

TERRESTRIAL FORAGING ECOLOGY OF RING-BILLED GULLS (Larus
delawarensis)

by

Clive V. J. Welham

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Department of Zoology, University of Manitoba, Winnipeg,
Manitoba

Winnipeg, Manitoba

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ISBN 0-315-33596-3

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(LARUS DELAWARENSIS)

BY

CLIVE V. J. WELHAM

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ACKNOWLEDGEMENTS

I wish to express sincere gratitude to my supervisor, Dr. Roger M. Evans, who saw in me a desire to learn. I'll not forget the valuable lessons he taught me about science. I am also grateful to the other members of my committee, Dr. J. H. Gee and Dr. R. A. Brust, for their contributions to the thesis.

My love and appreciation go to Leslie A. Baldwin who had the dubious distinction of living with me through the duration. And to Kenneth R. Kansas, for times and feelings that go beyond mere words. We always thought each looked better through the bottom of a beer glass. Your love and support helped immeasurably.

To all my colleagues at the University of Manitoba and elsewhere who contributed in many different ways, I thank you; in particular, A. N. Arnason, V. Converse, S. Cosens, L. S. Forbes, R. Kenny, A. W. Shostak, and R. C. Ydenberg.

Research was funded by a grant to R. M. Evans from the Natural Science and Engineering Research Council of Canada.

DEDICATION

This work is dedicated to my parents, Derek J. Welham and F. Marion Welham (nee Hewett) whose love and support have always matched my desire to succeed.

ABSTRACT

Ring-billed Gulls (Larus delawarensis Ord) breeding at Dog Lake, Manitoba were almost exclusively terrestrially-based in their foraging effort. Major prey items in late May to early June were earthworms and grain, and were obtained by foraging behind farm cultivating implements. Insects increased in importance as the season progressed, particularly in females. These were obtained by foraging along lakeshore ridges (mayflies) or behind haying implements (grasshoppers). Birds and mice, obtained from behind haying implements, comprised the predominant male diet in the latter part of the season. Behavioral observations and collections suggested that the larger males could outcompete females for these relatively valuable prey items. Chick diet (from late June to late July) closely paralleled that of adults, especially females. Food appears to be the most likely factor responsible for the moderate (2-fold) increase in numbers of Ring-billed Gulls breeding at Dog Lake over the past 30 years.

Two hypotheses relating colonial breeding in birds to their foraging system were tested in gulls. The Assembly Point Hypothesis, which states that colonies function to help maintain local densities at levels adequate to provide

benefits of group foraging, was supported by temporal and spatial grouping of arrivals and departures and by a demonstration of possible group-related benefits of foraging (local enhancement) using styrofoam models and live conspecifics. In addition, departure directions were significantly correlated with wind at intermediate velocities while arrival directions were not. Wind is postulated to "funnel" foragers in a uni-directional manner such that adequate forager densities are maintained far from the colony for local enhancement (or other group benefits) to operate effectively. Alternative predictions from the Information Center Hypothesis, which states that birds can find new food sites by following others out from the colony, were not supported due to a lack of correlation between arrival and departure vectors and colony direction and distance.

An optimality model was developed to determine whether gulls could maximize the rate of energetic intake (G/t) while foraging behind cultivating implements for earthworms (3 fields) or grain (1 field). From the G/t function, an optimal time in patch ($t_{p(opt)}$) was predicted and compared with actual departure times (t_p). Results suggest that Ring-billed Gulls are, to some extent, able to evaluate this cost-benefit function. As the predicted value of t_p increased, so did actual t_p , though at an increasingly disproportionate rate. There tended to be an inverse relationship between increasing peaks in the G/t function and its rate of

decline with increasing time in patch. It seems likely, therefore, that birds experienced greater difficulty in detecting the decline in intake rate as the G/t curves flattened out thus causing the delays in departure of increasing magnitude.

The optimality model yielded minimum relative benefits of at least double that of an alternative, non-optimal foraging model based on a null strategy of random patch residence times.

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GENERAL INTRODUCTION

The capability of Ring-billed Gulls (Larus delawarensis Ord) to adapt to a wide variety of conditions (Ludwig 1974) underlies their increasing numbers across most of North America in recent years (Conover 1983, Blokpoel and Tessier in prep.). Ring-billed Gull breeding range spans both coasts and extends north to Great Slave Lake (Vermeer 1970), and south to a line extending east from northern California (Conover 1983, Vermeer 1970). Breeding habitat is usually restricted to sparsely vegetated islands, both natural (Vermeer 1970) and man-made (Conover 1983, Scharf 1981), though gulls do breed on peninsulas (Blokpoel and Fetterolf 1978). Weir (1983) reported one instance of Ring-billed Gulls nesting at a garbage dump near Ottawa, Ontario. Wintering areas are the coastal regions of eastern (Southern 1974) and western North America (Vermeer 1970).

Concomitant with their widespread breeding range, Ring-billed Gulls also display a high degree of dietary breadth. Prey types include aquatic organisms such as fish (Ludwig 1966, Kirkham and Morris 1979) and emergent mayflies (Insecta: Ephemeroptera)(Jarvis and Southern 1976, this study). Terrestrial prey are commonly earthworms (Jarvis and Southern 1976, Haymes and Blokpoel 1978, this study), insects

(Baird 1976, Vermeer 1970, this study), mammals and birds (Blokpoel and Haymes 1979, Vermeer 1970, Baird 1976, Greenhalgh 1952, this study), and grain (Vermeer 1970, this study). In addition, refuse is an important food source during the winter (Burger and Gochfield 1983, Conover 1983).

The feeding studies cited above were based primarily on data gathered at the colonies through chick regurgitations and adult pellet analysis. There are surprisingly few detailed descriptions of gull foraging behavior on the foraging grounds themselves. This study was designed to examine this behavior in more detail. A terrestrially-based population, where observations could readily be made at various sites at close range, was selected for study. The first objectives of this study are to describe the prey types eaten by a particular inland population of Ring-billed Gulls and to determine where the prey were obtained. Chapter 1 addresses these subjects and relates the findings to published trends in population growth of the species. Subsequent observations were conducted to permit assessment of particular aspects of foraging theory of relevance to this population, as outlined below.

Ring-billed Gulls characteristically breed in large, dense colonies. Hypotheses of why birds breed colonially range from anti-predator adaptations (Lack 1968) to efficiency of food-finding (Crook 1965, Lack 1968). Recent food-based hypotheses of coloniality include the Information

Center Hypothesis (ICH)(Ward and Zahavi 1973) and the Assembly Point Hypothesis (APH)(Evans 1982a). As the name implies, the ICH argues that colonies act as information-centers whereby the knowledge of good feeding sites can be obtained by those lacking such information. According to the APH, on the other hand, colonially-breeding organisms enjoy a density-dependent net benefit from grouping on the foraging grounds (eg. local enhancement, Thorpe 1963). Regular reassemblage at a roost or colony serves to maintain adequate forager densities. A key distinction between these two ideas appears to be what animals do after the rejection of an unsuitable feeding site. The ICH would predict that birds should return to the colony for new information (Waltz 1982). Except for periodic reassembly of the population at a roost or colony, the APH predicts further dispersal in search of new sites when a current site becomes unsuitable. Chapter II is a test of these predictions. As a further test of the APH, I also examined how and to what degree Ring-billed Gulls use local enhancement to locate and evaluate potential food patches.

The efficiency with which organisms obtain energy from their environment has received considerable attention. Optimal Foraging Theory (Pyke et al. 1977) encompasses the idea that animals have evolved so as to maximize an energetic gain function (usually their net rate of energy intake) subject to certain constraints. Most tests of the theory

thus far have been conducted under very simple laboratory conditions and there remains doubt as to whether the theory has any heuristic value in the field (Morse 1980, Zach and Smith 1981, Schluter 1981). Chapter III is a test of an optimality model developed in a field situation where gulls were feeding for earthworms and grain exposed behind farm cultivating implements. The model poses the question of whether Ring-billed Gulls can maximize the rate of energetic intake by feeding at one location for an optimal time before departing to take up another location closer to the implement.

CHAPTER 1. DIET AND FORAGING IN RELATION TO POPULATION SIZE

INTRODUCTION

The dramatic increase in Ring-billed Gull (Larus delawar-
ensis) populations in recent years (Conover 1983, Ludwig
1974) has prompted efforts to determine the extent of the
change and, more importantly, those factors responsible.
Concern has also been expressed regarding the degree to
which a burgeoning gull population can affect reproduction
in economically important species such as waterfowl (Ander-
son 1965, Odin 1957, Vermeer 1970) and in non-economic but
threatened populations of other colonial species (Koonz and
Rakowski 1985, Kress et al. 1983). Gulls are also known to
consume grain (Vermeer 1970, this study) and cause damage to
cherry orchards (Behle 1958, Cottam 1935).

Food appears to be the main factor responsible for lo-
cal population increases studied to date (Conover 1983, Lud-
wig 1974) though creation of new nesting habitat by man-made
reservoirs has probably permitted the large scale range ex-
pansion of Ring-billed Gulls observed in the western United
States (Conover 1983). However, detailed analysis of the
relationship between foraging behavior and foods selected in
relation to population trends is lacking for this species.

The objectives of this portion of the study were to: (a) document the location of foraging of a particular population of Ring-billed Gulls throughout the breeding season (pre-egg stage to fledging), (b) determine prey selected, and (c) relate these findings to current food availability and population trends in this population, as documented from the literature.

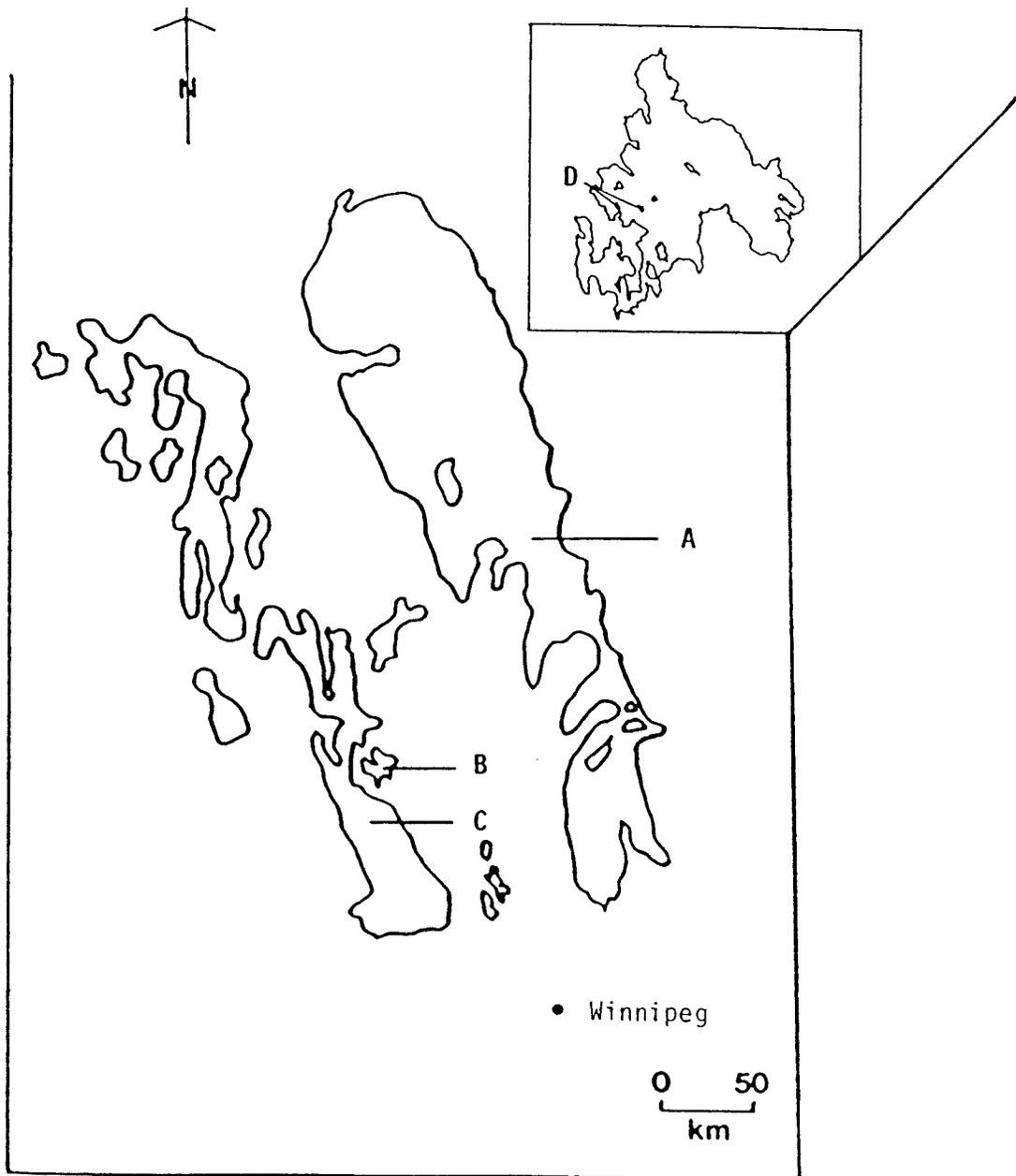
MATERIALS AND METHODS

Study area

The study area surrounded Dog Lake, Manitoba (51° 01'N, 98°29'W) (Fig. 1) containing three main Ring-billed Gull colonies with an estimated total of 3500 breeding pairs.

Soils are fairly homogeneous throughout the area (Pratt et al. 1961) while dominant vegetation includes poplar (Populus spp.), spruce (mostly Picea glauca), bur oak (Quercus macrocarpa), and willow (Salix spp.) in the higher areas and meadow grasses and sedges (Carex spp.) in the low areas. Agriculturally, the area is relatively poor with a high degree of stoniness and poor drainage. Less than half of the available land is utilized for agricultural crops, with most of the remainder used for cattle grazing. Of the total area in crop production, about 40% is sown to cereal crops, 40% tame hay, and 20% to oil seeds (Man.Dept.Agric. pers.comm.).

Figure 1. Map of southern Manitoba showing the location of Lake Winnipeg (A), Lake Manitoba (B) and Dog Lake (C). Inset shows the locations of Ring-billed Gull breeding colonies (D) on Dog Lake.



Forager distribution

The Ring-billed Gull population in this study is almost exclusively terrestrially-based in its foraging effort and therefore amenable to detailed examination on the foraging grounds. To assess the relative importance of different feeding sites during the breeding season (May to July 1983, 1984), pre-determined transects were driven by vehicle. The area was partitioned by halves (north/south) and two transect routes chosen to represent all possible habitat types (dumps, of which there were four in the Dog Lake region, pastures, arable land, marshes, and lake area). These routes extended out from the colony a maximum linear distance of 55 km, as previous observations on foraging in this population suggested that the usual maximum range was about 45 km (see also Baird 1976). Transects were run every 4-5 days with one full day devoted to each member of the pair. A total of 26 pairs were conducted. I varied direction and departure times as much as possible to reduce any systematic bias. Upon encountering gulls at a site I recorded habitat type, number of birds, status (numbers loafing vs feeding), and prey types, as determined by direct observation of foragers.

Prey

To verify observations of prey eaten, I collected 48 birds in 1984 from flocks representative of each habitat type, except those foraging on aquatic insects congregating on vegetation of beach ridges. Gulls foraging in this area were too wary to permit collection. In addition, 13 gulls that were flying towards the Dog Lake colonies were collected from four compass points (N,S,E,W) along the shore of Dog Lake. Collections were made throughout the season, except during the last half of June when heavy rainfall and thunderstorm activity precluded any cultivating or harvesting activities for 9 out of 15 days. No gulls were collected on the fields at that time, and only 2 were obtained en route to the colonies. Collected birds were sexed by internal examination.

I also entered the colony once every 7 to 12 days and collected a total of 17 chick regurgitations. These regurgitations, as well as prey types recovered from the proventriculus and gizzard of collected adults, were preserved in 10% formalin and later identified to Order. I determined the number, per cent frequency of occurrence and per cent volume for each type. All statistical analyses were by chi-square or Mann-Whitney U test (Conover 1971).

