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FORAGING STRATEGIES OF GLAUCOUS-WINGED GULLS IN A ROCKY INTERTIDAL COMMUNITY¹

DAVID B. IRONS² AND ROBERT G. ANTHONY

Oregon Cooperative Wildlife Research Unit, Department of Fisheries and
Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

AND

JAMES A. ESTES

United States Fish and Wildlife Service, Institute of Marine
Sciences, University of California, Santa Cruz
California 95064 USA

Abstract. Foraging strategies of Glaucous-winged Gulls (*Larus glaucescens*) were studied in rocky intertidal habitats of the western Aleutian Islands, Alaska. Daily foraging activity was most intense at maximum low tide, and was concentrated in the lowest intertidal zones available to the birds. Barnacles (*Balanus glandula*) and mussels (*Mytilus edulis*) comprised most of the gull's diet during neap low tides, but these species were almost entirely abandoned during spring low tides in favor of sea urchins (*Strongylocentrotus polyacanthus*), chitons (*Katharina tunicata*), and limpets (*Collisella pelta* and *Notoacmaea scutum*). Sea urchins, chitons, and limpets, which had positive prey selection indices, were most abundant in the lower intertidal zones; barnacles and mussels, which had negative prey selection indices, were most abundant in the upper zones. Gulls also generally selected the larger individuals from each prey species, although sea urchins larger than the commissural bill width were avoided and limpets were selected in proportion to availability. Variation in prey availability also occurred among study areas with varying densities of sea otters (*Enhydra lutris*). With increasing depression of invertebrate prey by sea otter predation, gulls fed on a more diverse prey resource, and they switched to neritic fishes under intense sea otter predation.

Preference experiments were conducted in the field, in which the common species and sizes of prey were made equally available to foraging gulls, thus eliminating search and capture times. In comparison with natural food choice, where sea urchins were most preferred, chitons became most preferred. We suggest that chitons are infrequent in natural diets because they adhere more strongly to the substratum than do sea urchins. Benefits of selective foraging were determined by comparing the net rate of energy gain of simulated random foragers with energy gained by selection of intertidal zones, prey species, and prey sizes. Observed selection patterns provided increased energy as gulls became more selective, and averaged 155% more than that obtained by the simulated random foragers. Results of the study support the two main predictions of optimal foraging theory in that (1) foraging patches (intertidal zones) and diets were selected such that net rates of energy gain were maximized, and (2) gulls became more selective foragers when energetically more profitable prey were more available.

Key words: Aleutian Islands; Glaucous-winged Gulls; intertidal communities; optimal foraging theory; prey preference; prey selection; sea otter; tidal variation.

INTRODUCTION

Since Emlen (1966) and MacArthur and Pianka (1966) first applied cost-benefit analyses to the study of foraging behavior, numerous papers have been published on the subject of optimal foraging theory (see Schoener 1971, Pyke et al. 1977, Kamil and Sargent 1981, Krebs et al. 1983, and Pyke 1984 for reviews). In most cases, predictions or hypotheses concerning foraging behavior have been generated by choosing a currency judged to be relevant, usually the net rate of energy intake, developing a cost-benefit function, and then solving for an optimum (Pyke et al. 1977). The overall objective of optimal foraging theory has been

to determine if animals forage by general decision rules (Krebs et al. 1983), which Pyke et al. (1977: 140) separated into the following four categories: "1) which patch type to visit; 2) how long to stay in each patch; 3) which food types to eat in each patch type; and 4) which foraging path to employ in each patch type."

Among these categories, the question of optimal diet has been the most rigorously and extensively studied, resulting in predictions (Krebs 1981: 29) "... that predators should (1) prefer more profitable prey, (2) be more selective when profitable prey are more common, and (3) ignore unprofitable prey that are outside the optimal set regardless of how common they are." The empirical evidence tends to support these predictions, although as Pyke et al. (1977) pointed out, most of the tests have been done in laboratories or in simple predator/prey systems where only the size or density of a single prey type varied. Because of this simplicity, op-

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² Present address: United States Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, Alaska 99503 USA.

TABLE 1. Average densities and sizes of intertidal invertebrates by zone at Massacre Bay and Chichagof Harbor, Attu Island, Alaska. n = number of $\frac{1}{4}$ m² quadrats sampled. Data are means and 95% confidence intervals.

Invertebrate types	Barnacle zone*		Mussel zone		Alaria zone		Laminaria zone	
	Number per $\frac{1}{4}$ m ²	Size (mm)	Number per $\frac{1}{4}$ m ²	Size (mm)	Number per $\frac{1}{4}$ m ²	Size (mm)	Number per $\frac{1}{4}$ m ²	Size (mm)
Chichagof Harbor								
	$n = 8$ quadrats		$n = 30$ quadrats		$n = 35$ quadrats		$n = 62$ quadrats	
Urchins	0.0	—	0.0	—	3.9 ± 1.1	19 ± 0.8	23.0 ± 3.0	22 ± 0.3
Chitons	0.0	—	0.1†	18†	10.3 ± 0.9	38 ± 0.8	5.6 ± 1.6	46 ± 1.1
Limpets	0.0	—	8.9 ± 0.9	15 ± 0.6	11.9 ± 1.7	17 ± 0.5	3.4 ± 0.9	18 ± 0.8
Mussels	$48.6 \pm 8.5\ddagger$	$10 \pm 1.4\ddagger$	852.3 ± 76.0	19 ± 0.2	1.7 ± 0.6	25 ± 1.7	0.6 ± 0.6	19 ± 1.6
<i>Balanus cariosus</i>	0.0	—	60.4 ± 3.3	$14 \pm 0.6\ddagger§$	132.9 ± 5.7	$14 \pm 0.6\ddagger§$	68.7 ± 5.3	$14 \pm 0.6\ddagger§$
<i>Balanus glandula</i>	2152.0 ± 328.8	$8 \pm 0.7\ddagger§$	168.0 ± 5.6	$8 \pm 0.7§$	0.0	—	0.0	—
Massacre Bay								
	$n = 25$ quadrats		$n = 25$ quadrats		$n = 25$ quadrats		$n = 25$ quadrats	
Urchins	0.0	—	0.0	—	0.8 ± 0.4	29 ± 3.4	35.2 ± 6.4	49 ± 0.7
Chitons	0.1†	55†	0.1†	55†	6.5 ± 0.6	$59 \pm 1.5§$	0.1†	$59 \pm 1.5§$
Limpets	9.3 ± 1.9	15 ± 0.4	9.3 ± 1.9	15 ± 0.4	10.9 ± 2.3	16 ± 0.4	1.9 ± 0.8	21 ± 1.0
Mussels	355.8 ± 71.2	11 ± 0.1	355.8 ± 71.2	11 ± 0.1	1.5 ± 0.8	17 ± 0.5	0.0	—
<i>Balanus cariosus</i>	0.0	—	0.0	—	41.5 ± 5.2	$14 \pm 0.6\ddagger§$	0.0	—
<i>Balanus glandula</i>	231.7 ± 18.2	$8 \pm 0.7§$	231.7 ± 18.2	$8 \pm 0.7§$	0.0	—	0.0	—

* Barnacle zone at Massacre Bay was depauperate and was not quantified.

† Confidence interval is undefined because sample size was one.

‡ From J. A. Estes (personal observation).

§ Sizes of invertebrates were not calculated separately for each zone.

Intertidal foraging theory has been criticized for not being applicable to more complex natural systems (Morse 1980, Schluter 1981, Zach and Smith 1981) in which such factors as nutrients (Belovsky 1978), predation risk (Sih 1980, Werner and Mittelbach 1981), accessibility of prey (Moermond and Denslow 1983), actual availability of prey (Menge 1972), and recognition time (Elner and Hughes 1978, Hughes 1979) have been shown to be important.

