

SPECIES ROLES IN MIXED-SPECIES FEEDING FLOCKS OF SEABIRDS

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Abstract.—Seabirds form mixed-species flocks above schools of juvenile Pacific Herring (*Clupea harengus pallasii*) in Barkley Sound, British Columbia. In 1983 each species played a unique and consistent role in flocks. Gulls initiated 57.1% of the flocks observed, and diving seabirds the remainder. Pursuit diving by Common Murres (*Uria aalge*) and Marbled Murrelets (*Brachyramphus marmoratus*) enhances foraging by gulls. Flocks with Common Murres were larger and more persistent than those without, but Marbled Murrelets participated in the smallest flocks, possibly to minimize disturbance from other species. Pelagic Cormorants (*Phalacrocorax pelagicus*) joined 45.1% of mixed flocks, but initiated only one flock and contributed little to the maintenance of flocks. The small-bodied California (*Larus californicus*) and Heermann's (*L. heermanni*) gulls were found most often among early arrivals when flocks formed, whereas the larger Glaucous-winged Gull (*L. glaucescens*) commonly arrived later.

EL ROL DE ALGUNAS ESPECIES DE AVES MARINAS, CUANDO SE ALIMENTAN EN GRUPOS MIXTOS

Sinopsis.—En un estudio que se llevó a cabo en Barkley Sound (Columbia Británica), se observó a grupos mixtos de aves marinas sobrevolar escuelas de juveniles de arenques (*Clupea harengus pallasii*). Durante el 1983 cada especie de ave tuvo un rol particular en el grupo. Las gaviotas iniciaron la formación de los grupos en el 57.1% de las veces, y las aves zambullidoras en el restante por ciento. La persecución bajo el agua por parte de *Uria aalge* y *Brachyramphus marmoratus*, acrecentó el forrageo por parte de las gaviotas. Grupos con individuos de *Uria aalge* resultaron ser más grandes y persistentes que bandadas sin estas aves. *B. marmoratus* participó en las bandadas más pequeñas, posiblemente para minimizar el disturbio por parte de otras especies de aves. El cormoran (*Phalacrocorax pelagicus*) se unió al 45.1% de las bandadas, pero tan solo comenzó un grupo y contribuyó muy poco al mantenimiento de las bandadas. Las gaviotas de poco tamaño como *Larus californicus* y *L. heermanni* se encontraron entre las especies pioneras en la formación de grupos, mientras que especies de mayor tamaño como *L. glaucescens*, por lo general, se unieron tarde a los grupos.

In Barkley Sound, British Columbia, seabirds form mixed-species flocks over schools of juvenile Pacific Herring (*Clupea harengus pallasii*). Our objective was to clarify the role that each species played in these flocks, emphasizing the numerically dominant gulls. In contrast to the momentary observations of feeding flocks from moving vessels that characterized many earlier studies of seabird flocks (e.g., Ashmole and Ashmole 1967, King 1970, Martin and Myres 1969), the current study adopted a more intensive approach. Each flock was observed from initiation until the participants dispersed after they ceased feeding.

Birds often feed in mixed-species associations that differ in the complexity of interactions between and among individuals. The simplest case

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involves birds of several species aggregating around a common resource, such as a swarm of army ants in the neotropics (Willis 1966). The most complex mixed-species flocks are those in which individuals forage together for cryptic, depletable prey. Many flocks of insectivorous passerines foraging in tropical forests limit attendance to one or two individuals of each species (e.g., Bell 1983, Jones 1977, Macdonald and Henderson 1977, Munn and Terborgh 1979, Powell 1979).

Mixed-species flocks of seabirds are somewhere near the midpoint of this complexity spectrum. Flocks form only after food has been discovered, but initiation and maintenance nevertheless are functions of the interactions between individuals. Flocks in Barkley Sound are relatively small, form over clumped food sources, are generally limited to inshore waters, and persist for no more than a few minutes (Porter and Sealy 1981, 1982), characteristics of Type I flocks (Hoffman et al. 1981).

