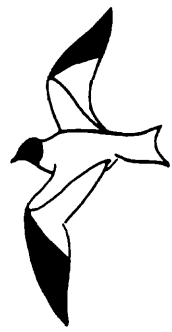


# WESTERN BIRDS



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## FEEDING BEHAVIOR OF CROWS AND GULLS ON A PUGET SOUND BEACH

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The shoreline bird community of the Pacific Northwest differs from many others in the world because an abundant member is not a waterbird but a crow, the Northwestern Crow (*Corvus caurinus*). Crows are known opportunistic feeders, as are gulls, and many crows throughout the world do feed at least occasionally along marine shores (Goodwin 1976). Consequently, the Northwestern Crow should be adapted to occupy a role as a member of the opportunistic beach feeding guild limited often to gulls. A guild is "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). Three gulls commonly feed in the intertidal areas of Puget Sound: Glaucous-winged Gull (*Larus glaucescens*), Mew Gull (*L. canus*) and Bonaparte's Gull (*L. philadelphia*). To compare the role of the crow with the roles of the gulls and to see how the members of this particular guild subdivide the available resources, I compared the feeding behavior of crows and gulls along a Puget Sound beach.

### STUDY AREA AND METHODS

This study was conducted in Kopachuck State Park, Pierce Co., Washington. The beach studied is typical of many Puget Sound beaches, as described by Weiser (1959), in that it is relatively sheltered from wave action, with the upper parts consisting of cobblestones and the lower parts (up to approximately the 2 m tide line for this particular beach) consisting of sand and mud. Driftwood logs ranging up to about 1 m in diameter litter the beach. The dominant surface animals are the Acorn Barnacle (*Balanus glandula*) and the Periwinkle (*Littorina sitkana*). Because the beach is within a state park, its invertebrate fauna is probably less diverse than it would be if within a less disturbed area. The beach is bordered on the east by a Big-leaf Maple (*Acer macrophyllum*) — Douglas-fir (*Pseudotsuga menziesii*) forest with scattered picnic tables.

## FEEDING BEHAVIOR OF CROWS AND GULLS

I gathered data on foraging crows and gulls during the nonbreeding season (September to March) in 1974 and 1975, and to a lesser extent in 1976. Birds were censused at hourly intervals and their positions on the beach noted: whether in deep water, in shallow water (birds could wade), just above the tide line (where water was still draining), on the middle beach (where the substrate was still wet), on the upper beach (substrate well drained), or on the extreme upper parts of the beach (usually only covered with water at high tide). If the birds were on exposed beach, I recorded whether they were on sand and mud or on rock. I obtained tide heights at census times from newspaper tide charts. Because Glaucous-winged Gulls were sitting most of the time and not feeding, their positions were noted only when they were seen taking food. Other species were almost always feeding when encountered on censuses. I censused only birds found on the beach or in adjacent water and ignored gulls flying or sitting well offshore or crows sitting in the trees along the beach. I made a further comparison between the crows and Mew Gulls by measuring the distance, estimated in body lengths, between food items taken by individuals on the beach at times other than when tides were below 0.7 m and food was superabundant.

## RESULTS

### NUMBERS AND FEEDING SITES

Results of the censuses for the three most common gulls and the crow are in Table 1. Other gulls, Herring Gull (*L. argentatus*), Thayer's Gull (*L. thayeri*) and California Gull (*L. californicus*), occurred in too small numbers to yield interpretable results. The results indicate that all species were most common at times of the lowest tides, with the crow and Mew Gull decreasing most in numbers as the tide height increased. Crows were the most abundant species on the beach at all but the two highest tide categories when their numbers dropped below those of the Glaucous-winged Gull. Numbers of Bonaparte's Gull were erratic.

The place where a species fed was closely associated with tide height. Bonaparte's Gull provided the clearest example, feeding almost entirely above the water line during the lowest tides and in deep water at all other times.