Based on these criticisms, Krebs et al. (1983) pointed out a need for more tests of the predictions of optimal foraging theory. Here we test two of these predictions for Glaucous-winged Gulls (*Larus glaucescens*) feeding in rocky intertidal communities. Gulls are excellent subjects for study as they are largely unaffected by the presence of human observers; their most common behaviors (e.g., searching, handling prey, resting, etc.) can be identified and quantified easily; and their prey usually can be identified when captured. Furthermore, gulls regurgitate many of the calcareous parts of their invertebrate prey, which permits determination of the sizes consumed. As a food base, the rocky intertidal community is also well suited for study because densities and size class distributions of prey populations are easily quantified. In addition, prey availability varies in several predictable ways. One of these is among

intertidal zones. Variation within zones is usually low while variation among zones is high (Table 1); therefore, foraging gulls have equal access to measurable food resources that vary markedly in density and species composition over short distances. Consequently, individual birds can move from patch to patch with little time or energy cost. Second, prey availability varies at weekly intervals according to the tides. The low spring tides expose the lowest intertidal zones that are inaccessible during the moderately low neap tides. Third, sea otter predation reduces the size and abundance of herbivorous invertebrates, principally sea urchins (Lowry and Pearse 1973, Estes and Palmisano 1974, Duggins 1980, Breen et al. 1982). The otters' influence extends into the lower intertidal zones (Estes et al. 1978: Fig. 4) and probably reduces populations of filter-feeding mussels and barnacles in the higher zones.

In this paper we describe foraging strategies of Glaucous-winged Gulls and test two hypotheses of optimal foraging theory. These hypotheses predict that gulls should (1) forage so as to maximize net energy gain and (2) become more selective foragers when energetically profitable prey become abundant. The tests are based on measurements of prey availability, prey quality, and observations of foraging gulls. These measurements and observations are of four main kinds.

First, we characterized differences in prey species composition, density, and size distribution among intertidal zones and among areas with different sea otter densities. Next, we described gull foraging behavior: the species and sizes of prey chosen; search and handling times for each of these; and the utilization of patches (intertidal zones) by gulls. From these two sets of data and measurements of energy values of prey, we then calculated net energy gain for the various prey and the relative benefits of selective foraging by patch type, prey species, and prey size. Last, we repeated some of these measurements and observations in a field experiment that eliminated variation in prey density and substrate adherence strength, thereby eliminating search time and making all prey equally available. To test the first prediction, we determined if the foraging patterns of gulls varied consistently so as to maximize net rate of energy gain. To test the second prediction, we compared foraging strategies of gulls between spring and neap low tides and among areas with different sea otter densities.

STUDY SITES

We conducted our research at Attu Island, Alaska (173° E, 53° N), with additional samples collected from Amchitka Island (179° E, 52°30' N) in the Rat Islands group. The Rat Islands have been densely populated with sea otters for the past several decades, following recovery from overexploitation during the 18th and 19th centuries (Kenyon 1969). The Near Island group, which includes Attu, was recolonized by sea otters around 1965 following extinction from overexploitation. Initially otters colonized the area near Chichagof Harbor on Attu Island. At the time of this study (summer 1980) ≈ 800 sea otters inhabited the northeastern coastline of Attu (J. A. Estes, *personal observation*), while the south coast of Attu remained unoccupied. Although growing rapidly, the population was undoubtedly far below equilibrium density (Estes et al. 1982). Sites with and without sea otters were studied intensively on Attu: Chichagof Harbor, near the center of the otters' distribution, and Massacre Bay, beyond the range of the sea otter. More limited observations were made at Kirilof Rocks on the northern coast of Amchitka Island where otters have existed in dense numbers for three or four decades (Kenyon 1969).

Distinct zones of invertebrates and algae characterize Attu's rocky intertidal community (Table 1). The zones at Chichagof Harbor are approximately equal in width and, from highest to lowest, are dominated by barnacles (*Balanus glandula*), mussels (*Mytilus edulis*), *Alaria crispa*, and *Laminaria* spp. *Balanus glandula* grows on many of the mussels, with the larger *B. cariosus* growing beneath and adjacent to the mussels. *Alaria crispa*, an upright brown alga, forms a virtually continuous cover in the next zone and is associated with barnacles (*B. cariosus*), chitons (*Katharina tunicata*), and limpets (*Notoacmaea scutum* and *Collisella*

pelta). The lowest intertidal zone is spatially dominated by the brown alga *Laminaria* spp. *Laminaria longipes* typifies the upper *Laminaria* zone, whereas other stipate species (*L. groenlandica*, *L. yezonesis*, and *L. dentigera*) form the lower *Laminaria* zone. *Balanus cariosus*, chitons, green sea urchins (*Strongylocentrotus polyacanthus*) and other less common species of invertebrates occur in the upper *Laminaria* zone (also see O'Clair 1977). The lower *Laminaria* zone supports a high diversity of invertebrate species, by far the most common of which is the green sea urchin.

The barnacle, mussel, and *Alaria* zones at Massacre Bay are structurally similar to those at Chichagof Harbor (Table 1). However, the *Laminaria* zone at Massacre Bay is more intensely grazed by sea urchins so that there are few organisms besides encrusting coralline algae (*Lithothamnion* spp. and *Clathromorphum* spp.) and urchins below the *Alaria* zone.

Amchitka's rocky intertidal community differs greatly from Attu and the other Near Islands (Palmisano and Estes 1977). Densities of the most common macroinvertebrates at the Rat Islands are much lower than they are at the Near Islands. For example, Estes and Palmisano (1974) provide the following comparison for Amchitka of the Rat Islands vs. Shemya of the Near Islands, respectively: 5 vs. 1215 *B. glandula*/m², 4 vs. 722 mussels/m², <1 vs. 38 chitons/m², and 8 vs. 78 urchins/m². Algal cover, however, is much higher at Amchitka Island. Estes et al. (1978) contended that sea otters largely accounted for these differences between the Rat and Near Islands.

METHODS

Foraging behavior and diets

Foraging behavior of gulls was observed during June through August, 1980. Field observations were made during spring (maximum tidal flux during new or full moon) and neap (minimum tidal flux during first or third quarters of the moon) low tides at Chichagof Harbor and during spring low tides at Massacre Bay. Foraging gulls were observed through spotting telescopes and binoculars. Scan samples (Altmann 1974) were taken at 30-min intervals to determine distribution and activity of gulls across the different intertidal zones. Individual foraging gulls were selected for focal animal sampling (Altmann 1974), for which we recorded the intertidal zone, search and handling times for each prey item, prey species and size, and resting time (i.e., any period interrupting active foraging behavior) until the bird left the intertidal zone or observation time exceeded 15 minutes. Because the gulls employed three conspicuously different techniques of handling urchins, we recorded how each urchin was consumed. The techniques included (1) swallowing the prey intact; (2) fracturing the urchin's test with the bill by repeated jabbing and pecking out the viscera (henceforth termed "pecking-out"); or (3) air-dropping the urchin to fracture its test (henceforth termed "air-drop-

ping"). Observations were made from approximately an hour before to an hour after low tide, when the birds usually quit foraging.

Gulls regurgitate, from their crops, pellets composed of the large undigested parts of their prey. These pellets were collected from one site on Amchitka once in September 1979 and three times during the summer of 1980. Pellets were also collected weekly after initial clearings from six locations on Attu, after spring and neap tide cycles. The locations included (1) a colony, (2) a site adjacent to the rocky intertidal zone, and (3) a loafing area near fresh water, at both Chichagof Harbor and Massacre Bay. All areas were within 5 km of the sites at which foraging behavior was observed. We recorded the occurrence of all recognizable prey in each pellet and collected measurable parts to determine prey sizes.

Dietary diversity of gulls foraging in different areas or at different times was calculated by Simpson's (1949) diversity index as modified by Greenberg (1956). Dietary equitability was measured using Heip's (1974) index with modifications (see Irons 1982). We used these indices to test the prediction that dietary diversity increased as net rate of energy gain (E_n) decreased in different habitats.

Intertidal invertebrates and algae were sampled at Chichagof Harbor and Massacre Bay on Attu Island. At each site, 25–35 0.25-m² quadrats were sampled in each of the intertidal zones. From each quadrat we recorded the density and size of all macroinvertebrates and the percent cover of macroalgae.

