

FEEDING BEHAVIOR OF THE GLAUCOUS-WINGED GULL ON AN ALASKAN SALMON STREAM

PETER MOYLE

EVERY year during the months of June through September millions of salmon (*Oncorhynchus* spp.) enter Prince William Sound, Alaska. Those that are not caught by commercial fishermen go up the numerous short streams that flow into the sound, where they spawn and die. These salmon, living and dead, are a superabundant food source that attracts to the spawning streams large numbers of predators and scavengers, among them bears, eagles, crows, ravens, gulls, and countless invertebrates. Despite their abundance and accessibility, the behavior of these animals has not been studied intensively on salmon streams. Perhaps the most conspicuous of the salmon stream scavengers are the gulls. On Olsen Creek, Prince William Sound, Alaska, the principal gull species were the Glaucous-winged Gull (*Larus glaucescens*), the Mew Gull (*Larus canus*), and the Bonaparte's Gull (*Larus philadelphia*). Because these gulls occurred in large numbers and remained in one area for several months, they could be studied using a blind and other methods normally reserved for breeding colonies. With the exception of Mossman (1958), however, virtually no systematic studies have been made of gulls on salmon streams, although the literature abounds with nonsystematic observations, as in Bent (1921) and Murie (1959). The nonbreeding behavior of gulls has received little attention compared to the intensively studied breeding behavior, with the exception of studies by Tinbergen (1956, 1960) and the Frings et al. (1957).

Since the Glaucous-winged Gull was the dominant gull on Olsen Creek, both in size and in numbers, this paper is concerned primarily with the behavior patterns of this species. Unfortunately, even the breeding behavior of the Glaucous-winged Gull is not well known. The only substantial paper on the subject, by James-Veitch and Booth (1954), was done without the benefit of Tinbergen's classical studies on gull behavior. The Glaucous-winged Gull, however, does belong to the Herring Gull group of Tinbergen (1959) and the behavior patterns observed on Olsen Creek fit nicely into the general patterns described for the group as a whole. Most of the behavior patterns observed on Olsen Creek appear to be closely related to those of the breeding season in form, although not necessarily in significance.

THE STUDY AREA

Olsen Creek is one of the principal spawning streams on Prince William Sound of the pink salmon (*Oncorhynchus gorbuscha*) and the chum salmon

(*O. keta*) and is the site of a U.S. Bureau of Commercial Fisheries research station, at which the author was employed. The study was carried out on free hours during the summers of 1963 and 1964, with most of the quantitative work using a blind accomplished during 1964.

The gulls were concentrated on the tidal flats, in areas along the stream where the largest numbers of salmon carcasses accumulated. These areas were different for the two summers, because the great Alaska earthquake of 27 March 1964 uplifted the entire region about five feet, moving the feeding areas downstream. The gulls were also affected by the lateness of the 1964 spring, as appreciable numbers of pink salmon did not appear in the creek until 11 July, nearly 10 days later than the previous year. (A few chum salmon were in the stream, however, on 16 June.) Thus, the number of Glaucous-winged Gulls during the first two weeks in July was lower in 1964, although the estimated maximum of 250 birds was reached in mid-August in both seasons. Large flocks of Bonaparte's Gulls appeared on 15 July in 1963 and on 22 July in 1964, reaching an estimated maximum of 100 birds during the first week of August. In both seasons Mew Gulls did not appear in any numbers until the third week of July and their maximum population never exceeded 40 birds. The lateness of the gulls' arrival on the stream in 1964 was probably due also to the lateness of the breeding season. Although there were no gulls breeding in the immediate vicinity of Olsen Creek, a colony of Arctic Terns (*Sterna paradisea*) nearby was still incubating on 21 June 1964, nearly 10 days later than noted in previous years. However, Gabrielson and Lincoln (1959) observed hundreds of fuzzy young Glaucous-winged Gulls in a Prince William Sound colony on 29 July 1945. Although this date seems exceptionally late, Bent (1921) gives egg dates for Alaska, south of peninsula, as ranging between 3 June and 16 July.