RESULTS

Forager distribution

The number of site-days for gull flocks observed in various habitats (excluding refuse dumps) is presented in Table 1, where a site-day is simply the presence of gulls at a site on a given day with no regard to number. In late May and early June, all observations of foraging gulls were made on agricultural land, either behind tilling implements (where the principal food was worms and grain), or on pastures (land used for grazing) where worms only were available. As the season progressed (late June onwards) the proportion of gulls on agricultural land declined steadily. From late June through the end of the season, marsh and ridge use increased in response to emergence of aquatic insects. Similarly, haying operations began at this time and gulls responded to prey uncovered by these implements. No significant differences exist between habitats chosen in early July vs late July but habitat use between other successive time periods were different (last 3 lines of Table 1) and there were significant differences across habitats for all months combined ($\chi^2=175.0$, $df=8$, $P<0.0001$).

There was a significant tendency for patches to be used during or immediately following periods of rainfall. Ratio of use:no use during rainfall was 23:4, compared with 3:28 during periods >3 days after rainfall ($\chi^2=30.3$, $df=1$, $p<0.0001$). On three occasions when pastures were used with

Table 1. Number of site-days of Ring-billed Gulls foraging in various terrestrial habitats during successive time periods in 1983 and 1984.

Habitat	May 16-31	June 1-15	June 16-30	July 1-15	July 16-31
Agricultural land					
Pastures	31(84) ^a	21(32)	4(12)	-----	-----
Cultivated land ^b	6(16)	42(64)	11(32)	8(13)	1(3)
Hay land ^c	-----	3(4)	14(41)	31(48)	12(40)
Marsh, ridge	-----	-----	5(15)	25(39)	17(57)
Totals	37(100)	66(100)	34(100)	64(100)	30(100)
X ²	25.612	34.500	14.000	3.517	
df	1	1	1	2	
P value	< 0.0001	< 0.0001	< 0.0009	> 0.1	

^aPer cent in brackets.

^bDiscing and seeding implements usually present.

^cCutting and bailing implements always present.

no rainfall, flock sizes were very small (30, 20 and 12 birds respectively) and all birds were loafing at the time of observation.

In both years, pasture use stopped in the latter part of June (Table 1). During this period, birds foraging on pastures became more skittish. Whereas in the early part of the season I observed flocks freely from my vehicle at close range (30 m or less), by late June, the whole flock would take flight at my approach and they always landed at least 100 m away. Upflights of the entire flock then occurred repeatedly at intervals of less than 1 or 2 min., often for no apparent reason. Measurements of grass height from four pastures in late June 1984, gave an average of 30.3 ± 4.6 (S.D.)cm (N=40), about equal to the height of a gull. Obscured visibility may have rendered the pastures unsuitable to foraging birds at this time.

On farm land, there were usually either many gulls or no gulls present. In contrast, a few gulls were almost always observed at each refuse dump. Under these conditions, the site-day statistic would have over-emphasized the relative importance of refuse as a prey item to the majority of the population and would not have been sensitive to differential use over the season. To assess the degree of dump use over the season, the maximum number of gulls observed during a given month is presented in Table 2. In 1983, peak use occurred in May then declined through June and July.

Table 2. Maximum daily number of Ring-billed Gulls at four major dumps in the vicinity of Dog Lake (distance to colony enclosed in brackets).

Date	Dump				Totals
	Ashern (25 km)	Vogar (10km)	Dog Creek (14km)	Narrows (10km)	
1983					
May	182	30	110	27	349
June	165	40	45	n.c. ^a	250
July	60	11	6	n.c.	77
August	10	8	2	5	25
Totals	417	89	163	32	701
1984					
May	0	n.c.	15	65	80
June	11	n.c.	3	67	81
July	21	n.c.	4	58	83
August	9	n.c.	n.c.	20	29
Totals	41		22	210	273

^an.c.=no census

Dump use in 1984 remained stable but relatively unimportant throughout the breeding season.

Prey

Table 3 shows frequencies and volumes of the major groups of prey. In late May-early June, earthworms were the dominant prey by volume (61%) followed by cereal grains (32%) for those birds collected while actually foraging on the habitat (Table 3, column 2). These prey were mostly obtained from pastures and cultivated land with active implements present (ploughs and seeders)(Table 1). Though insects were the most common prey type in the samples, they represented only 4% by volume. Insects were again the most frequent (77%) prey types in July for ground foragers (column 3), but mammals constituted the greatest volume (72%)(column 4). These were obtained by foraging behind haying implements (Table 1).

Prey types from collections of birds returning to the colony are also presented in Table 3 (last 4 columns). Insects accounted for 95% of the volume in June, dropping to 62% in July. This July diet contrasts sharply with that of July field-shot birds in which mammals are the predominant prey by volume (72%) with insects composing only 9%.

Table 4 shows that in the late May-early June period, of the small proportion of insects in the diet of birds col-

Table 3. Prey eaten by Ring-billed Gulls collected from the foraging grounds or en route to the colony.

Prey type	Ground foragers				Flying back to colony			
	May 16 - June 15		July 1 - 31		June 16 - 30		July 1 - 31	
	(1) Freq. (%)	(2) Vol. (%) ^a	(3) Freq. (%)	(4) Vol. (%)	(5) Freq. (%)	(6) Vol. (%)	(7) Freq. (%)	(8) Vol. (%)
Earthworms ^b	19 (73)	234.5 (61)	-----	-----	-----	-----	-----	-----
Insects	20 (77)	15.4 (4)	17 (77)	61.1 (9)	2 (100)	86.9 (95)	10 (91)	161.3 (62)
Birds ^c	-----	-----	3 (14)	61.1 (9)	-----	-----	2 (18)	54.6 (21)
Mammals ^d	-----	-----	13 (59)	488.5 (72)	-----	-----	2 (18)	28.6 (11)
Fish ^e	-----	-----	4 (18)	40.7 (6)	-----	-----	2 (18)	trace
Grain	17 (54)	123.0 (32)	1 (5)	trace	1 (50)	4.6 (5)	3 (27)	7.8 (3)
Frogs ^f	-----	-----	3 (14)	13.6 (2)	-----	-----	-----	-----
Debris	6 (23)	11.5 (3)	4 (18)	6.8 (1)	1 (50)	trace	3 (27)	7.8 (3)
Totals		384.4 (100)		678.5 (100)		91.2 (100)		260.1 (100)
Number of gulls	26		22		2		11	

^aAll volumes in ml.

^bMostly *F. Lumbricidae*.

^cAll Savannah Sparrows (*Passerculus sandwichensis*).

^dAll *Microtus* spp.

^eOne sample contained Perch (*Perca fluviatilis* Mitchill). 4 had Fat-head Minnows (*Pimaphelus promelas* Raf.).

^fAll *Rana pipiens*.

Table 4. Frequency and volume of insect composition in Ring-billed Gull diet from collections.

Order	Ground foragers				Flying back to colony			
	May 16 - June 15		July 1 - 31		June 16 - 30		July 1 - 31	
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
	Freq. (%)	Vol. ^a (%)	Freq. (%)	Vol. (%)	Freq. (%)	Vol. (%)	Freq. (%)	Vol. (%)
Odonata	-----	-----	1(6)	0.6(1)	-----	-----	-----	-----
Coleoptera	8(40)	2.5(16)	5(29)	1.9(3)	-----	-----	2(20)	trace
Homoptera	-----	-----	3(18)	5.6(9)	-----	-----	1(10)	4.8(3)
Orthoptera								
Acrididae	-----	-----	5(29)	48.8(78)	-----	-----	7(70)	132.3(82)
Ephemeroptera								
Ephemeridae	-----	-----	-----	-----	2(100)	86.2(100)	1(10)	1.6(1)
Diptera								
(adults)	1(5)	2.5(16)	-----	-----	-----	-----	1(10)	21.0(13)
(larvae)	1(5)	3.2(21)	-----	-----	-----	-----	-----	-----
Geophilomorpha	2(10)	0.2(1)	-----	-----	-----	-----	-----	-----
Unident. larvae	5(25)	6.5(42)	-----	-----	-----	-----	-----	-----
Unident. insect parts	7(35)	0.6(4)	8(47)	5.6(9)	1(50)	trace	-----	-----
Totals		15.4(100)		62.5(100)		86.2(100)		161.3(100)
Number of gulls	20 ^b		17		2		10	

^aAll volumes in ml.

^bSample size is derived only from gulls that consumed insects in Table 3.

lected on the ground (Table 3), 42% by volume were larvae (unidentified), 21% larval dipterans, and 16% adult dipterans and Coleoptera (beetles) respectively. In the July diet, Orthopterans (grasshoppers) predominated (78% by volume) followed by Homoptera (9%). One of the two birds collected en route to the colony in late June had stomach contents composed of 100% Ephemeroptera (mayflies) while the other had all mayflies except for a small volume of unidentifiable insect parts (Table 4, column 6). In the July diet of birds flying back to the colony, grasshoppers predominated (70% frequency, 82% by volume) followed by adult dipterans (13%).

Overall, collections showed that from late May through the end of June, birds consumed Coleopterans with the greatest frequency (36%) though mayflies constituted the greatest volume (85%). In July, grasshoppers were consumed by the largest number of birds and in the greatest volume (44% and 81% respectively).

Frequencies of prey selected were not significantly different between sexes in the late May-early June diet ($\chi^2=.462$, $df=2$, $P>0.05$) or for the combined July diets ($\chi^2=5.582$, $df=2$, $P>0.05$) (Table 5). During late May-early June, males had greater volumes of grain and also of earthworms than females ($P<0.01$, Mann-Whitney U test comparing actual volumes of all prey items). For ground foragers in July (columns 5 - 8), females consumed significantly greater volumes of insects than males (97 vs 2% respectively) with

Table 5. Frequency and volume of prey types for collected male and female Ring-billed Gulls.

Prey type	Ground foragers								Flying back to colony			
	May 16 - June 15				July				July			
	Male		Female		Male		Female		Male		Female	
	(1) Freq. (%)	(2) Vol. ^a (%)	(3) Freq. (%)	(4) Vol. (%)	(5) Freq. (%)	(6) Vol. (%)	(7) Freq. (%)	(8) Vol. ^b (%)	(9) Freq. (%)	(10) Vol. (%)	(11) Freq. (%)	(12) Vol. ^b (%)
Earthworms	8(67)	86.1(47)	11(79)	146.9(73)	-----	-----	-----	-----	-----	-----	-----	-----
Insects	10(83)	9.2(5)	10(71)	6.0(3)	13(72)	12.5(2)	4(100)	52.2(97)	3(75)	5.5(6)	7(100)	156.9(93)
Birds	-----	-----	-----	-----	3(17)	62.5(10)	-----	-----	2(50)	54.8(60)	-----	-----
Mammals	-----	-----	-----	-----	12(67)	487.3(78)	1(25)	0.5(1)	1(25)	28.3(31)	1(14)	trace
Fish	-----	-----	-----	-----	3(17)	43.7(7)	-----	-----	1(25)	0.9(1)	1(14)	trace
Grain	9(75)	84.3(46)	8(57)	40.2(20)	1(6)	trace	-----	-----	1(25)	1.8(2)	2(29)	5.1(3)
Frogs	-----	-----	-----	-----	3(17)	18.7(3)	-----	-----	-----	-----	-----	-----
Debris	3(25)	3.7(2)	3(21)	8.0(4)	3(17)	6.2(1)	1(25)	1.1(2)	-----	-----	3(43)	6.7(4)
Totals		183.2(100)		201.2(100)		624.7(100)		53.8(100)		91.4(100)		168.7(100)
Number of gulls	12		14		18		4		4		7	

^aAll volumes in ml.

mammals and birds comprising the bulk of the male diet (total of 88%) ($P < 0.01$, Mann-Whitney U test comparing actual volumes of all prey items in columns 6 and 8; Table 5). Similarly, for birds en route to the colony (columns 9 - 12), males consumed a significantly greater volume of birds and mammals than females (60 and 31% in males vs <1% for females) while 93% (by volume) of the female diet was insects (Mann-Whitney U test comparing actual volumes of all prey items in columns 10 and 12).

Since insects were an important component of the diet in July, Table 6 presents the insect compositions for each sex for this period. Forty six percent by frequency and 50% by volume of the insect diet in males collected from the fields was composed of miscellaneous insect parts. This is followed by volume percentages of 18 for Orthoptera (grasshoppers) and 16 for Coleoptera. The substantial insect component of the female diet under the same conditions shows frequencies of 50% grasshoppers and Homoptera and volumes of 90 and 9% respectively. For birds returning to the colony, the high insect component of females was again predominantly grasshoppers (82% by volume) followed by dipteran larvae (14%). In males flying back to the colony, the sample was composed of 98% grasshoppers. Overall, the data show that grasshoppers were the largest component of both male and female July diets, totalling 47 and 84% by volume, respectively, for all collections combined.

Table 6. Frequency and volume of insect composition in diet of male and female Ring-billed Gulls in July 1984.

Order	Ground foragers				Flying back to colony			
	Male		Female		Male		Female	
	(1) Freq. (%)	(2) Vol. ^a (%)	(3) Freq. (%)	(4) Vol. (%)	(5) Freq. (%)	(6) Vol. (%)	(7) Freq. (%)	(8) Vol. (%)
Odonata	1(8)	0.6(6)	-----	-----	-----	-----	-----	-----
Coleoptera	4(31)	1.6(16)	1(25)	trace	-----	-----	2(29)	trace
Homoptera	2(15)	0.9(9)	2(50)	4.7(9)	-----	-----	1(14)	6.3(4)
Orthoptera	3(23)	1.8(18)	2(50)	47.4(90)	2(67)	5.4(98)	5(71)	128.2(82)
Ephemeroptera	-----	-----	-----	-----	-----	-----	1(14)	trace
Diptera								
(adults)	-----	-----	-----	-----	-----	-----	-----	-----
(larvae)	-----	-----	-----	-----	-----	-----	-----	-----
Unident. insect parts	6(46)	4.9(50)	2(50)	0.5(1)	1(33)	0.1(2)	1(14)	trace
Totals		9.8(100)		52.7(100)		5.5(100)		156.3(100)
Number of gulls ^b	13		4		3		7	

^aAll volumes in ml.

^bSample size is derived only from gulls that consumed insects in Table 5.

The sex ratio of collected birds was variable in different habitats. Of those birds collected from behind tilling implements in late May-early June, the male:female sex ratio was not significantly different from unity (0.46:0.54) ($X^2=0.15$, $df=1$, $P>0.1$; $n=26$). The sex ratio of birds collected directly off a field with a harvesting implement, in contrast, was significantly different at 0.82:0.18 (male:female) ($X^2=8.91$, $df=1$, $P<0.005$; $n=22$). The ratio of 0.36:0.64 (male:female) for birds collected en route to the colony was not significant ($X^2=0.82$, $df=1$, $P>0.1$; $n=11$). Overall, males were larger (550.8 ± 45.8 (S.D.)g, ($n=33$) than females (466.7 ± 60.7 g, ($n=26$) and may have outcompeted them for the relatively valuable prey items (mice and birds) available by aerially searching behind harvesting implements. In agreement with this interpretation, all four females that were collected from fields in July were foraging on the ground. Of the two males that were also collected while on the ground, one weighed 448.1 g, almost 20 g. lighter than the average female weight, and its stomach contents were strictly insects. Thus light weight males may also have tended to use ground foraging sites rather than compete for mice and birds. The other male collected on a field weighed 620 g, considerably heavier than the average male weight. This bird had four freshly eaten Microtus spp. (90% by volume), the remains of a frog Rana pipiens (2% by volume) and a variety of insects (<1% by volume). Since I observed gulls capturing mammals only by spotting them from

the air, it seems likely that this large male was foraging by flying behind the implement but was collected while subsequently loafing on the ground.

Chick diets were fairly consistent with adult diets throughout the rearing period (Tables 5 and 7) which lasted from about mid-June to the end of July. Grains present in June were the same as found in adults during this period. Insect remains composed 100% of the volume in early and late July, only slightly less than found in adults at that time (cf Table 5). Insect composition included 99% Ephemeroptera (mayflies) in late June (Table 8) and they remained the principal prey through early and late July. Orthoptera (grasshoppers) made up 26% of the diet by volume in early July and fell to 16% in late July. Chick diets through July more closely follow adult female than male diets (cf Table 6) though mayflies were overrepresented in chick regurgitations relative to the female diet.

Table 7. Diet of Ring-billed Gull chicks in June to July 1983, based on regurgitations at the colonies.