Length and diameter of intact chitons and urchins, respectively, were regressed on the sizes of their calcareous parts. The regression equations then were used to estimate sizes of prey items in pellets. Demipyramid width was used to estimate urchin test diameter by the linear model $y = -6.19 + 19.81x$ ($r^2 = .97$), where y = test diameter and x = width of demipyramid. For chitons, log body length (y) was regressed against width of the anterior or posterior valves (x) as defined by the equation $y = -27.02 + 35.79 \ln x$ ($r^2 = .79$). Using posterior valves, the equation was $y = -7.55 + 34.94 \ln x$ ($r^2 = .84$). Maximum lengths of mussels, whelks (*Nucella* spp.), and limpets collected from pellets were measured directly.

The strength of adherence of chitons and urchins to the substratum was estimated by measuring the lateral force required to dislodge these organisms. This was accomplished by placing a metal rod vertically beside the organism and, while holding the top of the rod stationary, pulling toward the organism at the center of the rod, via a spring scale. In this manner the scale recorded twice of the force applied to the organism until it was dislodged from the substratum. We recorded the maximum reading on the scale and halved it. Various sized urchins and chitons were used to determine their ability to adhere to the substratum.

The energy values of different prey items were es-

timated from size–dry mass relationships, together with the energy values of edible body parts (see Irons 1982: Appendix II). Prey items were collected from the intertidal community at Massacre Bay, frozen, and transported to Oregon State University for analysis. Subsequently, the soft parts were dried to constant mass at 45°C, then ground into a powder. A Parr (Model 1101) oxygen bomb calorimeter was used to determine energy of soft (edible) body parts. Calorimetry procedures from Parr Instrument (1960) were followed. Energy values were converted from kilocalories per gram to kilojoules per gram (1 kcal = 4.184 kJ).

"Prey selection" refers herein to the process of prey choice by gulls in a natural setting. Selection of prey species and prey sizes by gulls was determined by using the odds ratio (Fleiss 1973) which relates the proportion of a prey species in the diet to that in the intertidal zones. Odds ratios were computed by using prey base data from the intertidal community (Fig. 4) and pellet contents or the dietary composition of gulls observed foraging in the intertidal during spring low tides. Gabriel's (1978) technique was used to determine if the odds ratios were significantly different ($P < .05$) from zero. Student's t test was used to determine both the significant differences in sizes of chitons, mussels, and urchins eaten by gulls at Chichagof Harbor as compared to Massacre Bay, and the sizes of chitons, mussels, and urchins occurring in the intertidal zones at Chichagof Harbor vs. Massacre Bay.

Prey preference experiments

"Prey preference" refers herein to prey choice when all prey are made equally available experimentally. We determined prey preference (as opposed to prey selection) by dislodging the most commonly consumed prey items from their substrata and locating them so that they were equally available to the gulls. This procedure was based on our perceptions that tenacious adherence to the substratum by many intertidal species deterred predation, and that variation in adherence strength among species and sizes of individuals had an important influence on prey selection by gulls. We used the three species of prey that occurred most frequently in the gulls' diets and selected sizes from the range of those available to gulls in the intertidal community. Thus the following seven prey types, freshly collected, were used in each experiment: a small, medium, and large urchin (mean test diameters ≈ 15 , 35, and 75 mm, respectively); a small and large chiton (mean lengths ≈ 25 and 55 mm, respectively); and a small and large mussel (mean lengths ≈ 25 and 55 mm, respectively). Prey items were arranged in a triangular pattern, ≈ 30 cm across. Birds foraging on the experimental array were observed through spotting telescopes from distances of between 10 and 30 m. Handling time for each prey item, and the sequence in which prey were handled or consumed, were noted. Success rates were de-

defined as the percentages of prey handled that were consumed. Correlation coefficients were calculated for prey size vs. success rates and average handling times.

Prey preference was determined from the proportion of experimental trials in which gulls handled a particular prey item first. If a prey item was handled more than once in a single experiment, only the first handling was counted. Preference was based on handling, rather than consumption, because we assumed that if a prey item was handled the gull intended to consume it. This assumption is valid because the results of experiments using actual consumption of prey were nearly identical to results based on handling of prey (D. B. Irons, *personal observation*). However, in the natural setting gulls often handled prey without consuming them because they could not remove them from the substratum. In our calculations of net rate of energy gain for the preference experiments, search time was considered to be zero. By using these methods, we removed factors (i.e., search time and adherence strength) that had differential effects on the availability of prey in the field, thereby permitting us to determine prey preference.

Student's *t* test was used to determine significant differences ($P < .05$) in handling times between different sizes of prey and between the same prey at Chichagof Harbor as compared to Massacre Bay.

Optimal foraging theory

Periods of active foraging were considered as search times and the intervals from initial physical contact with the prey until it was swallowed or abandoned as handling times. Net rate of energy gain (E_n) and giving up time (GUT; Charnov 1976) were determined for foraging gulls. E_n was defined as the average energy value (kilojoules) of a prey item divided by the average combined search time and handling time for that prey item. GUT was defined as the interval of continuous searching between the last prey capture and cessation of foraging in the study area.

The effects of selective foraging on E_n were determined by comparing E_n of randomly foraging gulls to E_n for their actual dietary composition. Random foraging was simulated for three cases. In the first case, gulls foraged randomly among all intertidal zones, all species, and all sizes of prey. In the second case, they selected specific zones but foraged randomly with respect to species and sizes of prey in each zone. In the third case, they selected zones and species but foraged randomly with respect to prey sizes. By comparing E_n for actual diets to those of the above situations, we estimated the energy benefits of foraging selectively by zones, by species within zones, and by sizes within species. We hypothesized that selective foraging at each of these three levels would be of some advantage to a gull. E_n for completely random (nonselective) foragers was calculated simply by assuming that gulls exploited zones, prey species, and prey sizes in proportion to their availability at spring low tide. The E_n acquired

through simulated zone selection (case 2) was calculated by weighting the E_n for each zone by the proportion of foraging gulls actually observed in that zone (i.e., barnacle zone, 2%; mussel zone, 7%; *Alaria* zone, 46%; and *Laminaria* zone, 45%). Similarly, the net rate of energy gain added to this by selecting prey species was calculated by using mean sizes (masses) of each prey species and weighting their E_n by the proportion of each species in the gulls' actual diets (i.e., urchins, 66%; limpets, 29%; and chitons, 5%). Finally, the E_n that gulls obtained by selecting zones, species, and sizes was determined by further weighting the E_n by the sizes of prey species that occurred in the diet.

To determine E_n from urchins consumed in the field by different foraging modes (i.e., swallowing-intact, pecking-out, or air-dropping), it was necessary to estimate the average size consumed by each of these modes. From our observations of gulls foraging, and measurements of the widths of their bills at the commissural point, we estimated that urchins up to ≈ 60 mm in diameter could be swallowed intact. Therefore, we used the mean size of urchins that were 60 mm or less in diameter, recovered from pellets, to calculate E_n from urchins swallowed intact. Similarly, we used the mean size of urchins larger than 60 mm to calculate E_n from those that were pecked-out and air-dropped.

Calculations of net rate of energy gain were based on (1) the average masses of prey species in the gulls' diets, (2) the average masses of prey that occurred within each intertidal zone, and (3) the masses of prey items used in prey preference experiments. Mean search times and handling times for the various prey species and sizes were used in these analyses.

GUTs, handling times, and search times at Chichagof Harbor and Massacre Bay were normalized by natural log transformations and tested for differences with Student's *t* test. Coefficients of determination were used to identify significant relationships between prey preferences and net rate of energy gain, size of prey and handling time, and the size of prey and success rates. Differences were considered significant at the .05 level.

RESULTS AND DISCUSSION

Time budgets and foraging behavior

Our observations of diet and distribution indicated that Glaucous-winged Gulls foraged almost entirely in or near the ocean during summer months. They selected invertebrates from the intertidal zones and fish from the neritic zone. Their foraging patterns changed over the summer and their diets shifted accordingly. When feeding nestlings during late June and early July, gulls infrequently foraged in the intertidal zones. During that time, prey regurgitated by nestlings ($n = 56$) was 96% fish and 4% zooplankton. In mid-July, after young had begun to fledge, gulls foraged more frequently in the intertidal zones.

