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BREEDING BEHAVIOR OF JAEGERS AND OWLS NEAR BARROW, ALASKA

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On the arctic coast in 1952, near Barrow, Alaska, Pomarine Jaegers (*Stercorarius pomarinus*) and Snowy Owls (*Nyctea scandiaca*) nested at the time of an upswing in numbers of the cyclic brown lemming, *Lemmus sibiricus*. In 1953, when lemmings were at peak abundance, these two important predators again nested, the jaeger in much higher density than in 1952, and in addition a third predator was common, the Short-eared Owl (*Asio flammeus*). A considerable amount of information on the breeding behavior of these species was obtained by us in those two years, and it is the purpose of this paper to report observations that add to the existing knowledge concerning them.

The breeding of the Pomarine Jaeger, Snowy Owl, and Short-eared Owl near Barrow (latitude 71° N.) as well as elsewhere on the coastal plain bordering the Arctic Ocean in America and Eurasia is correlated with numbers of the brown lemming. In the higher interior country of the arctic and at more southern latitudes, the two owl species depend also on other microtines. But on the lowlands close to the Arctic Ocean it may be said that any significant amount of breeding in a population sense appears to depend on the brown lemming. This is particularly true for the Pomarine Jaeger. Those aspects of the ecological relations of these avian predators having to do with their responses to lemmings as prey are dealt with in another paper (Pitelka, Tomich, and Treichel, 1955). In that paper data on relative abundance near Barrow in 1949-54, on breeding densities and nesting success in 1952-53, and on predation are given. This information will be referred to here only insofar as it relates directly to aspects of breeding behavior considered in this paper.

The numbers of nests found, many of them revisited a number of times, were as follows:

	1952	1953
Pomarine Jaeger	30+	80+
Snowy Owl	3	7
Short-eared Owl	0	28

Field work was underway from May 29 to September 12 in 1952, and from May 17 to August 24 in 1953. It should be emphasized, however, that what we offer here are notes on species still deserving intensive study, and our observations were obtained mainly in the course of censusing of bird populations on various areas and while other field work on birds and mammals was underway. In the choice and organization of observations worth reporting, we have been guided by the general works of Bent (1921, 1938), Witherby *et al.* (1940, 1941), Salomonsen (1951), and Dementiev *et al.* (1951), as well as by a number of original references.

Variation in plumage of Pomarine Jaegers is such that often the members of a given pair, trio, or even quartet can be distinguished in the field. This is made possible not only by differences between dark and light phases and intermediates between them, but also by a quantitative color dimorphism between sexes. Use of these characters is facilitated also by sexual dimorphism in size, the female jaegers averaging about

850 grams, the males about 650. In addition, subadult individuals are distinguished by incompletely developed central rectrices as well as other characters (see discussion in Pitelka *et al.*, 1955). Hence, it is possible in this jaeger to deal with behavior in the field in a more specific way than in most other species without artificial marking, and these circumstances made possible some of the observations summarized beyond.

POMARINE JAEGER

Near Barrow, the Pomarine Jaeger is in general the most numerous of the three jaeger species (Bailey, 1948:234). It occurs from late May to early September, although in certain years it may arrive in early May or remain into late September. In lemming years, jaegers appear in large numbers when lemmings are exposed at the time of the spring melt-off of snow, in late May or early June. Numbers then fall off as breeding gets started.

Habitat.—As a breeding species, the Pomarine Jaeger frequents coastal flats near the Arctic Ocean, in areas of small lakes and meandering rivers (Dementiev *et al.*, 1951:387). On the generally flat terrain of the Barrow area, breeding pairs may settle almost anywhere, but they settle in greatest density where marshy flats or poorly drained lowlands are most extensive. This is the habitat of their chief prey, the brown lemming. As Dementiev (*loc. cit.*) brings out, Pomarine Jaegers are not parasitic while breeding.

The nest is placed on slightly raised ground, as on a low shelf at the border of an extensive marsh or on the low ridge inclosing a low-center polygon. Occasionally the nest is on a level with the surrounding ground. A hollow is formed, perhaps merely as the result of the heavy bird settling on the soft moist ground that already offers some sort of a depression. Likewise, some nests with plant materials surrounding them or in their bowls seem to be thus provided only because of the chance presence of this material nearby. We have not observed jaegers deliberately forming a bowl or carrying nesting material.

Non-breeding jaegers wander widely over the tundra and over the ocean, along the shore or out some distance, using ice floes as rests. They are usually in small groups, but may occur singly or occasionally in fairly large, loose flocks of as many as 50 or 60 individuals. In summers of non-breeding, as 1951 and 1954 near Barrow, their occurrence is irregular and usually brief.

Breeding schedule.—The breeding cycle requires 10 or 11 weeks and breeding begun in mid-June, if successful, is not completed until the last week of August. For the population as a whole, the breeding season of 1953 was 10 to 14 days ahead of that of 1952. This is correlated with the fact that snow cover persisted late in 1952, and the first jaegers were not seen until June 9, whereas in 1953, jaegers were first seen on May 25.

In 1952, nesting began about June 20, on which date the first nest, with one egg, was found. All other nests were started within the next five days. First newly hatched young were found on July 17, and by the 20th, almost all nests contained young. In 1953, eggs were laid chiefly in the period from June 16 to 19, although some were probably laid earlier. Hatching records obtained later indicated that some were laid as early as June 10 or 11. In the main, young hatched in the period from July 10 to 15, but one hatching egg was reported on July 6.

