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# SHORT COMMUNICATIONS

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## PASSIVE INTERFERENCE COMPETITION BY GLAUCOUS-WINGED GULLS ON BLACK-LEGGED KITTIWAKES: A COST OF FEEDING IN FLOCKS

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*Abstract.* We analyzed data from two independent studies of foraging Black-legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound, Alaska. Our purpose was to determine if Glaucous-winged Gulls (*Larus glaucescens*) hindered prey capture by kittiwakes. At tightly aggregated feeding flocks, gulls remained on the water directly over the prey and foraged by making brief hop-plunges or surface-seizes. Kittiwakes, in contrast, fed by diving from the air into open spots in the flock or around its periphery. Data from both studies indicated that kittiwakes made fewer feeding attempts in flocks that had greater numbers of gulls. However, kittiwake success rate per feeding attempt did not change as the number of gulls increased. Kittiwakes were more likely to avoid flocks that had a greater number of Glaucous-winged Gulls. Gulls successfully pirated less than 1% of fish captured by kittiwakes. Our findings suggest that passive interference may be costly for smaller birds that feed in multispecies feeding flocks.

*Key words:* *Black-legged Kittiwake, Glaucous-winged Gull, multispecies feeding flocks, passive interference competition, Prince William Sound.*

### Competencia por Interferencia Pasiva de *Larus glaucescens* sobre *Rissa tridactyla*: El Costo del Forrajeo en Grupo

*Resumen.* Analizamos datos de dos estudios independientes sobre forrajeo de *Rissa tridactyla* en Prince William Sound, Alaska. El propósito de nuestro estudio fue determinar si *Larus glaucescens* impedía la captura de presas por parte de *R. tridactyla.* Las gaviotas permanecieron sobre el agua directamente sobre sus presas en bandadas de forrajeo altamente agregadas y forrajearon realizando zambullidos breves o capturas de superficie. En contraste *R. tridactyla* forrajeó lanzándose desde el aire a espacios abiertos entre la bandada o en su periferia. Los datos de ambos estudios indicaron que *R. tridactyla* realizó menos intentos de forrajeo en bandadas que tenían mayor número de gaviotas. Sin embargo, la tasa de éxito por intento de forrajeo no cambió con el aumento del número de gaviotas. *R. tridactyla* presentó una mayor probabilidad de evitar las bandadas con mayor número de gaviotas. Las gaviotas cleptoparasitaron exitosamente menos del 1% de los peces capturados por *R. tridactyla.* Nuestros resultados sugieren que la interferencia pasiva puede ser costosa para las aves más pequeñas que forrajean en bandadas multiespecíficas.

Competition has been seen as a primary structuring mechanism in bird communities from early on (MacArthur 1958). A fundamental principle of competition theory is that decreasing resources increase competition. A superior competitor may either exploit a prey patch more efficiently or deter others from using it through interference. Exploitation competition is more likely to occur when resources are rare and dispersed, whereas interference competition occurs more often when resources are concentrated (Maurer 1984). For seabirds feeding in flocks on aggregated prey, the latter scenario is often the case, and several factors may weigh on a bird's decision to join or pass by a feeding flock.

Interference competition is commonly divided into two major categories: active (Schoener 1983) and passive (Charnov et al. 1976). Active interference competition is manifested through aggressive interactions, food theft, and in extreme cases, the killing of a competitor. Active interference is commonly observed throughout many taxa (e.g., Kennedy and White 1996, Bardsley and Beebee 1998, Sunde et al. 1999). In contrast, passive interference competition, in which one

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species obstructs the availability of a resource to another species by nonaggressive behavior, is often difficult to detect (Maurer 1984). Yet, in surface or near-surface feeding seabirds it may be more readily observed due to their highly visible habits of feeding on nearly two-dimensional surfaces in localized areas. For example, Shealer and Burger (1993) have shown that Brown Noddies (*Anous stolidus*) interfere with Roseate Terns (*Sterna dougalli*) by blocking access to prey and hence reducing the number of feeding attempts by terns. Also, in the feeding guild of dabbling ducks, evidence exists of the passive exclusion of Northern Shovelers (*Anas clypeata*) by Green-winged Teals (*A. crecca*; Pöysa 1985).