Foraging behavior and time budgets of gulls were

TABLE 2. Percent of Glaucous-winged Gulls in each intertidal zone that were foraging, in relation to study site and tidal cycle on Attu Island, Alaska. Gulls that were not foraging were resting or preening.

Study site (tide cycle)	No. gulls observed	<i>Lami- naria</i> zone	<i>Alaria</i> zone	Mussel zone	Bar- nacle zone
Percent of gulls foraging					
Massacre Bay (spring tides)	4378	85	38	1*	1*
Chichagof Harbor (spring tides)	2916	96	63	29	1
Chichagof Harbor (neap tides)	1320	—†	92	74	1

* Mussel and barnacle zones at Massacre Bay were combined for counts of gulls.

† No gulls were observed in the *Laminaria* zone during neap tides.

strongly influenced by the tides. During spring tides, most gulls observed in the *Laminaria* zone and many in the *Alaria* zone were foraging (Table 2). In contrast, most of the gulls observed in the mussel and barnacle zones during spring tides were resting. A higher proportion of gulls in the *Alaria* and mussel zones were foraging during neap tides than during spring tides. On a daily basis, the highest proportions of gulls observed feeding during both spring and neap tides were in the lowest exposed intertidal zones (Fig. 1). Of all gulls observed foraging during spring low tides, most were in the *Laminaria* and *Alaria* zones (Fig. 2). During neap low tides, when the *Laminaria* zone was not exposed, most foraging gulls were in the *Alaria* and mussel zones. Gulls rarely foraged in the barnacle zone (Table 2, Fig. 2).

The gulls usually concentrated their foraging activi-

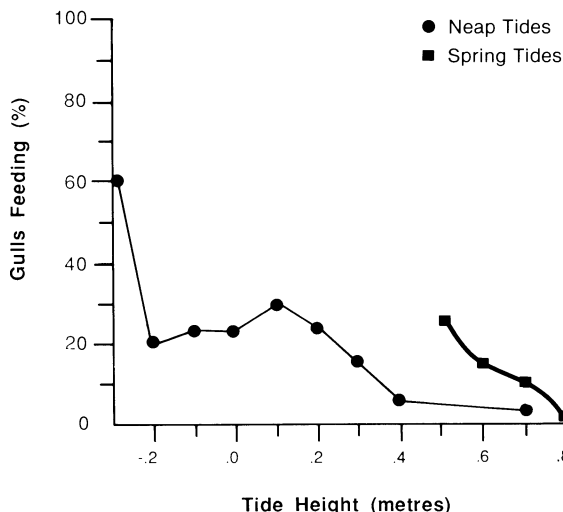


FIG. 1. Percentage of gulls feeding in relation to tidal height for spring ($n = 788$) and neap ($n = 161$) tides (data from observations at Chichagof Harbor, Attu Island, Alaska).

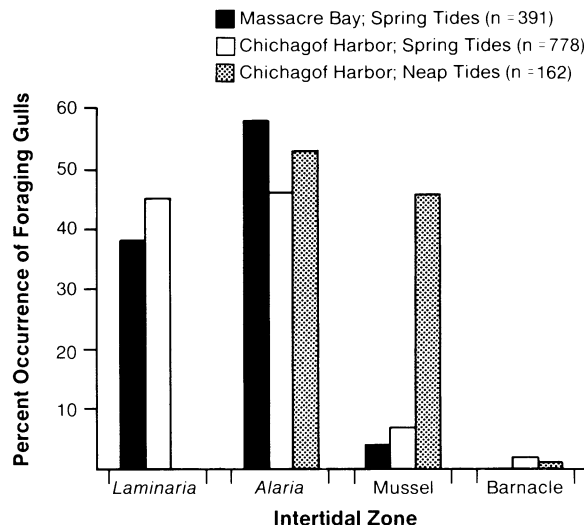


FIG. 2. Frequency of use of each intertidal zone by foraging gulls at Massacre Bay during neap tides and Chichagof Harbor during spring and neap tides, Attu Island, Alaska. Sample size is the number of gulls observed foraging.

ities around maximum low tide. However, even during low tides, only a small proportion of all gulls present in the intertidal zones was foraging (Fig. 1). Overall, a greater proportion of the birds fed during spring low tides (27%) than during neap low tides (12%). There are four possible explanations for this: (1) the gulls obtained food more quickly during neap tides than they did during spring tides; (2) assimilation time was longer for prey consumed during neap tides, thereby requiring the birds to wait longer between foraging bouts; (3) more foraging was done at sea during neap tides; (4) the prey available during neap tides were of lower energy value than those available during spring tides.

Explanation 1 is supported by the fact that combined search and handling times are greater for the prey taken from the lower intertidal zones during spring tides (e.g., urchins = 44 s; chitons = 41 s) than for those from the higher zones during neap tides (e.g., mussels = 22 s; barnacles = 16 s). Explanation 2 is supported by morphological differences between the prey types taken in high vs. low zones. Mussels and barnacles have heavy calcareous valves or plates that must be crushed in the gizzard; urchins and chitons have lighter and more easily crushed exoskeletons. Explanation 3 can be rejected because the occurrence of fish remains in pellets was similar between spring (6%, $n = 512$) and neap (5%, $n = 195$) tidal cycles. Explanation 4 cannot be rejected because the predicted net rate of energy gain (E_n) for randomly foraging gulls was lower in the upper zones (barnacle zone = 30 kJ/h; mussel zone = 160 kJ/h) than it was in the lower zones (*Alaria* zone = 464 kJ/h; *Laminaria* zone = 390 kJ/h). Consequently, gulls probably spent less time foraging during neap tides because of comparatively shorter search times,

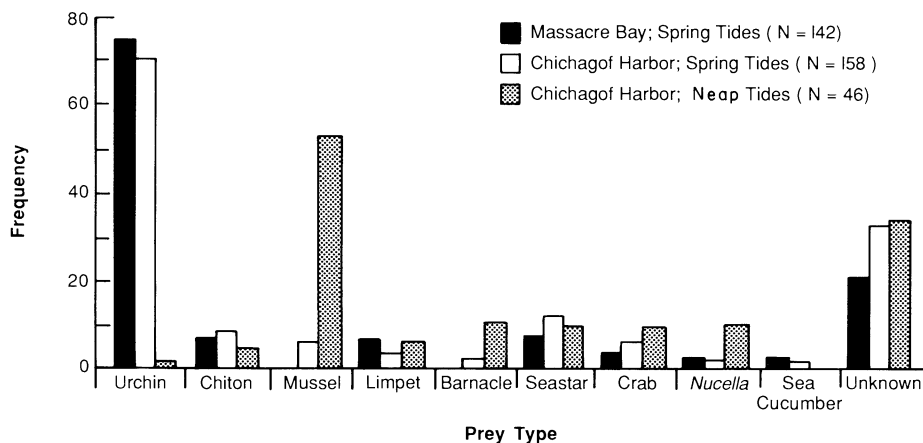


FIG. 3. Frequency of prey occurrence (%) in the diets of Glaucous-winged Gulls at Massacre Bay during spring tides and Chichagof Harbor during spring and neap tides, on Attu Island, Alaska. n = number of foraging bouts observed.

longer assimilation times, and lower energy value for mussels and barnacles taken during these times.

Diets

Gull diets, as determined by direct observation, also varied substantially between spring and neap tidal cycles in a manner consistent with the accessibility of intertidal zones (see preceding section). At Chichagof Harbor, for example, sea urchins constituted 70% of the prey selected by gulls during spring tides, but only 2% of the prey selected during neap tides (Fig. 3). Similarly, mussels and barnacles comprised 10% of the prey selected by gulls during spring tides and 65% of the prey selected by gulls during neap tides. Pellet composition following spring and neap tidal cycles showed this same pattern throughout the summer (Irons 1982: 30).

