

HUMAN DISTURBANCE OF AN AVIAN SCAVENGING GUILD¹

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Abstract. In order to investigate the effects of human activities on relationships within foraging guilds, we examined intraguild dynamics of eagles, crows, and gulls scavenging on spawned salmon in the Pacific Northwest. We examined several hypotheses that postulate the asymmetric foraging relationships of the three guild members and that reveal the influence of competition and facilitation in these relationships. Spatial and temporal patterns of resource use by the three primary guild members varied with the presence and absence of human activity at experimental feeding stations. At control (undisturbed) stations, eagles preferred to feed >100 m from vegetative cover, whereas gulls fed <50 m from cover. At experimental (disturbed) stations, eagles rarely fed, and feeding activity by gulls increased at both near and far stations. Crows often fed on alternate food sources in fields adjacent to the river, especially when salmon carcasses were scarce, whereas eagles and gulls rarely did so. We also examined if and how the behavior of single guild members changes in the presence or absence of other guild members. In the absence of eagles, gulls and crows preferred stations far from cover, numbers of both increased at feeding stations, birds were distributed nearer to carcasses, and they fed more. We emphasize that guild theory lends important insights to our understanding of the effects of human disturbance on wildlife communities.

Key words: aggression; American Crows; avian scavengers; Bald Eagles; foraging guild; Glaucous-winged Gulls; guild theory; human disturbance; niche shifts; Pacific Northwest; recreation; wildlife management.

INTRODUCTION

Comparisons of closely related species dominated studies of competition and community structure until the introduction of the foraging-guild concept. A guild has been defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967:335). Guilds emphasize overlap in resource use in groups of animals with different morphologies and behavior (Charnov et al. 1976), and group such species without regard to taxonomic positions. This perspective has stimulated studies of competition between distantly related organisms, such as heteromyid rodents and seed-eating ants (Brown and Davidson 1977, Davidson et al. 1980), hummingbirds and nectar-feeding insects (Brown et al. 1981), and foxes and raptors (Jaksić et al. 1981).

Here we describe the foraging dynamics of an avian guild that exploits rich concentrations of anadromous

salmon (*Oncorhynchus* spp.) that spawn and die along rivers flowing into the Pacific Ocean. The avian salmon-scavenging guild, primarily comprised of Bald Eagles (*Haliaeetus leucocephalus*), American Crows (*Corvus brachyrhynchos*), and Glaucous-winged Gulls (*Larus glaucescens*), forms along Pacific coastal rivers during winter when salmon carcasses are available, and disperses to alternate habitats and resources in spring (Stalmaster et al. 1979). This assemblage of species meets Root's (1967:335) key criterion for inclusion in a foraging guild in that the major portion of each species' diet comes from the same resource, even though individuals feed on varied food sources in other parts of their range and at other times of the year (Tangren 1982, Bayer 1984, Stalmaster 1987). This guild is not a passive gathering of individuals, but rather a highly interdependent assemblage, as we demonstrate below. In this assemblage, only eagles are large enough to open salmon carcasses, and food is available to crows and gulls only when the skin of carcasses is torn. In our experiments we opened carcasses, simulating the natural occurrence of partially eaten carcasses abandoned

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by eagles, thereby making food equally available to all guild members.

We also explore the importance of understanding guild relationships when assessing the effects of human-related activities on wildlife communities. Wildlife viewing and other recreational uses of important wildlife habitats are dramatically increasing (Brockman and Merriam 1973, United States Department of the Interior 1982) and present major challenges to natural resource managers. Our knowledge of the effects of such activities on wildlife communities lags far behind the growing problem. Many studies focus on single species and undertake to measure direct mortality, decreased reproductive success, and reduced populations in preferred habitats (Boyle and Samson 1983, Pomerantz et al. 1988) resulting from human activities. Here we focus on a more subtle effect of disturbance, the alteration of guild relationships.

The major impetus for this study came from concerns over winter recreational use of the Skagit River Bald Eagle Natural Area (SRBENA), northwestern Washington, owned and managed by The Nature Conservancy and the Washington Department of Wildlife (Skagen 1980, Knight and Knight 1984). Since the designation of the SRBENA preserve in 1976, thousands of people have visited the area to view eagles from commercial rafts, kayaks, canoes, and automobiles, and on foot. The increasing popularity of outdoor recreation has also led to substantial increases in human activity in other Bald Eagle wintering areas in the region (Knight et al. 1980).

We examined several hypotheses that postulate the asymmetric foraging relationships of the three guild members and that reveal the influence of competition and facilitation in these relationships. (1) When salmon are abundant, guild members are less likely to shift to alternate food sources than when salmon are scarce. If "coexistence" or concurrent use of a common food resource is possible because of spatial and temporal partitioning of the resources, we expect that (2) spatial patterns of resource use differ between guild members, specifically that guild members differentially use salmon near (<50 m) and far (>100 m) from vegetative cover, and that (3) temporal patterns of resource use differ between guild members. Furthermore, evidence of competition is provided by changes in features of resource utilization, in apparent response to the presence or absence of another species (Diamond 1978, Wiens 1983, 1989, Alatalo et al. 1986). We therefore examined if (4) spatial dimensions of foraging niches change in response to presence or absence of other guild members. We also examined if (5) crows and gulls benefit from feeding with eagles because salmon carcasses are easier to consume once the skin has been torn open.