STUDY AREA

Barkley Sound is the largest embayment on the southwest coast of Vancouver Island, British Columbia, Canada (see maps in Porter and Sealy 1981, Sealy and Carter 1984). The Sound supports breeding populations of Pelagic Cormorants (*Phalacrocorax pelagicus*), Glaucous-winged Gulls (*Larus glaucescens*), Marbled Murrelets (*Brachyramphus marmoratus*), and Pigeon Guillemots (*Cephus columba*). It is also an important post-breeding staging area for Common Murres (*Uria aalge*) and California (*L. californicus*) and Heermann's (*L. heermanni*) gulls (see Carter et al. 1984, Hatler et al. 1978).

METHODS

Most of our observations were made from an elevated position on southeast Sandford Island (68°52'N, 125°12'W), but some comparative observations were made from the top of unforested Taylor Islet (68°50'N, 125°12'W). Thirty-two d (159 h 25 min) of observations were made between 11 Jun. and 27 Oct. 1983. We attempted to record details of all feeding flocks within one km of the observation sites.

The flock initiator, time of initiation, duration, and the sequence of arrival of each participant were recorded. All participants were identified to species, and gulls were further identified to age class by plumage characteristics (Dwight 1925). Adult gulls were defined by their definitive plumage. Subadults were in at least their second calendar year, having not yet attained definitive plumage. Hatch-year birds were the products of the current breeding season.

Variation in flock size and persistence in the presence and absence of the most abundant flocking species was analyzed with two-sample *t*-tests. For each flock for which the sequence of arrival of each gull was documented, individuals were classified as either first-half or second-half arrivals around the median participant. Species and age class differences in timing of arrival were then examined with chi-square analysis.

TABLE 1. Species and age of individuals that initiated mixed-species feeding flocks in Barkley Sound, British Columbia ($n = 63$).

Species and age-class	Flocks initiated
Pursuit Divers	
Common Loon	1
Pelagic Cormorant	1
Common Murre	15
Marbled Murrelet	10
Total	27
Gulls	
Heermann's Gull	1
Mew Gull	1
Subadult California Gull	1
Adult California Gull	1
California Gull, unknown age	10
Subadult Glaucous-winged Gull	1
Adult Glaucous-winged Gull	5
Glaucous-winged Gull, unknown age	3
Total	36

RESULTS

One hundred and eight mixed-species feeding flocks were observed; 97 from Sandford Island, and 11 from Taylor Islet. On average, flocks persisted for 6.3 min, while mean attendance was 47.7 gulls of 2.1 species, and 5.8 non-larids of 1.3 species. The identity of the species of the individuals that initiated 63 flocks was known (Table 1). Of these, 57.1% were initiated by gulls, and 39.7% by alcids. In seven cases, the term "initiator" was not appropriate because large numbers of birds rested near the fish school as it ascended in the water column. Discovery by these individuals was essentially simultaneous.

Table 2 illustrates the differences in flock size and persistence with and without Common Murres, Marbled Murrelets, and Pelagic Cormorants. Gulls were present in all flocks, and so comparison of this sort is not possible.

When Common Murres were present in flocks, total attendance was greater ($t = 4.21$, $P < 0.001$) and flocks persisted longer ($t = 2.30$, $P < 0.025$) than when they were absent. Marbled Murrelets, on the other hand, were found in smaller flocks ($t = 4.59$, $P < 0.001$) that persisted for a shorter time ($t = 1.80$, $P < 0.1$). Pelagic Cormorants were found in larger ($t = 4.15$, $P < 0.001$), more persistent ($t = 3.21$, $P < 0.0025$) flocks.