As first suggested by Trapp (1979), the presence and density of sea otters had a profound effect on gull diets. Urchins were the most common prey among Glaucous-winged Gulls at Attu (Table 3) where otters were absent (Massacre Bay), or present at low densities (Chichagof

Harbor). Chitons, mussels, limpets, crabs, and barnacles were also important prey items there. Diets at Attu differed remarkably from those at Amchitka in that urchins were over 6 times as common at Attu and fish were 12 times as common at Amchitka (Table 3). Except for sea urchins, invertebrates were rare in the pellets collected from Amchitka. Sea otters effectively limit the size and density of sea urchins in the lower intertidal and shallow subtidal zones at Amchitka (Estes and Palmisano 1974, Estes et al. 1978). In contrast, urchin populations are strikingly more abundant at Attu. Within its range on Attu, the otter population has reduced the size but not the density of urchins (Table 1). Mussels (34%) and barnacles (16%) were important secondary prey of gulls at Chichagof Harbor, whereas crabs (16%) and chitons (15%) were relatively more important at Massacre Bay. Crab densities were lower at Chichagof Harbor than at Massacre Bay (Irons 1982: Appendix I). Sea otter predation may also be responsible for this difference because sea otters prey heavily on crabs in areas where they are available (Estes et al. 1981).

TABLE 3. Frequency of occurrence (%) of prey in regurgitated pellets of Glaucous-winged Gulls from two sites on Attu Island and from Amchitka Island, Alaska. n = numbers of pellets examined.

Prey item	Attu		
	Massacre ($n = 1244$)	Chichagof ($n = 1581$)	Amchitka ($n = 213$)
	Percent of prey items		
Urchins (<i>Strongylocentrotus polyacanthus</i>)	69.7	71.9	10.8
Fish (<i>Ammodytes hexapterus</i> , <i>Clupea</i> , <i>harengus</i> , and unidentified species)	7.5	7.3	90.6
Chitons (<i>Mopalia</i> spp.)	3.2	1.1	0.0
Chitons (<i>Katharina tunicata</i>)	15.0	10.6	0.5
Mussels (<i>Mytilus edulis</i>)	5.7	33.5	2.8
Limpets (<i>Collisella pelta</i> and <i>Notoacmaea scutum</i>)	5.1	10.2	2.3
<i>Nucella</i> spp.	1.8	7.5	3.8
Crabs (<i>Telmessus cheiragonus</i> , <i>Pugettia</i> spp., and unidentified species)	15.6	5.6	2.3
Barnacles (<i>Balanus glandula</i> and <i>B. cariosus</i>)	8.8	16.0	0.0

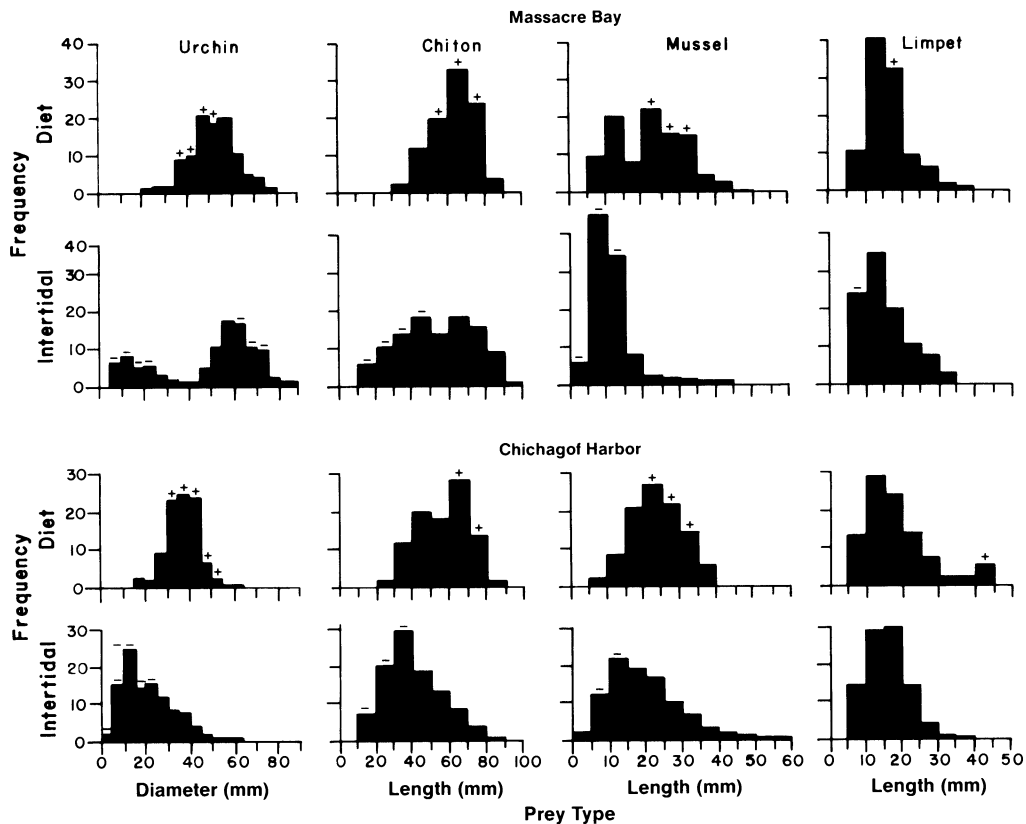


FIG. 4. Size frequency distributions of sea urchins, chitons, mussels, and limpets in intertidal areas and in gull diets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska. Sizes of urchins, chitons, and mussels in gull diets are estimates from remains in regurgitated pellets; the sizes of limpets in gull diets are based on pellets and stomach contents. +’s and -’s above histogram bars indicate significant selection and avoidance, respectively, in relation to availability (odds ratio, Gabriel 1978).

Prey selection

Glaucous-winged Gulls showed strong selection for prey species as well as intertidal zones. The odds ratio indicated that, at the respective sites of Massacre Bay and Chichagof Harbor, urchins (+3.8, +4.2), limpets (+2.2, +3.5) and chitons (+1.4, +1.8) were significantly ($P < .05$, Gabriel 1978) selected for, whereas barnacles (-15.5, -5.5) and mussels (-16.3, -1.0) were significantly ($P < .05$) selected against. The most highly selected prey species occurred in highest densities in the *Alaria* and *Laminaria* zones; those selected against occurred in highest densities in the mussel and barnacle zones. Thus gulls selected those zones in which to forage where their most favored prey occurred in greatest abundance.

In addition, gulls selected prey according to size. The size range of urchins consumed was ≈ 30 –55 mm test diameter at both Chichagof Harbor and Massacre Bay. In both cases, the selected size classes occurred in the diet in significantly ($P < .05$) different frequencies from those that were available in the intertidal community (Fig. 4). At Chichagof Harbor, selection was for the largest available urchins. At Massacre Bay, intermediate-sized urchins were selected because the larger size

classes had not yet been depredated by sea otters and were most abundant. Larger sized urchins were not selected because they could not be swallowed intact.

Gulls selected the largest available chitons at both Massacre Bay and Chichagof Harbor, and small chitons ($< \approx 20$ mm long) were not consumed at either site (Fig. 4). The average size of available chitons and the size consumed by gulls were significantly ($P < .05$) smaller at Chichagof Harbor than they were at Massacre Bay. Sea otters at Attu fed on chitons (Estes et al. 1981) and may have reduced the number of large individuals at Chichagof Harbor.

Similarly, gulls preyed on significantly ($P < .05$) larger mussels (i.e., 20–35 mm) at both sites, but the few largest mussels were not consumed (Fig. 4). Although the available mussels at Chichagof Harbor were larger ($P < .05$) than those at Massacre Bay, similar sizes of mussels were selected by gulls at both areas.

Limpets were consumed roughly in proportion to their frequency of occurrence in the intertidal community (Fig. 4) except for the avoidance of new recruits (< 5 mm), which occurred in very high densities. Apparently, individual gulls occasionally consumed large numbers of limpets from the blades of algae. For ex-

TABLE 4. Characteristics of intertidal zones at Chichagof Harbor, Attu Island, Alaska, during spring low tides.

