Black-legged Kittiwake Feeding Flocks in Alaska: Selfish/Reciprocal Altruistic Flocks?—Although Black-legged Kittiwakes (*Rissa tridactyla*) are important in the formation of mixed-species feeding flocks (Sealy 1973, Hoffman et al. 1981), the feeding biology of these kittiwakes (Belopol'skii 1957, Burtt 1974, O'Connor 1974) or of Red-legged Kittiwakes (*R. brevirostris*) (Siegel-Causey and Meehan 1981) has only been sketchily studied. Here, I examine the size and duration of kittiwake feeding flocks and the differences in feeding success of adults and subadults and of flock initiators and joiners. Finally, I discuss whether behavior in these flocks could be classed as selfish (i.e., it benefits the performer at the expense of others, Wilson 1975), altruistic (i.e., it costs the performer but benefits others, Wilson 1975), and/or reciprocal altruistic (i.e., it is altruistic when performed but the recipients behave altruistically to the original performer at a later time, Wilson 1975).

I watched Black-legged Kittiwakes in mixed-species or monospecific flocks from 22 July to 1 August 1976 along the Alaskan coast from Seward to Dutch Harbor. Observations were made from the 27-m research vessel *Acona* or its 5-m Boston Whalers. I distinguished between kittiwake adults (≥ 3 yr old) or subadults (1–2 yr old) by head color; adults had completely white heads, and subadults had a gray or black collar or a partial hood over the back of the head. I defined a feeding flock as 2 or more kittiwakes feeding within a visually estimated 10 m of each other. Flock duration (i.e., the time from the first dive to the last dive by 2 or more kittiwakes within 10 m of each other) and flock size (i.e., the maximum count of kittiwakes in a flock) were measured separately for each of 65 flocks, but samples of feeding behavior were pooled for each day or for all days because of small sample sizes for each flock.

In some areas kittiwakes were not seen during hours of cruising, but in other apparently similar areas, kittiwakes numbered in the hundreds or thousands. Foraging individuals typically flew in a meandering fashion within 20–40 m of the water and often over 100 m apart. When one kittiwake oriented to prey, a feeding flock often gathered at the site. Kittiwakes oriented to their prey (fish, probably capelin, *Mallotus villosus*) by hovering, tight circling banks, stoops, and/or active prey pursuit. While flying, a kittiwake stooped when it aborted a head-first dive before it reached the water. A kittiwake pursued prey by plunging, which consisted of a head-first dive into the water from an altitude of about 1–6 m. A plunging kittiwake did not penetrate the water deeper than about 1 m (see also

TABLE 1. Dive type and plunge success for adults (AD), subadults (SUB), or both age-classes (ALL) feeding in flocks (FL) or solitarily (SOL).

			Dives			Plunges		
	Date (July)	Age	n	Plunge (%)	Stoop (%)	n	Success (%)	Miss (%)
FL	23	AD	289	73[1]	27	210	88[2]	12
FL	23	SUB	78	76[1]	24	59	46[2]	54
FL	24	AD	103	78[1]	22	80	73[2]	27
FL	24	SUB	38	68[1]	32	26	81[2]	19
FL	23	ALL	367	73[3]	27	269	78[3]	22
FL	24	ALL	141	75[3]	25	106	75[3]	25
FL	29	ALL	262	27[3]	73	71	22[3]	78
FL	23, 24, & 29	ALL	770	58[4]	42	446	69[4]	31
SOL	27–31	ALL	73	44[4]	56	32	56[4]	44

[1] AD vs SUB; 23rd, $\chi^2 = 0.15$, df = 1, $P > .10$; 24th, $\chi^2 = 0.83$, df = 1, $P > .10$.

[2] AD vs SUB; 23rd, $\chi^2 = 45.27$, df = 1, $P < .01$; 24th, $\chi^2 = 0.34$, df = 1, $P > .10$.

[3] Dives, homogeneity, $\chi^2 = 156.24$, df = 2, $P < .01$; Plunge success homogeneity, $\chi^2 = 74.78$, df = 2, $P < .01$.

[4] FL vs SOL; Dives, $\chi^2 = 6.95$, df = 1, $P < .01$; Plunge success, $\chi^2 = 3.07$, df = 1, $P < .10$.