The order of arrival of every participating gull was known for 38 feeding flocks. Of the three most common larid species (Table 3), Heermann's and California gulls were found more often among early arrivals ($\chi^2 = 17.334$, $P < 0.005$). Adult birds were more common among early arrivals, while birds of combined hatch-year and subadult age classes entered flocks later (Table 4) ($\chi^2 = 19.93$, $P < 0.005$).

TABLE 2. Flock size and persistence in the presence and absence of Common Murres, Marbled Murrelets, and Pelagic Cormorants.

Species	Flock size		Flock duration (min)	
	Mean	<i>n</i>	Mean	<i>n</i>
Common Murre				
Present	79.0	46	7.8	46
Absent	17.3	52	4.1	50
Marbled Murrelet				
Present	22.1	17	4.8	17
	10.1 ^a	16	3.6 ^a	16
Absent	51.3	79	6.1	79
Pelagic Cormorant				
Present	82.2	42	8.7	45
Absent	18.9	56	3.6	52

^a Flock 18 eliminated (see text).

DISCUSSION

Moynihan (1962) studied mixed-species bird flocks in Panama, and found that each commonly occurring species played a characteristic and consistent role. Hoffman et al. (1981) devised a system of classification with specific reference to seabird feeding flocks. "Catalysts" are those species whose feeding behavior is highly visible to others. Catalysts usually initiate feeding flocks, and other flocking species use catalysts as indicators of feeding situations. Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous-winged Gulls were the most important flock initiators in seabird flocks in Alaska (Hoffman et al. 1981). The "divers" group includes those species that employ pursuit-diving and pursuit-plunging in prey capture. "Kleptoparasites" pirate food from other birds. The feeding behavior of flock "suppressors" decreases the availability of prey to other flock members.

Generally it is unclear what drives prey to the surface in Type I seabird feeding flocks. Most workers suggest that it is large predatory fish (e.g., Baltz and Morejohn 1977, Feare 1981, Sealy 1973). Indeed, in many cases, the concentrating agent for Barkley Sound flocks could only have been predatory fish. In several other studies (e.g., Bartholomew 1942, Grover and Olla 1983, Munro and Clemens 1931), the principal agent forcing small fish to the surface was pursuit by diving seabirds.

Flocks in which Common Murres participated were considerably larger and persisted longer than those in which they did not participate. Mean flock attendance by murres was only 4.2, and so the difference in flock size must be explained by variable participation by other species. This suggests that Common Murres enhanced the foraging of other seabirds, particularly the surface-feeding gulls. Underwater pursuit by murres probably caused fish schools to surface. As a case in point, flock 18 (5 September), initiated by a single Marbled Murrelet, was attended by

TABLE 3. Number of gulls in first-half and second-half arrivals to 38 mixed-species feeding flocks.

Species	Arrivals	
	First-half	Second-half
Heermann's Gull	40	30
California Gull	86	51
Glaucous-winged Gull	117	161

only 11 gulls, but after 70 murrees had arrived, the number of gulls in attendance rose to 119.

Common Murrees are important flock initiators, being first in attendance at 23.8% of feeding flocks. They do not fulfill the second requirement of Hoffman et al.'s (1981) "catalyst" category; their plumage is dull and their pursuit-diving is not as visible at a distance as the plunge-diving of gulls.

Another diving seabird with an important role as an initiator (15.9% of flocks) was the Marbled Murrelet. Flocks with murrelets were less persistent with fewer participants than those in which they did not participate. With their low attendance (maximum three), it is unlikely that murrelets suppressed flocking. Although surface feeding can be facilitated by the pursuit-diving of Marbled Murrelets, we believe that murrelets enter small flocks to minimize disturbance from larger, more numerous, and possibly more aggressive individuals of other species.