Intertidal zone	Percent daylight hours zone exposed	Number prey per ¼ m²*	Total energy of prey per ¼ m² (kJ)†	Net rate of energy gain, E_n (kJ/h)‡
Barnacle	100	2200.6§	301.2	30.1
Mussel	97	1035.6	823.0	158.6
<i>Alaria</i>	76	27.8	99.2	465.7
<i>Laminaria</i>	15	32.0	131.8	389.9

* Data totaled from Table 1.

† From Irons (1982).

‡ Of simulated randomly foraging gull.

§ From J. A. Estes (*personal observation*).

ample, the senior author observed a gull remove >60 small limpets (<25 mm) from a single plant in <2 min. The pellet samples suggested that this sort of behavior was typical, in that a few pellets contained numerous limpets, but most of them contained none. We never observed gulls consuming large numbers of limpets in rapid succession from the rocky substrate. Those that were eaten seemed to be larger and to require longer search and handling times than those taken from kelp, as limpets were most abundant in the mussel and *Alaria* zones (Table 1).

Generally, gulls selected the larger available individuals of each prey species (Fig. 4), which is consistent with the view that the rate of energy intake is maximized. The most notable exceptions were limpets (taken roughly in proportion to availability) and sea urchins at Massacre Bay (the largest sizes were avoided). The largest urchins were apparently avoided because

they required disproportionately more handling time. All but the largest urchins were swallowed intact; large individuals (>60 mm) were either air-dropped or pecked-out. Average handling times for the three modes of consumption (swallowing intact = 17 s; air-dropping = 128 s; and pecking-out = 310 s) were significantly ($P < .05$) different. Longer handling times reduced net rate of energy gain, and greatly increased the chance of piracy by other gulls (Maron 1982, Rockwell 1982; D. B. Irons et al., *personal observations*).

Benefits of selective foraging

We established that gulls preferred to forage as low as possible in the intertidal community (Fig. 1, Table 2). This behavior resulted in higher energy gain per unit of search and handling time than nonselective foraging, although the mussel and barnacle zones were higher in time of exposure, prey density, and energy content of prey per unit area (Table 4). The *Alaria* and *Laminaria* zones had higher E_n values even though prey in the upper zones required shorter search and handling times. This is because of the generally larger sizes and higher energy values of prey in the lower zones. In the sense that intertidal zones are prey "patches," gulls appear to select those patches that offer the highest E_n .

We also demonstrated that gulls were selective in their choice of prey species (see prey selection) and prey sizes (Fig. 4). What energetic benefits were derived from such selective foraging? The answer is suggested by a comparison of mean E_n 's for completely random foraging vs. selective foraging by zones, species, and size. Completely random foraging at Massacre Bay and Chichagof Harbor predicts E_n 's of 330 and 260 kJ/h.

TABLE 5. Results of prey preference experiments with adult Glaucous-winged Gulls at Massacre Bay (MB) and Chichagof Harbor (CH), Attu Island, Alaska. Prey items had been freshly dislodged from the substrate before being collectively exposed to gull predators. Prey were replaced after being eaten or abandoned by the focal gull, or eaten by another gull. n = number of experiments.

Prey item	Mean size (mm)*	Percent chosen first and second by each individual gull				Success rates (%)‡		Average handling time (s)§		Net rate of energy gain, E_n (kJ/h)	
		Massacre		Chichagof							
		1st† (n = 96)	2nd† (n = 70)	1st (n = 66)	2nd (n = 66)	MB	CH	MB	CH	MB	CH
Lg. Chiton	55	59	11	42	18	77	66	9.5 ± 1.5	9.1 ± 2.0	7109	7422
Med. Urchin	35	24	11	35	21	77	89	5.6 ± 0.7	3.6 ± 0.6	3092	4812
Sm. Chiton	25	6	43	4	12	88	85	1.7 ± 0.1	3.6 ± 1.0	3050	1439
Sm. Urchin	15	5	29	8	43	98	98	2.8 ± 0.6	1.6 ± 0.2	469	816
Lg. Urchin	75	3	1	11	6	42	20	310.7 ± 62.4	229.1 ± 36.9	573	778
Sm. Mussel	25	2	1	0	0	67	13	3.8 ± 0.8	1.2	1418¶	1418¶
Lg. Mussel	55	0	3	0	0	0	0	—#	—#	—#	—#

* Measurement is diameter for urchins, length for other prey types.

† Column does not add up to 100 because of rounding error.

‡ Success = eating of a prey that was handled.

§ Mean and 95% confidence interval.

|| Confidence interval is undefined because sample size was one.

¶ Handling times for Chichagof Harbor and Massacre Bay combined to increase small sample size ($n = 1$ and 6, respectively).

No data were available because large mussels were not eaten by adult gulls in experiments.

TABLE 6. Energy values of selected prey items and parameters describing foraging behavior of gulls at Chichagof Harbor and Massacre Bay, Attu Island, Alaska.

Study area and prey item	No. prey items	Search time* (s)	Handling time* (s)	Energy per prey (kJ)	E_n (kJ/h)	GUT* † (s)
Chichagof						
Urchins	252	35.8 ^c ± 2.6	8.3 ^d ± 1.6	7.45	606.7	
Chitons	19	37.9 ^f ± 12.7	3.1 ± 0.44	24.52	2153.9	
Limpets	111	9.9 ± 1.1	1.5 ± 0.1	2.93	1020.5	
Mussels	59	18.9 ± 2.8	2.9 ± 0.7	1.42	243.3	
Barnacles	14	14.1 ± 3.3	2.1 ± 0.3	0.16	27.6	
Urchins + chitons + limpets, weighted‡ mean	382	24.4 ^h	6.1 ^g	6.98	729.3	98.0 ± 14.6 ^h
Massacre						
Urchins (intact)§	100	48.8 ^e ± 5.5	16.9 ^d ± 1.8	14.60	837.2	
Urchins (air-dropped)§	38	22.1 ± 6.9	127.7 ± 8.2	34.52	830.1	
Urchins (pecked-out)§	9	54.6 ± 20.6	310.1 ± 51.7	34.52	341.0	
Urchins weighted‡ mean	147	40.2	63.3	22.38	778.2	
Chitons	8	123.7 ^f ± 47.0	3.0 ± 1.0	32.89	934.3	
Limpets	50	15.5 ± 2.6	1.7 ± 0.3	1.55	321.7	
Urchins + chitons + limpets, weighted‡ mean	205	37.7 ⁱ	45.5 ^g	16.99	734.3	163.2 ± 18.8 ^j

* Values are means with 95% confidence intervals.

† Giving up time (GUT) = period from last successful encounter until gull left intertidal area.

‡ For weighting protocol, see Methods: Optimal foraging theory.

§ Mode of consumption. Urchins that were swallowed intact were assumed to be ≤60 mm in diameter. Those that were pecked-out or air-dropped were assumed to be >60 mm.

d,e,f,g,h,i,j Values with the same superscript letter were significantly different at $P < .05$ (t test).

By selecting zones, but foraging randomly on available prey species and sizes, these respective E_n 's increase to 565 and 400 kJ/h. Selection by zones, species, and size further increases these predicted values to 736 and 728 kJ/h, increases of 126 and 181%, respectively, over the predicted rate of energy intake from completely random foraging. Selective foraging by zones, species, and sizes increased E_n 55% more for Chichagof Harbor than that for Massacre Bay. Consequently, selective foraging negated the effects of sea otters at Chichagof Harbor where E_n for simulated random foraging was 21% lower than it was at Massacre Bay. Although sea otters at Chichagof Harbor influenced the proportion of prey species and sizes in gull diets as compared to Massacre Bay, these influences were probably not energetically important, as gulls maintained an equally high E_n by foraging selectively. These results reflect a degree of plasticity in foraging behavior of Glaucous-winged Gulls.

Prey preference experiments

We experimentally eliminated species-specific differences in search and capture times (i.e., that component of handling time required to free a prey item from the substrate) by making prey equally available to the gulls. These experiments demonstrated distinct preferences for prey species and size by gulls. Large chitons were the most highly preferred prey, followed by medium urchins, small urchins, small chitons, large urchins, small mussels, and large mussels (Table 5). Preference hierarchies generally were similar at Chi-

chagof Harbor and Massacre Bay, except that large urchins ranked higher at Chichagof Harbor.