To reveal the effects of human activity on the foraging relationships of avian scavengers, we tested two additional hypotheses: (6) eagles, crows, and gulls differ

in their responses to human activity with the degree of sensitivity correlating positively with size, and (7) spatial and temporal patterns of resource use by guild members change in response to levels of human activity. Cooke (1980) has demonstrated a positive relationship between flight distances and body size in passerines, and other aspects of life history may also influence behavioral responses. We consider the effects of such differences on the ability of guild members to utilize the food resource.

STUDY AREA AND METHODS

Our study was conducted in December and January 1985–1986 and January 1987 along a 16-km segment (river miles 40.5–50.5) of the North Fork of the Nooksack River, Whatcom County, Washington (48°54' N, 122°08' W). Chum Salmon (*Oncorhynchus keta*) and Coho Salmon (*O. kisutch*) carcasses provide winter food for a transient population of 200–300 Bald Eagles as well as for numerous American Crows and Glaucous-winged Gulls. Other salmon scavengers, collectively consuming <10% of the salmon resource, include Common Ravens (*Corvus corax*), California Gulls (*L. californicus*), Red-tailed Hawks (*Buteo jamaicensis*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), and black bear (*Ursus americanus*). Because salmon carcasses are too heavy (≈ 3.7 kg, Stalmaster and Gessaman 1984) for the avian scavengers to carry away, birds in our study area must feed where salmon are deposited.

We censused birds along the river and in adjacent fields (i.e., "off river") at 4–7 d intervals between 0800 and 1300 Pacific Standard Time from observation points that provided views of nearly 90% of the study area. We recorded species, age class (when possible), location (on or off river, 0.8-km river section), and behavior (feeding, standing, perching, flying) of each individual sighted. We determined relative food abundance weekly by recording the number, position (submerged, partly submerged, exposed), and degree of consumption of every carcass along 20-m wide linear transects along five sloughs. We then calculated a food index (FI) as the number of salmon carcasses (or equivalents) per 100 square metres.

Feeding observations

We selected four observation areas with expansive views of the river where human activity was infrequent. Before first light we removed naturally deposited carcasses of spawned salmon from the observation areas, and arranged 3–5 salmon carcasses (averaging 13.1 kg in total mass [range 8.3–20.2 kg]) at each of two stations, one near (average distance 36 m, range 30–50 m) and one far (average distance 143 m, range 100–200 m) from shoreline vegetation. At each station, carcasses were cut open and half-submerged in water, 2–

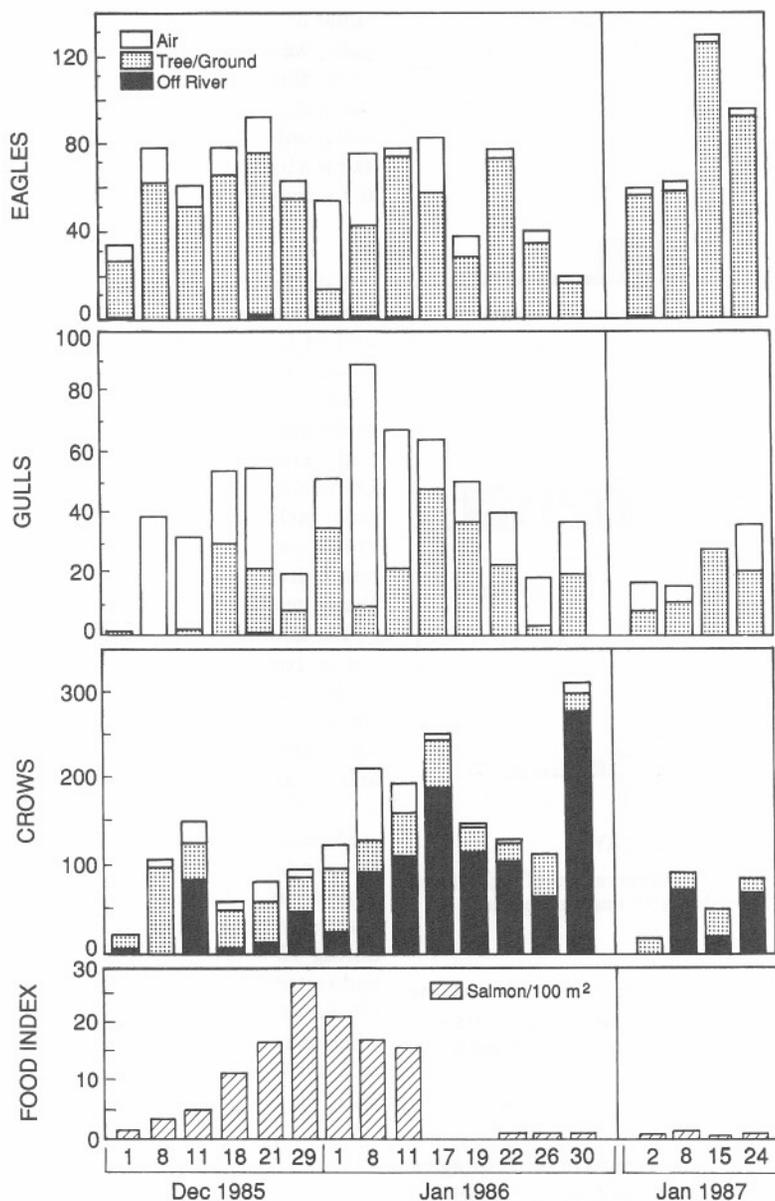


FIG. 1. Abundance and relative distribution of eagles, gulls, and crows, and of food (number of salmon carcasses per 100 square metres) during 18 surveys on the Nooksack River, Washington, December 1985–January 1986 and January 1987. “Off river” = in adjacent fields.

4 m apart. We opened carcasses to simulate carrion fed upon naturally, and to attract birds to areas where we could observe them.