Crows, on the other hand, fed almost entirely above the water line and only rarely waded into the water to feed (counted only once on a census, but also observed on other occasions). Once a crow was observed picking at a dead fish while standing on a small rock surrounded by water only a few inches deep. Apparently, crows avoid getting their feet in salt water. Crows also ranged higher on the beach than any of the gulls, picking over driftwood and debris left at the high tide line on the upper edge of the beach. However, they shifted closer to the water line at lower tide levels.

Mew Gulls showed an increasing tendency to feed above the water line as the tide level decreased, with only 21% feeding below the water line at the lowest tides. Mew Gulls began feeding above the line at the point where the

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tide began to uncover the sandy portions of the beach (94% of the Mew Gulls in contrast to 48% of the crows feeding above the water line fed on the sandy areas rather than on the cobblestones). At other nearby beaches where sand extends up higher, Mew Gulls were also more common at higher water levels.

Even at low tide levels, most of the Glaucous-winged Gulls' food came from below the tide line. The data for the Glaucous-winged Gull, however, were erratic due probably to the sampling method. Except at times of lowest tides, Glaucous-winged Gulls feeding above the line usually fed on carrion or other debris. Otherwise, they fed on live animals.

Hunt and Hunt (1973) found similar changes with Maine gulls. As the tide level decreased, uncovering mud, Laughing Gulls (*Larus atricilla*) moved onto the beach and other gulls switched from other substrates to the mud. In

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Table 1. Numbers of birds present during different tide heights and distribution of feeding places, Kopachuck State Park, Pierce Co., Washington, Sep.-Mar. 1974-75. Numbers of censuses were 10, 11, 15, 6 and 11 for increasing tide heights.

Tide Height (feet)	Mean Number Birds	Feeding place — Percent of observations					
		Deep Water	Shallow Water	Above Tide Line	Middle Beach	Upper Beach	Extreme Upper Beach
<b>Glaucous-winged Gull</b>							
< 2	5.9	44	33	6	17	0	0
2+ - 4	4.6	27	55	0	18	0	0
4+ - 6	2.9	17	0	50	33	0	0
6+ - 8	3.3	100	0	0	0	0	0
> 8	4.1	100	0	0	0	0	0
<b>Northwestern Crow</b>							
< 2	14.3	0	0	44	41	13	1
2+ - 4	6.3	0	1	23	29	38	9
4+ - 6	4.3	0	0	23	49	19	9
6+ - 8	2.3	0	0	33	33	33	0
> 8	0.8	0	0	67	0	17	17
<b>Mew Gull</b>							
< 2	7.1	3	18	8	69	1	0
2+ - 4	1.3	21	21	36	14	7	0
4+ - 6	2.1	82	0	14	4	0	0
6+ - 8	0.7	75	25	0	0	0	0
> 8	0.8	75	25	0	0	0	0
<b>Bonaparte's Gull</b>							
< 2	1.1	0	0	36	64	0	0
2+ - 4	0.2	100	0	0	0	0	0
4+ - 6	0.1	100	0	0	0	0	0
6+ - 8	1.7	100	0	0	0	0	0
> 8	0.6	100	0	0	0	0	0

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the present study, although only 48% of all crows foraged on the sand, 86% of those present during lowest tides foraged on the sand. This shift presumably occurred because during the lower tides, sand, which is the substrate most recently uncovered, is more productive than cobblestones.

### FOOD TYPES

The three gulls and the crow also fed on different foods as observed at binocular range (I did no stomach analyses, and my visual observations are biased toward large items). Although both gulls and crows are opportunists, and carrion and other debris may compose a significant portion of their diets, most of their food that I observed was live animals.