SPECIES DIFFERENCES

The different feeding habits of the three species resulted in a minimum of interspecific conflict. The dominant Glaucous-winged Gull either fed on carcasses pulled up on the stream bank or bobbed for drifting salmon eggs while swimming with the current. The Bonaparte's Gull generally flew up and down the spawning areas in flocks of 10 to 20 birds, lighting briefly on the water to dive for drift eggs. The Mew Gull occupied an intermediate position. Like the Bonaparte's Gull, they often fed on drift eggs by flying up and down over the spawning area. When no Glaucous-winged Gulls were nearby they tended to swim with the current to bob for eggs. They also would defend a riffle area or salmon carcass for short periods against all other Mew and Bonaparte's Gulls, if no Glaucous-winged Gulls were near enough to chase them off.

DISPLAYS AT SALMON CARCASSES

Most of the feeding behavior of the Glaucous-winged Gull at Olsen Creek occurred in the two distinct situations mentioned above. The displays centering around salmon carcasses were studied most intensively because of their close relationship to breeding season territorial displays described by Tinbergen (1959, 1960) and James-Veitch and Booth (1954). General descriptions of the Upright Display, the Oblique-cum-Long-Call Display, the Mew Call Display, and other displays mentioned can be found in Tinbergen (1959).

Upright Display.—This was the most common display observed. When assumed by an attacking or defending bird it was often sufficient to decide the issue by itself, the loser walking off, usually only a few paces, in the Hunched Posture. An Aggressive Upright Display was turned into an overt attack when the attacking gull began running towards the defending bird, neck stretched forward and wings partially out. In such an attack, an element of surprise was frequently the deciding factor, for, if the defending gull was not expecting the charge, it had little chance to do anything but jump out of the way.

The Upright Displays varied greatly in appearance. A gull feeding on a salmon carcass often stretched its neck only half as far as it would when extremely provoked, as a warning to another gull walking or flying by. Such a semi-upright posture could also be assumed by a defender towards a gull approaching in a "full" Aggressive Upright Display. In such a case, the defending gull almost always yielded to the aggressor.

When an attacking bird assumed such a semi-upright posture, the dispute usually ended in its favor. The attack was signaled as much by the aggressor's approach in a rapid walk as by its posture, which was often indistinguishable, at the beginning of the attack, from normal walking posture. The defender almost always walked off at the first sign of such an attack, most likely because it was familiar with the aggressor, and had lost a more vigorous dispute with it earlier. Thus, when a row of fish five feet apart was placed in front of the blind, it was common to observe the following:

Two adult gulls begin feeding, gull 1 on fish A, gull 2 on fish B. Gull 2 assumes a semi-upright posture and charges gull 1. Gull 1 immediately jumps back and stands by with hunched shoulders a few paces off. Gull 2 feeds at A. Gull 1 now circles around and begins feeding at B. Gull 2 stops feeding and looks at gull 1, which also stops feeding. Both gulls resume feeding. Gull 2 suddenly begins walking in a semi-upright posture towards gull 1, which quickly steps a few feet away. Gull 2 begins feeding at B, while gull 1 circles around and begins feeding at A.

The whole performance may be repeated several times, ending only when one of the two gulls leaves the area. Occasionally an attack by one gull on its immediate neighbor resulted in a chain reaction with four or five gulls switch-



FIG. 1. Typical Oblique-cum-Long-Call Display, gull on left defending.

ing fish. The stimulus for the attack was the presence of another gull feeding nearby. Gulls not feeding were seldom disturbed, as long as they were behaving in a nonaggressive manner.

Although the above behavior seems, in many respects, like the pecking order behavior described for other bird species, any order established in the study area was only temporary, because the individual gulls in one area changed constantly. Not only did individual birds leave the feeding area to roost and preen when their hunger had been satisfied, but they often left to feed someplace else on the stream. Furthermore, the number of gulls in the study area (which was above the reach of most high tides), varied with the height of the tide and the time of day. When the tide was high or the hour early, there tended to be more gulls in the area than at other times. Also, individual gulls with conspicuous identifying plumage characteristics were never observed feeding continuously in one area for longer than two weeks. Thus, the feeding rights to fish were constantly being established and re-established as new gulls came in and others left. This instability of local social orders resulted in numerous Oblique-cum-Long-Call and Mew Call Displays, as well as outright fights.

