveniles (Appendix F). Banding records indicated that juveniles tend to disperse farther (Butler *et al.*, 1980). Migrants were few and mostly resident and(or) wintering species were present. The total number of species dropped to 24 species and there were 25.76 birds recorded per km.

Appendix E. Species composition of the Deer Group Transects.

Species[1]	Birds per km per month						Total
	May	Jun	Jul	Aug	Sep	Oct	
COLO	0.05	*	*	*	*	0	0.01
ARLO	0.17	0.02	0.01	0	0.44	0.06	0.12
RTLO	0	*	0	0	0	0	*
RNGR	0	0	0	0	*	0.01	*
HOGR	0	0	0	0	0	0.07	0.01
WEGR	0	*	0	*	0	0.05	0.01
SOSH	0	0	0	*	0	0	*
DCCO	0	0.01	*	0	0.02	0.51	0.08
BRCO	0.23	0.27	0.06	0.06	0.30	0.31	0.20
PECO	2.00	0.73	0.30	0.18	2.86	8.62	2.27
Cor. spp.[2]	2.30	1.06	0.43	0.27	3.41	10.50	2.79
GBHE	0	0.01	0	0.02	0.04	0.02	0.02
HADU	0	0.01	*	0.01	0.28	0.39	0.12
WWSC	0.02	*	0	0.01	0	0.18	0.03
SUSC	0	0	0	0.03	0.54	0.28	0.15
BLSC	0	0	0	0	*	0	*
BAEA	0.22	0.36	0.16	0.11	0.03	0.04	0.15
OSPR	0	0.01	0	0	0	0	*
BLOY	0.12	0.12	0.10	0.08	0.19	0.16	0.13
BLTU	0	0	0	0	0.13	0.09	0.04
WATA	0.04	0	0	0	0.01	0	0.01
WESA	0	0	0.02	0	*	0	*
NOPH	0	0	0.07	0.02	0.02	0	0.02
GWGU	2.29	0.94	0.44	0.54	6.54	6.02	2.78
WEGU	0	0	0	0	0.01	0	*
HERG	0.02	0.01	0.01	0.20	0.11	0.06	0.08
CAGU	0	0.04	0.85	19.93	16.33	0.41	7.40
RBGU	0	0	0.01	0	0	0	*
MEGU	0	0	0.04	0.03	0.01	0.13	0.03
BOGU	0	0.01	0	0.04	0.02	0.01	0.02
HEEG	0	0	0.01	0	0.12	0.91	0.16
Gull spp.[3]	2.32	1.31	2.81	29.31	66.80	10.71	21.58
COMU	0.01	0.01	0.02	3.65	20.70	3.02	5.28
PIGU	0.45	0.19	0.29	0.19	0.05	0.11	0.19
MAMU	1.41	1.45	0.58	0.72	0.43	0.06	0.75
CAAU	0	0	0	0	0.02	0.01	0.01
RHAU	0.03	0.02	*	0.08	0.13	0	0.05
Total	7.12	4.60	4.52	34.51	93.24	25.76	31.47
No. km	127.6	242.2	216.8	255.2	255.2	191.4	1288.0