Crows fed on animals that ranged in size from small unidentifiable items that could be swallowed in one bite with no further handling to items several times the length of a crow's beak and requiring 10 or more minutes to consume. Items much larger than a crow's beak were uncommon, and perhaps were limited to what the crows could carry in their beaks during flight. Foods commonly taken by the crows included crabs (*Hemigrapsus oregonensis* and *Cancer productus* were identified), sand dollars (*Dendraster excentricus*), cockles (*Clinocardium nuttallii*), rock cockles (*Protothaca semidecussata*), small Moon Snails (*Polinices lewisii*) and unidentified amphipods. This diet is similar to, although not as diverse as, the one Butler (1974) described for the Northwestern Crow from pellets. Many prey animals found by Butler were not present in my study area. Sand dollars were not listed by Butler, but were a major food of crows in this study, particularly in late winter. The crows simply picked them off the surface and opened them as gulls open shells by dropping them on rocks while in flight. The crows found most of their food by searching under seaweed and by digging down into the cobblestones with their bills. On a few occasions, crows picked up bits lost by Glaucous-winged Gulls feeding on large items such as crabs.

In contrast to the crows, Glaucous-winged Gulls fed mostly on large items requiring some handling time (e.g., 22 minutes timed for a large cockle), but as with the crow, bill size apparently limited food size. Small items were taken only during the lowest tides when these items are abundant. The gulls usually captured larger items in the water by either diving while flying several meters above the water or dipping while either sitting or wading in water. The gulls then flew or swam back to the beach where they consumed the food. Foods taken by the gulls included small fish, crabs (same species as taken by the crows but apparently with a larger proportion of the larger *C. productus*), cockles and starfish (*Piaster ochraceus*). I never saw gulls feeding on sand dollars.

Cockles were a major food of both crows and Glaucous-winged Gulls, as evidenced by an abundance of broken shells strewn on the beach. Cockles usually remain close to or on the surface of the sand (Ricketts and Calvin 1968) and thus make easy prey.

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Mew Gulls fed on items that could usually be swallowed whole with no handling. The few items I could see were small unidentified crabs, amphipods and unidentified worms. Mew Gulls usually found food by walking or swimming along the beach and picking up food from either the water's or the sand's surface, by searching under seaweed, or by foot-paddling (when the gull treads wet sand with its feet, as discussed by Buckley 1966). In this study, foot-paddling occurred in late winter, the same season Williams (1933) observed it in California. A water-sand medium is evidently required for gulls to foot-paddle efficiently.

Bonaparte's Gulls fed on food that was too small to identify, but on several occasions they caught insects while flying swallow-like over the water.

### FOOD DISTRIBUTION AND SOCIAL BEHAVIOR

A fourth difference in foraging behavior between these species was the apparent reactions to the dispersion of their food. The larger items that Glaucous-winged Gulls fed on were much more widely spaced on the beach and in the water than were the foods of the other species. Mew Gulls' food was more clumped than the crows' food (Figure 1). These differences, however, were not as distinct at the lowest tide levels when all species were feeding on the abundant and highly aggregated food. A difference in food dispersion usually is not considered a means by which interspecific competition is lessened but rather is another indication that different foods are being chosen. Cody (1974), for example, combined bill measurements and food dispersion into one variable in his studies.

Differences in food dispersion can also lead to differences in sociality, because sociality is important in the strategy animals use to exploit their environment (E.O. Wilson 1975, Wiens 1976). As resources become more unpredictable and less defensible, animals tend less to defend territories and tend more to aggregate, with the flock forming the most stable unit. Corresponding differences were seen in this study.

Mew Gulls fed solitarily when on the beach, except at lowest tides, and usually chased away any other Mew Gulls that approached. For a Mew Gull, food is limited and easily defended in the small patches. When feeding on the beach during lowest tides and at most times out over the open water of the adjacent bay, Mew Gulls fed in flocks or aggregations, which frequently included other bay and shore feeding birds.

In contrast, Northwestern Crows were almost always in small flocks or aggregations, which is often noted as a characteristic of the Northwestern Crow relative to other crows (Johnston 1961). Often several crows moved together along the beach searching for food. When food was found, the group stopped moving and broke down into a loose aggregation, which was joined by other crows. Because of the food's slightly dispersed nature, a crow cannot find and defend it all efficiently, as Mew Gulls can. Consequently, a crow can share food and, besides, will reduce its risk of not finding sufficient

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food by later feeding with other crows that have found food (Thompson et al. 1974). Flocking is also advantageous in providing more eyes to look for predators (Willis 1972).