The incubation period of this jaeger is not known. Our efforts to determine it were not completely successful for any one nest, but for several the error in estimate was no more than one day. From three such records the incubation period was determined as 27 or 28 days. In the light of data reported for the smaller species *parasiticus* (Witherby

et al., 1941:124), this estimate is reasonable, and in any event more closely determined incubation periods of *pomarinus* will probably be found to vary over several days.

In 1953, additional nests were started later than June 19, as evidenced by the following observations: Copulation was observed as late as June 23, and the nest of this pair, with two eggs, was found on June 29. A new territory was established on June 22 in an area visited daily, and the nest with two eggs was discovered on July 8. Finally, a nest already containing two eggs on June 18 was found destroyed on June 24; the same pair started a second nest which contained one egg on July 2 and only one after that date. Thus, on a population basis, breeding was less synchronized in 1953 than in 1952.

Young are able to leave the nest after the second day and usually do so by the fourth, wandering in the vicinity of the nest site. They are fairly easy to locate until after the first week. By that time, they move fast, hide well, and are no longer necessarily near a marked nest site. Birds about one week old enter small ponds freely and swim rapidly. Young begin to fly when they are five to six weeks old. First young were seen on the wing in 1952 on August 25, in 1953 on August 13. They are attended by parents for at least a week more. Feeding of young by adults continues after the former are able to hunt for themselves. This period of semi-independence could not be determined exactly, but it is safe to state that it lasts at least a week. The repeated observation in 1952 of only one adult attending any one young bird suggests that toward the end of the period of fledgling dependence, only one adult feeds any given young, but this point also requires further study in the field.

Adults share in incubation and in the care of young, as previous observers have reported. Young are fed largely, if not exclusively, on morsels of meat torn from lemmings (*Lemmus*). Such pieces were regurgitated by some of the young handled during banding.

Clutch size.—In 1952, all nests found contained two eggs. In 1953, a fair number contained only one egg, perhaps five to ten per cent, but no definite data were gathered on this point. Although Bent (1921:9) states that clutches may consist of "two or three . . . , usually the former," there appears to be no basis for any statement or implication that three eggs may be laid by one bird. Witherby *et al.* (1941) advance their statements more cautiously, but credit the Parasitic Jaeger (*Stercorarius parasiticus*) with even four eggs per clutch, "very rarely." The fact is that specimens of both sexes of breeding *S. pomarinus* collected by us showed two distinct, bilaterally placed brood patches, 3x6 cm. in size, each large enough to accommodate one egg, and it seems that these jaegers must regularly incubate no more than two eggs. We note that Salomonsen (1951), in his treatment of the jaegers, credits none of them with more than two eggs per clutch in spite of the writings of earlier compilers. Dementiev *et al.* (1951:388) likewise point out there is no evidence of clutches larger than two.

In view of the chronic enthusiasms of old-school oölogists, as well as carelessness of some collectors with data, should not records for clutches in excess of two be checked thoroughly? In part, the notion that jaegers may lay more than two eggs may be traced to early writers such as Kumlien (1879:95), who, in other connections, made some fantastic observations (see, for example, comments of Salomonsen, 1951:261). There is a possibility, of course, that extra eggs may be laid by a second female, as indeed is suggested by Witherby *et al.* (1941:124) for the Great Skua (*Stercorarius skua*). This we are inclined to doubt for the Pomarine Jaeger because the species is so strongly territorial and any intruder is repulsed so promptly by either or both sexes that it is difficult to see how any intruding female would be tolerated long enough to lay an egg! It should be remembered that both members of a pair remain on the territory con-

stantly. These comments are made even though we have, ourselves, found a five-egg nest of the Red Phalarope (*Phalaropus fulicarius*) and know that the H-shaped incubation patch of the male is formed to accommodate no more than four. In this species the loose organization of the breeding population actually allows for the occasion of a second female entering one nest. However, in the case of our five-egg nest, after a few days the extra egg was found a few inches outside the nest, which then was still active.

Territoriality.—Pomarine Jaegers are strongly territorial, and in this respect they resemble the Long-tailed Jaeger, *Stercorarius longicaudus* (Manniche, 1910:175). They occupy territories any time from the last week of May through the first two weeks of June, one to two weeks before eggs are laid. Both members of a pair act in defense of a territory, and such behavior continues through the period that young are dependent on their parents. Foraging is normally confined to the territory, throughout the nesting cycle, and adults defend their territories into August with almost as much vigor as earlier.

Once a pair is established and nesting is begun, the birds are generally silent. The fact of an occupied territory is advertised merely by the presence of the occupants cruising slowly over the area or standing erectly on the ground or some slight promontory if such is available. If there is a threat of intrusion, a jaeger at rest and settled on the ground may merely rise and erect itself. It may also call or it may raise its wings in a threat display as it calls. Or it may take wing, flying toward the threatened approaching intruder; if the jaeger is on wing, cruising slowly, it will increase its speed and fly directly toward the intruder, usually calling. The typical call is a harsh, gull-like *yowk, yowk, yowk*, variable in pitch and tempo, becoming a series of high-pitched, sharp screams when the jaeger is excited. If an intruder enters the territory, the jaeger, or usually both members of a pair, call persistently and swoop down or dive over the intruder, wheeling back over the territory rapidly, and then, with accelerated flight and another sequence of screaming calls, again swoop over the intruder. The intruder may be struck with the dropped feet as the jaeger passes over. This ultimate in aggressive behavior of the Pomarine Jaeger is addressed to humans, to vehicles, to owls grounded or flying slowly over a territory, or on occasion to larger birds on the ground, such as Brant (*Branta nigricans*). If the intruders are other jaegers or gulls, those merely moving across an area in long distance flights accelerate their speed and fly on silently. Territorial action then consists merely of the chase and calls. But if the occupant jaeger is already more or less excited, or if the intruder is reluctant to leave or is contentious, the jaeger may swoop over or toward such casual intruders and double back to repeat this. Such behavior is commonplace between competing neighbors with much yelling, swooping, and wheeling over the contested area by all four members of the competing pairs.