We examined data from two independent studies on the feeding strategies of Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous-winged Gulls (*Larus glaucescens*) in Prince William Sound, Alaska. Glaucous-winged Gulls are larger (66 cm in length) than kittiwakes (43 cm) (Harrison 1983). In many cases, larger species outcompete smaller ones (Persson 1985) and thus can monopolize a greater proportion of resources as their numbers increase or food supply decreases. Their apparent competitive disadvantage may be the primary impetus for many kittiwakes to pass by feeding flocks, where food is obviously available, and forage on their own. The purpose of this study was to investigate the extent of passive interference competition among surface-feeding seabirds in Prince William Sound and compare it with active interference such as aggressive interactions and food piracy. Specifically, we wished to determine if the larger Glaucous-winged Gulls hindered prey capture by the smaller Black-legged Kittiwakes.

## METHODS

Both studies were conducted in Prince William Sound (60°30′N, 147°00′W), a large estuarine embayment of the northern Gulf of Alaska that provides important foraging and breeding habitat for many seabirds (Isleib and Kessel 1973). In the summers of 1995 and 1996, we examined the behaviors of seabirds at feeding flocks encountered along systematically run transects in Prince William Sound. Observations were conducted aboard an 18-m vessel during daylight hours, and observers used 7 × 40 and 10 × 42 binoculars. Two observers continually scanned for the presence of seabird activity within 500 m of either side of the vessel. Upon encountering a feeding flock, we departed from our transect to make detailed observations of seabird behaviors from a distance of 50 to 100 m. During 1995 we surveyed a systematically selected combination of offshore and nearshore transects varying in length (See Ostrand et al. 1998 for details). In 1996, we concentrated our efforts on nearshore transects in randomly selected 12 × 1 km blocks (Haldorson et al. 1998) because most feeding flocks were found close to shore (Maniscalco et al. 1998).

A feeding flock was defined as an aggregation of three or more seabirds actively feeding, e.g., alcids surfacing with fish in their bills or larids plunging or dipping into the water. Flock types were loosely classified following Hoffman et al. (1981): (1) small, short-duration flocks over tightly clumped prey; (2) large, persistent flocks over more broadly dispersed prey; and (3) flocks associated with sites where forage was concentrated by downwelling or other hydrophysical influence, determined by a subjective evaluation of oceanographic features. We concentrated our analyses on Type 1 flocks, where gulls and kittiwakes fed together.

Upon encountering a feeding flock we noted species composition and their positions in the flock, i.e., flying, on the water, over the fish school, or on the periphery. We quantified the frequencies and types of feeding strategies for Glaucous-winged Gulls and Black-legged Kittiwakes by continually scanning the entire flock and using a voice recorder or videotape. Feeding was categorized as three strategies: (1) plunge-diving (diving into the water from a hovering or flying position), (2) piracy, and (3) surface-seizing (grabbing prey while remaining on the water; Ashmole 1971) or hop-plunging (making brief hops off the water and immediately back down into the water; Hoffman et al. 1981). We did not record aborted dives or swoops because of uncertainty as to their cause. We did record feeding frequency (number of dives bird$^{-1}$ min$^{-1}$) and feeding success (number of prey captured per total number of dives) of kittiwakes when our position and the prey type facilitated those observations. We remained with each flock until it broke up naturally or became disturbed by our presence.

In 1997 we gathered data from 17 radio-tagged kittiwakes from Shoup Bay, a large colony in northeastern Prince William Sound. In this study we used a boat and telemetry-receiving equipment to maintain visual contact and record the foraging activities of radio-tagged kittiwakes (see Suryan et al. 2000 for methodology). Using those data, we compared the species composition of flocks joined with those passed by, focusing on individual kittiwakes as the sample unit (Irons 1998). We did not use data from flocks associated with fish processors because these flocks were intermittent and artificial in nature.