Prey types	June 16 - 30		July 1 - 31	
	Frequency (%)	Volume ^a (%)	Frequency (%)	Volume (%)
Earthworms	-----	-----	-----	-----
Insects	2 (67)	51.7 (76)	10 (100)	102.0 (100)
Birds	-----	-----	-----	-----
Mammals	-----	-----	-----	-----
Fish	-----	-----	-----	-----
Grain	1 (33)	16.3 (24)	-----	-----
Frogs	-----	-----	-----	-----
Debris	-----	-----	-----	-----
Totals		68.0 (100)		102.0 (100)
Number of chicks ^b	3		10	

^aAll volumes in ml.

^bOnly one sample was taken from a given chick.

Table 8. Composition of insects present in diet of Ring-billed Gull chicks in June to July 1983, based on regurgitations at the colonies.

Order	June 16 - 30		July 1 - 31	
	Frequency(%)	Volume ^a (%)	Frequency(%)	Volume(%)
Odonata	1(33)	0.5(1)	-----	-----
Coleoptera	2(66)	trace	-----	-----
Homoptera	-----	-----	2(20)	1.0(1)
Orthoptera	-----	-----	5(50)	23.5(23)
Ephemeroptera	2(66)	51.5(99)	5(50)	73.4(72)
Diptera				
(adults)	-----	-----	1(10)	4.1(4)
(larvae)	-----	-----	-----	-----
Totals		52.0(100)		102.0(100)
Number of chicks ^b	3		10	

^aAll volumes in ml.

^bOnly one sample was taken from a given chick.

DISCUSSION

Forager distribution

The observed distribution of foraging gulls in this study indicates a pattern closely tied to the agricultural activities of man. Despite widespread observations of dump feeding by a variety of species (Sibly and McCleary 1983a, see Burger and Gochfield 1983 for other references) there has been little attempt to relate the accessibility of these sites to breeding birds and their degree of use versus alternate sources of food (Sibly and McCleary 1983b). Use of refuse sites was constant but minimal in this population (Table 2) with daily maxima at all major sites totalling less than 5% of the estimated breeding population for any given month. This was not unexpected since all five refuse sites serviced a combined human population of only about 1600 (Statistics Canada 1982). Wesoloh et al. (1983) recorded no use of dumps by Ring-billed Gulls from mid-April to mid-July in the Lower Great Lakes, and an increase in dump use in July and August. Blockpoel and Tessier (in prep) reviewed five other studies of Ring-billed Gull diets in the Great Lakes and St. Lawrence region during the breeding season and in only one of seven locations was garbage cited as one of the main constituents. In an Alberta population, Vermeer (1970) recorded a low incidence of refuse in May and June diets and a predominance in July. I have no data to determine whether a small number of gulls on my

study area were specializing on refuse feeding (Hunt 1972). The breeding status of gulls at dumps was not determined directly, but I rarely observed individuals in sub-adult plumage, suggesting that they could have been members of the breeding population.

Cultivation of fields in late May and early June provided abundant sources of earthworms and grain at relatively close distances to the breeding colony (usually <40 km). During periods of rainfall when fields were too wet for tillage, earthworms became available on pastures throughout the day and were heavily utilized at this time. The relationship between predator behavior, moisture levels and earthworm availability is well established in Herring Gulls (Andersson 1970, Sibly and McCleery 1983b), badgers (Meles meles) (Kruuk 1978) and foxes (Vulpes vulpes) (Macdonald 1980). Macdonald (1980, Fig. 4) noted a first order relationship between mean number of worms on the surface and time since the last rainfall. About 40 hours following precipitation there were essentially no worms on the surface (and thus available to foragers). This time period correlates well with the drop in pasture use after rainfall found in this study. In contrast, Sibly and McCleery (1983b) observed at least some gulls regularly foraging on pastures in the early morning. Since their study was coastal, it may be that overnight moisture levels were sufficient to bring worms to the surface.

Late June represented a transitional period in available foraging habitat. By this time most tilling activities were finished for the season. Farmers began to cut the first crop of hay and gulls followed the haying implements and used them as a mechanism for flushing or exposing small birds, rodents and insects. Large aquatic insect hatches provided an additional food source along lake shores at this time. This trend became well established in July.

The wide variety of prey items in gull stomachs in this study confirms what has been found in other Ring-billed Gull populations (Baird 1976, Jarvis and Southern 1976, Vermeer 1970) and other species of gulls, both on this continent (Anderson 1965, Baird 1976, Greenhalgh 1952, Pasquier 1977, Snell 1981, Threllfall 1968, Vermeer 1970), and in Europe (eg. Harris 1965, Mudge and Ferns 1982, Sibly and McCleery 1983b). The degree of behavioral flexibility that Ring-billed Gulls possess was particularly well illustrated by their success in foraging behind agricultural implements and by abrupt changes in diet as the season progressed (Table 3). However, the population at Dog Lake appears to differ from some others studied to date in one major respect. Populations breeding around large freshwater bodies, such as the Great Lakes, have fish as a significant component of both the adult and chick diets (Haymes and Blokpoel 1978, Kirkham and Morris 1979, Ludwig 1974, Jarvis and Southern 1976). Only traces of fish were found in stomach contents of

this study even though the colony is situated very close to large freshwater areas known to contain fish. Both Dog Lake and Lake Manitoba are fished commercially and both lakes support sizable populations of fish-eating Common Terns (Sterna hirundo), American White Pelicans (Pelecanus erythrorhynchos), and Double-breasted Cormorants (Phalacrocorax auritus) (Koonz and Rakowski 1985). I verified that fish were not commonly used on my study area by many hours of observations along and over the nearby lakes. The Dog Lake Ring-billed Gulls may have become "local specialists" (Fox and Morrow, 1981) as agriculturally-based foragers. Fox and Morrow (1981), in regard to herbivorous insect species, define as local specialists "species that, over their entire geographical ranges, are generalized in the sense of feeding on a variety of species, but which have more restricted diets within particular communities." It may be that the lack of complementary data of behavior at the foraging sites and methods of lumping results of stomach analysis over an arbitrary time period or even over an entire breeding season (Anderson 1965), have obscured local population specializations of the sort observed in this study.

Late season differences in stomach contents between males and females, and the variation in sex ratios in different habitats at that time, suggest competition between the sexes. One method that gulls used to obtain prey at this time was by aerially following a haying implement and

capturing items that were flushed (birds) or uncovered (mice). Gulls also walked on the field picking insects off the swath. The high levels of aggression exhibited by aerial foragers and the differential size between the sexes probably prevented females from exploiting this rich food source made available by the haying implements, at least in the presence of males. Gulls behind tilling implements were collected while on the ground. Since the prey were small, abundant, and probably not economically defendable, a sex ratio very close to unity would be expected and did indeed occur in this context. The latter situation could best be described as a scramble strategy with each bird attempting to consume the maximum number of prey before localized depletion occurred (see Chapter III). Burger (1983) reported differential sex ratios in Franklin's Gulls (Larus pipixican) feeding behind a plough. However, in her study only 6 of 63 birds collected on the field were actually foraging on the ground. Hence, the method of collection largely differed from this study, rendering comparisons difficult. The July sample size of birds returning to the colony is insufficient for meaningful comparison between sexes though the sex ratio is slightly skewed toward females. Differences in stomach contents between males and females were distinct, however (Table 5), and reinforce those observed from field foragers.

Chick regurgitations were exclusively arthropod with mayflies as the predominant insect species. As one might ex-

pect, this diet varied considerably from that reported in the Great Lakes regions where fish are the principal food source, particularly in the latter part of the rearing period (Haymes and Blokpoel 1978, Kirkham and Morris 1979). In Alberta, Vermeer (1970) found arthropods were the dominant food type in June (50% by volume) but were replaced by refuse in July (66%). Bird remains and rodents accounted for a further 23% in the latter month followed by plant material (10%) and arthropods (1%). Vermeer (1970) also reported a high degree of overlap between the chick and adult diets, as was found in my study. Chick diets in my study followed the adult diet of both sexes in June but more closely resembled that of the female in July. It is therefore possible that in this particular population, females play the principal role in feeding chicks, at least in the latter part of the rearing period. An alternative explanation, however, is that my sampling period (1000 - 1800) may not have corresponded to the peak activity patterns (Conover and Miller 1980) or chick visitation rates (Kirkham and Morris 1979) documented in other populations (Conover and Miller 1980, Kirkham and Morris 1979), at least for males.

Population levels and limiting factors

Ring-billed Gulls have undergone increases in numbers in almost all areas of their breeding range. Ludwig (1974) reported more than a 100-fold increase of breeding pairs

from 1930 to 1967 in the Great Lakes. Conover (1983), in an extensive historical review of the western United States, estimated a 22-fold increase in breeding individuals. Population trends in Manitoba are less clear. Bent (1921) commented that in 1913 Ring-billed Gulls were common on most lakes in Manitoba though he gave no specific estimates. The most extensive survey of colonial waterbirds in Manitoba to date has been the 1979 survey of Koonz and Rakowski (1985). They reported that "populations (of Ring-billed Gulls) in Manitoba are considered high and on the rise at present", but no quantitative comparative figures exist (W.H. Koonz pers.comm.). Specific data for Dog Lake is also sparse but Moynihan (1956) estimated 4000 birds in 1955. If Moynihan's figures are acceptable as a rough estimate, then the Dog Lake population has approximately doubled in the last 30 years with an estimated 3500 nests or 7000 individuals present during my study.

Conover (1983) has outlined three major factors that could limit gull populations: predation, lack of available breeding habitat, and food. I will now discuss these factors in relation to the Dog Lake population.

1. Predation pressure. Since gulls are now protected under Canadian law, few people shoot them or disturb their breeding colonies, a practice that Bent (1921) thought was responsible for their decline in the 1800's. Also, most major colonies are located on small, rocky islands more than

0.5 km from the shore, far from the range of mammalian predators (see Southern et al. 1982). In 1983, a Dog Lake colony of approximately 1600 pairs was visited regularly by a Great-horned Owl (Bubo virginianus) (pers. obs.). From three separate visits I counted a total of 34 freshly decapitated adults in the colony proper and the remains of three more adults beneath a tree on one side of the island. This particular island was unusual in being close to the mainland (approx. 150 m), was much larger than the other colony islands and had extensive tracts of mature trees and other vegetation. It was occupied as a result of the flooding of a nearby traditionally-used reef site during a period of high water levels in the 1970's (R.M. Evans pers. comm.). The colony suffered complete reproductive failure in 1983 and the island was not reoccupied in 1984, when tracks of mammalian predators were also noted on the island. In contrast, gulls breeding on small rocky reefs further out in Dog Lake enjoyed high reproductive success and little or no evidence of predation in either year. It seems likely, therefore, that predation does not represent a serious, overall long-term threat to the Ring-billed Gull population on Dog Lake.

2. Lack of available breeding habitat. Ludwig (1974) noted the facility with which Ring-billed Gulls abandoned unsuitable colony sites between years and thus maintained high reproductive rates; a strategy he interpreted as an ad-

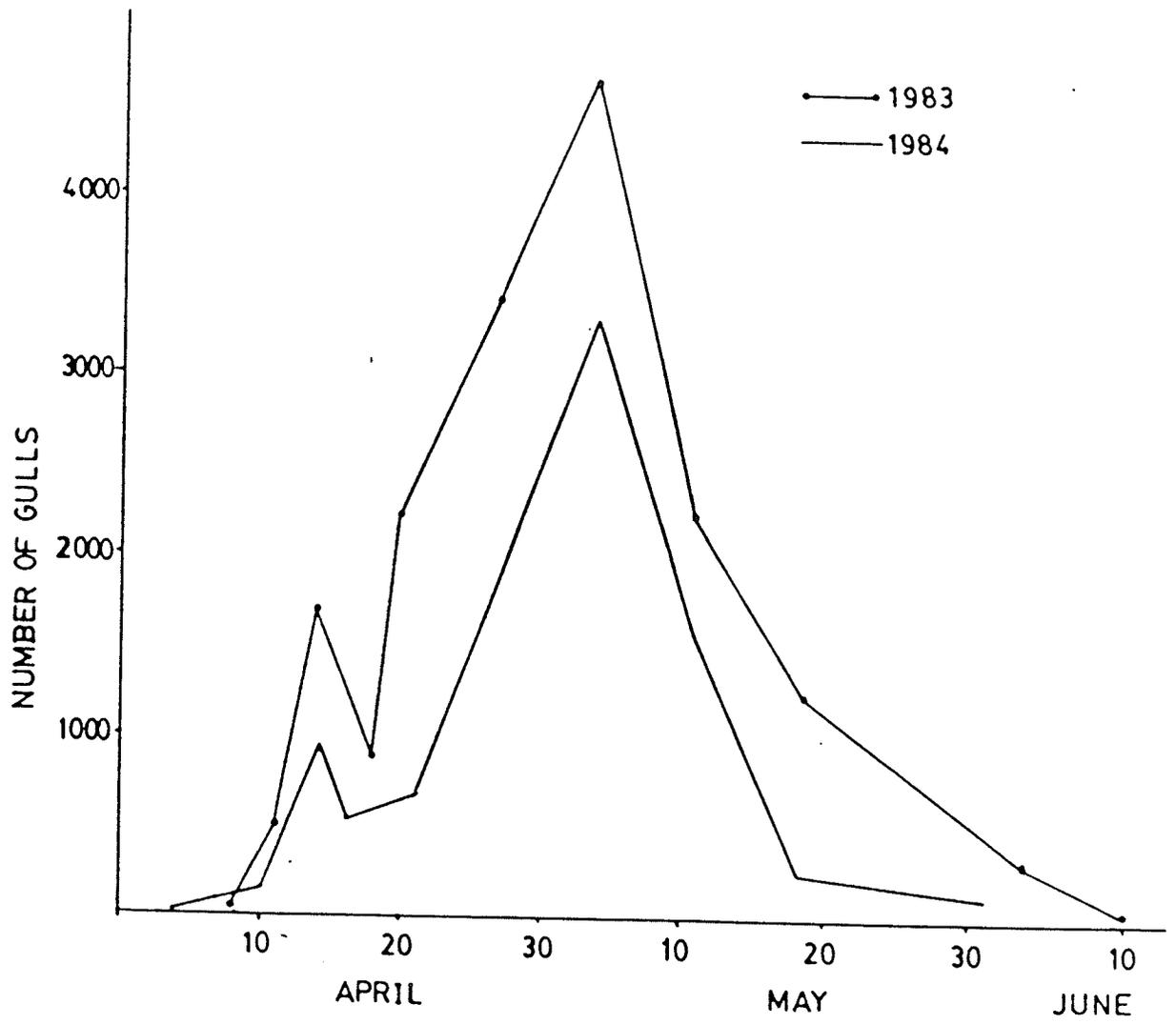
aptation to unstable water levels. The change in colony location noted in the previous section attests to this capability in Dog Lake gulls. As new and better breeding habitat becomes available or old sites become unsuitable, Ring-billed Gulls are evidently able to change sites and thereby adapt to changing conditions. A survey of possible breeding habitat within several kilometers of present colonies revealed three similar islands, one of which was occupied by approximately 50 Common Terns and 30 Ring-billed Gulls. Hence, there appears to be adequate breeding habitat on Dog Lake. In addition, gulls at the three main colonies occupied less than 90% of the available area on each island thus strengthening the argument against habitat limitation.

3. Food. Recent studies of population trends in gulls indicate that greater food availability is responsible for population increases in North America (Conover 1983, Ludwig 1974). For inland-breeding populations that are terrestrially-based in their foraging effort, increasing human populations with concomitantly greater amounts of refuse and greater agricultural exploitation have provided much of this expanded food base (Conover 1983). At Dog Lake, only the use of agricultural land appears to successfully explain the recent increases in the Ring-billed Gull population. Patterns of land use for Manitoba indicate a 21% increase in total area of crop production for the period 1951 - 1981 (Man. Dept. Agric. Handbook 1983). Similarly, the amount of tame

hay production has increased 68% while summer fallow acreage has declined 41%. The increases in total agricultural production area mean that more land is cleared and cultivated in early spring for seeding to crops, thus expanding earthworm and grain foods. The decline in summer fallow area further emphasizes this trend as economic conditions force more intensive use of available growing area. Similarly, increases in tame hay production ensure more food later in the season for chick-rearing and pre-migratory lipogenesis.