Glaucous-winged Gulls during times of higher tides were territorial. Winter territories are not uncommon in this species (Vermeer 1963, Barash et al. 1975). However, most were not territorial, and those that were, were adults (as is the usual case for winter gull territories; Drury and Smith 1968). Furthermore, the winter territories were not as strict as breeding territories usually are. When large flocks of gulls were present in aggregations in the adjacent

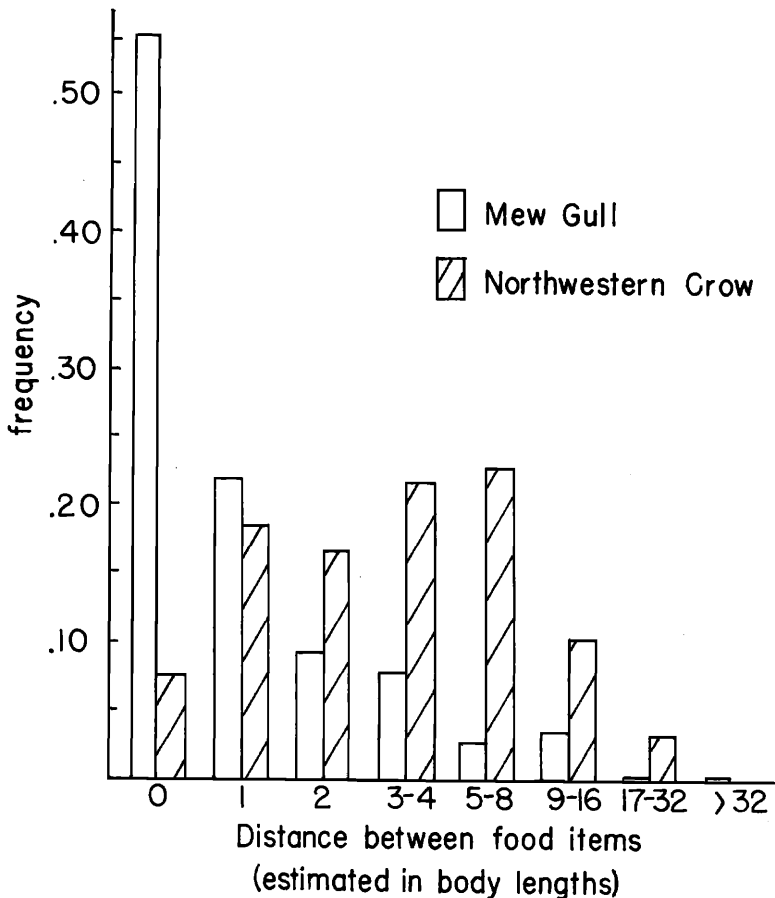


Figure 1. Frequency distributions of the distances between food items for the Mew Gull and the Northwestern Crow, Puget Sound, Washington. Sample size is 209 for the gull and 96 for the crow.

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bay, the gulls on the beach were either absent or were seen flying out to join the aggregation. For Glaucous-winged Gulls, food is probably plentiful enough in the shallow water along the beach to form a predictable and defendable source. At times of the lowest tides, territories were not defended at all, probably because food is then abundant. A similar system of territorial and nonterritorial individuals in winter has been well described for wagtails (*Motacilla alba*) by Zahavi (1971) and Davies (1976); when food is abundant, aggregations form, but when food is limited and defendable, territories form.

Among the four species, a dominance hierarchy existed with the larger species dominating the smaller ones (also described by Moyle 1966 for the same three gulls). Mew Gulls especially were often supplanted by crows or by Glaucous-winged Gulls, although apparently only place and not specific food items were in dispute. Glaucous-winged Gulls also attempted to steal food from the crows. However, on two occasions when a Glaucous-winged Gull landed in the midst of a group of feeding crows, the crows chased away the gull. Once, when the crows were feeding on carrion, a crow that appeared to be a dominant individual, because it was in the center of the group, attacked the gull by grabbing one of the gull's wings in its beak and pulling on it.