In the prey preference experiments, handling times increased ($r^2 = 0.71$) and success rates declined ($r^2 = 0.74$) significantly ($P < .05$) with increasing prey size (Table 5). These results demonstrate that gulls were more efficient consumers of small than large prey. Thus, there was a trade-off between efficiency and net rate of energy gain as prey size increased, which caused the birds to choose intermediate-sized prey.

Preference rankings for urchins and chitons were significantly ($P < .05$) correlated ($r^2 = 0.78$) with E_n at both sites (Table 5) indicating the importance of E_n in prey preference of gulls. Most of the deviation ($r^2 = 0.22$) in this correlation was contributed by mussels, which were lowest on the preference hierarchy but intermediate in E_n . Unlike urchins and chitons, mussels have a tough calcareous shell surrounding their edible portion, which must be crushed in the gizzard. Gulls, like other carnivorous and piscivorous birds, have small, weak gizzards compared with granivores and molluscivores (Welty 1975). Thus, gulls probably incur a greater cost of assimilation for mussels than for urchins and chitons, and therefore avoid them more than would be predicted based on E_n alone.

In addition to differences among prey in assimilation cost, our results suggested that foraging experience, which may lead to specific search images, had an influence on prey preference. For example, gulls at Massacre Bay ate more large urchins, and gulls at Chichagof Harbor ate mainly medium and small urchins in ex-

periments (Table 5), which was consistent with differences in availability. Second, medium and small urchins were more highly preferred at Chichagof Harbor than they were at Massacre Bay (Table 5). Third, handling times for medium and small urchins were significantly ($P < .05$) lower at Chichagof Harbor than at Massacre Bay, and success rates for medium urchins also were higher at Chichagof Harbor. These results are similar to those of Rabinowitch (1969) who found that experience influenced prey preferences in zebra finches. In addition, 84% of the gulls that handled a medium urchin first at Chichagof Harbor handled a small urchin second (Table 5). In contrast, 52% of the gulls at Massacre Bay chose a small urchin after having chosen the medium one first. Small chitons were handled after large chitons were taken first in 39 and 42% of the experiments at Chichagof Harbor and Massacre Bay, respectively. There are two notable points to be made from these results. First, gulls sequentially chose the same species more often than expected (i.e., with six prey items remaining in an experiment, the probability of randomly choosing any one of them is 0.17), even though more highly preferred prey remained available on the grid. Second, gulls chose medium and small urchins sequentially more often at Chichagof Harbor than they did at Massacre Bay. This suggests that search images for small urchins were stronger in gulls with more experience foraging on small urchins, and thus that prey size as well as species are important in the formation of a search image. The formation of size-specific search images in the foraging behavior of gulls is to be expected because size selectivity is highly beneficial in terms of increasing E_n .

Preference vs. selection of prey

Large chitons were ranked highest in prey preference experiments whereas, in nature, gulls selected urchins more strongly than chitons. This difference demonstrates a real dichotomy between prey preference and prey selection. Although many factors may influence prey availability, in this case the difference probably resulted from differing forces by which urchins and chitons adhered to the substratum. The shear force required to dislodge chitons was 102 N ($\bar{X} = 53$ mm length, $n = 103$); that required to dislodge urchins (18 N) of roughly the same size ($\bar{X} = 47$ mm test diameter, $n = 105$) was significantly less ($P < .05$). Even though large chitons were abundant and apparently encountered frequently by foraging gulls, their actual availability as prey apparently was reduced because of their great ability to adhere to the substratum.

Sea otter predation and foraging behavior of gulls

We have shown that the presence of sea otters influences the size (Chichagof Harbor vs. Massacre Bay; Table 1) and proportion of sea urchins (Amchitka vs. Attu; Table 3) in gull diets. In addition, prey abundance (both species and size), as influenced by sea otters, may

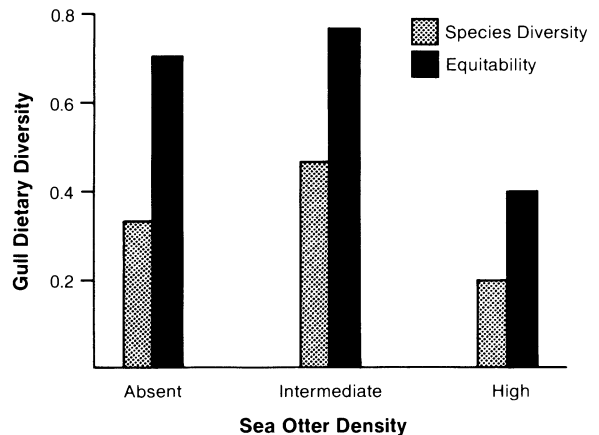


FIG. 5. Relationship between sea otter density and dietary diversity of Glaucous-winged Gulls in the western Aleutian Islands, Alaska. Spacing of the intermediate data set was arbitrarily placed midway between zero and high density. Diversity was measured by Simpson's (1949) index D , as modified by Greenberg (1956).

affect the learning of foraging behaviors of gulls. In prey preference experiments, gulls more often chose those prey items that were naturally most abundant (Table 1) than other prey items, and they were more efficient in foraging on these items as well (Table 5).

Mean search times for most prey items were not significantly ($P > .05$) different between Chichagof Harbor and Massacre Bay, but mean handling times for all prey items were significantly ($P < .05$) longer at Massacre Bay (Table 6). Search times for urchins < 60 mm and chitons were significantly ($P < .05$) longer at Massacre Bay than those at Chichagof Harbor. Handling times for urchins < 60 mm were also longer ($P < .05$) at Massacre Bay. As a result, net rate of energy gain (E_n) for the various prey items differed between Chichagof Harbor and Massacre Bay, but the influence of selective foraging by gulls resulted in similar E_n 's for all common prey items combined at Chichagof Harbor (728 kJ/h) and Massacre Bay (736 kJ/h). These differences in foraging behavior by gulls appeared to result largely from the differences in size frequency distributions of urchins between Chichagof Harbor and Massacre Bay. Large urchins at Massacre Bay had not been removed by sea otters, and they required longer handling times but provided higher E_n than those at Chichagof Harbor (Table 6).

Giving-up time (GUT), the period of continuous searching between last prey capture and cessation of foraging, was significantly ($P < .05$) longer at Massacre Bay than at Chichagof Harbor (Table 6). Therefore, giving-up times were longer where urchins had a higher E_n (Massacre Bay). This result is consistent with optimal foraging theory which predicts that a predator can afford to use more energy to find a prey item that has a higher energy content. GUTs were also 2–3 times longer than average search times at both areas, sug-

gesting that gulls hunted by expectation (see Gibb 1958, Krebs et al. 1974 and Zach and Falls 1976a, b, c for further discussion on this topic).

Diversity and evenness of gull diets were also related to sea otter density (Fig. 5). Dietary diversity of gulls was low at Amchitka Island, where otter density was highest, and at Massacre Bay, where otters were absent. Dietary diversity was highest at Chichagof Harbor, where otters were present, but in low density.

GENERAL DISCUSSION

Optimal foraging theory

In this study, we have examined two of the general predictions of optimal foraging theory in a complex natural community. The assumption that net rate of energy intake is an important currency in determining an animal's foraging behavior leads to the prediction that predators prefer the energetically most profitable prey (Krebs 1981). Our results provide three lines of evidence to support that prediction. First, prey selection hierarchies (based on dietary composition and prey abundance) were positively correlated ($r^2 = 0.44$) with species-specific net rates of energy intake (Fig. 6). Second, prey selection by gulls in the natural environment changed in response to varying prey availability in ways consistent with maximizing net rate of energy intake. Third, prey preference, as determined experimentally, maximized net rate of energy gain, but in a way that was different from prey selection in the natural environment.