TABLE 2. Dive type and plunge success of flock initiators and joiners on 29 July.

	Dives			Plunges		
	n	Plunge (%)	Stoop (%)	n	Success (%)	Miss (%)
Initiator	39	85[1]	15	33	30[2]	70
Joiner	218	17[1]	83	36	11[2]	89

[1] $\chi^2 = 74.69$, df = 1, $P < .01$.
[2] $\chi^2 = 2.82$, df = 1, $P < .05$.

Belopol'skii 1957). If successful, a kittiwake swallowed the prey at the surface or while flying away.

Although kittiwake feeding flocks were conspicuous visually (up to several km) and audibly (up to 0.8 km), kittiwakes did not appear to signal these flocks in any manner other than by their own feeding activities (e.g., hovering, flying in circling banks, stooping, or plunging) and consequent flashing of their white plumage or by aggression. A kittiwake seemed to call only after it had been joined by others, and then calls commonly occurred during flight chases. Though some of these chases were kleptoparasitic attempts (see below), many chases did not involve food but may have been attempts to jockey for position at a site where food was available (i.e., a site where prey were detected and were close enough to the water surface to be captured). Similarly, others have also reported seabird feeding flocks to be signalled by flashing white plumage, feeding calls, or feeding activities (Frings et al. 1955, Simmons 1972, Gould 1974, Hoffman et al. 1981).

Kittiwake feeding flocks were of short duration and small. Flock duration averaged 8.2 s (SD = 11.1 s, range 3–90 s, n = 65 flocks), and flocks were probably brief because when prey became available the feeding activities of the kittiwakes drove the prey beyond the kittiwakes' plunging (see also Hulsman 1978, Hoffman et al. 1981). The average flock size was 8.9 birds (SD = 10.9, range 2–80, n = 65 flocks). Flock size correlated directly and significantly with flock duration ($r = 0.92$, $t = 18.12$, df = 63, $P < .01$) and seemed to be a function of prey availability rather than of the availability of kittiwakes to form flocks because there were always at least 20 kittiwakes milling about during my observations.

Kittiwake feeding success in flocks varied from day to day (Table 1). Kittiwakes on 29 July had a significantly lower proportion of dives that were plunges and successful plunges than on 23 or 24 July. Overall, flock feeders had a significantly greater proportion of dives that were plunges and a higher plunge success rate than did solitary kittiwakes (Table 1). This may vary from day-to-day, however, as solitary kittiwakes overall did better than flock kittiwakes on 29 July.

Flock initiators (i.e., the first 2 kittiwakes at a flock) had significantly greater proportions of dives that were plunges and successful plunges than did joiners (Table 2). Because each plunge lasted about 2–5 s and most flocks were brief, initiators also had a greater chance than joiners to plunge repeatedly at a given site before prey became unavailable.

When adults and subadults were compared, the proportion of dives that were plunges did not differ significantly on either 23 or 24 July (Table 1). The success of plunges was not significantly different on 24 July, but adults were significantly more successful than subadults on 23 July (Table 1). Others have generally found adults to be more successful than younger birds (see references in Burger 1980).

Within a feeding flock, kleptoparasitic interactions consisted of 1–5 kittiwakes chasing another kittiwake with a fish. These chases generally lasted 5 s or less (86% of 22 chases, maximum of 25 s). Although some chasers successfully stole food on some days, none of the 38 attempts on 24 and 29 July was successful, but in 8% of these attempts the victim dropped the fish and none of the birds recovered it.

Subadults seemed more vulnerable to kleptoparasitic attacks than adults. A higher proportion of successful subadults (62% of 21 subadults) than successful adults (38% of 58 adults) were chased, although the difference was not significant ($\chi^2 = 2.68$, df = 1, $P > .10$). Further, a higher percentage of subadults lost prey when chased (15% of 13 subadults attacked) than adults (5% of 22 adults attacked), but sample sizes were inadequate to test this difference statistically.