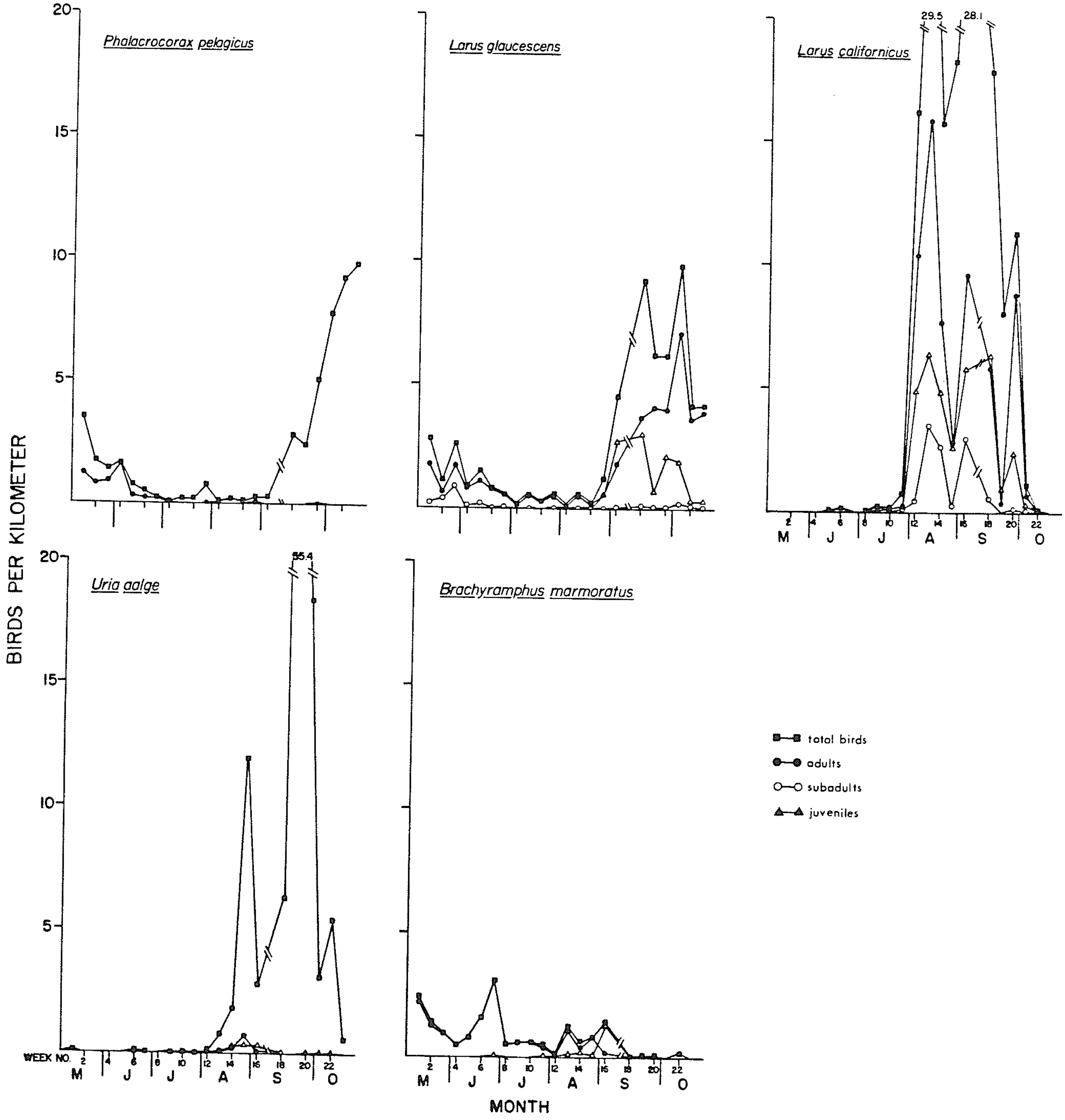
[1] Common and scientific names given in Appendix C.

[2] Cor. spp. includes all the birds in the previous three rows, plus some unidentified cormorants, assumed to be one of those species.