From a blind we recorded the use of the salmon stations by scavengers. At 10-min intervals we recorded the species, behavior (feeding, standing, perched on driftwood, perched in tree, flying), and distance from the salmon carcasses (within 1 m, 1–5 m, 5–15 m, >15 m) of each individual at each station. For each observation area we randomly conducted 5–10 disturbances, during which one observer approached the feeding stations on foot. We recorded the time that elapsed be-

tween flushing and subsequent reuse of the stations by each species.

Between scans we observed foraging interactions for 5 min (after Altmann 1974) to record occurrence and outcome of intra- and interspecific aggressive interactions. We considered an encounter successful when the recipient was displaced from food or space by the aggressor. We also recorded aggressive interactions ad libitum.

To document preferences of crows and gulls for open or intact carcasses, we conducted 23 trials of a choice experiment in which we provided pre-weighed open

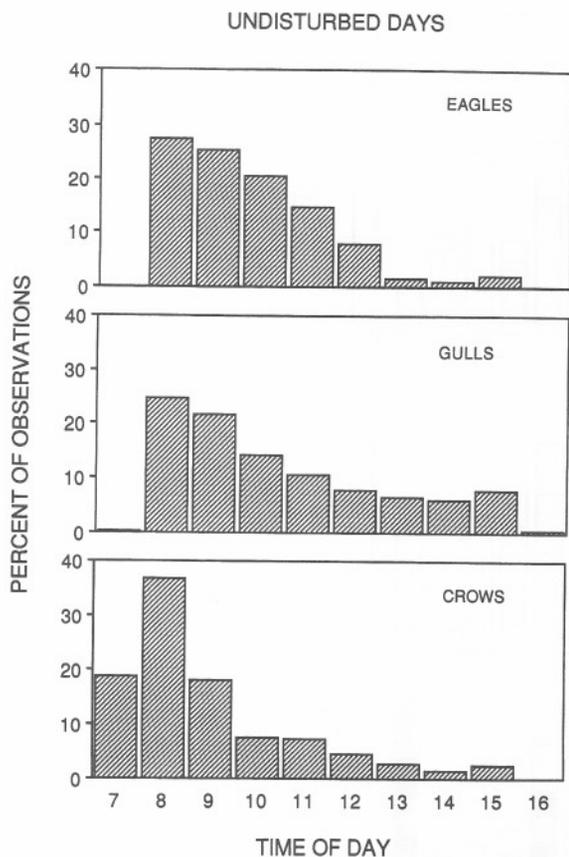


FIG. 2. Percentage of feeding observations of eagles, gulls, and crows from 0730 to 1630 on 10 undisturbed days.

and intact salmon carcasses. We then recorded the number of bites taken from each carcass by crows and gulls and reweighed carcasses at the end of each observation period.

Flight distances

We approached in full view groups of birds foraging on naturally deposited salmon and on carcasses we placed along the river. We recorded group composition (species, numbers), and noted when the first and last bird of each species flew away. We then paced the distances between the observers and the salmon station (or to stone markers placed at 100-m intervals from the salmon) when the birds flew.

Estimates of salmon consumption

We calculated the quantity of salmon consumed by species i as: $S_i = (\text{bird-minutes of feeding})_i \times (\text{bites per bird-minute of feeding})_i \times (\text{grams consumed per bite})_i$. For eagles, the value of 62.5 g/min, derived from foraging data of M.V. Stalmaster (*unpublished manuscript*), was substituted for the last two terms of the

² Hereafter "bird-minutes of feeding" is abbreviated as "bird-min."

equation. Because no such values exist for crows and gulls, we determined the number of bites per minute of feeding by observing videotapes of foraging crows and gulls. To determine salmon consumption per bite, we recorded the number of bites taken from pre-weighed salmon by foraging crows and gulls, and then reweighed the salmon at the end of each observation period.

RESULTS

Bald Eagles were most numerous in our study area between mid-December 1985 and mid-January 1986, and in late-January 1987 (Fig. 1). Gull populations peaked in early to mid-January 1986, and were relatively low throughout January 1987. Crows became more numerous as the 1985–1986 season progressed, and were relatively low in number in January 1987. Of the total birds that were in trees and on the ground (and excluding birds in the air) during the surveys, crows used off-river habitats more often than eagles and gulls ($F = 45.37$, $df = 52$, $P < .0001$, Kruskal-Wallis test); eagles and gulls rarely were seen in fields.

The abundance of salmon carcasses (food index, FI) varied considerably during our study, ranging from 0 to 26.8 salmon/100 m² (Fig. 1). During 14 surveys in the winter of 1985–1986, there was no linear relationship between the number of eagles in the study area and the amount of available food ($F = 1.254$, $df = 13$, $P = .285$). Similarly, gull ($F = 2.496$, $df = 13$, $P = .135$) and crow ($F = 0.004$, $df = 13$, $P = .955$) numbers were independent of food abundance. In support of hypothesis 1, however, the distribution of crows did change in response to variation in food availability during 18 surveys in the study. More crows foraged and rested in fields when salmon carcasses were scarce (76.8% of 1216 crows in 10 surveys when $FI < 3$) than when salmon were more abundant (47.6% of 824 crows in 8 surveys when $FI \geq 3$; $\chi^2 = 184.5$, $df = 1$, $P < .001$; Fig. 1).