As previously mentioned, refuse sites in the Dog Lake area were of little importance to this population. However, use of refuse sites further south during spring migration may provide a food source at a critical point in the breeding cycle since birds are near the end of their northward migration and may need to build up or maintain pre-breeding weights. Alternate food sources may not be available early in the season. Bent (1921) stated that the earliest date for spring migration in southern Manitoba was 21 April with a mean of 25 April. Figure 2 shows the number of Ring-billed Gulls present at one of five major dumps in Winnipeg, Manitoba in early spring (approx 150 km southeast of Dog Lake). By the first week in April, birds had already begun arriving and peak numbers were achieved on 4 May in both years. Winnipeg's population has increased from 176,230 in 1916 (Statistics Canada 1918) to its present level of about 600,000 (Statistics Canada 1982). Presumably the amount of

Figure 2. Number of Ring-billed Gulls reported at one Winnipeg City dump in 1983 and 1984 (R.M. Evans, used with permission).



refuse has been proportional to this increase. Tilling activities at Dog Lake do not usually become general before the first or second week in May. Hence, the presence of a predictable food source at dumps relatively close to and near the migratory route to the colony, may have permitted birds to migrate north earlier, remain in good physiological breeding condition and track the availability of other food sources (ie. agricultural activities) with greater precision. Comparison of first arrival dates for the Alberta Ring-billed Gull population shows similar results. Bent (1921) placed the earliest arrival date at 9 May for northern Alberta while Vermeer's (1970) earliest arrival dates at a dump in Edmonton (approx. 35 km from his colony site) for 1964 - 1967 are 29,30 and 28 March, and 2 April respectively. Hence, that population may also utilize predictable refuse sites as convenient stopovers early in the breeding season.

The date of first laying may also be taken as an indicator of the health of a population (see Baird 1976, p.16). The data of Bent (1921) are again the only source available for comparison. He gave 17 records of egg dates between 4 to 23 June for Saskatchewan and Manitoba. On 10 May, 1983 the author and R.M. Evans counted 39 nests with eggs present (23 1-egg, 4 2-egg, 2 3-egg clutches) at one colony on Dog Lake. Peak laying occurred between 25 May and 7 June. Observations in 1984 revealed that most nests had eggs present by

15 May with peak laying from 21 to 26 May. Data for both years are considerably advanced over those previously reported. The date of first laying in Alberta populations is about 7 to 10 days further ahead than in Manitoba (Vermeer 1970). This is not surprising since, as previously mentioned, this population arrives in the general area of the colony by about late March while the Manitoba population only arrives in Winnipeg (approx 150 km south of the study area) in early April.

In summary, it appears that the moderate (2-fold) increase in the Dog Lake Ring-billed population in the past 30 years can be attributed to an increase in food made available by agricultural practices. In addition, the abundance of food from refuse sites south of the breeding grounds may have permitted gulls to migrate earlier in the spring and to better track availability of alternate prey types as indicated by the degree of agricultural activities. As more land is cleared and put into production one would predict further increases, particularly in those populations such as at Dog Lake, that are terrestrially-based in their foraging efforts.

CHAPTER 2. RING-BILLED GULL ARRIVAL AND DEPARTURE CHARACTERISTICS

INTRODUCTION

Possible food-related benefits of coloniality have received considerable attention. The first hypothesis to generate widespread interest was probably that of Ward and Zahavi (1973) whose information center hypothesis (ICH) proposed that unsuccessful foragers could derive knowledge of profitable feeding sites by following previously successful foragers as they departed a central place such as a colony or communal roost. However, a conclusive test of the hypothesis has proven difficult and results so far are equivocal (Bayer 1982). Evans (1982a) has suggested that colonies act as "Assembly Points" "where dispersed foragers can reunite for purposes of subsequent group feeding activities." While not precluding the operation of an ICH, this hypothesis was proposed as a possible alternative explanation for the evolution of coloniality in birds. The overall objective of this part of my study was to discriminate between these two hypotheses by examining a colony of Ring-billed Gulls (Larus delawarensis) that are terrestrial in their foraging habits. Previous tests of the Assembly Point model are lacking though Evans (1982b) and Evans and Welham (1986) provided evidence consistent with its predictions.

Most tests of the possible food-related benefits of coloniality were concerned with measuring patterns of dispersal from the colony site. However, as Waltz (1982) has demonstrated on theoretical grounds, a critical component of the foraging system concerns the behavior of birds after the rejection of such a patch. For example, under the ICH, birds leaving an unsuitable patch would be predicted to return to the colony for new information. The Assembly Point hypothesis (APH), on the other hand, predicts further dispersal in search of new patches regardless of distance, at least until the usual time (eg. evening) when the foragers reassemble at the colony site.

The APH also assumes the presence of some benefit of grouping while foraging; the ICH permits but does not require such group-related benefits (Ward and Zahavi 1973). Anti-predator adaptations may be one such advantage (Rand 1954). However, as recent evidence indicates, local enhancement is probably one of the most widespread group-related benefits in both single (Krebs 1974, Anderson et al 1981) and mixed species flocks (Kushlan 1977, Caldwell 1981, Porter 1983). Waite (1981) has demonstrated that local enhancement can occur on both a "coarse" and "fine-grained" level depending on whether a potential forager is attracted to a field or to specific areas in that field, respectively. Demonstrating the existence of local enhancement or some equivalent group benefit at the food site is therefore an important aspect of any test of the APH.

To help discriminate between the ICH and APH, I examined arrival and departure characteristics of foragers in relation to food patches and the influence of wind as a possible mediator of departure direction (Evans and Welham 1986). Failure to show any systematic departure trend from depleted sites back to the colony would provide evidence contrary to the ICH. In addition, I used styrofoam models, and the presence and feeding behavior of live conspecifics, to document "coarse-grained" local enhancement and determine possible cues that may be used to assess patch quality. An absence of local enhancement or other group-related foraging benefit, and/or a tendency for birds leaving a depleted patch to go primarily towards the colony, would provide evidence contrary to the APH.

MATERIALS AND METHODS

Directions and timing of arrivals and departures at foraging sites

I examined the directions and times of arrivals and departures at terrestrial foraging sites (fields) from May to July in 1983 and 1984 in the vicinity of Dog Lake, Manitoba (see Chapter 1). A 360° circle around each field was divided into eight equal sectors (N,NW,W,SW,S,SE,E,NE). Only fields that provided a complete unobstructed view of all arrivals and departures were included. Wind direction was recorded by sector at the beginning and end of each observation period. In 1984, I determined wind velocity using a

hand-held anemometer (MET-5500, Le Naturaliste, Rimouski, Quebec), whereas in 1983 velocity was estimated by per hour averages calculated from three weather stations within 108 km of the study area (100 km W, 108 km SE, 108 km NE). I used my 1984 wind velocity estimates to verify that the weather station data were representative of conditions on the study area.

Analysis was by time period (morning: dawn to 1100 hr; mid-day: 1101 to 1700 hr; evening: 1701 hr to dark). The timing of departures was tested for randomness against a Poisson distribution. To examine arrival and departure directions, I used the length of the mean vector, r (Batchelet 1981:31), calculated for all fields separately. Chi-square statistics were used to further test whether birds had a significant tendency to arrive from or depart to the colony sector. Expected values for this test were derived by dividing a 360° arc into 8 equal sectors and assuming a $1/8$ chance of birds arriving from or departing to the colony sector. Hence there was a $7/8$ chance of a bird being counted in the remaining sectors if departures were random. Rayleigh tests (Batchelet 1981) were then used for testing against randomness. Circular correlations with wind were also calculated (Batchelet 1981:190). Wind analysis used axial data, a procedure whereby all angles are doubled, then reduced modulo 360° (see Batchelet 1981:21 for details). Axial data analysis is appropriate whenever a biologically

meaningful response can occur in either of two opposite directions (upwind or downwind in this case).

Local enhancement

To test the hypothesis that foragers use the presence of other foragers on the field as a cue when settling at a food patch (ie. local enhancement), I set out 25 styrofoam gull models. Models were made by pouring liquid styrofoam components into a plaster of paris mold that had been formed around life-sized clay models of a feeding and loafing Ring-billed Gull. For a test, models were distributed in a set pattern (Fig. 3) between 23 May and 12 June 1984, at four different distances (4, 11, 14, and 24 km) from the colony. The procedure followed is outlined in Table 9. Each location selected was a tilled field that I was certain had no birds on it for at least 2 days prior to the experiment. Models were then set out (experimental period)(see Table 9) and observations begun. Data were gathered continually and tabulated by the minute. For the experimental periods, I recorded the number of birds flying over the field, the number flying over the models (no perceptible response), and the number circling and/or landing at the models. For the control periods (Table 9), I simply recorded the number of birds flying over the field and the number that circled or landed on the field.

Figure 3. Distribution pattern of Ring-billed Gull models. Solid arrows represent feeding postures (n=19 models), broken arrows represent loafing postures (n=6 models). The head of an arrow indicates the direction the model was facing.

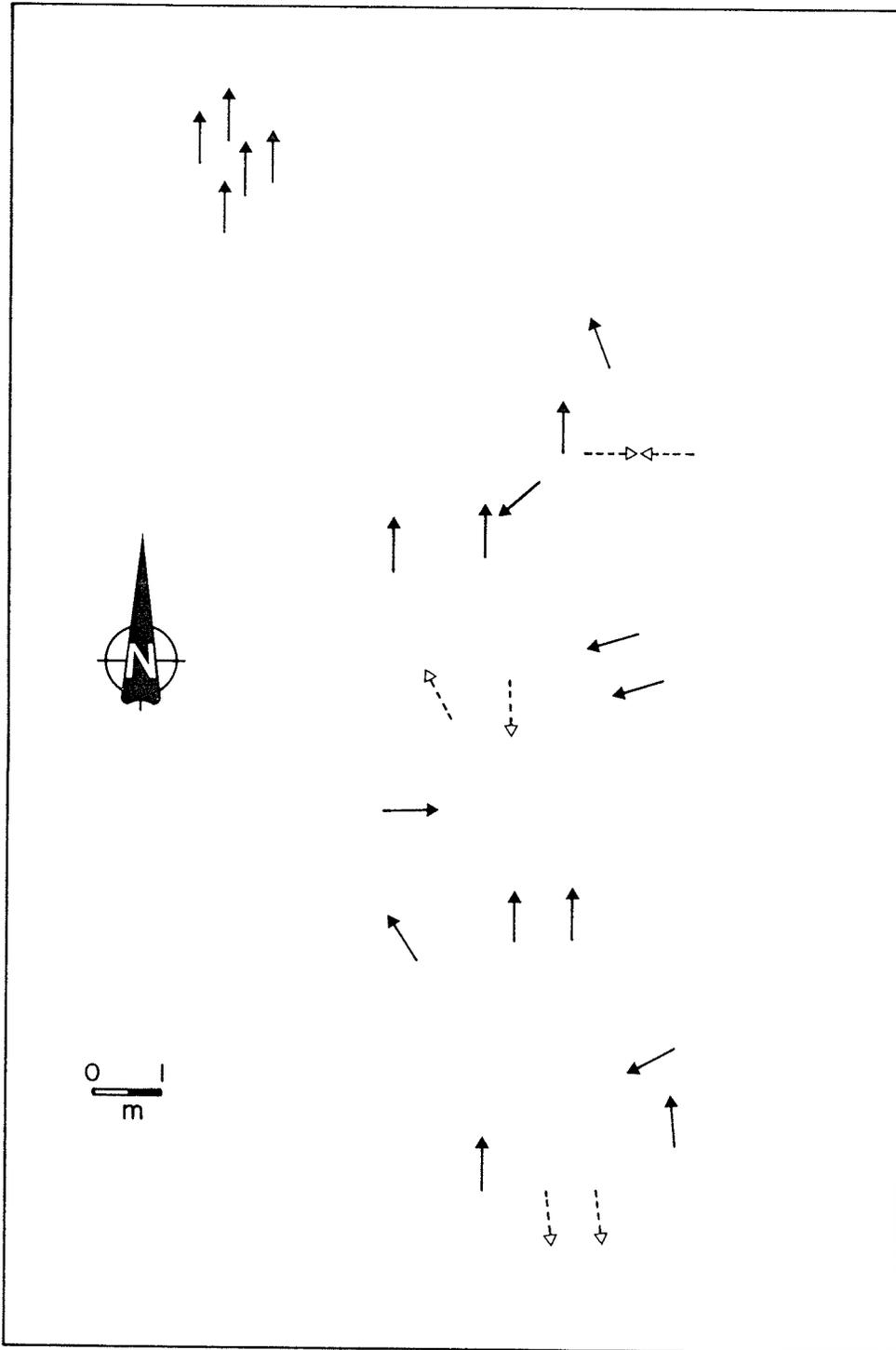


Table 9. Timing (hr) of tests with gull models present (experimentals) and absent (controls).

days	experimentals	controls
I and III	0700 - 0800 1030 - 1130	0815 - 1015
II and IV	0815 - 1015	0700 - 0800 1030 - 1130

Detailed observations of foraging behavior on fields having different forager densities were gathered in 1984 to further assess the local enhancement hypothesis. In 1983, I had observed two fields, about 8 km from the colony and .5 km apart, that had substantial differences in flock sizes (<10 versus >100). I therefore made arrangements in 1984 for both fields to be tilled on different days in as short a period as possible (one day for each field). It was assumed that foragers attracted to the better feeding site would experience higher feeding rates and thereby exhibit less of a tendency to depart, which would also result in an increasing flock size. Comparable data were gathered at approximately the same time each day (1300 hr) and for equal duration. I recorded peck rates, time spent feeding and not feeding, and flight times of randomly selected focal birds (Altmann 1974), arrivals and departures, and flock size at the end of the sampling period.

RESULTS

Directions and timing of arrivals and departures at foraging sites

Fig. 4 and 5 show frequency distributions and chi-squared values of observed and expected (if random) distributions of the numbers of Ring-billed Gulls arriving at and departing from fields at three times of the day. In all cases, arrivals and departures were significantly different from random, with differences being as expected where clumping

Figure 4. Frequency distributions of the number of minutes with 0, 1, 2, ... arrivals of Ring-billed gulls at terrestrial feeding sites for morning (dawn - 1100 hr), mid-day (1101 - 1700 hr), and evening (1701 hr - dark) periods from May to July 1983, 1984.