Parasitic Jaegers (*Stercorarius parasiticus*) and Glaucous-winged Gulls (*Larus glaucescens*) also occasionally harassed kittiwakes with or without fish. Interspecific kleptoparasitic attempts on kittiwakes (attacks on 6% of 79 successful kittiwakes in flocks), however, occurred significantly less frequently than intraspecific attempts (attacks on 40% of the same kittiwakes) ($\chi^2 = 26.60$, df = 1, $P < .01$). Jaegers were also joined sometimes by kittiwakes to form mixed-species kleptoparasitic flocks. In such flocks, jaegers have been reported as successfully causing kittiwakes to drop prey, but at least sometimes other kittiwakes following the jaeger swallowed the dropped prey (Hoffman et al. 1981).

Kittiwake behavior in feeding flocks may be interpreted as being both selfish and reciprocal altruistic. There was much selfish behavior (e.g., aggression, jockeying for position, and kleptoparasitism) in flocks, and the only overt cooperative behavior within a feeding flock was when kittiwakes joined together to attempt to kleptoparasitize fish from others (but they did not share any food obtained among themselves). Nevertheless, the feeding activities of the kittiwakes coupled with their white plumage (which may have evolved for signalling, see Simmons 1972) acted to signal a feeding site to other kittiwakes, which may then join these flocks because they would then have a better chance of obtaining food than by searching independently. This signalling behavior could be interpreted as altruistic because flock joiners could decrease the amount of food available to the original signallers by causing the prey to descend. A more appropriate, but untested, interpretation could be that this behavior is reciprocal altruistic because signal recipients for one flock could signal new feeding sites to previous signallers at a future time. This could occur because these flocks were widely enough dispersed that a single kittiwake would probably not be the first to detect every site of prey availability. To test between altruism and reciprocal altruism, however, would require monitoring individually-marked kittiwakes in flocks during several days to determine if kittiwakes alternated in being signallers and recipients, but this was beyond the scope of this study.

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Prolonged Incubation by a Long-eared Owl.—Prolonged incubation has been reported for a number of bird species (e.g., Skutch 1962), but I am aware of only one record for an owl. East (1930) observed a Common Barn-Owl (*Tyto alba*) that incubated 10 eggs for 12 weeks.

On 24 March 1981 I found a female Long-eared Owl (*Asio otus*) that appeared to be incubating at a nest in the Snake River Birds of Prey Area along Fossil Creek, Owyhee County, Idaho. I visited the nest 7 times in 8 weeks and observed the female in an incubation position each time. I neither flushed the female nor observed nest contents during any of these visits. On my eighth visit, on 27 May, I flushed the female and collected 6 stained, infertile eggs.

Barn-owls and Long-eared Owls begin incubation with the first egg, and a meaningful definition of incubation might be the time between laying and hatching of the first egg in a clutch. Using that definition, the 65-day interval from my first to last nest visit represents a prolongation of at least 37 days beyond the normal incubation period (26–28 days, Mikkola 1973) of the Long-eared Owl. The barn-owl incubated for at least 51 days beyond the normal incubation period (33 days, Prestt and Wagstaffe 1973).

Long-eared Owl eggs hatch asynchronously and the laying (and thus hatching) interval can be irregular. Whitman (1924) reported Long-eared Owls laying on alternate days, and Armstrong (1958) recorded laying intervals of 1 to 5 days. Given the variability in laying interval, a 6-egg clutch might hatch over a period of 1 to 2 weeks. A similar or perhaps longer hatching period would be required for a clutch of barn-owl eggs.

Prolonged incubation provides a margin of safety for eggs that take longer than normal to hatch (Holcomb 1970), and many species will incubate unhatchable eggs for 50 to 100% longer than the normal incubation period (Skutch 1962, Holcomb 1970). Holcomb (1970) suggests that excessive prolongation would be nonadaptive for birds that can renest after a nest failure. The prolongations reported for the barn-owl and Long-eared Owl represent about 150% of the normal incubation periods and thus might be considered excessive, especially since both species can renest after failure during incubation (Marti 1969, and pers. observ., respectively). I suggest that prolonged incubation behavior is related to the time interval in which an entire clutch would normally hatch. Species laying large clutches that hatch asynchronously (e.g., some owls) may be more likely to prolong incubation more than species whose eggs hatch in a short time interval.

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