Foraging patterns in the absence of human activity

Consistent with hypothesis 3, that temporal patterns of resource use differ, eagles and gulls fed primarily (95.5% and 80.6% of feeding activity, respectively) between 0800 and 1300 (Fig. 2). No eagles and only 1 gull fed before 0800. In contrast, 18.9% of crow feeding activity took place before 0800. Afternoon (1300 until dusk) was less important for feeding by eagles (4.5%), crows (6.9%), and gulls (18.4%). Temporal patterns of feeding activity (grouped into 3 time periods, before 0800, 0800–1259, and 1300 until dusk) differed significantly ($\chi^2 = 262.88$, $df = 4$, $P < .0001$) among species.

When presented a choice, crows and gulls used open rather than intact carcasses in all of 23 trials. On average, $91.5 \pm 5.14\%$ (mean \pm SD; $n = 6875$) of bites by gulls and $86.8 \pm 6.69\%$ ($n = 10876$) of bites by crows were taken from opened salmon, also suggesting

TABLE 1. Number of crows (C), gulls (G), and eagles (E) at stations near and far from shoreline vegetation under conditions of varying species composition in n scan samples on undisturbed mornings.

Species present*	n	Near		Far		t	P †
		\bar{X}	SE	\bar{X}	SE		
C	103	C: 2.1	0.76	9.0	3.25	-2.23	0.027
- G	84	G: 0.2	0.11	1.0	0.34	-2.96	0.004
- E	128	E: 0.5	0.08	1.0	0.20	-2.42	0.016
C G	144	C: 3.1	0.71	8.3	2.45	-2.19	0.029
		G: 0.5	0.12	1.3	0.27	-3.44	0.001
C	237	C: 2.3	0.43	5.0	1.46	-1.95	0.049
		E: 1.1	0.14	1.3	0.17	-1.42	0.152
- G E	185	G: 1.1	0.22	0.8	0.19	1.15	0.250
		E: 0.4	0.06	1.5	0.18	-5.38	<0.001
C G E	371	C: 2.9	0.31	4.5	0.99	1.71	0.083
		G: 1.3	0.15	0.9	0.13	2.10	0.035
		E: 0.9	0.11	1.7	0.14	-5.43	<0.001

* Scan samples were omitted if species represented by dashes were present.

† Level of significance of differences (from t tests on paired data).

that crows and gulls are either unable or reluctant to tear open the skin of salmon carcasses. Additionally, most naturally deposited salmon carcasses showed little or no signs of use when food was relatively abundant. In 71.8% of a sample of 6650 available carcasses, only eyes (averaging $0.32 \pm 0.013\%$ of total salmon body mass, $n = 10$) or small amounts of flesh around the gills and vent had been eaten, and 14.1% of the carcasses were completely intact. The remaining 14.1% of the carcasses were in varying (5–95%) states of consumption, and were probably opened by eagles.

A size-related dominance hierarchy existed among guild members. Eagles were always successful when initiating aggressive interactions with both gulls ($n = 57$) and crows ($n = 57$). Gulls succeeded in displacing crows in 91.0% of 166 gull-initiated encounters, whereas crows successfully displaced gulls in only 25.5% of 51 crow-initiated interactions. Crows and gulls rarely initiated interactions with eagles.

Eagles often landed near or flew low (<10 m) over feeding stations. We recorded responses of 89 groups of crows (averaging 19.4 birds, range: 1–100) and 54 groups of gulls (averaging 5.8 birds, range: 1–15) to eagle movements. On average, 52.3% of crows and 76.6% of gulls flew away and only 21.2% of crows and 41.4% of gulls soon resettled at the station.

Spatial patterns and shifts in resource use

We examined spatial-use patterns of crows, gulls, and eagles in all possible combinations by forming subsets of the scan data according to presence and absence of the three species (Table 1). When only one species was present in the focal feeding area, crows, gulls, and eagles all exhibited a preference for the feeding station far from shoreline (i.e., significantly more birds were present at far stations, Table 1). When all species were potentially present (the entire scan data set was used), gulls shifted in numbers to the near

station (Table 1). Overall, eagles spent more time ($t = 3.84$, $df = 15$, $P < .005$) feeding at the station far from shoreline cover, whereas gulls spent more time ($t = 3.06$, $df = 15$, $P < .01$) feeding near shoreline cover (Fig. 3). Although crows were more prevalent at far stations ($P = .083$, Table 1), feeding by crows was fairly equal at the two types of stations ($t = 0.52$, $df = 15$, $P < .50$).

Gulls and eagles were negatively associated at both near and far stations (Table 2). In contrast, crows were positively associated with gulls at stations near shoreline when eagles were absent, and positively associated at stations with eagles near shoreline when eagles were present. Crows were unassociated with other species at far stations.

To view spatial patterns on a smaller scale, we inspected behavior and distribution of crows and gulls around the carcasses relative to the presence or absence of eagles (when 0 eagles, 1–2 eagles, and ≥ 3 eagles were

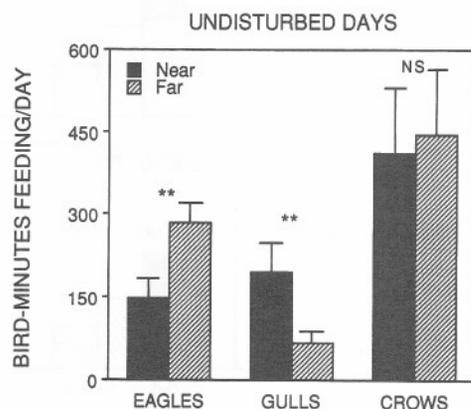


FIG. 3. Feeding effort (bird-minutes of feeding per day) by eagles, gulls, and crows at stations near (<50 m) and far (>100 m) from shoreline cover in absence of human activity ($n = 16$ d). Data are means + 1 SE. ** $P < .01$, NS=not significant (t tests).