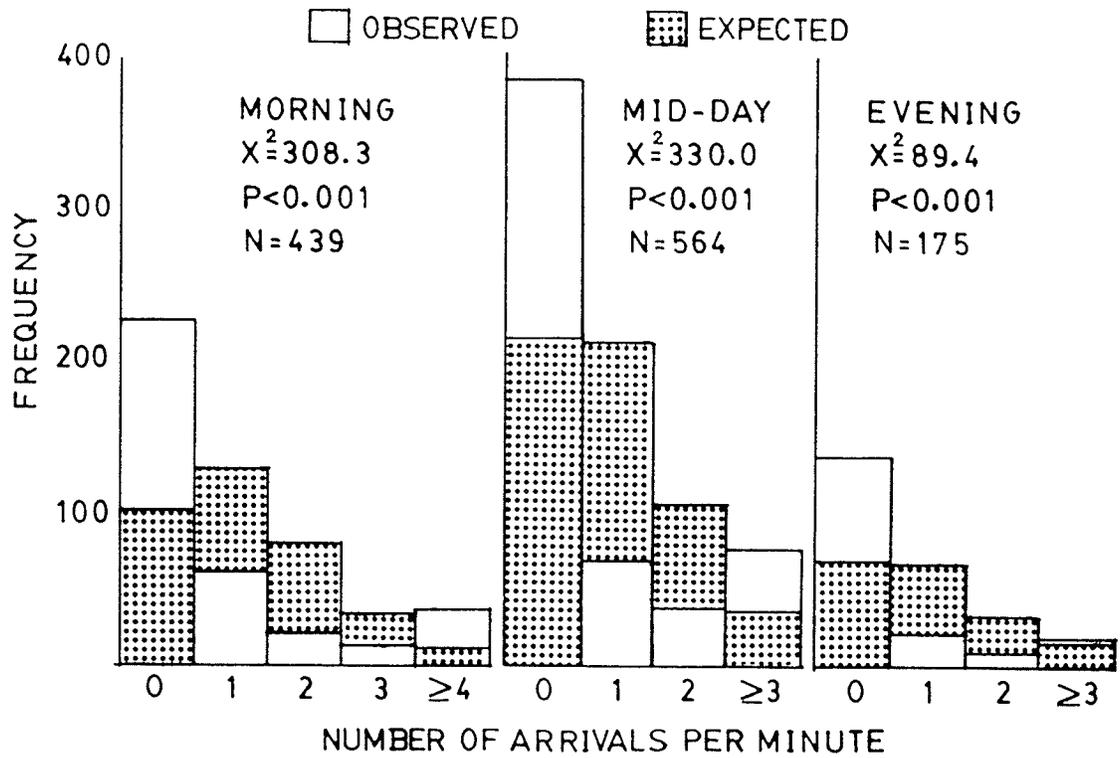
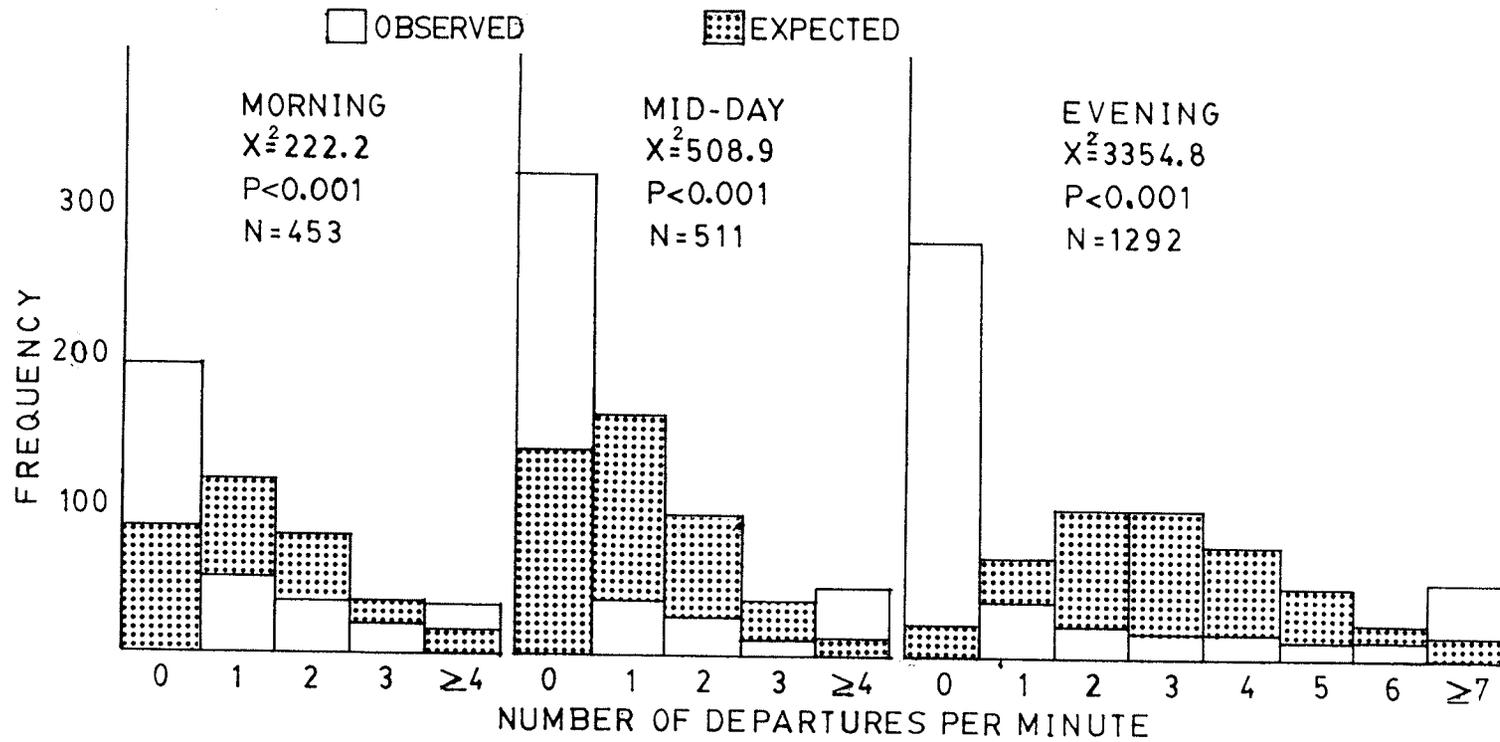


Figure 5. Frequency distributions of the number of minutes with 0, 1, 2, ... departures of Ring-billed gulls at terrestrial feeding sites for morning, mid-day and evening periods from May - July 1983, 1984 (see Fig. 4 caption).



(flocks) occurred. Flock size distributions did not differ significantly between morning and mid-day arrivals ($X^2=2.879$, $df=2$, $P=0.24$), mid-day and evening arrivals ($X^2=4.080$, $df=2$, $P=0.13$), or between morning and mid-day departures ($X^2=2.012$, $df=2$, $P=0.37$). Similarly, morning arrivals vs departures and mid-day arrivals vs departures did not differ significantly ($X^2=6.832$, $df=3$, $P=0.08$, and $X^2=1.244$, $df=2$, $P=0.54$ respectively). Only evening arrivals vs departures and mid-day vs evening departures showed significantly different patterns of flocking ($X^2=12.073$, $df=2$, $P=0.0024$ and $X^2=10.806$, $df=2$, $P=0.0045$, respectively).

Table 10 shows significant clumping for most arrivals and departures during all time periods. Only evening departures showed a significant directional preference for the colony sector (Table 11). For morning and mid-day departures combined, a total of 16/20 (80%) departure vectors differed from the colony sector (Table 12). Departures toward the colony also showed no systematic trend with distance (Table 12). These results suggest that some factor other than colony location was responsible for arrival and departure directions.

Circular correlations between departure and wind directions are presented in Table 13. Departures from morning through mid-day are significantly correlated with wind direction while evening departures and all arrival data are not.

Table 10. Number of significant Rayleigh tests for randomness of arrival and departure directions at terrestrial foraging sites (fields) at different times of the day (May to July 1983, 1984)^a.

	Arrivals				Departures			
	P<0.001	P<0.01	P<0.05	n.s. ^b	P<0.001	P<0.01	P<0.05	n.s. ^b
Morning	5	0	0	1	8	0	0	0
Mid-day	5	0	1	2	9	0	0	2
Evening	2	0	0	0	8	0	0	0
Totals	12	0	1	3	25	0	0	2

^aNote that in a given time period, each test represents a different day.

^bn.s.=not significant.

Table 11. Chi-square tests of the hypothesis that arrivals and departures were significantly oriented from or to the colony direction in terrestrial feeding sites from May to July 1983, 1984 (see text).

	Arrivals from colony sector			Departures to colony sector		
	Morning	Mid-day	Evening	Morning	Mid-day	Evening
X ²	.95	.50	a	0	2.19	41.1
P value	>0.05 ^b	>0.05	-----	>0.05	>0.05	<0.001
N	6 ^c	8	2	8	12	7

^aBoth fields in this column had arrivals from the colony direction, but sample size was too small to permit statistical analysis.

^bDf=1 in all cases.

^cFor each time period, N is the number of days pooled for analysis.

Table 12. Number of samples for which departure vectors coincided with colony direction during three time periods, in relation to distances of feeding sites from colony (see text).

Distance to colony (km)	Number of departures							
	To colony				Not to colony			
	Mo ^a	Md	E	Totals	Mo	Md	E	Totals
0-5	--	--	-	--	--	--	-	--
5.1-10	0	1	1	2	1	2	0	3
10.1-15	0	0	0	0	1	2	0	3
15.1-20	1	2	3	6	4	2	0	6
20.1-25	0	0	1	1	1	0	0	1
25.1-30	0	0	0	0	0	3	1	4
30.1-35	0	0	0	0	0	0	0	0
35.1-40	0	0	1	1	0	0	0	0
Totals	1	3	6	10	7	9	1	17

^aMo=morning

Md=mid-day

E=evening

Table 13. Circular correlations between wind and arrival or departure directions at terrestrial feeding sites from May to July 1983, 1984.

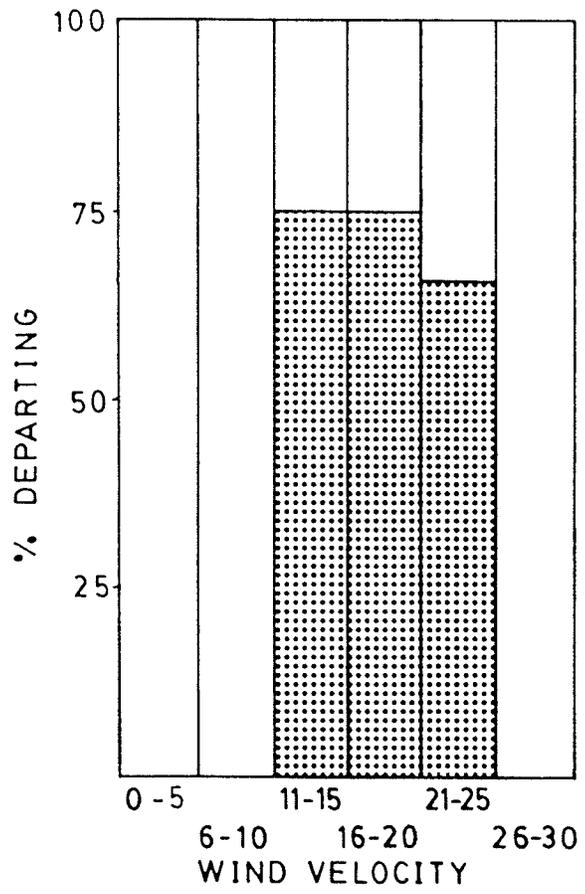
Time of day	Statistic	Arrivals	Departures
Morning		7.3189	10.6665
	N ^a	5	8
	P	P > 0.136	0.027 < P < 0.04
Mid-day		3.3566	10.8562
	N	5	8
	P	P > 0.261	0.027 < P < 0.04
Evening		b	6.3962
	N	-----	5
	P	-----	P > 0.136

^aN equals the number of pairs. Df=4 in all cases (Batchelet 1981: 178).

^bInsufficient data pairs.

Under high wind conditions, I noticed that birds tended to depart by "quartering" into the wind ie. departing at about a 45° angle. Fig. 6 shows that a high percentage of birds departed either into or with the wind ($<20^\circ$ of wind direction) at intermediate wind velocities (11 to 25 km/hr) and that most departures in other directions occurred either at low (0 to 10 km/hr) or high (>25 km/hr) wind velocities. Evidently wind strength as well as wind direction, is an important variable influencing departure direction.

Figure 6. Percent of all departures (n=16 days) $\leq 20^\circ$ (stippled) or $>20^\circ$ (open) from an upwind or downwind direction as a function of wind velocity.



Local enhancement

Significantly more Ring-billed Gulls flew over the fields when conspecifics were present (experimental; 71%; n=206) than when they were absent (control; 29%; n=84) ($\chi^2=6.5$, $df=1$, $P<0.025$). Gulls during experimental periods had significantly different arrival and departure directions than control birds; for experimentals, the proportion that changed direction was 0.33, while the proportion that did not was 0.67. For controls, the corresponding proportions were 0.01 and 0.99 ($\chi^2=16.3$, $df=1$, $P<0.001$, $n=290$). No gulls landed at the site during control periods. In contrast, during experimental periods, significantly more birds landed at or circled the models (146) than flew directly over the field (61) ($\chi^2=34.9$, $df=1$, $P<0.001$, $n=207$).

Table 14 presents comparative data on potential local enhancement cues displayed by foragers on two fields. The maximum flock size attained on field #1 never exceeded 21 foragers and fluctuated continually. Field #2, however, exhibited a steady increase in numbers from the beginning to the end of the observation period, to at least 79 foragers. Similarly, other factors such as peck rate and time spent foraging on the ground were higher on field #2. Also, on field #1, I noted that a bird usually landed to investigate potential prey. When, after landing, the prey was rejected (by picking up and dropping) or consumed, the bird usually stood still and visually scanned its immediate surrounding.

Table 14. Comparative behavior of Ring-billed Gulls on two fields of varying quality.

Field	Maximum flock size ^a	Number of birds sampled	Mean peck rate per minute	Proportion focal animal samples ending in a flight ^b	Mean \pm S.D. time spent on ground (s) ^c	Net arrival rate per minute ^d
1	21	16	.92	1.0	49 \pm 34	.17
2	79	23	4.75	.35	>88	.67

^aDetermined at the end of observation periods.

^bIncludes both birds that departed field or flew closer to implement.

^cMean time spent foraging before bird took flight or sample ended.

^dObtained by subtracting departure rate from arrival rate.

My observations indicate that birds on field #1 spent 78% of their time on the ground in a standing position; this compares with only 19% in birds on field #2. On the latter field, a bird tended to follow the same sequence of events in that, upon landing, prey were rejected or consumed, followed immediately by a scanning position. However, within several seconds, new prey were usually spotted and the bird walked over and began the event sequence again. Hence the two fields generated wide variation in forager behavior and offered different local enhancement cues to other foragers as to their suitability.

DISCUSSION

Directions and timing of arrivals and departures at foraging sites

How birds depart a food patch is relevant to discriminating how (or if) breeding or roosting aggregations can function to enhance individual feeding success. According to the information center hypothesis, one might expect most departures to be in the colony direction. Hence, given that patches were ephemeral, occasionally superabundant and existed for slightly more than one day (chapter 1) it is relevant that I observed no systematic departure trend in the colony direction for morning and mid-day periods. All evening departures but one were in the colony direction regardless of wind. Since I never observed gulls terrestrially foraging at night, evening departures were probably related

to other nocturnal activities (such as roosting). From a previous study (Evans and Welham 1986) it is known that departures from the colony did not tend to correlate on successive days suggesting that even the evening departures towards the colony were not likely related to an information center function. The data appear to be consistent with the APH, which predicts dispersal away from depleted food sites by searching foragers except when birds are reassembling at the colony.

The lack of significant differences between flock size distributions of arriving and departing foragers for morning and mid-day periods at the foraging sites also lends support to the APH since foragers would presumably derive the same benefits from flocking when departing a food source to search for another, as they did prior to discovery of the original site. If the colony were acting in the context of an information center, there would be no reason to expect flocking among birds heading back to a colony of known location. One could argue that flock mates would be beneficial to spotting new food sites that may have developed closer to the colony but this is not a prediction of the ICH. Moreover, at least one information center model (Waltz 1982) has assumed that birds fly directly back to the colony when unsuccessful and not in the meandering fashion that was characteristic of Ring-billed Gull foragers departing a food site (pers.obs.).

The significant difference between flock size distributions for arrivals and departures in the evening period suggests that flock departures function in a different context at this time. As darkness approached, large upflights of the entire flock from the field were common, and were usually followed by departures of most, if not all, birds. Birds spent the night either roosting near the colony on Dog Lake or adjacent portions of Lake Manitoba (pers.obs.).

That wind strength and direction were the major correlates of departure direction during the day has implications for the APH. By responding to wind direction, foragers would, in effect, be funneled into two major departure directions thus increasing forager densities in those portions of the habitat so that local enhancement or other group foraging benefits could operate effectively as required by the APH. This "funnel effect" should become increasingly important as birds move further from the colony (up to 38 km in this case) since area increases as the square of the distance with a correspondingly greater chance of reduced forager density at these greater distances, unless countered by some density-maintenance mechanism such as that proposed here. One might argue that even though the initial departure direction was influenced by wind, subsequently birds changed direction. From protracted observations of individual departures, I saw no evidence for this. On one occasion, R.M. Evans (pers.comm.) was able to track high forager

densities as gulls moved out from the colony in a unidirectional south-easterly manner for a distance of 54 km from the colony.

Responses to wind direction and strength could also have implications for the energetic balance of foragers. Of particular importance are the thermoregulatory and energetic benefits of wind travel (see Tucker 1975, for a review). Gulls were observed to utilize a variety of soaring techniques (Pennycuick 1975) that reduce the costs of locomotion. These possible energetic benefits could, presumably, complement or enhance any benefits arising from improved food search.

Local enhancement

The use of model birds to test experimentally for attractions to conspecifics at foraging sites (ie. local enhancement, Thorpe 1963) is being used with increasing frequency. In Ciconiiformes, the attractiveness of a potential foraging site was significantly enhanced by the presence of one or more models (Krebs 1974, Kushlan 1977, Caldwell 1981). Andersson et al. (1981) demonstrated that Black-headed Gulls (Larus ridibundus) were attracted to models and also groups of live conspecifics, whose natural presence at a food source increased its chances of discovery by searching gulls. Porter (1981) used California Gull (Larus californicus) models in a marine situation. No differences were

reported in the degree of attractiveness between a single model and a large group (23 - 26 models) but in each condition, the presence of models attracted significantly more birds to the model site and for longer periods of time than occurred during control periods. Similarly, the significant attractiveness of model Ring-billed Gulls observed in this study indicates that birds are not just responding to some external stimulus (eg. a cultivating implement; see Chapter I) but that the presence of conspecific models can be attractive, presumably as indicators of a potential food patch.