## DISCUSSION

The pattern in food-size consumed is the same as that commonly observed between members of a guild. Smaller species will take food from a range of smaller sizes, and as the species become larger in body size, the range in food is expanded to include larger sizes but still includes the smaller food sizes fed upon by the smallest species (D.S. Wilson 1975). However, the larger species usually prefer larger food items because of higher nutritive content. The limit of food size of an individual animal is determined by the size of whatever that animal uses to catch or handle its food. In gulls and crows, bill size is apparently important, with the smaller Bonaparte's and Mew gulls unable to handle the larger crabs and mollusks that are important in the diets of the crow and the Glaucous-winged Gull. To open mollusks, crows and gulls need to be able to pick them up and to take flight with them, so that they can be dropped.

The importance of bill size in separating the foods of these species can be seen by the ratios of bill sizes in Table 2. A ratio of 1.3 is commonly found in comparing members of the same guild (Horn and May 1977). The small ratio between the Mew Gull and the Bonaparte's Gull may be one reason why Bonaparte's Gull feeds on the beach only at the lowest tides. Food is more abundant then, and competition thereby lessened. Also, while the North-western Crow is smaller in body size than western races of the Common Crow (*Corvus brachyrhynchos*), of which the Northwestern Crow is often

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Table 2. Bill lengths (of males) and their ratios for the four members of the beach scavenging guild of Puget Sound, Washington. Bill lengths from Ridgway (1919).

Species	Bill length (mm)	Ratio
Glaucous-winged Gull	58.3	1.24
Northwestern Crow	47.0	1.29
Mew Gull	36.4	1.17
Bonaparte's Gull	31.2	

considered to be a race, the bill size is similar (Johnston 1961). A smaller bill would cause more competition with the Mew Gull.

The work of Hunt and Hunt (1973) reveals that the opportunistic beach feeding guilds in both Maine and Europe, although filled mostly by gulls, are organized in the same way as is the Puget Sound guild. They found that in the intertidal usually only three or four species fed and that these fell into three general body size categories. Other gulls with similarly sized bodies were confined to other habitats and were only infrequent visitors to the intertidal. In addition, they found a pattern between body size and ecological role that was repeated in this study. The large species feeds mostly in the water, the medium species feeds mostly on the beach, the small species feeds mostly on mud or sand, and, if there is a second small species, it feeds in the intertidal only during the lowest tides. Table 3 lists the ecologically equivalent species. The Mew Gull, which is found in both Puget Sound and Europe, shows a role change, from the first small species in Puget Sound to the second in Europe. The Black-headed Gull (*Larus ridibundus*), a close relative of the Bonaparte's Gull, fills the role of the first small species in Europe. The Herring Gull shows a habitat shift from Maine and Europe to Puget Sound, where it is common but not in the intertidal.

Examples of ecological equivalence such as this are common (Cody 1974, Cody and Diamond 1975). Cody (1974) states that equivalence is found most often in structurally simple habitats where there is less opportunity for variation in niche patterns. For birds the intertidal is a simple environment. The pattern of bill size in the beach scavenging guilds indicates that differences in food size may be the primary mechanism easing competition and allowing the four species to co-exist. The beach is not stratified sufficiently to allow height or depth criteria to separate resources; this is in contrast to the case in most avian communities, including muddy intertidal areas (Recher 1966). The tide cycle, however, contributes complexity to the availability of resources and, thus also, to resource division by members of the guilds. In Washington, only at the lowest tides is a fourth species (Bonaparte's Gull) able to feed on the beach. Then, apparently, as the tide increases and



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perhaps food decreases, differences in range of food size are not sufficient to ease competition. Further tide increases lead to another species (Mew Gull) being unable to feed efficiently on the beach, leaving only two species, which are separating resources also by place. Finally, when the beach is almost completely inundated, in Puget Sound at least, the third species (Northwestern Crow) drops out and only one species (Glaucous-winged Gull) is left, and individuals defend the area against conspecifics.