The diet of the Pelagic Cormorant consists mainly of nonschooling fish that are found in close contact with rocky substrates or kelp beds (Ainley et al. 1981, Robertson 1974). This species participates in mixed-species feeding flocks opportunistically, and did so in 45.1% of flocks observed in 1983. They entered the largest flocks which persisted the longest, but unlike Common Murrees, they apparently did not enhance the foraging of individuals of other species. Alcids generally foraged from the periphery of the flock (see also Porter and Sealy 1982), possibly to decrease the incidence of kleptoparasitism by gulls. This behavior may delay the descent of schooling fish in the water column (Hoffman et al. 1981). Pelagic Cormorants, on the other hand, dived from the center of the flock (see also Porter and Sealy 1982).

With only one recorded initiation, Pelagic Cormorants did not play a major role in discovering herring schools. With limited participation (maximum five) and dull plumage, this cormorant was neither a "catalyst" nor a "diver" that enhanced surface foraging. A closer examination of Pelagic Cormorant feeding behavior may reveal them to be flock "suppressors."

In general, foraging seabirds of different species are dispersed in terms of the depth at which they forage and the distances they fly to search for food (Furness and Birkhead 1984, Pearson 1968). When these species come together to feed on schools of fish, the potential for competition

TABLE 4. Combined number of California and Glaucous-winged gulls of different age classes in first-half and second-half arrivals to 38 mixed-species feeding flocks.

Age class	Arrivals	
	First-half	Second-half
Adult	167	133
Hatch-year and subadult	36	79

becomes more apparent. In some situations, gulls of different sizes may be able to use food of different sizes within a given region (Hunt and Hunt 1973), but in this case, one prey species of one age class is being captured by similar foraging techniques (see also Sealy 1973). In those feeding situations where food may be most easily obtained, large-bodied gulls may dominate the smaller species. When comparing first-half and second-half arrivals (Table 3), it seems that Glaucous-winged Gulls may have adopted an assessment approach, judging the quality of flocks before leaving terrestrial roosting sites. The smaller-bodied Heermann's and California gulls may avoid competitive interactions by entering flocks early while attendance is low.

Many studies have demonstrated that the foraging skills of waterbirds improve with age (e.g., Bayer 1983, Dunn 1972, Searcy 1978). Porter and Sealy (1982) found that adult California Gulls had significantly greater percent capture success in mixed-species feeding flocks than their younger conspecifics. This may help to explain why adult gulls joined feeding flocks earlier than younger birds in the current study (Table 4). While adult birds await flock-feeding opportunities, young birds may concentrate their efforts on some other feeding activity, such as intertidal foraging, and so, join flocks later. This sort of behavior was documented by Burger and Gochfeld (1983); young Laughing Gulls (*L. atricilla*) foraged in situations where their feeding success most closely approximated that of adults.

An El Niño event is described as the appearance and persistence of anomalously warm water in the Eastern Tropical Pacific (Barber and Chavez 1983). An intense El Niño began in 1982 and persisted through 1983. This event resulted in widespread seabird mortality and nesting failure (Hodder and Graybill 1985, Schreiber and Schreiber 1984). While the breeding success of seabirds other than Pelagic Cormorants was not specifically documented in Barkley Sound in 1983, fledging hatch-year birds of all flocking species were observed in the Sound (pers. obs.). The El Niño was not thought to have influenced flocking behavior in Barkley Sound in 1983.

Each species of seabird foraging in flocks of mixed composition plays a unique and consistent role. An analysis of flocks in Barkley Sound has allowed us to elucidate these roles. Adult gulls have conspicuous white plumage, and when combined with their plunge-diving, they serve "as an automatic signalling device indicating to other individuals areas in

which a comparatively abundant food supply is temporarily available" (Armstrong 1971). Hoffman et al. (1981) describe gulls as flock "catalysts." Common Murres and Marbled Murrelets have dull plumage and forage inconspicuously by plunge diving, yet they were important flock initiators. Pelagic Cormorants are "divers," but neither initiate flocks, nor enhance foraging by gulls. Because of the complexity of interactions, it is difficult to categorize species of seabirds according to their roles in feeding flocks.

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