Oblique-cum-Long-Call Displays.—The Oblique-cum-Long-Call (Fig. 1) occurred primarily in three situations: (1) when a gull was highly motivated (i.e., hungry) in the defense of a salmon carcass or in an attack on a feeding bird; (2) when a gull was issuing a general challenge; and (3) when a gull was extremely frustrated or excited. Unfortunately, the exact nature of a Long Call was often very difficult to determine. This was particularly true of the second category, for even though a general challenge appeared to be directed towards any individual gull that happened to be nearby, it was really a challenge to all the gulls in the vicinity. Such a Long Call was seldom followed by an attack. Thus, with the exception of Long Calls given after a victory (which were apparently not aimed at individual gulls), all category two Long Calls were also analyzed as part of category one. Analysis for all categories was made in terms of Long Call performances, i.e., any display that included Long Calls was considered as one performance no matter how many single vocalizations were given (32 per cent of the performances involved more than one Long Call). Out of 100 such performances, 51 were begun by the attacking bird, 37 by the defending bird; nine were challenges given by adults to juveniles, and three were given by victorious birds after a conflict.

The temporary social superiority of a gull giving an Oblique-cum-Long-Call Display is indicated by the fact that, overall, a gull initiating a conflict by giving a Long Call came out ahead 65 per cent of the time. If the initiating gull was defending a carcass, however, it won 80 per cent of the time; if attacking, only 50 per cent of the time. These figures are striking when compared to the combined win-lose percentages for all the carcass conflicts on the creek. Normally, a carcass was defended successfully only 33 per cent of the time. The reason for this difference is probably that any defending gull that had to be attacked with a Long Call had already been sized up by the attacking bird as a formidable opponent. Otherwise an Aggressive Upright posture would have been sufficient. If the defending gull responded to the intruder with another Long Call, the two birds were probably equal in most respects, for a fight (Fig. 2), or a Mew performance, ensued, from which either bird could emerge the winner. Occasionally, the defending bird simply delivered a quick jab at the Long Calling intruder, which hastily retreated.

General challenge Long Calls were given either by gulls in possession of a carcass as a severe warning to any nearby or approaching gulls or by gulls landing in a new feeding area, presumably to test the aggressiveness of the birds already feeding. Long Calls given by a victorious bird after a conflict were also of the general challenge type. A defending bird that gave a general challenge Long Call was usually exceptionally aggressive and would often leave its fish temporarily to attack other gulls feeding nearby.



FIG. 2. A fight over a salmon carcass, gull on right trying to flee. Such fights usually last only a few seconds.

Long Calls that occurred under stress are discussed under encounters with juveniles and under gull-bear relationships.

Mew Call Displays.—The Mew Call Display (Fig. 3) was one of the most noticeable displays on the salmon stream, both because of its comparatively long duration and because of the long, monotonous cries that accompanied it. Three general types of Mew Call Displays were observed: conflict, sexual, and threat. In the conflict Mew Call Displays Glaucous-winged Gulls walked side by side in a deliberate manner, necks arched, with one or both gulls Mewing continuously. A Mew walk began when one gull, giving Mew cries, approached another feeding. If the dispute did not end immediately with a sudden jab by one of the birds, the defending gull would join the intruder in a Mew walk. Frequently, one of the gulls climbed up on the disputed fish and then ate and vocalized (in a muffled sort of way) simultaneously. The other gull slowly paced around the fish and its owner, Mewing constantly, until the dispute was settled, either by a jab, a fight, or by one gull walking away.