To a potential forager attempting to assess the quality of a patch, the behavior exhibited by those already on a field could be an important energy and time-saving cue (cf Krebs and Davies 1983). Results (Table 14) indicate that the cue provided to a potential gull forager, at least in the initial stages, may be simply the amount of time that committed foragers spend on the ground. The presence of loafing flocks, which commonly form adjacent to the rich food patches (pers. obs.), could function in a similar manner.

The strong evidence for local enhancement in this study and elsewhere is consistent with the interpretation that gulls obtain benefits from foraging in groups as assumed by the APH. Colonial breeding, combined with the funnelling effect of wind at both colony (Evans and Welham 1986) and

foraging sites (this study) can be expected to help maintain sufficient forager densities far from the colony for efficient employment of local enhancement. This complex of behavior appears to constitute an effective overall foraging strategy enabling Ring-billed Gulls to efficiently exploit this environment.

CHAPTER 3. A TEST OF AN OPTIMAL FORAGING MODEL IN RING-BILLED GULLS FEEDING BEHIND AN IMPLEMENT

INTRODUCTION

Optimal foraging theory (OFT) (Pyke et al 1977) has attempted to predict how animals forage under the assumption that this behavior has been shaped by natural selection, subject to certain constraints. When expressed in terms of an energetic currency (Schoener 1971) an animal usually has been assumed to maximize its fitness by maximizing its net rate of energy intake while feeding (Krebs et al 1983). A logical dichotomy in OFT models, at least to date, has been to separate the decision of which food patch to feed in and for how long, from which prey items to select and reject (Krebs et al 1983). This chapter addresses the first of these issues. In particular, I attempt to determine whether or not Ring-billed Gulls (Larus delawarensis) maximize their rate of energy intake while foraging for patches of earthworms (Lumbricus spp.) exposed by a farm implement.

The gull population in this study is terrestrially-based in its foraging effort, at least throughout the breeding season (see Chapter 1). Food types vary seasonally (Chapter 1), with earthworms being the dominant prey type from May through early June. At this time, gulls obtained

worms primarily by feeding behind ploughing and seeding implements on agricultural land. In a typical foraging scenario, the tractor proceeded in a somewhat circular path around the periphery of the field, gradually working into the center. Gulls attracted to the field for feeding usually flew immediately to the implement and landed as close behind it as possible. As flock sizes increased, in some cases up to several hundred birds, a dense line of foragers developed in the most recent path of the implement. Individuals employed a strategy whereby a bird would land behind the implement, actively feed for a time, then fly again towards the tractor. This cycle was then repeated.

Since there are a finite number of worms on the surface at any given location on the field, I postulated that depletion effects would result in a cumulative intake function that was decreasing at a monotonic rate, of the form assumed by Charnov's (1976, Fig. 2) marginal value theorem. In addition, since the tractor is in essentially constant motion, there is necessarily a direct relationship between the time spent on the ground and the distance an individual forager has to travel to catch up to the implement. Both conditions operate together such that for a gull to maximize its rate of energy intake, an optimum time on the ground can be predicted from OFT. In this study, I first determined the energy intake of gulls foraging behind an implement to verify the shape of the cumulative food intake function. A model

was then developed from OFT to make predictions about the time that should be spent in a patch before flying on. Comparisons were then made between the predictions and actual gull foraging behavior.

MATERIALS AND METHODS

Field choice

In May 1984, I observed four fields being prepared for that summer's grain crop. Three fields (locations 29, 34, and 37) were being ploughed and one (location 10) seeded in barley (Hordeum distichon). These fields were judged suitable for detailed analysis since they were (a) roughly rectangular in shape and cleared of all stands of trees, (b) large enough (at least 65 ha.) to permit the implement to make at least 10 passes around the field with essentially constant circumference time, and (c) had a well-established feeding flock (> 100 gulls).

Data collection

When a field was selected, I positioned myself about one third of the distance down its longest side, sufficiently concealed in peripheral vegetation so as not to disturb the foraging gulls. As the tractor passed by my location, I selected the first gull that landed behind the implement and conducted a focal animal sample (Altmann 1974) with the aid of a 15X spotting scope. I was able to identify the prey,

whether earthworms or grain, as it was selected, and could determine if a peck was successful or unsuccessful. The observation period ended either when the bird took flight towards the implement or after 60 s if it did not fly by that time. I then selected another focal bird from the same location and continued to sample under the same criteria. This process was continued until there were either no birds at that location or those that were remaining had stopped foraging (ie. were only loafing or preening). Preliminary analysis indicated that 240 s after the implement passed usually resulted in termination of a sampling bout. At the beginning and end of each observation period I recorded flock size and tractor speed, the latter by measuring the time required for the tractor to pass two points of known distance. At the end of each observation period, I recorded the total time required for the tractor to make one complete circuit of the field.

Earthworm abundance was sampled at the end of each observation period by walking four 10 m transects, beginning immediately behind the tractor. One transect was conducted in the immediate area of the focal animal samples, while the starting points of the others were selected using the estimated dimensions of the field (in meters) as coordinates and choosing coordinate pairs from a random numbers table. The total worm sample for each location was lightly washed, padded dry, then weighed and preserved in 10% formalin. These

collections were then used to determine the average wet weight of earthworms on each location. Earthworm dry weight was calculated by assuming that each worm was composed of approximately 83% moisture (French et al 1957). I multiplied the estimated dry weight by a value of .5584 kcal/g dry weight (Cummins and Wuychek 1971) to obtain an estimate of average caloric value per earthworm. Caloric values per grain of barley were calculated by multiplying a sample of known weight from location 10 by 2775 kcal/kg (Anonymous 1977, Scott et al 1976) and dividing by the number of grains in the sample.

For purposes of analysis and model development, I assumed that the immediate surroundings of the bird were its "patch" and that time in the patch started from the instant the bird landed behind the implement until it again departed in pursuit of the implement. Flight speed was estimated from frame by frame analysis of 8 mm movies taken of 67 gulls foraging on four fields. Flight time, calculated from flight speed and distance to tractor, was taken from the time the gull departed the patch until it landed behind the implement. One feeding cycle consisted of one bout of feeding plus one flight to the implement.

Cumulative intake curves

A statistical model used to fit all cumulative intake curves in this paper is the monomolecular growth function (Richards 1959) which is of the form:

$$G = a/b(1 - e^{-bt_p}) \quad (1)$$

where G is the cumulative intake, a/b determines the asymptotic value of the function, b the spread of the curve along the time axis, t_p is the time spent feeding in the patch, and e is the base of natural logarithms.

All functions were fitted using a least squares non-linear iterative reweighting procedure employing the Marquardt algorithm (Conway et al 1970). The procedure itself is written in APL and available in the public library of the University of Manitoba Computing Services. This method incorporates a weighting factor, derived from Taylor's Power Law (Taylor 1961) to estimate the variance at each t_p . Calculation of the weighting factor was done by using the inverse of the predicted variance at the predicted intake rate at each t_p , ie.

$$w = 1/(G^b/Nt_p) \quad (2)$$

where W is the weight, G = equation (1). The exponent, b , derived from Taylor's Power Law, is the slope of the double log plot of the means and variances of the cumulative intake rates and Nt_p is the sample size at each t_p (see Shostak et al 1985, for further details).

The fitting procedure involved entering initial estimates of parameters a and b obtained by hand calculation. After the first iteration the computed values for a and b were re-entered. This process was continued until there was no change in residual variance up to five significant digits (usually after 4 - 6 iterations). Residual analysis was then employed to determine the suitability of the fit.

The model

If a gull foraging at a particular location after a tractor had passed by had a monotone decreasing intake rate of the form expressed in eq. (1), it would become progressively less worthwhile to forage at that spot. At some point it would seem, intuitively, to be more efficient to fly after the tractor and thereby regain an initially high intake rate. To this end, very frequent flights should be most effective. There must, however, also be some minimum time at or near the patch required to land, consume the prey, and become airborne again without wasting excessive time in these aspects of the foraging cycle. It follows that there should exist an optimal time in patch that maximizes the rate of energy intake. This relationship, as detailed in Appendix 1, is of the form:

$$G/t = \frac{a/b(1 - e^{-bt_p})}{t_f + t_p} \quad (3)$$

where t_f =time in flight, t_p =time in patch, and $t=t_f+t_p$. A graphical way of showing this result is illustrated in Fig. 7. A mathematical solution (detailed in Appendix 2) is obtained by first expressing t_f in terms of t_p .

$$t_f = 2/9.3 t_p + 4.54/9.3 \quad (4)$$

Combining (3) and (4) and factoring out $11.3/9.3$, the expression becomes:

$$G/t = \frac{a/b(1 - e^{-bt_p})}{11.3/9.3(t_p + 4.54/11.3)} \quad (5)$$

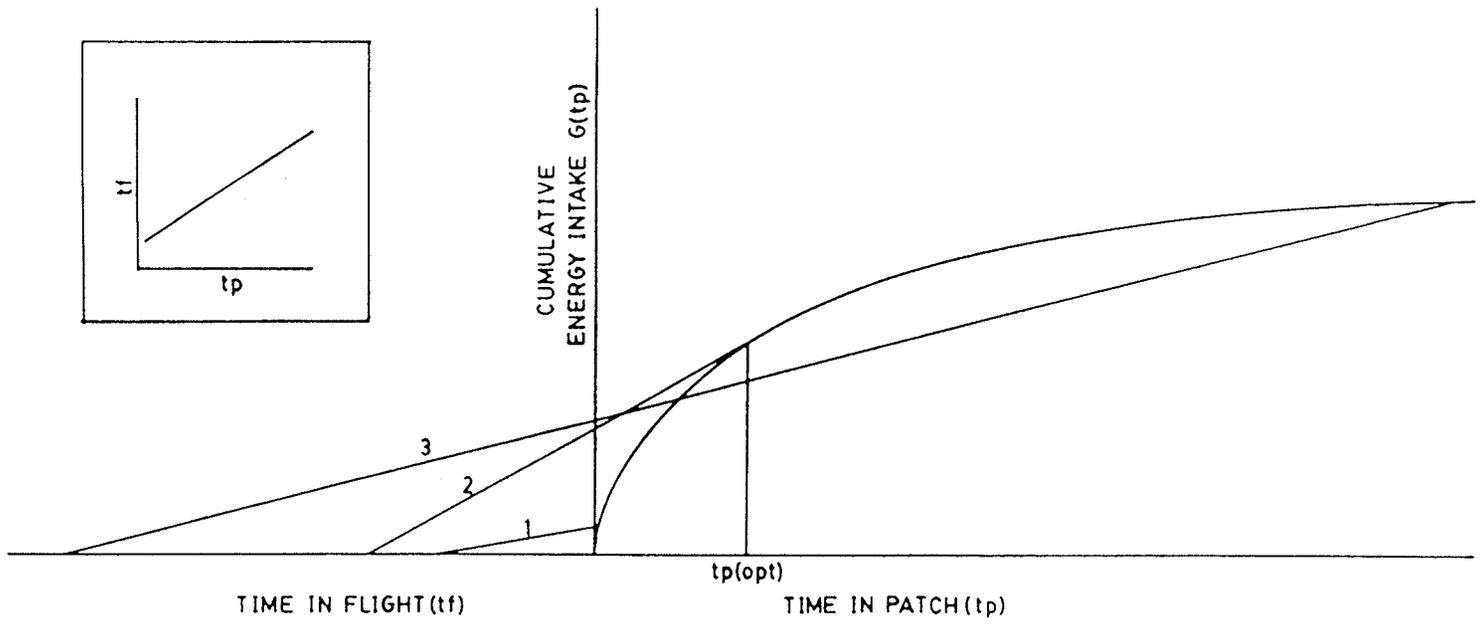
Taking the derivative, $\frac{dG}{dt}$, and setting it equal to zero gives the following optimality solution:

$$0 = bt_p e^{-bt_p} + 4.54/11.3 b e^{-bt_p} + e^{-bt_p} - 1 \quad (6)$$

One can then solve for t_p using standard numerical techniques.

To compare the observed optimal solution with alternative, especially random solutions (Aronson and Givnish 1983), I employed a simple null hypothesis of random arrivals to and departures from locations (patches) within the most recent cultivated furrow left when the tractor went around the field once. Patches selected were then irrespective of the exact location of the tractor at that time. This strategy of random selection of and departure from

Figure 7. A graphical solution of optimal time in patch ($t_p(\text{opt})$). The energy intake function, $G(t_p)$, is the same for each patch in the habitat. t_f is a function of t_p (insert, and eq. 4). The optimal solution ($t_p(\text{opt})$) is found by constructing the steepest possible line between $G(t_p)$ and its corresponding t_f (line 2 in this illustration).



patches is analytically equivalent to a bird landing behind the tractor and foraging in that patch for the duration of the complete tractor cycle. I therefore calculated the predicted gain per unit time by using equation (3) and substituting total circuit time for time in patch (t_p). Note also that the denominator, t , is no longer equivalent to $t_f + t_p$ but simply t_p (= total circuit time). In fact this approach will tend to err in favor of the null hypothesis since the costs of flying up, expressed in terms of time lost for foraging, are not included.

The energy measurement commonly employed in tests of OFT is the net rate of energy intake (Krebs and Davies 1983) whereby the energetic cost of foraging is subtracted from the gain before being expressed as energy per unit time foraging. Using metabolic estimates from the literature, of flight and walking costs in gulls (Berger et al. 1970, Brackenbury 1984, Gessaman 1973, Kendeigh 1970, Schmidt-Nielson 1972, Tucker 1970, 1972), I found that energetic costs would be negligible relative to the gains obtained by gulls in this study (a maximum of 12.5% of total energy gain for a gull feeding in a patch on location 10 for one second before flying on. Maximum costs were only 2.6 to 8.1% on other fields and would be less for gulls remaining >1 s in the patch). Energetic costs of foraging were therefore not incorporated in the analyses.

RESULTS

Fig. 8 shows the mean cumulative intake for successive 20 s periods in a given patch (t_p) for the four locations. Calculated calorific values used in these and all subsequent calculations were .3675 kcal/worm (for locations 29, 34, and 37) and .1371 kcal/kernel (for location 10). cursory examination shows that the functions are monotone decreasing and likely rising to an eventual asymptote. Table 15 contains the least squares parameter estimates and slope coefficients of Taylor's Power Law for each curve. Fig. 9 a,b show the results of the curve-fitting procedure using equation (1). Location 29 has the greatest rise to asymptote followed by locations 34 and 10. Location 37 has only a slight decline in intake rate over the period shown.

Fig. 10 illustrates the expected relationship between G/t , or food intake rate, and time spent in patch for the four locations, calculated from equation 5. The peak in each G/t curve defines the predicted optimum t_p for that location. For locations 29, 34, 10, and 37, these are 2.8, 4.3, 4.7, and 12.4 s, respectively. From Fig. 10 it is clear that location 29 had the highest optimal food intake rate and the sharpest decline in G/t values. In contrast, location 37 and 10 had the lowest optimal G/t values and show slight declines in G/t values with increasing time in patch. The fact that G/t dropped less quickly at 37 than at 10, while optimal G/t was appreciably higher at site 37, in-

Figure 8. Mean cumulative intake as a function of time in patch (tp) for locations 37, 29, 34, and 10 (curves fitted by eye).