The aggression among jaegers is chiefly bluff, and rarely does it lead to bodily clash. But it definitely may among birds occupying compressed territories, as was observed in one area in 1953 when the activity centers of three neighboring territories were no more than 400 to 500 feet apart (see west side of plot 1 in fig. 5, Pitelka *et al.*, 1955). Between two of these pairs, on June 17 and again on June 23, a boundary contest went on through most of an hour or so which one of us spent nearby while censusing a study plot. At this time actual combat occurred several times with two jaegers clashing in the air and dropping to the ground in a struggle. The observer was not close enough actually to see the bills in use, but it seemed clear from all other features of these fights that they were used, as in many similar situations in other birds.

Other, more routine territorial actions among neighbors may now be described.

There are what we may term challenge flights, usually silent, when a jaeger (A), apparently at this moment aware of a particular neighbor, approaches the periphery of his territory in the direction of the neighbor. This prompts the neighbor (B) already in flight to swing over toward the boundary in a retaliatory flight. No calling need occur, and there is therefore a good deal of territorial assertiveness manifest merely in the movements of the birds. If A moves close to the territorial limits, B may call as he reasserts by his flight his occupation of the area momentarily challenged. From observations of many such engagements, it appears that there is more or less of a neutral zone between territories, sometimes one or two hundred feet wide, as when a natural physiographic break such as a low ridge separates the preferred lowland habitat. Usually it is narrower, and occasionally very narrow or even nonexistent, as between the crowded pairs mentioned earlier.

Members of either of two neighboring pairs may venture in such a neutral zone with the possible consequences just described. If A moves through this zone to B's boundary, the retaliatory chase of B will proceed into the zone but not so far, usually, that the antagonism is reversed. When this occurs with A undertaking the chase instead, and after many such occasions, one way or the other, the fact of a neutral zone becomes clear, in spite of the monotony of the terrain over which it is difficult or impossible to detect what jaegers respond to as markers. In these situations, also, the aggravated jaeger typically ends a chase with calling and with a sudden burst of speed close to the boundary, then wheels sideways in a steep bank and returns. Persistent aggravation of a territorial bird provokes repeated and rapid attack flights, almost always accompanied by loud calling, as already described.

Territorial actions of the two sexes appear to be similar. Members of a pair regularly cooperate in the defense of the home area, as they do also in incubation and care of young. One adult on the wing may chase an intruder, calling as the chase occurs; its mate may support his aggression by calling from the ground or by calling and taking wing to participate in the chase or by merely following its mate, turning back when the latter does. The incubating adult will call in warning or alarm from the nest when an intruder approaches but will usually not take wing as readily as the other, free member of the pair. Like the free member of a nesting pair, the one settled on eggs may also raise its wings in threat display as it calls, but this it does without rising from the eggs. The incubating bird typically offers this display in support of the aggressive behavior of the mate on wing.

It is clear now that the territorial behavior of the Pomarine Jaeger resembles that of many passerines, but lacks song, or at any rate a regularly delivered vocal announcement. The challenge flights and retaliatory flights, the latter reinforced or not by calls, are in effect types of aggressive display functioning in territoriality. The territory of the Pomarine Jaeger subserves functions of both reproduction and self-preservation (Armstrong, 1947:274), from at least the time pairing is already completed and copulation is yet to occur, through nesting and rearing of young. It is not possible now to say to what extent, on a population basis, prenuptial display and pairing occur on the territory. Events of 1953, about June 1, suggested that some jaegers may arrive already paired. But it is certain that on some territories, prenuptial display and pairing occur as well as all the remaining activities of the breeding cycle.

In 1952, observations that continued through August and early September provide certain facts about territoriality in the latter part of the nesting cycle. In the first week of August, and hence in the period young were being fed, changes in the limits and areas of territories were occurring, and at least those pairs noted by us were enlarging their foraging ranges. This was true of pairs with territories near the ocean shore, which

now were noted feeding along the shore. It was also true of a pair marked with paint by D. Q. Thompson which extended its hunting over an area frequented by us and not earlier used regularly by that pair, or by other jaegers. This spread of hunting effort occurred when young were two or three weeks old, and the general mid-summer scarcity of lemmings was apparently responsible for it. Defense of some territories continued as late as August 30, when, on at least two territories, young were attended singly by an adult. At several territories close to Elson Lagoon, young left to fly out over the lagoon where they chased Glaucous Gulls (*Larus hyperboreus*) and picked up food disgorged by the gulls. Young thus roaming and foraging were observed to return to adults whose own movements were still local and who usually did not accompany the young away from the territory. The indications are that adults on territories with advanced young may remain attached to these areas while young are already progressing toward independence.