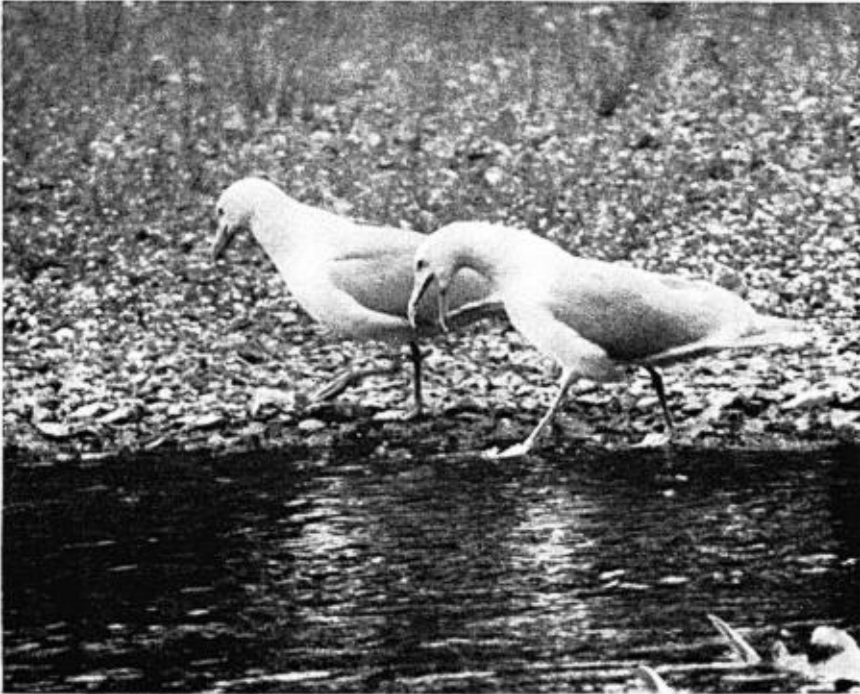


FIG. 3. A Mew walk. Gull on left is losing interest and walked away from other gull immediately after picture taken.

The sexual displays were similar in form to the conflict displays, except they did not center around a salmon carcass and they seldom ended with a jab or fight. They occurred primarily in areas where feeding was not taking place and their only obvious cause was the mutual attraction of two gulls. In seven sexual displays that occurred near the study area (which was almost exclusively a feeding area), three were accompanied by Choking, one by Head Tossing, and one was preceded by Long Calling by both birds. During the breeding season, Mewing, Choking, Long Calling, and Head Tossing are all part of pair formation or territory defense (Tinbergen, 1959).

Conflict Mew Call Displays always occurred in the vicinity of a fish on which one of the disputants was feeding. One of the gulls usually retained possession of the fish at the end of the display (in 27 of 32 displays analyzed). There was no sharp separation, however, between conflict and sexual displays and sexual motivation was probably at least partially responsible for many conflict displays. Choking occurred in six of the 32 cases analyzed. In one instance, when one of a pair of Mewing gulls began Choking, the other bird,

which had climbed on top of the disputed fish, reached down and grabbed the Choking bird by the tail. In other cases, Choking occurred only as a short interruption of a Mew walk, with both birds Choking. Five of the 32 Mew Call conflicts began with the intruding bird giving a Long Call to which the defender immediately responded with a similar Long Call. Half (16) of the Mew Call conflicts ended with a fight; 10 of these were won by the attacker, six by the defending bird.

Although the number of conflict displays subjected to detailed analysis was small, tentative conclusions about them have been made from these and other more general observations. In a conflict Mew Call Display the two contenders are strangers, but recognize, from each other's size and actions, that they are approximately equal in strength and aggressiveness. During the Mew walk they discover more exactly the extent of their equality. If one gull then discovers its superiority to its opponent, it jabs out abruptly and the other bird flees without further ado. If, on the other hand, the Mew walk is unsuccessful in establishing the stronger bird, a breast-to-breast, or bill-pulling, fight results, winner take all. Such a fight usually lasts only a few seconds, although if one birds gets a good grip on another's bill it may last over two minutes. In 11 disputes (out of 32) in which the attacker gained the fish, 10 were won only after a fight, indicating that the defending bird had a slight advantage in being the possessor. This is further indicated by the fact that 16 of the Mew conflicts were won by the defending bird and only six of these by combat. The remaining five conflicts ended indecisively, with neither gull going back to the original fish, possibly because the Mew Call Display was partially sexual in origin. There is the distinct possibility that most conflict Mew Call Displays occur between birds of the opposite sex, and that the display itself results from a conflict between sex and hunger drives.

The third category of Mew Call Display, threat, perhaps better belongs under Upright Displays. Its exact origin is still uncertain, although it appears to be an intermediate threat display, i.e., stronger than an Upright Display but less intense than a Mew or Long Call Display. During a threat Mew Call Display, the neck is in a Mew or Semi-oblique position and the attacking bird walks towards its opponent giving one or two short Mew cries. The defending gull immediately either yields or jabs at the threatening gull, which then retreats. In nine of the 32 such threats analyzed, the defending bird responded first with another threat Mew Call Display and in four it responded first with a Long Call. The conflict, however, was decided immediately after that with a jab or a yield. Twenty-eight of the threats were given first by attacking birds, yet they succeeded in gaining the fish only 44 per cent of the time.