Our results also support the prediction from optimal foraging theory that animals are more selective foragers as profitable prey become more common (Krebs 1981). At Attu Island, the most profitable prey types (urchins, chitons, and limpets) occurred largely or exclusively in the lower littoral zones and were exposed only on spring low tides. In contrast, less profitable prey (mussels and barnacles) occurred in higher zones where they were exposed during both spring and neap low tides. We used this situation to test the hypothesis that gulls forage more selectively when profitable prey are most common. During neap tides at the Chichagof Harbor site, 47% of foraging gulls occurred in the mussel and barnacle zones, and 63% of the gulls' diet consisted of barnacles and mussels. However, during spring tides <0.2 m above mean lower low water only 6% of foraging gulls occurred in the mussel and barnacle zones, and no barnacles and mussels were observed to be eaten. We conclude that when energetically valuable prey were unavailable, the gulls fed predominately on less valuable mussels and barnacles. However, when energetically valuable prey were abundant, mussels and barnacles were excluded from the diet, even though some gulls fed in the immediate vicinity of these prey.

Although diets of numerous gull species have been studied extensively, few of the published accounts have tested predictions of optimal foraging theory. Herring

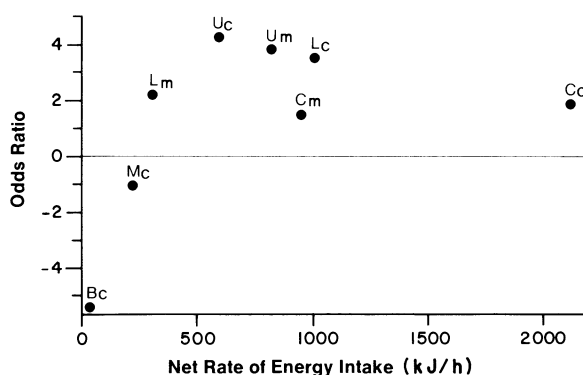


FIG. 6. Relationship of prey selection hierarchies of Glaucous-winged Gulls to net rates of energy gain, E_n (energy value divided by search plus handling times) for different prey species at Attu Island, Alaska. B, M, L, U, C refer to barnacle, mussel, limpet, urchin, and chiton, respectively; subscript letters identify the site: m = Massacre Bay, c = Chichagof. The odds ratio is equal to: [(proportion of diet comprised by a given prey taxon) $\times$ (proportion of food complex in environment comprised by all other taxa)] $\div$ [(proportion of food complex in environment comprised by the given taxon) $\times$ (proportion of diet comprised by all other prey taxa)] (Fleiss 1973).

Gulls (*Larus argentatus*) in England have been shown to select seastars (*Asterias rubens*) over less profitable mussels (Sibly and McCleery 1983a) while foraging in intertidal habitats, but fewer gulls than expected abandoned the intertidal zones to feed on highly profitable refuse dumps when the dumps became available (Sibly and McCleery 1983b). In Florida, Herring Gulls chose the largest available scallops (*Argopecten irradians*) and cockles (*Trachycardium egmontianum*) to air-drop (Kent 1981), which were likely the most profitable, since Zach (1979) showed that the large whelks (*Thais lamellosa*) that were selected and air-dropped by Northwestern Crows (*Corvus caurinus*) were also the most profitable.

Predictions of optimal foraging theory have been tested more extensively for other species of shorebirds that forage in intertidal habitats or pasture-lands. Lapwings (*Vanellus vanellus*) and Greater Golden-Plovers (*Pluvialis apricaria*) chose the most profitable size classes of worms (*Lumbricus rubellus*, *Allolobophora chlorotica*, and *A. caliginosa*) (Thompson and Barnard 1984). Furthermore, in the presence of kleptoparasitic Blackheaded Gulls (*Larus ridibundus*), they shifted to smaller sizes of worms in a manner that continued to maximize energy intake while accounting for the risk of theft by gulls (Thompson and Barnard 1984). Redshanks (*Tringototanus*) chose the most profitable size classes of worms (*Nereis diversicolor* and *Nephtys hombergi*) (Goss-Custard 1977a), but chose less profitable amphipod crustaceans (*Corophium volutator*) over the worms (Goss-Custard 1977b). Black Oystercatchers (*Haematopus bachmani*) have been shown to select the most profitable prey, based on biomass rather than energy content, and to be more selective when prey abundance increases (Groves 1982,

Sutherland 1982). Results from these field tests are generally consistent with our findings for Glaucous-winged Gulls, thus indicating that the predictions of optimal foraging theory are valid for many shore-feeding birds. However, the inconsistencies deserve note as well. These inconsistencies suggest that energy gain is an inadequate or inappropriate currency for the study of foraging behavior in some complex natural systems (Goss-Custard 1977b, Schluter 1981, Pyke 1984).

The influence of sea otters

In contrast with Attu, fish were the most important component of the gulls' diet at Amchitka Island. This is similar to dietary differences of sea otters between the two islands (Estes et al. 1982), and no doubt has the same explanation. That is, sea otters, which are abundant at Amchitka Island, reduce the size and density of sea urchins (Lowry and Pearse 1973, Estes and Palmisano 1974, Breen et al. 1982), and enhance the growth of marine algae (Dayton 1975, Estes et al. 1978, Duggins 1980). Population levels of many nearshore fishes are positively correlated with algal abundance (Quast 1968, Simenstad et al. 1977, 1978, Ebeling and Laur 1985, Ebeling et al. 1985). Furthermore, populations of intertidal invertebrates at Amchitka Island are limited by sea otter predation and perhaps indirectly by various physical effects of extensive kelp beds (Palmisano and Estes 1977). Differences in the gulls' diets between Attu and Amchitka islands reflect the resulting differences in prey availability.

Diets of gulls at Massacre Bay and Amchitka Island probably represent extremes in the range of influences by sea otters. The community at Amchitka Island has supported an equilibrium density population of sea otters for the past four decades (Kenyon 1969), while sea otters were absent from Massacre Bay. Chichagof Harbor represented an intermediate situation, having been reinhabited by sea otters in the mid-1960's (Jones 1965) and being well below equilibrium density at the time of our study. Sea otters at Chichagof Harbor had reduced the size of invertebrates (Table 1, Fig. 4), although this had not been sufficient to promote the extensive development of kelps (Simenstad et al. 1978, J. A. Estes, *personal observation*). Among these three sites, the dietary diversity of gulls was highest at the site of intermediate sea otter density, and lowest at the two extremes (Fig. 5). These observations probably are explained as follows. Where sea otters are absent, intertidal invertebrates are abundant and gulls forage selectively on the most energy-rich species. A reduction in prey abundance in the low intertidal zones closely follows the re-establishment of sea otters. Gulls continue to feed mostly on intertidal invertebrates, but they select less valuable species, such as mussels, whelks, and barnacles. The number of species (species richness) consumed is unchanged, although their evenness in the diet is increased. High otter densities greatly reduce prey abundance in the littoral zones, resulting directly

from predation on sea urchins and related ecological processes (e.g., see Palmisano and Estes 1977). Under this circumstance intertidal invertebrates are largely forsaken by foraging gulls in favor of neritic marine fishes, which results in a substantial drop in the gulls' dietary diversity and evenness. These results parallel, both in form and process, other examples of the intermediate disturbance model of species diversity (Paine and Vadas 1969, Lubchenco 1978, Hixon and Brostoff 1983). The conceptual analogues are between species diversity and dietary diversity on one hand, and between competitive hierarchies and prey selection hierarchies on the other.

Rocky intertidal communities are probably recent and temporary foraging habitats for Glaucous-winged Gulls. Before sea otter populations were effectively eliminated from the rim of the North Pacific by human exploitation, intertidal community structure in the central and western Aleutian Islands was likely similar to that presently occurring at Amchitka Island. Based on the fossil record this situation may have been the predominant condition from the late Miocene or early Pliocene (Repenning 1976). Ironically, we have learned a great deal from perturbations to this system by the ravages of fur hunters. Indeed, the remarkable variation in foraging strategies by Glaucous-winged Gulls among areas at differing stages of sea otter population recovery provides another example of the sea otter's influence on the organization of coastal marine communities in the northeastern Pacific Ocean.

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