Contrary to Salomonsen (1951:262, 270), then, the organization of breeding populations in the Pomarine Jaeger should not be referred to as "colonial"; nesting pairs are territorial in every sense of the word. This matter is discussed by us more fully elsewhere (Pitelka *et al.*, 1955).

Pairing display.—On numerous occasions in June, birds in two's on the ground performed together or singly a display evidently significant in pairing or maintenance of the pair-bond. In some instances later events indicated the pair was still unformed, whereas in others, the two birds continued to associate and to respond to others as a pair. Other displays, overtly similar in certain features, are also mentioned here, but the full repertoire of display behavior, by modern standards of ethology, remains to be described.

In the display associated with pairing, one jaeger receives another that is about to alight by raising and pulling back its head, puffing its breast feathers, raising and spreading its tail slightly, and then elevating the two elongate rectrices above the plane of the tail. Also, the bill may be lifted and lowered, but this was never seen to occur rhythmically. What vocalizations other than the usual loud calls accompany this display cannot be said; usually in the field the wind prevented hearing any soft notes. Occasionally both of two birds would perform this display facing each other; then one would turn and perhaps also walk a short distance away. The erected rectrices appeared to be a focal point in the display. On one occasion (June 18, 1952), two jaegers on a mound, vibrating their wings and holding their heads high, alternately displayed before each other. In the course of an attempted but unsuccessful copulation watched on June 24, 1953, the male would hold his head high facing forward and puff his neck feathers prior to advances thwarted by the female moving forward. On other occasions, copulation was preceded by the display with raised central rectrices, as described. Still other copulations were not preceded by any visible display actions.

The pairing display was also seen in groups of three birds, at a spot later occupied by a breeding pair, and two of these would display before the third. Such a group, witnessed several times, would break up soon, with two or all three taking wing, and in a few instances, flight would occur as a result of aggressive gestures of one toward the second displaying bird. The aggressive bird, in extreme instances, would pull its head back and down, raise its wings partly, and dash at the other, pecking at it. Typical loud calling would occur prior to the aggression and flight. Or, two standing birds would be seen, one displaying, and a third would come along and chase the displayer, then return and remain in the area with the passive bird.

While we can only describe these incidents briefly, it is clear that a display ritual, with variations, occurs early in the breeding cycle and is significant in pairing and

apparently also in the maintenance of the pair-bond, inasmuch as through June, with pairs clearly settled on an area, the display would be seen presumably after pairing had been completed. Certain elements in this display apparently have no relation to territorial contests, except insofar as one member of a forming pair repulses a single bird which may be from a neighboring area attempting to associate with it. On the other hand, the raised-wing display, a gesture of aggression used in the course of pairing, is used subsequently by territorially established birds, as described. A raised-wing display occurs also in the Great Skua, and with similar function (Murphy, 1946:1026, 1032; Witherby *et al.*, 1941:124). In many features of display, the Pomarine Jaeger also resembles some of the larger gulls, but information available for the jaeger is too fragmentary to justify comparisons now.

Distraction display.—*Stercorarius pomarinus* does not perform a distraction display, and aggressive actions described under territoriality are the only ones manifest when a human approaches a nest. Near time of hatching, both members of a pair, but particularly the female, merely become more ferocious. In this respect, *pomarinus* contrasts with *parasiticus*, which has a routine distraction display; this was witnessed in a single nesting pair, both members displaying, at Barrow in 1952 (see also Salomonsen, 1951:271). *S. longicaudus* is stated by Witherby *et al.* (1941:138) to have a distraction display. Manniche (1910:173) does not mention or even hint at one, Soper (1946:234) reports he never observed *longicaudus* in such display, and Salomonsen (1951:282) states flatly that the species "does not feign injury as the Arctic Skua" (Parasitic Jaeger); but Birulya (1907:60), Deichmann (1909:152) and Sutton (1932:167) can be cited in support of Witherby *et al.* In this respect, then, *longicaudus* appears to be variable and thus contrasts with the other two species, of which one has a well-developed distraction display whereas the second has none.

Other notes on behavior.—Study of the accounts of the Great Skua written by Selous (1901), Pitt (1922), Murphy (1936), and others impresses one with the fact that in many basic traits of behavior, *Stercorarius skua* and *S. pomarinus* resemble each other closely. Among these traits are the generally hawk-like behavior of both, their massive strength combined with maneuverability, vigorous defense of territories and nests, their aggressive diving and manner of striking, their persistence in attacking an intruder, their raised-wing display, their lack of a distraction display, their clamorousness, and various aspects of behavior referred directly to nest or young. Murphy (1936:1029) noted that wounded skuas did not utter cries. This we found true also for Pomarine and Parasitic jaegers, for those lamed in collecting as well as for those found lamed with a broken wing or caught in a fox trap. Comparative investigation of behavior may bring out differences in details between *skua* and *pomarinus*. But a fact worth emphasizing here is that while their general behavior patterns are similar, there is a significant difference between them at the population level, in spatial organization and food dependences of breeding pairs, *skua* being properly termed a semi-colonial species, whereas *pomarinus* is not colonial but rather territorial in all senses of the word.