TABLE 1
FEEDING PERIODS OF THE GLAUCOUS-WINGED GULL, OLSEN CREEK

Time interval (sec)	Number of feeding periods
15-60	34
61-120	12
121-180	7
181-240	6
241-300	4
301-360	2
361-420	4
421-480	4
481-540	2
541-600	1
601-660	2
661-720	1
721-780	1

RELATIONSHIP TO BREEDING BEHAVIOR

With the possible exception of a few Mew Call Displays, all displays centering around the salmon carcasses were what Tinbergen (1959) terms "distance increasing displays," displays that, during the breeding season, permit the existence of territories by keeping rival birds apart with a minimum of physical encounter. On the salmon stream, however, these displays existed in the absence of true territories. Instead, individual carcasses or small groups of carcasses were defended. Furthermore, the carcasses were defended only for very short periods of time and attacking gulls seemed to have an overall advantage over those defending.

One of the main characteristics of a breeding territory is that it is defended for most of the breeding season. In contrast, a salmon carcass at Olsen Creek was held by an individual gull only for an average of three and one-half minutes. This figure was determined by timing 70 feeding periods to the nearest five seconds. A feeding period was considered the time between a gull's arrival on a carcass to the time it left, usually as the result of an encounter with another gull. The period was not necessarily one of continuous feeding but might have been interrupted by fights and threats. Even though periods under 15 seconds were arbitrarily discarded as exploratory, 43 per cent of the periods were still under one minute (Table 1). These were balanced by a few long periods, ranging up to 12.1 minutes. The shortness of the average feeding period is not surprising, because a hungry gull can eat an extraordinary amount of food in a very short period. Furthermore, when salmon carcasses were very abundant, a gull would often defend one only long enough to devour the eyes and viscera.

Another characteristic of a breeding territory is that the defending gull has the odds for winning in its favor. Out of 218 disputes over salmon carcasses, however, the attacking bird gained possession 145 times, 67 per cent of the total. (A dispute is defined as any encounter between two adult birds in which one, or both, of the gulls shows definite hostile intentions to the other by an Upright, Mew, or Long Call Display.) The intruding gull's advantage, in part, can be explained by the feeding gull's steadily decreasing motivation to defend a carcass as its hunger is satisfied. Similarly, the aggressiveness of an attacking gull was most likely to be stronger the hungrier it was. The attacker's advantage appeared mainly in the form of Aggressive Upright Displays to which the defending gull yielded with little protest, either because its hunger had been satisfied or because it had been defeated by the attacker in a previous fight. When a hungry gull had just begun feeding, the odds for winning an encounter were in its favor. Thus, in an analysis of 151 Mew Call and Long Call Displays, which indicate one or both gulls was highly motivated, 57 per cent were won by the defender, and 40 per cent by the intruder, leaving 3 per cent inconclusive. A feeding bird generally had to have an aggressive appearance in order to provoke a Mew Call or Long Call Display by an attacker. In extreme cases, such a bird attacked or threatened every gull in its immediate neighborhood, actually spending more time displaying than feeding. If one of its opponents also happened to be highly motivated, a wing-flapping, bill-pulling fight ensued, from which either bird could emerge the winner. When exceptions to the preceding occurred, they were often spectacular. A gull occasionally finished feeding and then walked for a few minutes among the other feeding birds, challenging, chasing, and fighting every gull it met, before finally settling down to preen and roost. Other gulls were chased from one carcass to another by more aggressive neighbors and never protested, no matter how eager to feed they appeared.

Despite these differences the relationship between breeding behavior and that observed on the salmon streams is undoubtedly very close. In many cases the motivation for a salmon stream display may have been purely sexual, as in the Head Tossing Displays that were occasionally seen on the tide flats. This also applies to many Mew Call Displays, particularly those preceded by Long Call performances or interrupted by Choking or Head Tossing. Any sexual displays on the salmon stream during June and July could be the result of feeding gulls still being in breeding condition, such as unmated birds, mated birds that had lost their brood, second- and third-year juveniles, or birds coming from nearby breeding colonies to get food for themselves and their young. Once the breeding season is over any sexual behavior could be the result of sexual recrudescence, similar to that of the Herring Gull (Tin-



FIG. 4. Gull waiting for black bear to finish feeding on female pink salmon. Note Long-Calling gull at center.

bergen, 1960). There is, however, no direct evidence for this in the Glaucous-winged Gull.