### STATISTICAL ANALYSES

Numbers of birds participating in flocks are expressed as means ± SD. We used chi-square statistics to examine frequencies of the different types of feeding behaviors and foraging success. Changes in the rates of feeding attempts in relation to the proportion of Glaucous-winged Gulls in the flock were estimated using Spearman rank correlations. All analysis of the 1997 radio-telemetry data used averaged data for each individually tracked kittiwake. We also compared the mean number of flocks joined and flocks passed by in 1997 with a two-sample $t$-test assuming equal variances.

## RESULTS

### SCAN SAMPLES AT FEEDING FLOCKS (1995 AND 1996)

The majority of feeding flocks encountered (34 of 44 in 1995 and 1996 combined) were tightly aggregated Type 1 flocks with a mean of 57.1 ± 48.7 birds participating (range 3 to 194). Twenty-two of these flocks (65%) contained both Black-legged Kittiwakes (mean = 23.9 ± 15.8) and Glaucous-winged Gulls (mean = 9.5 ± 9.5). Other members of the Laridae, which comprised less than 5% of the birds in flocks, included Mew Gulls (*Larus canus*), Bonaparte's Gulls (*L. philadelphia*), Arctic Terns (*Sterna paradisaea*), and Parasitic (*Stercorarius parasiticus*) and Pomarine (*S. pomarinus*) Jaegers. Marbled Murrelets (*Brachyramphus marmoratus*), Tufted Puffins (*Fratercula cirrhata*), and Pigeon Guillemots (*Cepphus columba*) also commonly took part in the flocks.

At Type 1 feeding flocks, Glaucous-winged Gulls foraged most frequently by hop-plunging compared to Black-legged Kittiwakes, which most frequently plunge-dived ($\chi^2_2$ = 962.9, $P < 0.001$). The positions of each species within flocks also differed. Gulls often remained on the water over the center of a concentrated prey source while kittiwakes typically circled or hovered above the water ($\chi^2_1$ = 321.0, $P < 0.001$, data from 1996 only). Glaucous-winged Gulls maintained their position in the flocks by hop-plunging and surface-seizing for their prey 87% of the time; they also plunge-dived 7%, and pirated (inter- and intraspecifically) 7% of the time ($n$ = 802). Conversely, kittiwakes hop-plunged and surface-seized 14%, plunge-dived 80%, and pirated (inter- and intraspecifically) 6% of the time ($n$ = 883). On two occasions kittiwakes were denied feeding opportunities at flocks where several gulls were centered over the prey. Active interference between these two species was rarely observed and only in the form of piracy, where gulls stole less than 1% of prey captured by kittiwakes.

In Type 1 flocks that contained both kittiwakes and Glaucous-winged Gulls, the number of feeding attempts by kittiwakes decreased by as much as 14% as the ratio of gulls to kittiwakes increased (range of ratio 0.04 to 2.66, $r_s$ = −0.30, $n$ = 15, $P < 0.05$, Fig. 1a). There was not a significant difference in the feeding success of kittiwakes in flocks without Glaucous-winged Gulls (73%) as opposed to those with (74%, $\chi^2_1$ = 0.2, $P > 0.5$).

FOCAL OBSERVATIONS OF RADIO-TAGGED KITTIWAKES (1997)

Feeding flocks that kittiwakes joined had a mean of 4.6 ± 5.8 ($n$ = 15) Glaucous-winged Gulls as opposed to 9.4 ± 5.5 ($n$ = 14) gulls in flocks that were passed by ($t_{27}$ = 2.0, $P$ = 0.03).

In flocks that were joined, kittiwakes reduced their feeding attempts as much as 36% in the presence of greater ratios of Glaucous-winged Gulls to kittiwakes (range of ratio 0.01 to 0.79, $r_s$ = −0.33, $n$ = 16, $P$ = 0.05, Fig. 1b). There was no relationship between the feeding success of kittiwakes and the relative number of Glaucous-winged Gulls in the flock ($r_s$ = 0.002, $n$ = 23, $P > 0.5$). We did not examine the feeding methods during this portion of the study.