The crow does not leave the beach at higher tides solely because it is not a water bird, because in Europe, the Herring Gull, the medium-sized species, also is reduced in numbers at times of higher tides (Verbeek 1977). Body size is correlated with the order in which species respond to the tide cycle, both in this study and in Hunt and Hunt (1973). Several factors create this pattern response. First, the interspecific dominance hierarchy may be one factor because the larger birds, which are present on the beach at more times are dominant over the smaller birds. Another factor may be food size. Where the beach changes from cobblestone to sand, there is a corresponding change in the invertebrate fauna (Wieser 1959). A third factor may be that both the crow and Herring Gull (Verbeek 1977) are able to dig with their bills into the cobblestones, something smaller gulls are apparently unable to do.

Consequently, the crow appears to be exploiting a niche in Puget Sound that in many parts of the world would be a gull niche. But does the crow exclude a medium-sized gull? Four medium-sized gulls do occur along the Pacific Coast in winter. These are listed with bill lengths in Table 4. Because

Table 3. The ecologically equivalent species found at a Puget Sound beach<sup>1</sup>, in Maine<sup>2</sup> and in northwestern Europe<sup>2</sup>.

Niche	Puget Sound	Maine	Europe
Large body, feeds mostly in water	Glaucous-winged Gull	Great Black-backed Gull	Great Black-backed Gull
Medium body, feeds mostly on beach	Northwestern Crow	Herring Gull	Herring Gull
Small body, feeds mostly on mud or sand	Mew Gull	Laughing Gull	Black-headed Gull
Small body, feeds only in area at low tide	Bonaparte's Gull	None	Mew Gull

<sup>1</sup>From this study.

<sup>2</sup>From Hunt and Hunt (1973).

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Table 4. Bill lengths of some male Pacific Coast gulls.

Species	Bill length (mm)
Herring Gull	54.2 <sup>a</sup>
Thayer's Gull	52.2 <sup>b</sup>
California Gull	49.8 <sup>a</sup>
Ring-billed Gull	44.3 <sup>a</sup>

<sup>a</sup>From Ridgway (1919)

<sup>b</sup>From Dwight (1925)

Thayer's and Herring gulls both approach the Glaucous-winged Gull in size (Table 2), they may be excluded by competition from feeding in the intertidal because their diets would overlap too much with that of the Glaucous-winged Gull. Ring-billed and California gulls, however, are both much more similar in size to the crow. These last two gulls are common in migration through the Puget Sound region, but are uncommon in winter, increasing in numbers south of 46°N latitude (Table 5), which is also approximately the same latitude given as the southern boundary of the Northwestern Crow's range (AOU 1957). That these two gulls tend to be more terrestrial than most gulls may allow the crow to more readily exclude them by competition. The crow

Table 5. The average numbers of California and Ring-billed gulls per 10 party-hours on 1975 Christmas Bird Counts<sup>1</sup> from the coastal Pacific Northwest, by latitude.

Lat (°N)	Counts	California Gulls	Ring-billed Gulls
50	2	0.0	0.0
49	8	+	2.1
48	6	0.3	0.2
47	3	11.1	2.9
46	2	0.6	0.7
45	3	12.2	16.0
44	1	50.2	17.3
43	1	17.3	22.3

<sup>1</sup>From *American Birds*.

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may also be able to exclude them because it is a permanent resident in the Pacific Northwest. For one species, such as the crow, to competitively exclude another one, it must limit that other species' population more than it does its own. For the case of competition between migrants and residents, in general, migration hazards can reduce populations of migrants to the point that the permanent resident population can do just that (Willis 1966). The crow could thus actually limit abundance of Ring-billed and/or California gulls in Washington and farther north during the nonbreeding season.

### SUMMARY

Four species of birds composing the beach scavenging guild of a Puget Sound beach, Northwestern Crow, Glaucous-winged Gull, Mew Gull and Bonaparte's Gull, separate their foods by responding to the tide cycle in different ways, by feeding in different places in the intertidal, and by choosing foods of different sizes. Differences in food dispersion and in the resulting socialities also indicate the use of different foods. Species in this guild are ecologically equivalent to species in similar guilds in Maine and Europe. Apparently, the Northwestern Crow exploits a typical gull niche, and possibly to the exclusion of a medium-sized gull.