BEARS

Most of the described displays, except the Long Calls of the Glaucous-winged Gull, were of little value when the carcass involved was that of a freshly caught salmon, left behind by a fishing black bear (*Ursus americanus*). The desirability of such salmon to the gulls arose from the sloppy but selective eating habits of the bears. They seldom devoured a salmon completely, leaving the scraps for the gulls. When the salmon became abundant in the stream, the bears often captured unspawned females. With these, the bears squeezed, sucked, or tore out the eggs, spilling many in the process. Those eggs that the bears failed to lick up were left for the gulls, along with the remains of the salmon. Thus, any bear that dragged a freshly caught salmon up on the bank was quickly surrounded by Long Calling gulls (Fig. 4). When the bear left, there was a general rush for the remains of the fish. If the salmon was

left in pieces, those gulls that could each grabbed one and tried to carry it away. The other gulls gave Long Calls and tried to snatch the pieces away. Fights were frequent and a gull often dropped a hard-won piece of fish when it tried to give a Long Call in response to a challenger. If the salmon was still whole, five to 10 birds could end up grouped around it, alternately feeding, challenging, and fighting. If the bear had spilled large numbers of eggs, the gulls present pecked frantically, generally ignoring the challenges of late-comers, until the eggs were gone. The gulls reacted in the same manner with Long Calls and fights when a bear fed on an old carcass that the gulls had rejected previously. The remains of such a carcass, however, were quickly deserted by the gulls after a few initial squabbles.

CARCASS SELECTION

Most of the salmon carcasses defended by the Glaucous-winged Gulls of Olsen Creek were originally dragged out of the water by the gulls themselves. When large numbers of salmon were spawning and dying, the gulls tended to feed more extensively on female carcasses. The Glaucous-winged Gull's preference for female salmon was also noted by Mossman (1958) on red salmon (*O. nerka*) streams of Bristol Bay, Alaska, where gulls preyed on live fish splashing through shallow water. Mossman found that nearly four times as many female salmon were killed as males. On Olsen Creek, there was no significant predation on live salmon, but nearly twice as many female carcasses were dragged up on the bank as males. Out of a total of 387 pink and chum salmon carcasses examined on two separate days, 133 were male and 254 were female. All the carcasses were in areas above the mean high tide mark where large numbers of gulls had been observed feeding. It was assumed that any carcass on the stream bank had been dragged there by the gulls.

On the first examination date (29 July 1964) the number of dead pink salmon was small, so only chum salmon carcasses were examined. The carcasses were arbitrarily divided into three categories to determine if the gulls also ate larger portions of individual female carcasses: (1) carcass in good shape, usually just eyes eaten; (2) carcass partially eaten, viscera gone; (3) carcass with only head, bones, skin, and fins; most of edible parts gone. It was found that 96 per cent of the female carcasses belonged to classes 2 and 3 (87 per cent to class 3 alone), contrasting with 61 per cent for the males (36 per cent to class 3). Thus, an apparent preference for female carcasses is shown, despite the fact that only 53 per cent of the 159 carcasses examined were female. The tendency to eat more of a female carcass was probably caused by the gulls' preference for salmon eggs, small numbers of which were usually retained in the visceral cavity of the female salmon after spawning.

Once a gull had torn into a fish to get the viscera, it would be easier for it to continue to feed on the same fish than it would be to tear open a new one, particularly if the number of carcasses was small. A preference for eggs is also given by Mossman (1958) as the principal reason for selective predation by Glaucous-winged Gulls on female red salmon.

On the second examination day (3 September 1964) both chum (45 fish total, 65 per cent female) and pink salmon (183 total, 77 per cent female) were examined. However, it is not known if the high percentages of female pink salmon carcasses were caused by a high percentage of females in the run itself, as indicated by Helle, Williamson, and Bailey (1964), by selection by the gulls, or by a combination of both. Among the chum salmon censused 55 per cent of the females were in classes 2 and 3 (10 per cent in class 3) as opposed to 25 per cent for the males (6 per cent in class 3), indicating, despite the small number of carcasses, the gull's preference for females. This is not so clear among the pink salmon because 36 per cent of the females and 30 per cent of the males belonged to classes 2 and 3. The low number of chum salmon in the sample is due to the small number spawning in the stream at this time and not to a preference by the gulls for pink salmon.

ROLE OF JUVENILE GULLS

Gulls in immature plumage were generally forced by adult birds to feed in the less desirable areas, either upstream from the prime areas or on the tideflats away from the stream, where occasional fish were left by the tide. Consequently, certain areas along Olsen Creek were characterized by the constant presence of groups of 20 to 30 juvenile birds. These birds, however, also spent much time patrolling the adult areas in the submissive Hunched Posture, feeding momentarily on unguarded fish or on carcasses rejected by the adults. Usually an adult gull had no trouble driving a second- or third-year juvenile from a fish, for they seemed to react to all the adult threat displays and even used them in juvenile-to-juvenile conflicts. Although vocalizations of the juvenile Long Call Displays were just a series of hoarse squeaks, adults and other immature birds reacted to them or, at least, to the posture. In rare cases an aggressive juvenile could actually drive an adult off a fish with a threat display.