TABLE 2. Associations (r) of crows (C), gulls (G), and eagles (E) at feeding stations near and far from shoreline vegetation. n represents the number of scan samples of four combinations of species on undisturbed mornings.

Species present†			n	Species compared	Cover proximity	
					Near	Far
C	G	-	144	C:G	0.254**	-0.011
C	-	E	237	C:E	0.164*	-0.059
-	G	E	185	G:E	-0.144*	-0.066
C	G	E	371	C:G	0.039	0.020
				G:E	-0.157**	-0.102*
				C:E	0.105*	0.074
				C:(G + E)	0.103*	-0.042
				G:(C + E)	-0.003	0.006
				E:(C + G)	-0.070	0.087

* $P < .05$, ** $P < .01$ (significance of r).

† Scan samples were omitted if species represented by dashes were present.

present at feeding stations) on undisturbed mornings. Distributions of gulls and crows around salmon carcasses changed significantly in response to the presence of eagles ($\chi^2 = 46.6$, $df = 4$, $P < .001$ and $\chi^2 = 228.8$, $df = 4$, $P < .0001$ for gulls and crows, respectively; Fig. 4a,b). When no eagles were present, 60.8% of gulls and 51.2% of crows were within 1 m of the salmon,

whereas only 25.0% of gulls and 26.3% of crows were within 1 m when >2 eagles were present. Furthermore, feeding activity by gulls and crows at the stations also varied inversely with the number of eagles ($\chi^2 = 17.14$, $df = 2$, $P < .001$ and $\chi^2 = 36.13$, $df = 2$, $P < .001$ for gulls and crows, respectively; Fig. 4a,b). In the absence of eagles, the distribution and feeding behavior of crows

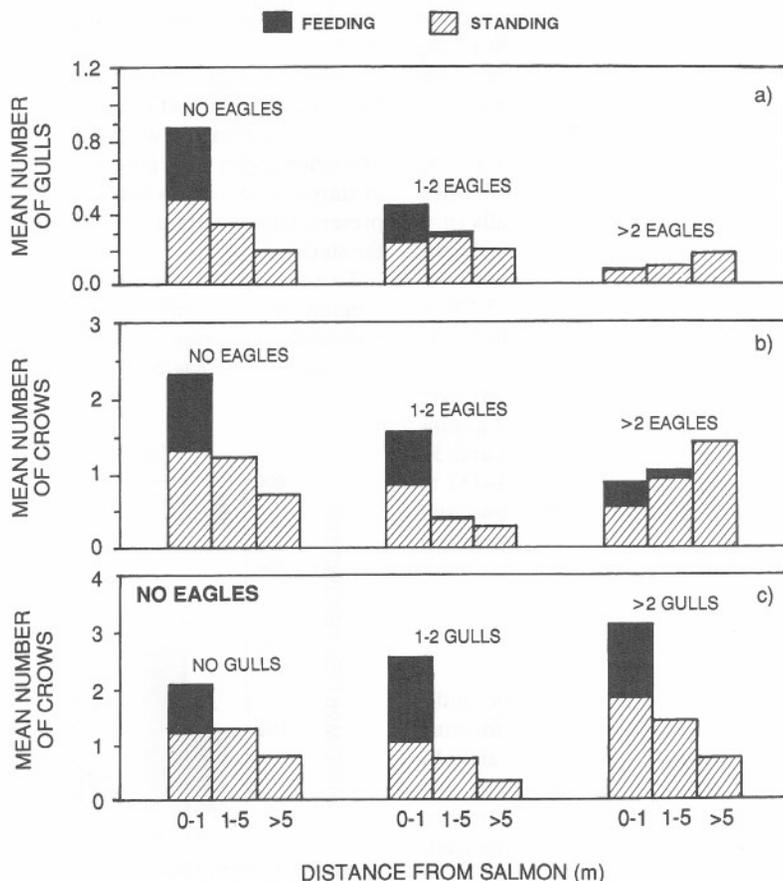


FIG. 4. Numbers, behavior, and distribution of (a) gulls and (b) crows at salmon stations relative to the presence of Bald Eagles. Only undisturbed, morning scan samples ($n = 446$, 153, and 143) are represented. (c) Numbers, behavior, and distribution of crows at salmon stations relative to the presence of gulls, in the absence of Bald Eagles.