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### LITERATURE CITED

- American Ornithologists' Union. 1957. Check-list of North American birds, 5th ed. Am. Ornithol. Union, Baltimore, MD.
- Barash, D.P., P. Donovan & R. Myrick. 1975. Clam dropping behavior of the Glaucous-winged Gull (*Larus glaucescens*). *Wilson Bull.* 87:60-64.
- Buckley, P.A. 1966. Foot-paddling in four American gulls, with comments on its possible function and stimulation. *Z. Tierpsychol.* 23:395-402.
- Butler, R.W. 1974. The feeding ecology of the Northwestern Crow on Mitlenatch Island, British Columbia. *Can. Field-Nat.* 88:313-316.
- Cody, M.L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, NJ.
- Cody, M.L. & J.M. Diamond eds. 1975. Ecology and evolution of communities. Harvard Univ. Press, Cambridge, MS.
- Davies, N.B. 1976. Food, flocking, and territorial behavior of the Pied Wagtail (*Motacilla alba yarrellii* Gould) in winter. *J. Anim. Ecol.* 45:235-253.
- Drury, W.H., Jr., & W.J. Smith. 1968. Defense of feeding areas by adult Herring Gulls and intrusion by young. *Evolution* 22:193-201.

## FEEDING BEHAVIOR OF CROWS AND GULLS

- Dwight, J. 1925. The gulls (Laridae) of the world; their plumages, moults, variations, relationships and distribution. *Bull. Am. Mus. Nat. Hist.* 52:63-401.
- Goodwin, D. 1976. *Crows of the world*. Cornell Univ. Press, Ithaca, NY.
- Horn, H.S. & R.M. May. 1977. Limits to similarity among coexisting competitors. *Nature* 270:660-661.
- Hunt, G.L. & M.W. Hunt. 1973. Habitat partitioning by foraging gulls in Maine and northwestern Europe. *Auk* 90:827-839.
- Johnston, D.W. 1961. *Biosystematics of American crows*. Univ. Washington Press, Seattle.
- Moyle, P. 1966. Feeding behavior of the Glaucous-winged Gull on an Alaskan salmon stream. *Wilson Bull.* 78:175-190.
- Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47:393-407.
- Ricketts, E.F. & J. Calvin. 1968. *Between Pacific tides*, 4th ed., revised by J.W. Hedgpeth. Stanford Univ. Press, Stanford, CA.
- Ridgway, R. 1919. *The birds of North and Middle America*. U.S. Natl. Mus. Bull. 50, part 8.
- Root, R.B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecol. Monogr.* 37:317-350.
- Thompson, W.A., I. Vertinsky & J.R. Krebs. 1974. The survival value of flocking in birds: a simulation model. *J. Anim. Ecol.* 43:785-820.
- Verbeek, N.A.M. 1977. Comparative feeding ecology of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. *Ardea* 65:25-42.
- Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island, B.C. *Occas. Pap. Brit. Col. Prov. Mus.* 13:1-104.
- Wieser, W. 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnol. and Oceanogr.* 4:181-194.
- Wiens, J.A. 1976. Population response to patchy environments. *Annu. Rev. Ecol. Syst.* 7:81-120.
- Williams, L. 1933. A peculiar feeding habit of the Short-billed Gull. *Condor* 35:161.
- Willis, E.O. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187-231.
- Willis, E.O. 1972. The behavior of Spotted Antbirds. *Ornithol. Monogr.* 10:1-162.
- Wilson, D.S. 1975. The adequacy of body size as a niche difference. *Am. Nat.* 109:769-784.
- Wilson, E.O. 1975. *Sociobiology*. Harvard Univ. Press, Cambridge, MS.
- Zahavi, A. 1971. The social behavior of the White Wagtail *Motacilla alba alba* wintering in Israel. *Ibis* 113:203-211.

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