The first-year juveniles occupied a more ambiguous position, for they usually didn't react to adult threat displays. Furthermore, their Hunched Posture tended to inhibit any direct attacks by the adults except under extreme provocation. As a result, feeding adult gulls became noticeably uneasy in the presence of persistent juveniles and often left a fish previously defended against other adults. In one case, three juveniles were observed feeding on a carcass claimed by an adult. The adult gave repeated Long Call

Displays and was completely ignored by the feeding juveniles. If the adult charged, the juveniles only scattered briefly. As soon as it began feeding again the juveniles would return and begin feeding also. The adult finally walked off, giving a Long Call to another adult feeding over 30 feet away.

The Head Tossing Display used by begging first-year juveniles was also observed frequently, although regurgitation feeding of a juvenile by an adult was observed only once.

DRIFT EGG FEEDING

Much of the Glaucous-winged Gull's time on Olsen Creek was spent bobbing for loose salmon eggs that rolled along the stream bottom, carried by the current. These eggs were primarily those which were dug up by salmon spawning at a site where other salmon had spawned previously. When drift egg feeding, a gull swam with the current until it spotted an egg. If the egg had been forced to the surface by an eddy or a digging salmon, the gull simply ducked its head and grabbed it. If the egg was deeper, the gull jumped up from the surface of the water and dived headfirst after the egg, often completely submerging. The gulls would also stand in shallow riffles and catch eggs rolling by. A gull intercepting eggs on a riffle appeared to have interactions with other gulls very similar to those centering around carcasses. A swimming gull, however, was exceptionally vulnerable to an attacking bird. When the attack came from the air, the swimming bird was helpless. It either had to fly up at the low-flying approach of an attacker or be bowled over, for the attacker always tried to land on top of the swimmer, throwing it off balance in the water and making it practically helpless before further onslaught. Thus, in all of 58 such attacks, the swimming gull either flew up at the approach of another gull coming in low over the water or, if caught by surprise, was knocked off balance, fleeing as soon as it could.

Another behavior pattern associated with riffle egg feeding was paddling (reviewed by Tinbergen (1960)) in which the gull stood in one place and trod rapidly in shallow water. Tinbergen concluded that for Black-headed Gulls (*Larus ridibundus*) feeding in shallow pools, the primary purpose of paddling was to stir up invertebrates, which then revealed themselves by moving. In Olsen Creek, paddling usually occurred when a Glaucous-winged Gull was standing in a shallow riffle. Its apparent purpose was to loosen salmon eggs from the surface gravel, although it was observed both before and after a gull had bobbed for an egg.

SUMMARY

The feeding behavior of the Glaucous-winged Gull was studied on Olsen Creek, a salmon stream flowing into Prince William Sound, Alaska. It was found that feeding

took place in two distinct situations: (1) on the banks of the stream on salmon carcasses pulled up by gulls or bears and (2) in the stream itself, on salmon eggs drifting with the current. The behavior patterns centering around the defense of salmon carcasses appeared to be very similar to the territorial displays of the breeding season with these exceptions: actual territories did not exist, the carcasses were defended only by hungry birds, and the attacking gull won more often than the defender in disputes over a carcass. Upright Displays, Oblique-cum-Long-Call Displays, and Mew Call Displays were all observed frequently during carcass defense. The effectiveness of such behavior, however, tended to break down in the presence of bears feeding on freshly caught salmon, particularly when the salmon were females. The gulls also seemed to exhibit preference for female over male carcasses of spawned out salmon. Birds in immature plumage usually could not defend a salmon carcass against adult gulls, although first-year juveniles had a certain immunity to attack by their unresponsiveness to adult threat displays. Apparently, even adults cannot defend themselves against other adult gulls while diving for drift eggs in the stream. At the approach of a low-flying attacker, the swimming gull must either fly up or be bowled over. If drift egg feeding occurs in a riffle, however, the riffle can be defended like a salmon carcass. Paddling, probably to stir up salmon eggs caught in the surface gravel, also occurred in the riffles.

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