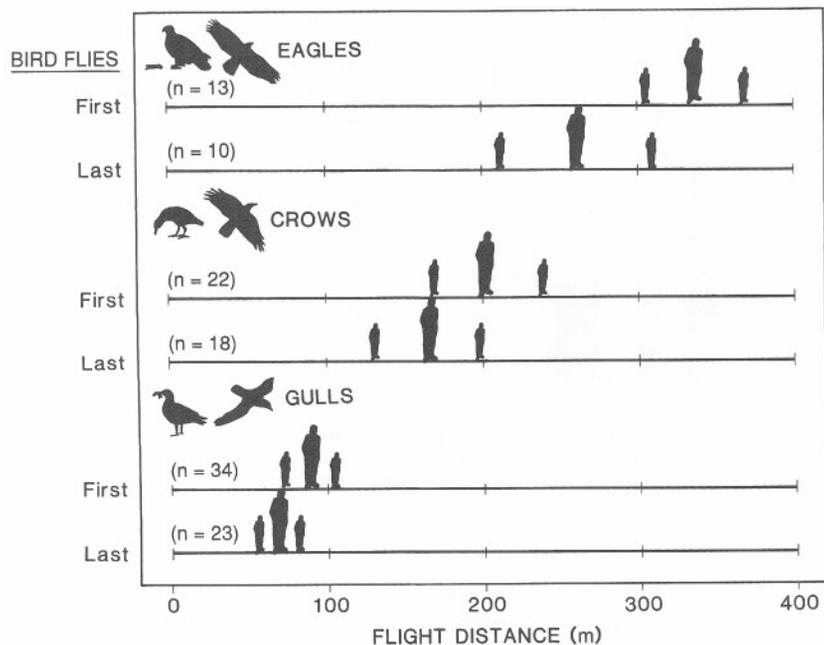


FIG. 5. Flight distances (mean and 95% CI represented by large and small persons, respectively) of the first and last birds of foraging groups of eagles, crows, and gulls to fly in response to approach of people on foot. n = sample sizes of first and last birds to respond.

did not change as gull numbers increased from 0–2 to >2 ($\chi^2 = 0.881$, $df = 2$, $P = .64$, and $\chi^2 = 0.370$, $df = 1$, $P = .54$ for distribution and feeding, respectively; Fig. 4c).

Changes in guild relationships due to human activity

We recorded flight distances for 13 groups of eagles (average group size 3.2 ± 0.54 birds [$\bar{X} \pm SD$]), 22 groups of crows (average size 7.7 ± 2.26 birds), and 34 groups of gulls (average size 6.3 ± 1.21 birds). The first eagle to fly in response to an approaching human did so at a significantly greater distance (337.9 ± 15.9 m) ($F = 71.64$, $df = 66$, $P < .001$) than did the first crow (201.9 ± 18.3 m), which in turn flew at a greater distance from humans than the first gull (90.3 ± 8.66 m; Fig. 5). The same trend held for the last bird of a group to fly ($F = 38.79$, $df = 48$, $P < .0001$).

After a disturbance, eagles seldom returned to feed that day, so we were unable to record subsequent use of a feeding station by eagles effectively. Gulls returned to stations within 7.3 ± 0.91 min ($n = 38$), which was sooner ($F = 9.74$, $df = 59$, $P < .001$) than crows (15.5 ± 3.04 min, $n = 23$).

Eagles fed at a site more on days of no disturbance than days when feeding was disrupted ($t = 7.60$, $df = 43$, $P < .0001$; Fig. 6). Although there was a 10-fold difference in feeding effort by eagles between undisturbed and disturbed days, the relative proportion of feeding effort at the far station remained the same (68.0% of 434.4 bird-min/d and 70.2% of 43.9 bird-

min/d; Fig. 7). In contrast, disturbance appeared to enhance feeding opportunities for gulls ($t = 5.37$, $df = 43$, $P < .0001$), especially at the far station. When undisturbed, 26.5% of the average feeding effort of gulls (264.3 bird-min/d) occurred at the far station, whereas 55.5% of an average of 1607.5 bird-min/d occurred at the far station on disturbed days. Crows did not feed more when undisturbed ($t = 1.25$, $df = 43$, $P > .10$) nor did their distribution at near and far stations change (51.7% of 857.5 bird-min/d vs. 48.7% of 625.7 bird-min/d).

Eagles, gulls, and crows fed more in the afternoons

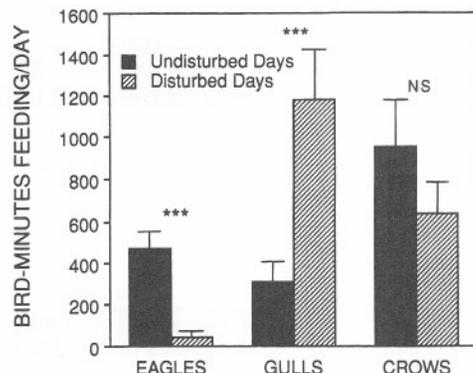


FIG. 6. Feeding effort (bird-minutes of feeding per day) by eagles, gulls, and crows on 16 undisturbed and 28 disturbed days. Data are means + 1 SE. *** $P < .001$, NS = not significant (t tests).

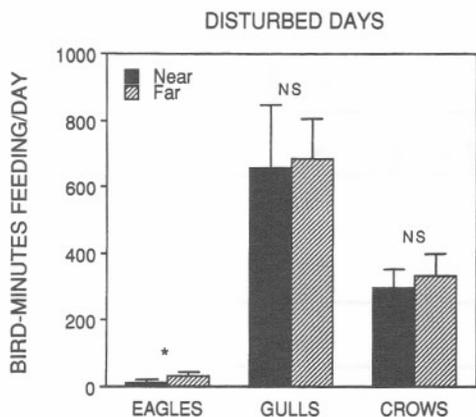


FIG. 7. Feeding effort (bird-minutes of feeding per day) by eagles, gulls, and crows at stations near and far from shoreline cover on 28 disturbed days. Data are means +1 SE. * $P < .05$, NS = not significant (t tests).

on disturbed days (Fig. 8) than on days with no disturbance (Fig. 2) (34.8% vs. 4.5%, 41.0% vs. 10.1%, and 31.4% vs. 6.9% for eagles, gulls, and crows, respectively; $\chi^2 = 89.27, 52.68, \text{ and } 211.99, df = 1, P < .001$).