In 1953, when Brant nested abundantly in the Barrow area, their nests were not molested by jaegers even though these were easily located when the female was incubating and even though the eggs were occasionally left uncovered. A pair of jaegers regularly and persistently harried a male Brant when one of us entered their territory. In this action, the Brant would stoop and run ahead slightly to avoid the plunging jaeger. It would grunt repeatedly, particularly if incited to face the jaegers directly; then it would raise its wings slightly to meet the threat. Occasionally, it would take wing in brief sallies when the jaeger came close, and this was the most aggressive retaliation. The Brants' nest was about 75 feet away from that of the jaegers, and

after observation of several sequences of the behavior described, it became clear that the close association of these birds was normally peaceful, but that in the presence of a man, the jaegers addressed their aggression to the Brant rather than to the man. If the female Brant left its nest and the pair then moved at least two or three hundred feet away, the jaegers would leave them alone and then fly over the man if he remained nearby. At no time was there any gesture of molestation by the jaegers at the Brants' nest, and the young goslings were led away from the area successfully. Dementiev *et al.* (1951:397), however, state that the Parasitic Jaeger preys on eggs of the White-fronted Goose (*Anser albifrons*).

Juvenal jaegers harass other birds soon after learning to fly. Their attacks on Glaucous Gulls in early September were mentioned earlier. In addition, on September 8, 1952, three juvenal jaegers were observed attacking a juvenal Snowy Owl, which then was able to fly well.

SNOWY OWL

As elsewhere in the arctic, in northern Alaska the Snowy Owl is a resident species, remaining through the winter when lemmings are common (Bailey, 1948:265). The literature on the Snowy Owl is far more extensive than that on the Pomarine Jaeger, and what information we gathered agrees closely with reports of earlier observers (Pleske, 1928; Murie, 1929; Sutton, 1932; Bent, 1938; Witherby *et al.*, 1940; and Salomonsen, 1951).

Habitat.—One feature of nest location detected among the 10 sites near Barrow in 1952 and 1953 does not receive any comment by previous writers. There, nests are placed on high polygons or on raised parts of better-drained ground, as a low ridge, and in eight of these sites, the nest was placed with reference to a slope bordering a drainage axis so that the incubating owl had what for the flat tundra terrain was a relatively generous vista. As we observed, the female leaving the nest could slip off, flying low and even coasting along the slope into the drainage axis, then moving up on the other side; or it could fly back away from the nest, over polygons or a ridge. Two nests were located on high polygons in areas not immediately sloping off into a drainage axis, but not more than several hundred yards from one. As nesting is begun early, a spot of bare ground is of course most likely to be available on raised ground and also near slopes where snow drifting would result in thinner snow cover on the adjacent high ground. These factors must figure not only in location of the nest site but also in the effectiveness of the owl in hunting. But it is our impression that more is involved, since the very physiography of these sites enables the owl to give itself what little measure of protection the terrain can offer in that it can leave or approach a nest with good chance of avoiding detection, at least through May and in early June. The fact was that in 1953 the subtleties of this physiographic configuration around a Snowy Owl nest were sufficiently impressed upon us so that on June 16, when the last four nests were found, two of them were spotted directly, in an area occupied by owls, by mere choice of what seemed to be the most "ideal" part of the terrain!

Breeding schedule.—The nesting cycle lasts over three months, probably $3\frac{1}{2}$ months. Nesting begins in the latter half of May or early June. From hatching records as well as nests found early, we estimated that in 1952 clutches were begun in the period from June 5 to 10, whereas in 1953, they were begun in the period from May 15 to 20.

The incubation period is 32 to 33 days (Pleske, 1928:166; Murie, 1929:8). Eggs hatch in late June and the first half of July. When 20 to 25 days old, young may wander from the nest mound and remain nearby. According to Witherby *et al.* (1940:310), young in captivity begin to fly at ages of 51 to 57 days, and on this basis, young at

Barrow, in such a year as 1953, would not take wing earlier than about August 10. We were unable to determine directly the age at which young take wing, but one young kept by us in an outdoor cage and given opportunity to move about almost daily performed its first successful short-distance flight on August 13 when it was about seven weeks old. One juvenile in 1952 observed on September 8 was in flight and unattended by adults.

The lengths of the periods over which young are dependent and then semi-dependent are not known, hence the uncertainty indicated concerning the length of the nesting cycle. On the basis of the situation at Barrow, it would appear reasonable that the young are largely if not entirely independent by the last week of August or the first week of September. This is a guess, however, which we have ventured in the interest of a usable approximation of the time required by nesting.

Territorial behavior and display.—In 1953, hooting and pairing activity at Barrow was recorded from May 17 (earliest date of field work) to May 28. In 1952, no regular hooting was heard in late May or early June, but occasional hooting was recorded in middle and late June. We did not witness the large-scale hooting of territorial birds described by Sutton (1932:206), but the breeding population observed by him was evidently much denser than the one near Barrow.

Nesting pairs near Barrow were widely spaced out, usually one to four miles apart, or even farther. No territorial conflict between known neighboring pairs was witnessed. It is likely, however, that what territorial differences occurred were largely settled in April or May, well before our field work began. The areas occupied by nesting pairs were mutually exclusive, so far as we could judge by their local movements. The available evidence on territoriality, ours as well as that in the literature, is scant and largely circumstantial, but there is no reason to expect that this owl would differ from temperate-zone owls.

On May 27, 1953, in one area near the ocean shore some distance away from nesting areas, one male repeatedly chased a second, dark bird, which may have been a female or a young male. The latter returned the chases several times, and on one such occasion, the male, remaining on the ground, faced its approaching opponent by stooping slightly and holding its wings out partly. This was evidently a threat display, which incidentally resembles the courtship display. Later, the light-colored bird took wing and the dark bird followed, swooping toward the first in a mid-air dash. The former continued its flight while the dark bird returned to the area. Owls did not nest in this area, but the behavior observed is probably typical of territorial bickering.