DISCUSSION

Flock-feeding in seabirds is common and has been shown to increase foraging efficiency by keeping prey concentrated, thereby making prey capture easier (e.g., Grover and Olla 1983, Mahon et al. 1992, Mills 1998). Joining flocks decreases time used searching for prey individually (Hoffman et al. 1981), and in some cases capture rate can increase with an increase in aerial predators (Gotmark et al. 1986). However, there appear to be costs associated with feeding in flocks. Inter- and intraspecific kleptoparasitism are common among gulls in small, closely aggregated flocks (Maniscalco and Ostrand 1997), and jaegers commonly steal prey from birds in large feeding flocks (Hoffman et al. 1981, Maniscalco and Ostrand 1997). Yet the low rates of interspecific aggression and piratical success by Glaucous-winged Gulls suggest that active interference may have a minor effect on kittiwakes compared to passive interference.

Passive interference may occur in the form of blocked feeding opportunities (e.g., Duffy 1986, Shealer and Burger 1993) or dispersal of prey by "suppressors" (flock participants that disrupt foraging) such as shearwaters (*Puffinus* spp.; Hoffman et al. 1981) or Blue-footed Boobies (*Sula nebouxii*; Mills 1998). Here we inferred the existence of passive interference by an increased number of gulls monopolizing fish schools (which diving birds held in tight balls near the surface, Maniscalco and Ostrand 1997), which resulted in a reduced number of feeding attempts by kittiwakes. Neither of our independent studies revealed significant differences in the feeding success of kittiwakes in the presence of gulls. Thus, reduced feeding attempts essentially reduced overall capture rates by

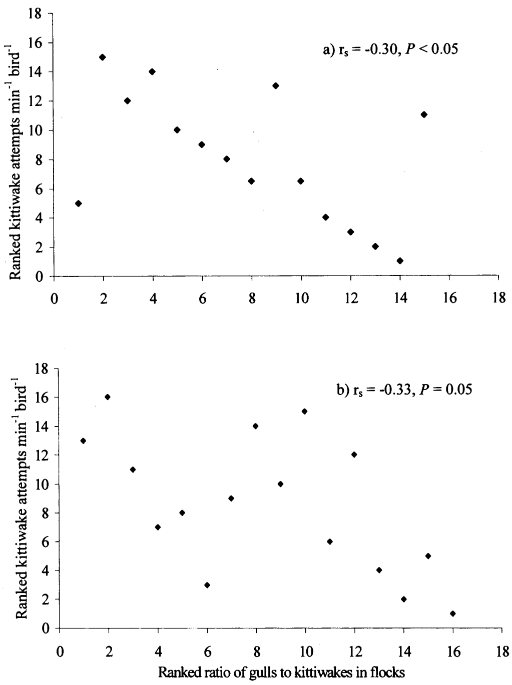


FIGURE 1. Relationship between the number of feeding attempts by Black-legged Kittiwakes and the ratio of Glaucous-winged Gulls to kittiwakes in the feeding flock in Prince William Sound, Alaska: (a) feeding flocks encountered by observers on transects in 1995 and 1996 (data represent means for 15 flocks), and (b) feeding flocks joined by radio-tagged kittiwakes in 1997 (data represent individual means for 16 kittiwakes).

kittiwakes. Further, our 1997 radio-tracking data suggests that kittiwake foraging was sufficiently impaired by passive interference to merit avoiding flocks that were dominated by gulls.

Although active interference can have obvious and serious detrimental effects on the inferior species (e.g., Kennedy and White 1996), no such evidence exists in regard to passive interference, to our knowledge. At Shoup Bay colony in northeastern Prince William Sound, reduced productivity of kittiwakes in 1997 compared to 1996 may be attributed primarily to lower prey abundance (Roby et al. 1998). We could not ascertain negative effects on the survival of kittiwakes due to interference competition. However, our study does imply that passive interference may be a primary factor (more so than active interference) that deters kittiwakes from using multispecies feeding flocks and may compound the negative effects of low prey availability.

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