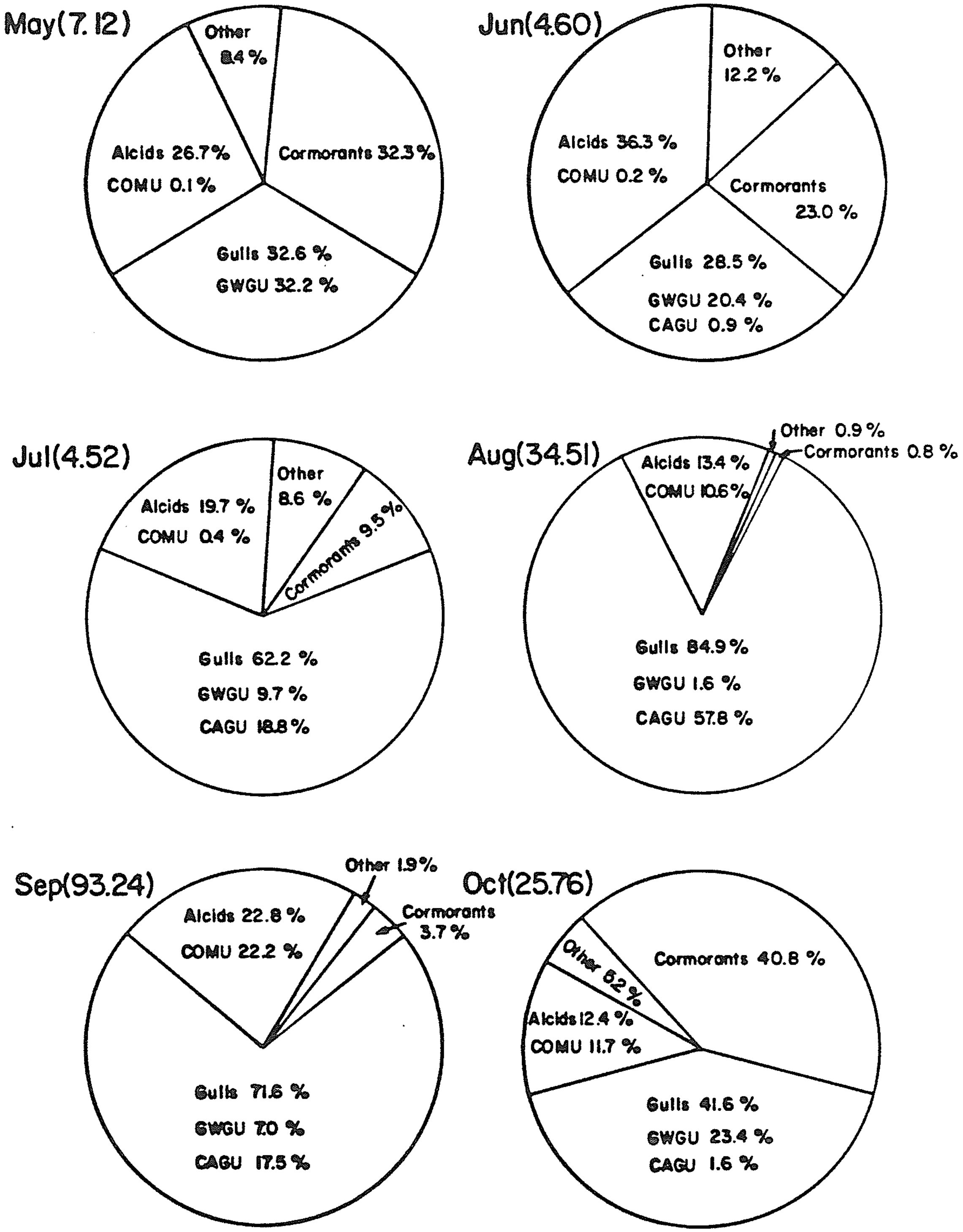
[3] Gull spp. includes all the birds in the previous eight rows, plus some unidentified gulls, assumed to be one of those species.

*Present, but less than 0.005 birds per km.

Appendix F. Abundance of five species on the Deer Group Transects. Age classes plotted in species where these categories were recognized.



Appendix G. Relative abundance of species or species groups on the Deer Group Transects. Numbers in parentheses are the numbers of birds per km each month. Common and scientific species names are given in Appendix C.



Appendix H. Average body weights of individuals of each species in multispecies feeding flocks on the regular[1] transects.

Species	Body weight (g)	Source
Arctic Loon	2500.0	Palmer, 1962
Western Grebe	1474.0	Palmer, 1962
Pink-footed Shearwater	787.0	Palmer, 1962
Sooty Shearwater		
Brandt's Cormorant	2426.0	Palmer, 1962
Pelagic Cormorant	1868.0	Palmer, 1962
Northern Phalarope	34.4	U.M.Z.M.[2]
Glaucous-winged Gull	1373.5	U.M.Z.M.
Herring Gull	1134.9	Belopol'skii, 1959
California Gull	719.8	U.M.Z.M.
Bonaparte's Gull	171.7	U.M.Z.M.
Heermann's Gull	419.2	U.M.Z.M.
Gull spp.[3]	850.0	
Common Murre	982.1	Bédard, 1969
Pigeon Guillemot	450.0	Drent, 1965
Marbled Murrelet	219.9	Sealy, 1975b
Cassin's Auklet	171.3	Manuwal, 1974
Rhinoceros Auklet	519.8	Vermeer and Cullen, 1979

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[1] Deer Group plus Inner plus Outer.