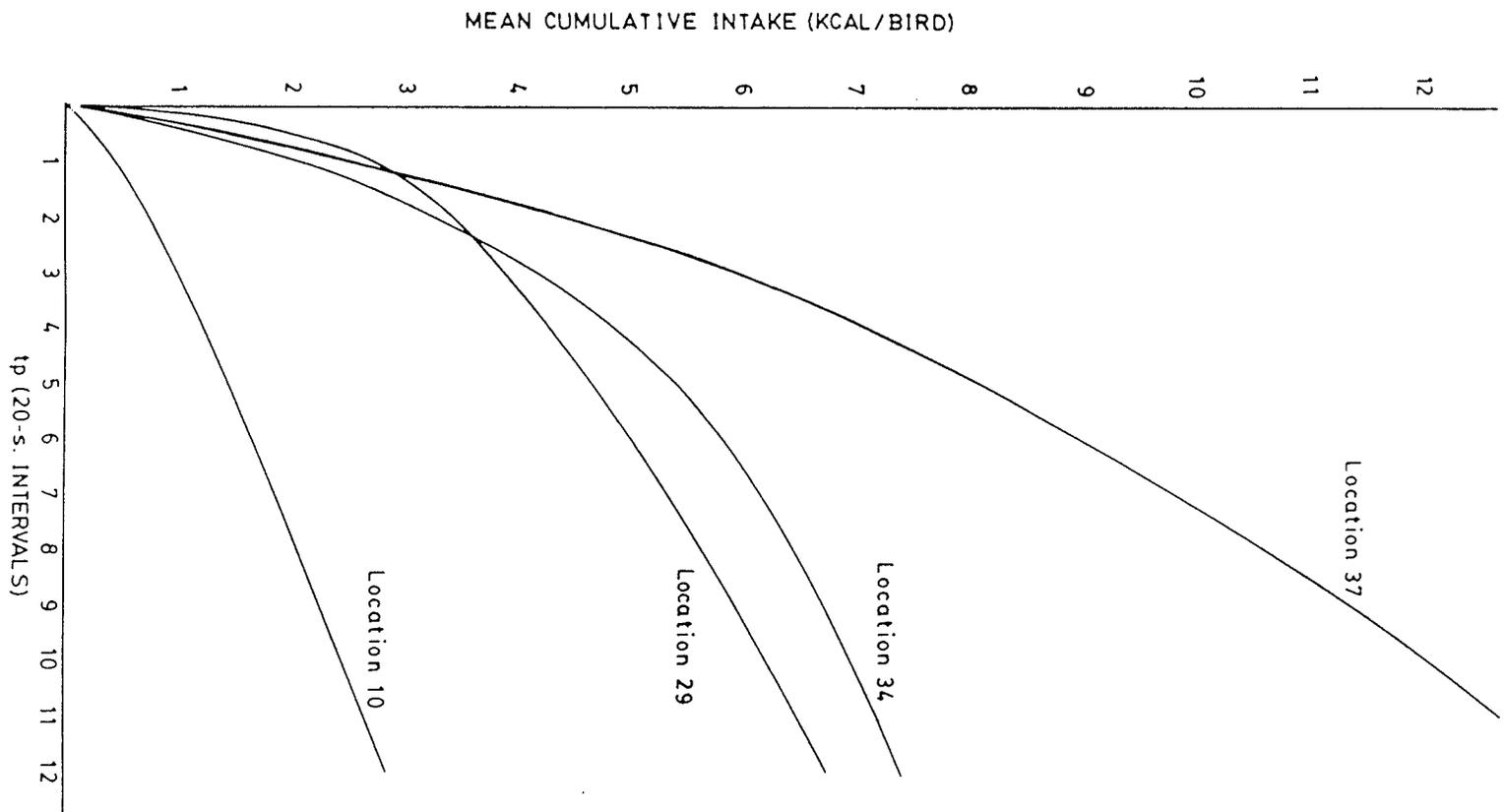


Table 15. Parameter estimates from Taylor's Power Law and non-linear fit.

Location	Parameter		
	<u>b</u>	a (\pm S.E.)	b (\pm S.E.)
37	1.508	.054 (\pm .002)	.005 (\pm .001)
10	1.358	.024 (\pm .001)	.034 (\pm .003)
34	1.186	.086 (\pm .004)	.041 (\pm .004)
29	1.378	.172 (\pm .007)	.091 (\pm .005)

Figure 9. Predicted (solid lines) and observed (points) cumulative gain per 2-second interval as a function of time in patch (t_p) for locations 37 and 10 (a) and 29 and 34 (b). Predicted curves derived from equation 1 (see text).

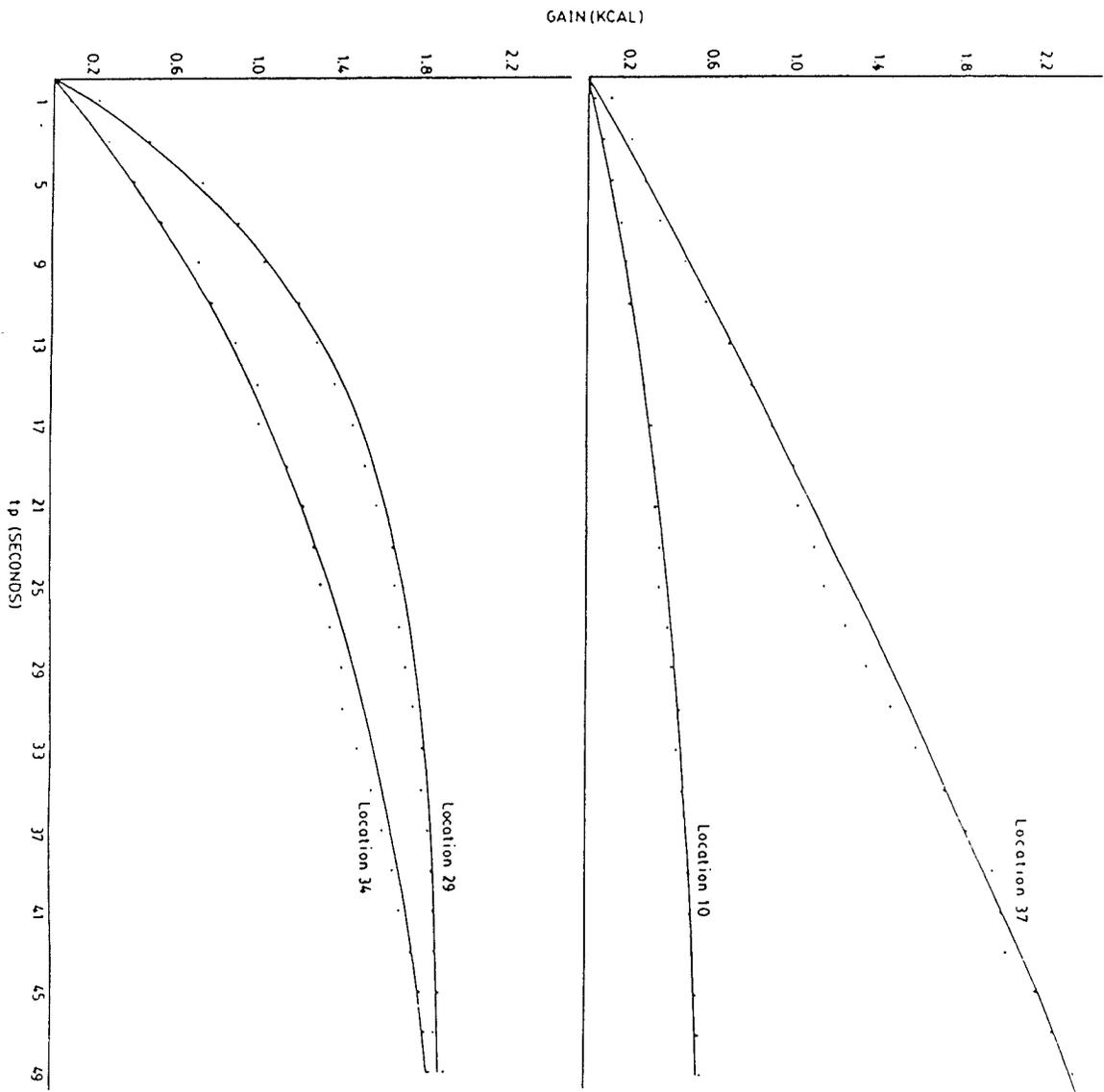
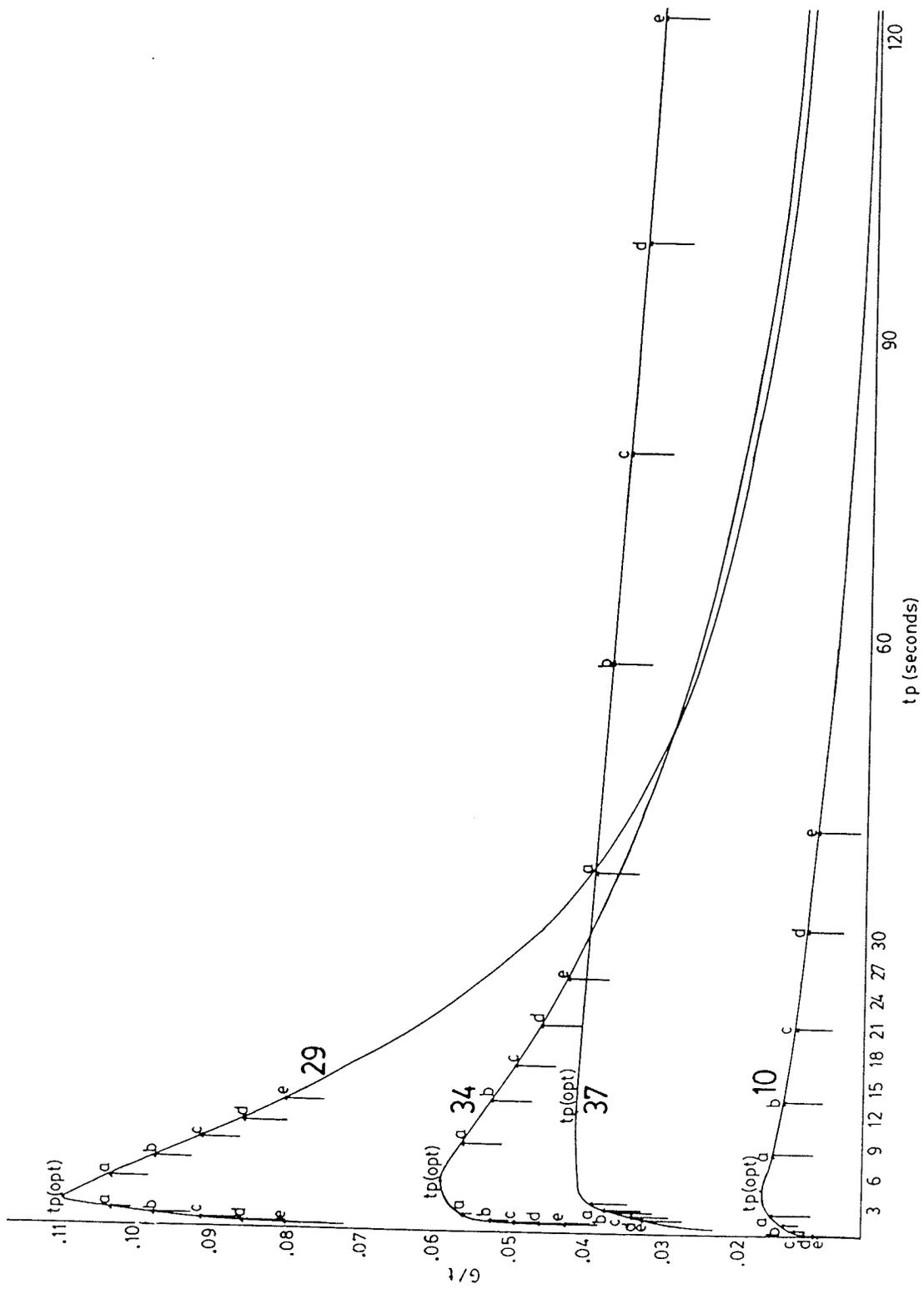


Figure 10. G/t values as a function of time in patch (t_p) for each of the four locations. Pairs of lowercase letters define the range of t_p that would enable a gull to obtain food at a rate equal to or greater than some percentage of optimum G/t. The percent of optimum G/t shown are: a=.95%, b=.90%, c=.85%, d=.80%, and e=.75%.



dicates that there was not always a simple direct relationship between peak G/t values and the rate G/t declined as t_p increased.

Frequencies of gull departures from patches along with the modal classes and means (\pm S.D.) in relation to time since the tractor passed (t_p) are shown in Fig. 11 for all four locations. Fig. 12 shows the relationships between the observed and predicted mean and modal patch residence times. Predicted optimal t_p was always low (2.8 to 12.4 s), and varied only slightly among patches. Actual t_p 's were always highly variable (Fig.11) and the mean and mode greater than predicted (Fig. 12). With one exception (mean of location 29), actual mean and modal t_p values were similar to predicted values in relative rank among locations (Fig. 12).

Fig. 13 is the proportion of birds departing the food patch that achieved a G/t value as great or greater than a given percentage of the predicted optima. To derive this figure, I first determined the range of t_p values that would permit a gull to achieve a G/t as high or higher than a given percent of the optimum G/t (see Fig. 10). I then calculated the cumulative percentages of actual departures that occurred in the respective t_p ranges. A steeper slope in Fig. 13 indicates more birds were closer to the predicted $t_p(\text{opt})$ value. Locations 37 and 34 exhibit a reasonable fit to the predicted departure times, with 80% of the birds departing so as to achieve 81.5 and 67.5% or better of the G/t

Figure 11. Gull departure frequency from patches in relation to time since the tractor passed by the patch (tp) for each of four locations. Horizontal lines indicate the mean time of departure (dots) \pm S.D. (calculated from actual times). Vertical arrows indicate the modal class.

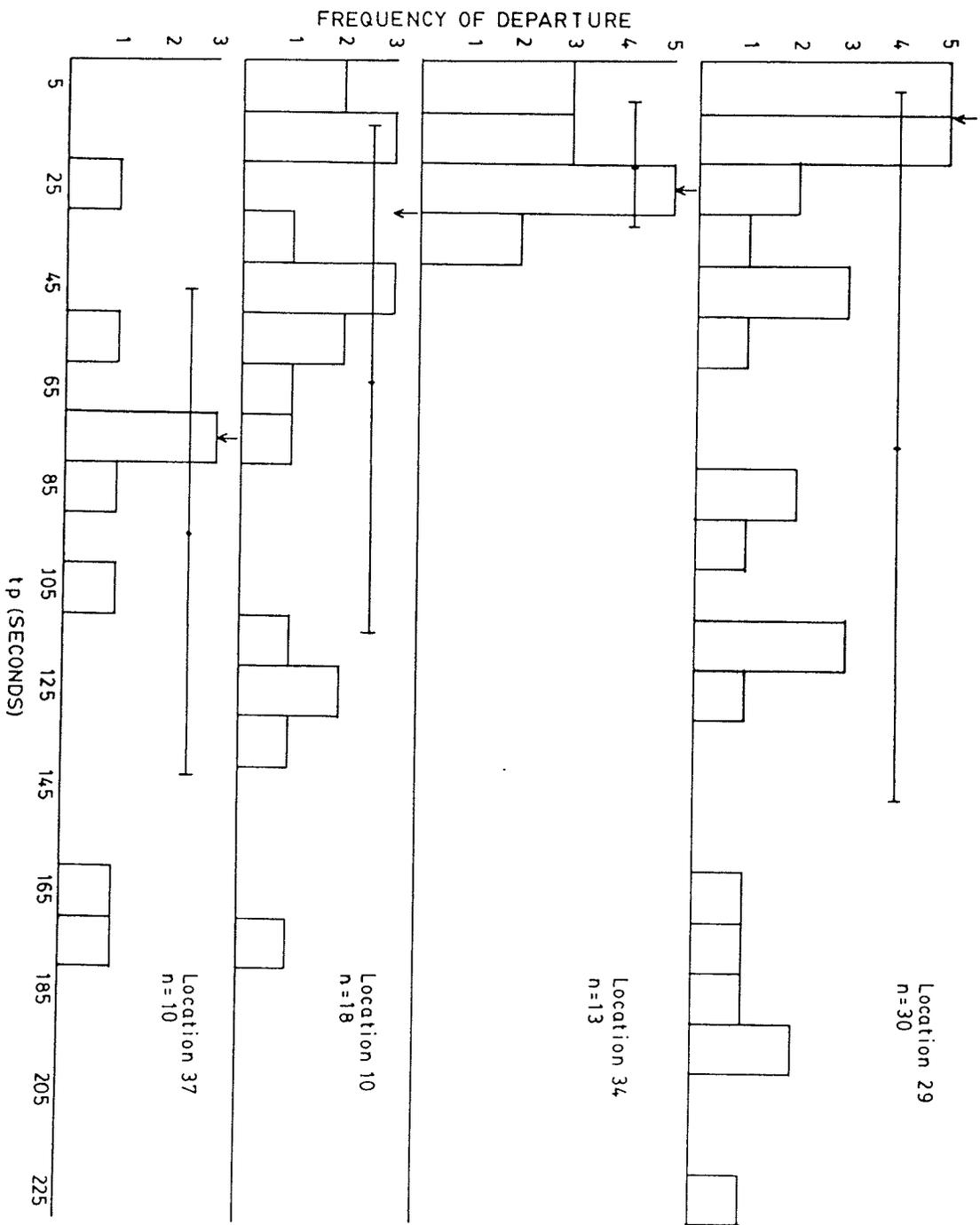


Figure 12. Comparison of predicted and observed patch residence times for the four locations. (\blacktriangle) represent means, (\blacksquare) are the modal classes, while (\bullet) are the predicted optimal tp. Patches are arranged by increasing magnitude of predicted optimum tp for the four locations.