Non-breeding owls do not react to each other aggressively, and indeed may occur in local concentrations. Thus, in 1953, on several occasions in mid-June, 20 to 30 owls were seen scattered and resting on areas of no more than 50 to 75 acres. Smaller local concentrations were seen in 1952, as well as later in 1953. Thus, while Salomonsen (1951:467) may be correct in saying this owl "is not gregarious," it is not anti-social, so to speak, to the extent that individuals habitually isolate themselves.

The "courtship antics" described by Sutton (1932:209) consist only of the territorial hooting in which the male, in the manner of the Horned Owl (*Bubo virginianus*), calls with lifted tail. A pairing display witnessed by us on two occasions we do not find described in the literature. A sequence observed on May 24, 1953, is described in Tomich's original notes as follows: "A brown-plumaged bird [female] was making short flights across the snow, evidently hunting lemmings. Its manner was to hop four or five feet, or ten feet, with the aid of the wings. A white owl [male] then came over the ridge at an angle and alighted on snow some 50 feet from the first owl. It carried a dark object, likely a lemming, in its bill, and the brown owl flew immediately to it,

perching behind it. The white owl stood with its wings raised and leaning forward about a minute. Then it turned to one side, maintaining the raised-wing attitude. The brown owl stood quietly." A similar sequence was witnessed on May 28, although we were unable on that date to ascertain whether the white individual held anything in his bill.

SHORT-EARED OWL

Near Barrow, the Short-eared Owl occurs rather irregularly (Bailey, 1948:268). In 1953, it nested commonly and was present from May 24 until observations were stopped in August. In the main, breeding behavior witnessed by us was similar to that already described in the literature, but for so widely distributed a species, the available information is surprisingly limited. For this reason, and because we are dealing with a population at a high latitude, a complete summary of our observations is given here.

Habitat.—Although Short-ears could be encountered almost anywhere on the tundra, they were most numerous in areas of broken tundra where slight rises provided good vantage points. Nest sites were characteristically on relatively high ground, on ridges or polygons, where a coarse grass (*Arctogrostis latifolia*) generally ignored by lemmings provided just about the only cover the owl could use to some advantage. Even so, the nests were conspicuous and easily seen from overhead as the old grass culms and blades forming the shelter for the nest were rarely more than six to eight inches long and then rather sparse and more or less inclined. A few nests were placed on lower ground, on better drained parts of marsh flats, where remains of dense growths of grass (*Dupontia*) and sedges (*Carex* and *Eriophorum*) provided a site for the nest bowl. In all cases, once the location of the nest was known, the incubating bird usually could be seen from a distance of 50 to 100 feet.

Breeding schedule.—Pairing and establishment of territories occurred in the first week of June. The first records of eggs, on June 11, as also the span of time over which new clutches were started, are shown in figure 1. On the basis of the time intervals indicated in that figure, eggs are laid usually one every two days, and according to Witherby *et al.* (1940:333), this is the general rule. But in some clutches, certain intervals may be shorter, approaching one day (nest 4); others may be longer — as many as four days (nest 3). Longer intervals "of up to a week" are known (Witherby). In all these estimations allowance is made for the possibility that any given egg may have been laid on an earlier date which is blank in the record (fig. 1).

On the basis of data and estimates just given, first eggs were laid in 1953 near Barrow from June 6 to June 22 or 23. In addition to data given in figure 1, two females collected on June 8 were in pre-laying stage and contained enlarged ova, to 12 and 5 mm., in a first-year and an adult individual, respectively. Both of these females, 406 and 475 grams in weight, had light fat. Age distinction is based on the presence of worn flight feathers and wing coverts of the juvenal plumage in first-year birds (Witherby *et al.*, 1940:331).

Females occupy the nest site in incubating position before the first egg is laid and probably after that egg is ovulated. At nest 4 (fig. 1), the female was found thus on June 20, and the nest contained one egg on June 23 (not checked the 21st or 22nd). At a second nest site, on June 9, a "broody" female flushed from an empty nest gave a single low, grunt-like hoot and actually performed a distraction display for three or four seconds about 50 feet from the nest before again taking wing and flying farther away.

Pair 4 was regularly present on a small area at the north end of census plot 1, and our repeated, unsuccessful efforts to find the nest puzzled us when other nests were found

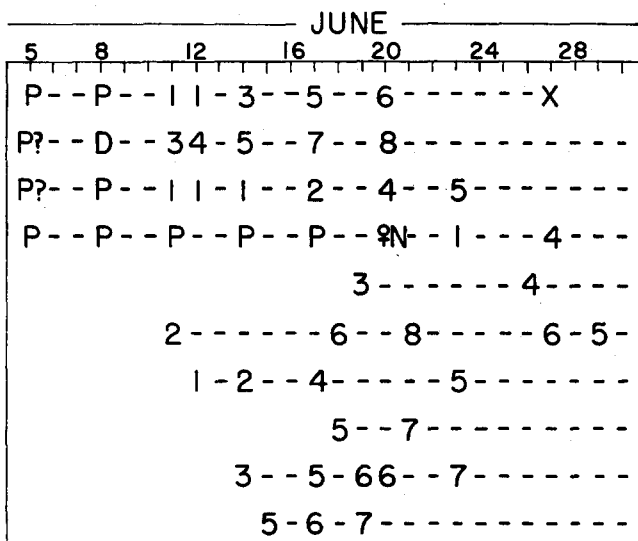


Fig. 1. Time records of establishment of pairs and egg-laying in ten nests of Short-eared Owls near Barrow, Alaska, in 1953; P, pair present near site where nest was later found; D, pair in display over nesting area; ♀N, female on nest cavity; numbers indicate counts of eggs on successive visits to nests; X, nest found destroyed. At nest 6, female continued incubating through period when three eggs disappeared, but the nest with five eggs was found deserted on August 5.

so easily. As is shown in figure 1, this pair was actually present on a territory fully two weeks before its nesting was started.