[2] University of Manitoba Zoology Museum.

[3] Gull spp. includes all of the birds in the previous five rows, plus some unidentified gulls, assumed to be one of those species.

Appendix I. Seasonal use of terrestrial loafing sites on the Deer Group Transects.

	Location[a]																									Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
May																										
No. species	0	0	0	0	0	3	0	0	3	3	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	3
No. individuals/ transect	0	0	0	0	0	24	0	0	11	11.8	0	0	0	9.5	0	0	0	0	0	0	8.8	0	0	0	0	65.1
No. transects loaf sites used (4)	0	0	0	0	0	3	0	0	2	2	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	12
Jun																										
No. species	0	0	0	0	6	1	0	1	2	1	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	6
No. individuals/ transect	0	0	0	0	19.9	1.8	0	0.6	5.6	3.9	0	0	3.1	4.5	0	0	0	0	0	0	0	0	0	0	0	39.4
No. transects loaf sites used (8)	0	0	0	0	6	2	0	1	3	2	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	20
Jul																										
No. species	0	0	0	0	2	0	0	0	0	4	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	4
No. individuals/ transect	0	0	0	0	1.1	0	0	0	0	2.3	0	0	0	2.6	0	0	0	0	0	0	0	0.7	0	0	0	6.7
No. transects loaf sites used (7)	0	0	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	6
Aug																										
No. species	3	0	1	2	4	2	0	0	0	4	0	0	0	4	2	1	0	1	1	2	0	3	0	0	0	4
No. individuals/ transect	303.9	0	17.5	28	0	8.9	0	0	0	15.1	0	0	0	54.9	11.4	15.1	0	11.6	0.9	38.9	0	79.3	0	0	0	585.5
No. transects loaf sites used (8)	7	0	2	3	4	2	0	0	0	3	0	0	0	3	1	1	0	3	1	2	0	4	0	0	0	36
Sep																										
No. species	4	4	3	2	4	4	2	2	3	5	2	3	4	3	0	4	2	2	2	1	4	1	0	3	1	5
No. individuals/ transect	494.6	13.5	18.9	106.3	10.6	9.9	5.3	28.0	18.4	14.5	30.3	3.5	16.6	16.8	0	12.1	27.3	54.8	27.3	61.8	6.5	148.3	0	52.3	11.8	1189.4
No. transects loaf sites used (8)	7	2	4	2	4	6	2	4	6	4	4	2	6	6	0	3	2	4	4	4	2	5	0	3	3	89
Oct																										
No. species	7	0	2	3	5	2	2	1	4	2	2	1	2	3	0	4	1	1	0	2	1	4	2	0	2	7
No. individuals/ transect	58.2	0	0.3	31.8	16.0	21.0	56.3	49.2	68.5	4.7	21.8	1.0	25.5	24.7	0	19.8	1.3	13.8	0	2.2	0.3	26.1	6.8	0	2.5	451.8
No. transects loaf sites used (6)	6	0	2	2	5	4	6	5	4	2	2	1	3	6	0	5	1	2	0	2	1	5	2	0	2	68
Total																										
No. species	7	4	3	4	7	4	3	2	5	6	3	4	5	4	2	6	2	2	2	2	4	4	2	3	2	7
No. individuals/ transect	164.3	2.6	7.1	30.9	10.2	7.9	9.3	12.8	15.8	8.8	9.1	0.8	7.6	19.8	2.2	8.2	5.5	15.0	5.5	20.0	2.2	40.3	1.0	10.2	2.7	427.8
No. transects loaf sites used (41)	20	2	8	7	20	17	8	10	15	14	6	3	11	25	1	9	3	9	5	8	4	16	2	3	5	231

[a] Refer to Figure 4.