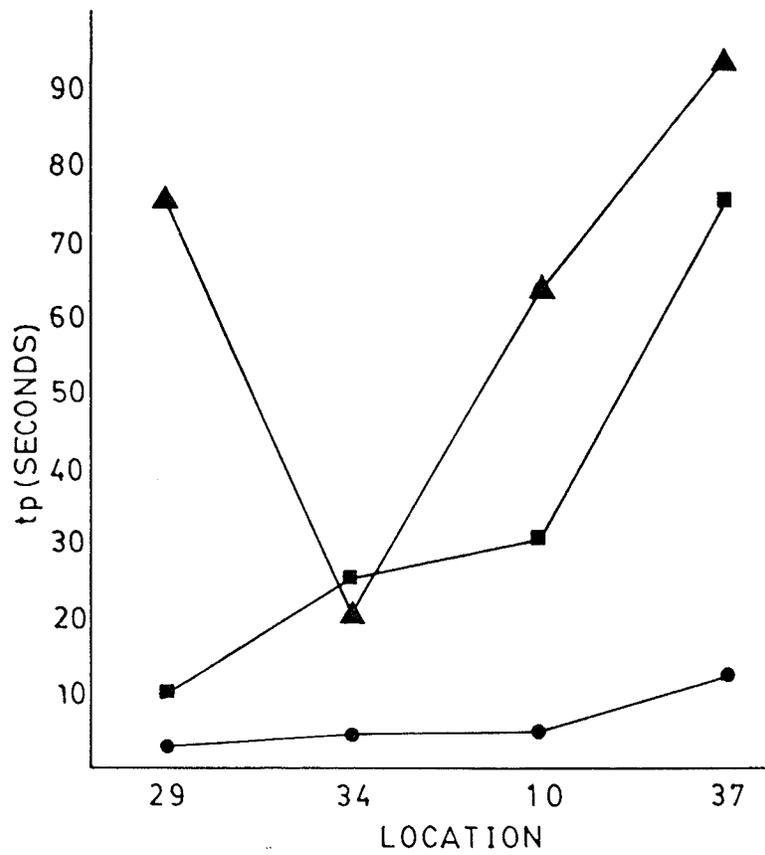
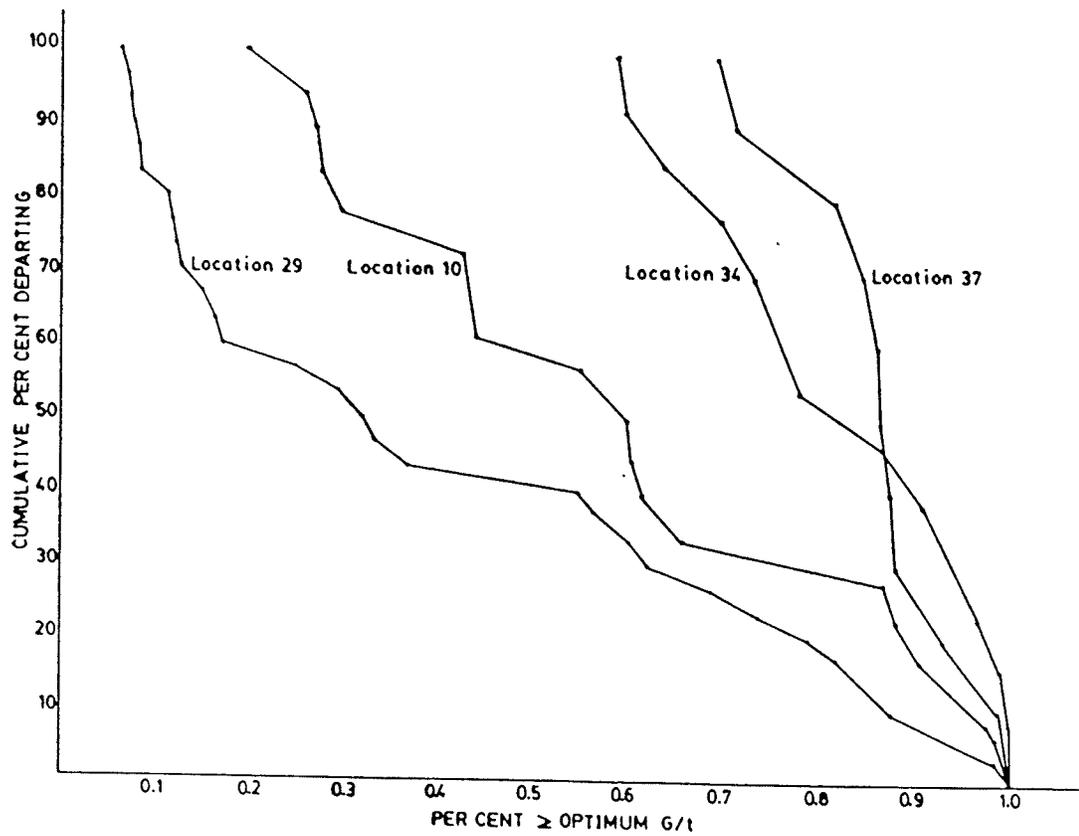


Figure 13. Cumulative percent of birds that achieved a given percentage (or better) of optimum G/t for each of the four locations (see text for details).



optimum respectively. Birds at site 10 and especially 29 clearly did much poorer than predicted by the optimality model.

Table 16 (first line of entry) shows the proportional difference of G/t values under an optimal strategy over that of the null hypothesis. Differences range from 3.2 to 31.7 fold in favor of the optimal strategy. Similarly, using calculated G/t values for the last bird to depart a patch shows differences ranging from 2.0 to 10.1 fold over the null hypothesis. I also compared expected G/t values for all departures on a given field against the null hypothesis using a sign test. In all cases, calculated G/t values from the null hypothesis were smaller than the actual G/t values ($\chi^2=10$ $p<0.005$ for location 37, $\chi^2=18$ $p<0.001$ for location 10, $\chi^2=13$ $p<0.001$ for location 34, $\chi^2=30$ $p<0.001$ for location 29, $df=1$ in all cases). Although Ring-billed Gulls did not forage optimally, they clearly foraged more efficiently than they would have if selecting their food patches at random.

Table 16. G/t ratios for optimal departure times and final departure times of the last bird to leave the patch, in relation to the null hypothesis of random arrival and departure times (see text).

Departure time	Location			
	37	10	34	29
tp(opt)	3.2 ^a	31.7	15.9	26.8
tp final ^b	2.5	2.0	10.1	5.3
Total circuit time (s) ^c	793	1114	561	546

^aIn each case, the statistic represents a ratio calculated from G/t for the type of gull indicated divided by G/t in a randomly departing bird.

^bCalculations based on the departure time of the last bird to leave the patch in pursuit of the tractor.

^cThe time required for the tractor to complete one revolution of the field.

DISCUSSION

According to the marginal value theorem (Charnov 1976) a bird should depart a depleting patch when the capture rate in the patch falls to that for the habitat at large. Many tests of this theorem to date have involved manipulating travel time between patches and then determining how closely patch residence times approach the predicted optimum. For example, Cowie (1977) simulated longer travel times by placing lids on food trays within artificial patches that were either "hard" or "easy" to remove. The Great Tits (Parus major) in his study maximized their net rate of energy intake by staying longer in the patches with increasing travel times (see Krebs et al 1983 for further references). Other studies (Cook and Cockrell 1978, Hodges and Wolf 1981, Lima 1983, Pyke 1978, Whitman 1977) have shown organisms to depart patches before they were totally depleted when net energy intake rates had fallen below the expected net rate for the habitat (Sih 1980).

In contrast to these types of studies where travel and patch residence times have been treated independently, optimally foraging gulls in the context studied here would have to take account of the fact that travel time was directly dependent on time in patch due to the continuous movement of the tractor. The optimal decision process therefore required joint assessment of declining intake rates and steadily increasing travel time between patches. This scenario

is analogous to a diving time problem in which an air-breathing organism that must return to the surface to replenish depleted oxygen stores spends greater and greater amounts of recovery time on the surface with increasing dive length (Houston and McNamara 1985). The results of this study suggest that Ring-billed Gulls are, to some extent, able to evaluate this cost-benefit function and depart food patches under a strategy that increases the rate of energetic intake relative to a random foraging pattern. Moreover, as the predicted time in patch increased so did the observed modal time in patch, though at a disproportionately greater rate. A similar trend was present for mean departure times at three of the four locations. A partial explanation for the increasingly high values of observed relative to predicted time in patch is provided by Fig. 10, which shows that larger $t_p(\text{opt})$ values were associated with flatter G/t curves. It seems likely that birds would have experienced greater difficulty detecting the decline in intake rate as the G/t curves flattened out, thus causing delays in departure of increasing magnitude for the sites with larger $t_p(\text{opt})$ values. Even for the steepest G/t curve (location 29), actual time in patch still exceeded the predicted value, indicating that the model employed is in some way incomplete, or that Ring-billed Gulls, although able to forage significantly more efficiently than random, are unable to actually maximize energy intake under the conditions of this study.

Recently, several authors have stressed the importance of testing alternative non-optimal models against their optimality counterparts (Aronson and Givnish 1983, Janetos and Cole 1981, but see also Houston and McNamara 1984). The relative efficiency of the foraging strategy actually used by gulls in this study is illustrated by the fact that even with the high degree of variability present in the data (Fig. 13), all birds still achieved at least double the intake rate over the null strategy.

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Appendix A

The cumulative gain to an organism, G , after feeding in a patch for time t_p , is given by equation (1) (see equation (1) in text):

$$G = a/b(1 - e^{-bt_p}) \quad (1)$$

To express this equation as a rate of gain per unit time foraging, G must be divided by, in this case, the length of time a bird forages in a patch, t_p , plus the flight time required to fly to the tractor (t_f) before resuming feeding. This represents one complete feeding cycle. Hence the rate of gain per feeding cycle is:

$$\frac{G}{t_f + t_p} = \frac{a/b(1 - e^{-bt_p})}{t_f + t_p} \quad (2)$$

By letting $t = t_f + t_p$ on the left hand side of the equation, we have:

$$G/t = \frac{a/b(1 - e^{-bt_p})}{t_f + t_p} \quad (3)$$

However, as detailed in Appendix B below, t_f can be expressed in terms of t_p as:

$$t_f = 2/9.3 t_p + 4.54/9.3 \quad (4)$$

By substitution:

$$G/t = \frac{a/b(1 - e^{-bt_p})}{113/93tp + 454/93} \quad (5)$$

Now, by factoring out 11.3/9.3, the expression becomes:

$$G/t = \frac{a/b(1 - e^{-bt_p})}{11.3/9.3(tp + 4.54/11.3)} \quad (6)$$

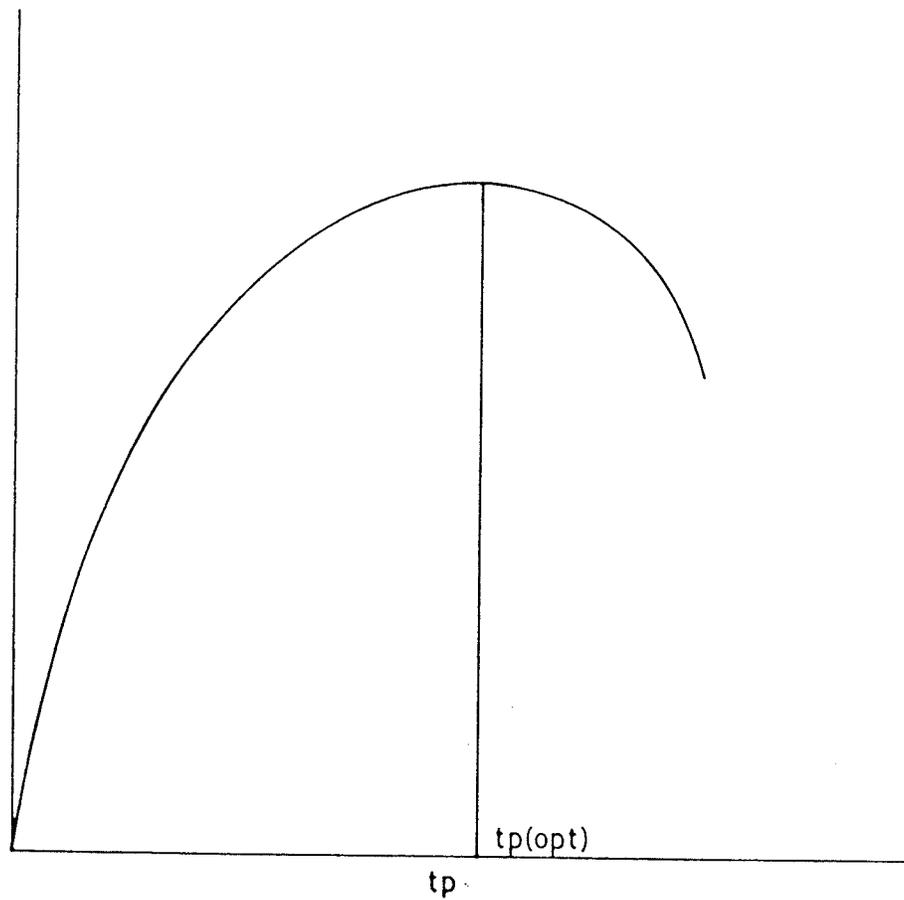
Varying the length of t_p yields different rates of gain (G/t values). However there should be a certain t_p that yields the highest possible rate. This can be illustrated by plotting G/t values for various t_p 's (from equation 4) against those t_p values. For example, a curve may result such as the one shown in Fig. 14. Hence, the t_p corresponding to the highest G/t value is the optimal time to stay in a patch ($t_p(\text{opt})$). In order to find this $t_p(\text{opt})$, one must calculate the first derivative of equation 4, and set it equal to 0.

$$dG/dt = bt_p e^{-bt_p} + 454/113 b e^{-bt_p} + e^{-bt_p} - 1 = 0$$

One can now solve this equation for t_p using standard numerical techniques.

Figure 14. Hypothetical G/t curve as a function of patch residence time (t_p) (see Appendix A).

$$\frac{G}{t} = \frac{a/b(1 - e^{-bt_p})}{\frac{11.3}{9.3} \left(t_p + \frac{4.54}{11.3} \right)}$$



Appendix B

Calculation of time in flight

Total flight time, t_{ftotal} , can be expressed as:

$$t_{ftotal} = t_f + t_t + t_l = t_f + c \quad (1)$$

where t_f =time in constant horizontal flight (chf), t_t =time required from takeoff to chf, t_l =time required to decelerate from chf and land, and $c=t_t + t_l$.

Let s_t and s_l = the distances required to reach and decelerate from chf for takeoff and landing respectively. Furthermore, let $s_t + s_l = k$. Notice that c (above) and k are assumed to be fixed regardless of t_f . Now, the tractor moves all the time the gull is in a patch, and covers a distance of $V_t t_p$, where V_t =velocity of the tractor, and t_p =time in patch. The tractor also moves while the gull is in flight ($t_f + c$). The sum of these distances is the total distance moved by the tractor in one cycle, which must equal the distance the gull flies. Hence:

$$V_t t_p + V_t(t_f + c) = V_g t_f + k \quad (2)$$

where V_g = average speed of a gull at chf, and all other variables are defined as above. Equation (2) can be reexpressed as:

$$t_f = \frac{V_t t_p + V_t c - k}{V_g - V_t} \quad (3)$$

From 8 mm films and direct measurement, the following estimates were obtained: $V_t=2.0$ m/s, $c=1.64 + 1.57 = 3.21$ s, $k=1.50 + 0.38 = 1.88$ m, and $V_g=11.3$ m/s. Substituting into (3) gives:

$$t_f = 2/9.3 t_p + 4.54/9.3 \quad (4)$$