The difference in patterning between males and females (Bent, 1938:174), particularly that in the wing, was sufficiently clear that while our field work was in progress, we noted that without exception only the female incubates. This agrees with Witherby and also with Dementiev *et al.* (1951:387), but not with Bent (1938:172). Saunders (1923:122) also states that only the female attends the nest, in this case a nest with young. This matter deserves emphasis since Bent's error is perpetuated in the recent extensive study of incubation behavior by Kendeigh (1952:215).

Incubation periods estimated from successive nest observations are as follows:

Nest	Egg	Period	Dates
2	1st	At least 26 days	June 6-July 2 ¹
3	Last (5th)	At least 37 days	June 22-July 29 ²
11	1st and 2nd	30 days	June 6-8 to July 6-8
10	1st and 2nd	About 28 days	June 9-11 to July 6-8

¹ Egg still unhatched.
² Egg hatched no earlier than 29th.

For mid-latitudes, as given by Witherby *et al.* (1940:333), the incubation period is 24 to 28 days. The period given by Bent (1938:172) is shorter and probably unreliable. For the Barrow region, so far as the data go, incubation evidently may take no longer than it does at lower latitudes, but the average, as also overall variation, is probably greater. There is no mistake about the 37-day calculation given above.

On the basis of an average incubation period of 26 days, in the most advanced nests near Barrow in 1953, newly hatched young would be expected about July 3. The first young found was hatched on July 6 from a clutch the earliest egg of which we estimate was laid on June 6. All other hatchings occurred later. Thus, all indications are that incubation requires longer than 26 days.

Although both sexes care for the young, the female alone broods and continues this even after young leave the nest cavity. Thus, brooding still occurred on July 30, when a female was observed over the two youngest owls which had moved from their nest four feet away, while at distances of 20 to 100 feet farther away, five older ones rested. Where thriving young were observed in July and August, both adults were usually seen.

According to Witherby *et al.* (1940:333), young leave the nest after 12 to 17 days. It may be expected that at higher latitudes the period of nestling life would average longer. Heat quantities are lower and we have already seen that what evidence is available suggests that the incubation period may average slightly longer at higher latitudes. Regarding nestling period, we know that at one nest when the five young were 21 to 31 (± 1) days old, none had yet left the nest. On the other hand, at another nest the oldest young, known to be 16 or 17 days old on July 22, was found on that date 20 feet from the nest, which then contained three other young and two eggs. Thus, what evidence we have indicates that young may leave the nest after intervals as short as some recorded at mid-latitudes but others may remain in the nest longer.

We did not succeed in determining the age at which young begin to fly; according to Witherby, this is 24 to 27 days, while Urner (1923:33) estimates it at 31 to 36 days. On the basis of these estimates, near Barrow young would not be seen on wing any earlier, in 1953, than the last week in July. Our first record for a young bird in flight was August 8.

The period of dependence *after young take wing* is apparently unknown. According to Urner (1923:32), this is at least one to two weeks [or the difference between 31 to 36 days and six weeks after hatching, not six weeks after young are able to fly, as misstated by Bent (1938:172) in citing Urner]. In a medium-sized owl, the estimate of one to two weeks is surely conservative; for the better known Long-eared Owl (*Asio wilsonianus*), the period of dependence after flight is said to be three to four weeks (Bent, 1938:158). At Barrow we were unable to observe young in late stages of development, but in the light of facts just given, it is unlikely that any would have become independent before the middle of August.

Counting from the first week of June, then, we arrive at a minimal estimate of 11 or 12 weeks for the nesting cycle.

Territorial behavior and display.—The aerial display of territorial birds, circling over home areas, was seen many times in the period from June 5 to 11. During mid-day on June 5, the wing-flapping sound of displaying birds could be heard from all directions over and in the vicinity of a census plot on a beach ridge along which nest sites were relatively numerous. In the lower light of the evening on the same date, owls were grounded.

The most frequent call given in the aerial display was a single-noted harsh scream, like that of the Barn Owl (*Tyto alba*) uttered in flight over its foraging area, but the note of the Short-ear was less drawn out and lower pitched. This is presumably the harsh flight note mentioned by Witherby *et al.* (1940:332). It is a note evidently significant in situations of aggression, as it was heard most frequently on June 5 and 6 when displaying and chasing occurred generally. The hooting given on wing often just before a dive and wing-flapping sequence, consisted of 9 to 12 notes given about three

per second. These were short, sharp hoots, delivered regularly. Hooting and flight displays were observed essentially as described by various authors (Dubois, 1924; Francis Harper in Bent, 1938:170; Witherby *et al.*, *loc. cit.*).