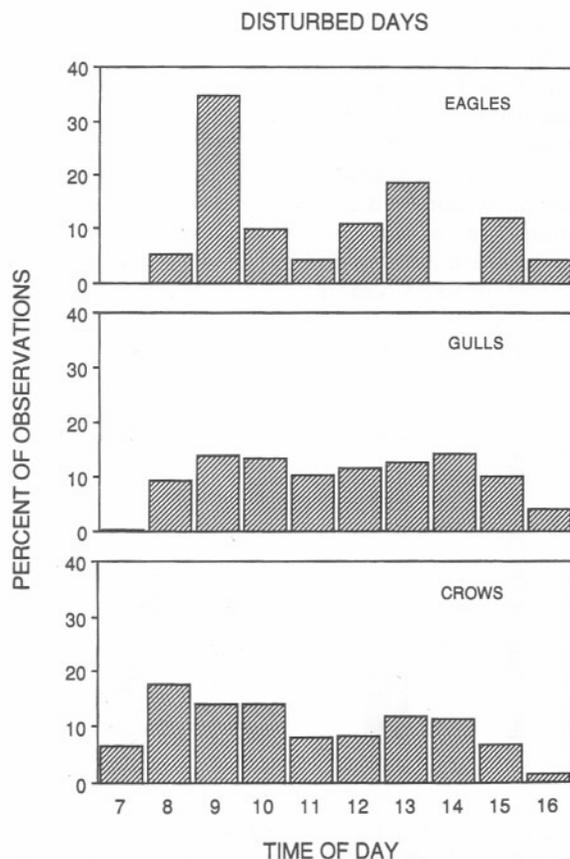


FIG. 8. Percentage of feeding observations of eagles, crows, and gulls from 0730 to 1630 on 25 disturbed days.

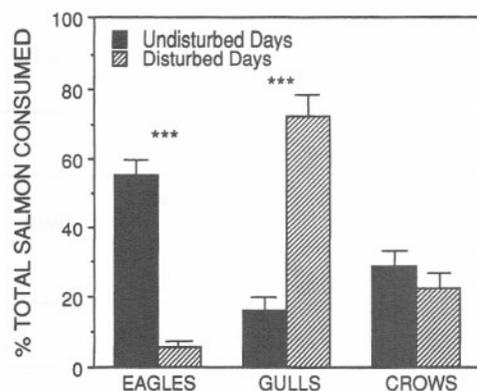


FIG. 9. Estimated percentage of open salmon carcasses consumed by eagles, gulls, and crows relative to human disturbance. Data are means +1 SE. *** $P < .001$, NS = not significant (t tests).

Effects of disturbance on salmon consumption patterns

On average, individual gulls took 23.8 bites/min ($n = 103$) and crows took 28.9 bites/min ($n = 130$) of feeding on opened carcasses. Gulls consumed 1.3 ± 0.14 g/bite ($\bar{X} \pm SD, n = 25$) and crows 0.6 ± 0.13 g/bite ($n = 9$). Because consumption from intact carcasses by crows and gulls was negligible, we were unable to determine rates.

The total amount of salmon consumed by crows, gulls, and eagles at the feeding stations did not differ between disturbed days and undisturbed days ($t = 0.66, df = 42, P = .51$), but the relative amounts consumed by the guild members did vary. We estimate that eagles ate only 5.7% of the salmon consumed on disturbed days in contrast to 55.3% on undisturbed days (Fig. 9; $t = 11.72, df = 42, P < .0001$). Gulls accounted for nearly 72.1% of the daily salmon consumption when disturbed and only 16.0% when undisturbed ($t = 9.48, df = 42, P < .0001$). Consumption by crows did not vary significantly in response to disturbance (28.6% when undisturbed, 22.2% when disturbed; $t = 1.11, df = 42, P = .275$).

DISCUSSION

Feeding within guilds or other mixed-species groups may enhance foraging efficiency or anti-predator defenses. Increased foraging efficiency is accomplished in several ways, including enhancement of food availability (flushing of prey by groups of insectivorous birds [Perrins and Birkhead 1983:179], larger guild members opening carcasses for subordinates [Hewson 1981, Wallace and Temple 1987]), and interspecific aid in locating food (eagles using crows to locate food [Knight and Knight 1983]).

Foraging efficiency of crows and gulls is enhanced by associating with eagles, which are necessary to open carcasses. Other scavenging guilds in which actions of one species enhance the foraging efficiency of other

species include mammalian carnivores and gulls (Hewson 1981) and New World Vultures (Wallace and Temple 1987). The primary disadvantage to crows and gulls of associating with eagles, however, is interference with foraging. Crows and gulls avoided feeding at stations with many eagles present, and many deserted the salmon when eagles approached the stations. Interspecific dominance hierarchies, responsible for this interference, occur among other foraging guilds, for example insectivorous birds (Perrins and Birkhead 1983) and Old World and New World Vultures (Kruuk 1967, Houston 1975, Wallace and Temple 1987).

Another possible advantage to interspecific foraging groups is increased vigilance to detect predators. Black-headed Gulls (*Larus ridibundus*) provide early warning to Lapwings (*Vanellus vanellus*) and Greater Golden-Plovers (*Pluvialis apricaria*) (Thompson and Barnard 1983). Two lines of evidence strongly suggest that eagles avoid feeding in places where danger from people or other large mammals is high. First, eagles exhibited a strong preference for feeding stations far from shoreline vegetation, and they flew away from humans approaching from distances exceeding that of the stations from shoreline. Second, the increased vigilance of eagles feeding near shoreline and in disturbed areas (Knight and Knight 1986) suggests that birds feed more efficiently when farther from danger.

We have only minimal evidence at this time to address anti-predator defenses in the salmon-scavenging guild. All three species preferred the station far from cover, suggesting that predation is a consideration in choice of foraging location. Crows and eagles were positively associated when feeding at near but not at far stations (Table 2), suggesting a possible predation defense benefit to one or both species of this association. We also noted that eagles feeding with crows often look up from feeding when crows suddenly fly away.

Patterns of guild structure

Experimental evidence of shifts in the time and locations of use of food resources can be a strong indication of the role of competition in structuring foraging guilds (Alatalo et al. 1985, Alatalo et al. 1987). Our study experimentally examined foraging shifts on several scales, including changes in behavior, microhabitat use, and habitat use. The interpretation of such experiments is simplified if presence or absence of the putative competitors is the only factor varying between experimental and control sites (Alatalo et al. 1986), as we believe is the case here. When present alone, eagles, crows, and gulls preferred feeding at stations far from shoreline cover. Both gulls and crows altered microhabitat choices and feeding behavior in response to the presence of eagles. Because eagles are socially dominant to gulls, gulls fed near the shoreline when eagles were present. Because there was substantial temporal overlap in feeding by eagles and gulls, this spatial shift by

gulls may be especially important in promoting coexistence.

Crows, the most subordinate guild member, exhibited the most flexibility. Many crows arrived at feeding areas early, presumably to feed on scraps and carcasses opened the previous day without interference from the two dominant guild members. Crows used both near and far stations when gulls and eagles were present, but were farther from carcasses and fed less when eagle numbers increased. Crows also shifted to off-river areas when food resources were scarce.

An alternative explanation for the observed spatial shifts, that subordinates perceive eagles as potential predators, would affect the intensity but not the direction of their responses. Although intraguild predation can be important in structuring guilds when food availability is low (e.g., desert scorpions, Polis and McCormick 1987), and eagles prey on gulls in other seasons and locations (S. Skagen, R. L. Knight, and G. H. Orrians, *personal observation*), we did not see evidence of gull predation by eagles during our study.

If birds fed elsewhere when food was depleted at our feeding stations, we may have underestimated afternoon feeding effort. Stalmaster and Gessaman (1984) established, however, that eagles forage primarily in the morning.

Management implications of foraging changes

A guild approach can bring useful insights to management perspectives and practices. This paper focuses on interactions among species that might otherwise not be suspected because the interactors are not closely related. In the salmon-scavenging guild, for example, human recreational activity favors consumption of open salmon carcasses by the more tolerant guild members. We predict that in areas of frequent human disturbance, densities of gulls and crows would increase in response to the greater availability of partly consumed salmon carcasses abandoned by eagles. This becomes increasingly important as food supplies diminish. In many winters, flood waters wash carcasses downstream and eliminate the food supply. If floods occur early in the spawning season, carcasses become available once flood waters recede, whereas late-season floods generally mark the end of salmon abundance. Periodic cold weather and heavy snowfalls freeze or cover carcasses, rendering them inaccessible to scavengers. In assessing food resources for threatened populations of Bald Eagles, consideration should be given not only to the effects of diminishing natural salmon runs in the Pacific Northwest rivers, but also to the interacting factors of floods, increasing human disturbance, and increases in crow and gull populations.

Shifts in the timing and spacing of resource use may be especially important in highly fragmented landscapes with disjunct areas of suitable habitat. Fragmentation or separation of suitable habitat patches may

make it much more difficult for subordinate species to find and utilize other patches. This fragmentation was not a problem for the crows in this study because pastures close to the river provided alternate food sources when salmon were scarce.

This study illustrates the importance of examining the more subtle effects of wildlife viewing, a flourishing recreational activity that is generally regarded as compatible with wildlife protection. Many people view wildlife because of a strong interest or concern for the resource, yet the possible detrimental effects of human presence are often undetected. In a 1987 survey of 381 anglers and eagle viewers along the Skagit River, Washington, only 5% considered their activity a frequent disturbance to eagles (Stalmaster 1989:668). Clearly, the ethics of wildlife viewing need to consider subtle negative effects of viewing activities.

*Applications of guild theory:
a perspective*

Since the guild concept was introduced in ecological studies (Root 1967), ecologists have actively pursued theoretical and empirical studies of resource partitioning among guild members (Schoener 1974). The aims of many of these studies were to describe community patterns and to elucidate the evolutionary processes and causal mechanisms underlying these patterns. Interpretations of findings were based on the assumption that populations or communities are saturated and in equilibrium (Wiens 1989).

Recently, guild theory was proposed as a promising tool for environmental assessment and management (Severinghaus 1981, Landres 1983), with early attention paid to the effects of forestry practices on vertebrate communities (Mannan et al. 1984, Verner 1984, Szaro 1986, Karr 1987). This recent application of guild theory differs from earlier ecological studies in several ways. First, the major goal of such applications is to develop predictive models that enable resource managers to assess the effects of management regimes rather than to understand evolutionary history and process. Second, the assumption of community stability and equilibrium is clearly inappropriate in the face of dynamic and extensive human-induced perturbations. Third, as a means of streamlining assessment tasks, groups of species are administratively designated as "management guilds" (Severinghaus 1981, Verner 1984:3) based on similar responses to environmental change rather than similarities in resource use (Root 1967, Jaksić 1981, MacMahon et al. 1981). This grouping mechanism, however, can mask important ecological relationships.

In contrast to the management-guild approach, our study emphasizes the importance of examining intra-guild dynamics, dominance relationships, and differences in species' responses to environmental changes. Human disturbance of natural communities is proceeding at an unprecedented pace, and this study

clearly shows that wildlife viewing, although generally well-intended, can subtly disrupt community dynamics. Species differences in responses to human disturbances could lead to unexpected changes in the abilities of some guild members to persist in the face of human activity.

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