Hooting and aerial display occurred at considerable heights above the ground, easily two or three hundred feet, where the owls were above the traffic of jaegers and were ignored by them. Short-ears display at such heights likewise at mid-latitudes; hence, this habit does not appear to have any direct adaptive relation to the presence of jaegers. Still it is interesting that some locally settled owls in attempting to elude jaegers on the wing did so by climbing higher when harassed.

Territorial behavior occurred clearly only in conjunction with the aerial display given at the beginning of the nesting cycle. Thus, in the period from June 5 to 11, when birds in display were observed frequently, they circled over their respective territories, announcing themselves with hoots and wing-flapping and intermittently giving the aggressive note mentioned above. Occasionally a displaying male swerved over to chase a neighboring bird, often giving the aggressive note in the course of the chase. These chases were deliberate and vigorous, and there seemed to be no doubt that although the birds were flying at a considerable height, their behavior was referred to some fairly definite area below. In the course of the high flights, particularly on June 5 and 6, on some territories two birds of a pair or forming pair would be on wing, both circling more or less independently, the male dropping into a flapping sequence when he happened to be close to the other bird as well as at other points in his circling. So far as we could tell, but one bird, presumed to be the male, did all the displaying and most if not all the calling.

Aerial display continued until June 11, and then was witnessed only a few times until the 20th. Such late display occurred in particular near one site on a census plot visited regularly. There the nest with the first egg was found on June 23.

No aggressive behavior among Short-eared Owls was observed after this period in which most nests were started. None occurred among owls flying about low when disturbed or in the course of their normal movements about the tundra. Indeed, certain flights of owls harassed by jaegers or flushed by one of us occurred over distances of up to $\frac{1}{4}$ or $\frac{1}{2}$ mile, and there was no doubt in these instances that the owl was crossing the areas occupied by other Short-ears. Thus, a dispersion of breeding pairs achieved early in the nesting cycle was not abetted by persistent aggression among neighbors. An ornithologist coming to the tundra after June 11 might think these owls were non-territorial. But the facts are that the breeding population became dispersed through available habitat in the course of a week's time when the owls in display were actively territorial.

Once the period of active aerial display was over, the activity areas of the owls were still largely separate, and the long flights just mentioned occurred relatively infrequently. This situation, incidentally, is similar to that in the Lapland Longspur (*Calcarius lapponicus*), which some writers state is non-territorial, presumably because of the amount of overlap in activity areas of neighboring pairs in the latter part of the nesting cycle.

Distraction display.—Distraction display or "injury feigning" was not observed in any conspicuous or persistent form. One instance has already been mentioned — that of a "broody" female flushed from a nest cavity. Another, flushed from a nest in the egg-laying period, flew over the observer and called *ki-rrr*. This shrill note was given several times followed by bill snapping, then another series of calls followed by bill snapping again. At a second nest, a female left and flopped along on the ground for a short distance before taking wing. No wing clapping of the type used in aerial display was

witnessed when the female was flushed from the nest. On all of the other and many occasions when a bird was flushed from its nest, it simply took wing and flew some distance before settling down or circling back and coming down several hundred feet from the observer and nest.

Witherby *et al.* (1940:333) state "injury feigning" is frequent. It seems possible that the fact of infrequent observation of injury feigning in the Barrow region Short-ears may be significant in view of the risks suffered by owls' nests in the presence of abundant jaegers. In general once a clutch was completed, owls disturbed from them left in an undemonstrative way. But the white eggs left exposed were conspicuous, and losses of nests with eggs were considerable, due probably as much to the degree of disturbance suffered by the owls because of intrusions by ecologists and Eskimos as to subhuman enemies!

SUMMARY

Noteworthy observations on breeding behavior of the Pomarine Jaeger, Snowy Owl, and Short-eared Owl near Barrow, Alaska, in 1952 and 1953, are reported. The breeding of all three depends here on the availability of brown lemmings, which in 1953 passed through a cyclic high.

Breeding pairs of the Pomarine Jaeger establish territories on marshy flats and extensive lowlands characteristic of the arctic coastal plain. Clutches of 1 or 2 eggs are laid; there is no satisfactory evidence that clutches in this species may be larger. Incubation lasts 27 to 28 days. Young are dependent for at least six or seven weeks. The nesting cycle lasts 10 or 11 weeks. Territories subserve functions of reproduction and self-preservation. Territorial behavior, comparable in the two sexes, continues throughout the nesting cycle. In all basic features except vocal announcement, which is lacking, the territorial behavior of this jaeger resembles that of many passerines. A display ritual apparently functioning in pairing and pair-bonding is described. This species of jaeger does not perform a distraction display.

Near Barrow, Snowy Owls typically place nests on high ground adjacent to a gently sloping drainage axis. Breeding pairs are spaced out and in this sense truly territorial, as might be expected with a large predator, but good evidence on defensive and aggressive behavior is lacking. The nesting cycle is estimated to last three months, probably 3½ months. A courtship display of the male is described.

By contrast with the other two avian predators depending on lemmings, Short-eared Owls nested near Barrow in 1953 but not in 1952. Territories were established in early June. First eggs were laid from June 6 to 23. Incubation required 28 to 30 days, the female alone incubating. Young unable to fly left the nest cavity at ages of 17 to 30 days. Early in June aerial display serving in territorial establishment and announcement was frequent, as also aggression among neighboring owls; but such behavior was not recorded after June 20. The nesting cycle spanned 11 or 12 weeks. Distraction display occurred infrequently; in this respect the Short-ears of the Barrow area appeared to contrast with those of mid-latitudes.

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