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THE SPRING BEHAVIOR OF WILD STELLER EIDERS

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Very little has been published on the behavior of the Steller Eider (*Polysticta stelleri*). Observations on general behavior and feeding habits of this species were made by Dr. H. M. S. Blair in Norway and by Lord William Percy in Siberia (reported in Bannerman, 1958). Brandt (1943) included a few notes on behavior in his study of nesting birds in Alaska. In 1959, the species was first brought into captivity and small flocks were established at the Delta Waterfowl Research Station in Manitoba, Canada, and at the Wildfowl Trust in England. The displays of these captives have been described by Johnsgard (1960, 1962, 1964), but no detailed account has been published on the behavior of wild birds.

In the spring of 1958, I watched Steller Eiders at Izembek Bay and Nelson Lagoon on the north shore of the Alaska Peninsula (fig. 1). From March 31 to April 28, large numbers of adults and subadults (birds in their first spring) were present at Izembek Bay. Many adults were in pairs, but the high frequency of courting flights indicated that some birds were still engaged in pair formation. A 30-mile boat trip on April 10 revealed 15 flocks, varying in size from about one thousand to several thousand individuals, giving an estimated total of 20,000 birds. A mass departure from this wintering area occurred at the end of April: large flocks were still present on April 28, but a survey by boat on April 30 showed less than 100 birds.

Small numbers of nonbreeding subadults have been seen in Izembek Bay in summer (Murie, 1959) and, at least in some years, large flocks of adults return from the breeding grounds in late August to molt in the area (Mr. Robert D. Jones, Jr., personal communication).

I spent from May 10 to 29 at Nelson Lagoon and, during the first few days, there were excellent opportunities to study a flock of about 800 Steller Eiders, and I obtained 500 feet of 16 mm. film. Most of these birds were subadults, but small numbers of adult pairs and a few courting parties were seen.

My observations at Izembek Bay were made with the aid of 20 × binoculars, but the birds were often so far away that I was unable to see all the details of postures and movements. At Nelson Lagoon, I was much closer to the birds and 10 × binoculars were used. Field notes were dictated to a Midgetape recorder and transscribed later to notebooks. Several details of behavior were checked and studied further in the captives held at Delta in 1959 and 1960.

ACKNOWLEDGMENTS

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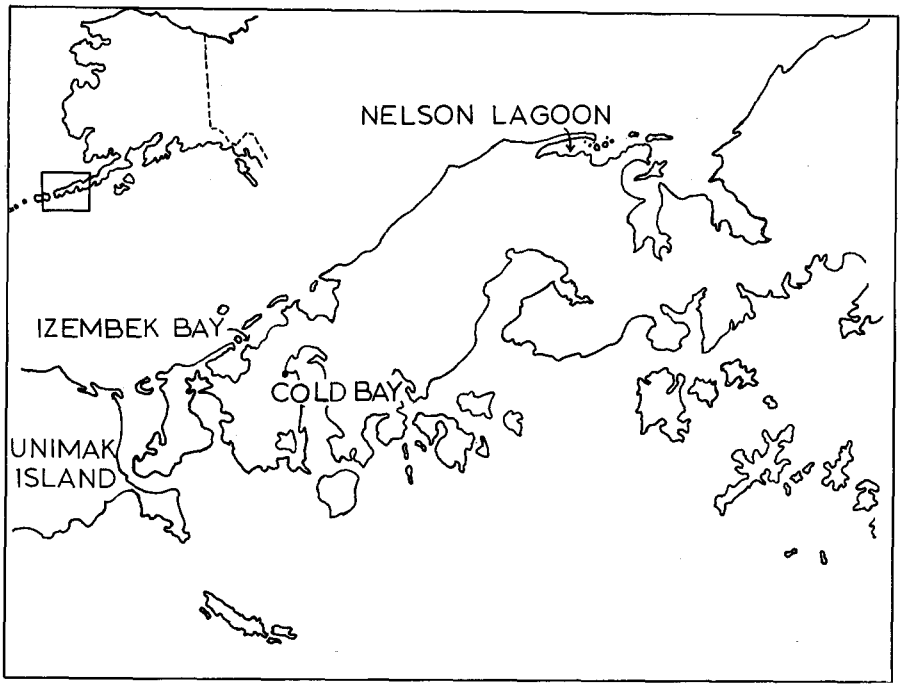

Fig. 1. Izembek Bay and Nelson Lagoon on the Alaska Peninsula where observations were made.

Dr. E. LeFebvre and Dr. N. Tinbergen for their comments on the paper and Dr. P. Johnsgard for the loan of films made at Slimbridge.

GENERAL BEHAVIOR

The Steller Eider is the smallest member of the eider group. The flight is swift and birds can take off quickly from the water with an agility similar to that of small ducks such as the Bufflehead (*Bucephala albeola*). When a large flock takes to the air there is a loud roar of wings, at times audible a mile away, as the birds rise steeply. In April, social tendencies were very strong and flying flocks "decoyed" readily to other groups on the water. Solitary birds and pairs seldom remained long away from companions.

Flocks were easily disturbed, flying up on the approach of a Bald Eagle (*Haliaeetus leucocephalus*), Gyrfalcon (*Falco rusticolus*), or even sometimes a hovering Glaucous-winged Gull (*Larus glaucescens*). Alerts were contagious and often a number of flocks would rise from one area, coming together in the air to alight in a single massed group. After alighting, the birds swam a few inches apart in a densely packed raft, with much shaking, wing-flapping, and restless swimming about with heads erect. Some minutes later, if there was no further alert, they gradually spread out and resumed feeding. After an hour or so without a disturbance, flocks would be strung out in long lines, usually along a feeding area exposed by the receding tide.

Steller Eiders spend much time feeding in shallow water. They wade or swim about, dabbling on the surface, up-ending, or feeding with the head under water. At Nelson Lagoon, a flock fed for several days on an accumulation of dead shrimps in

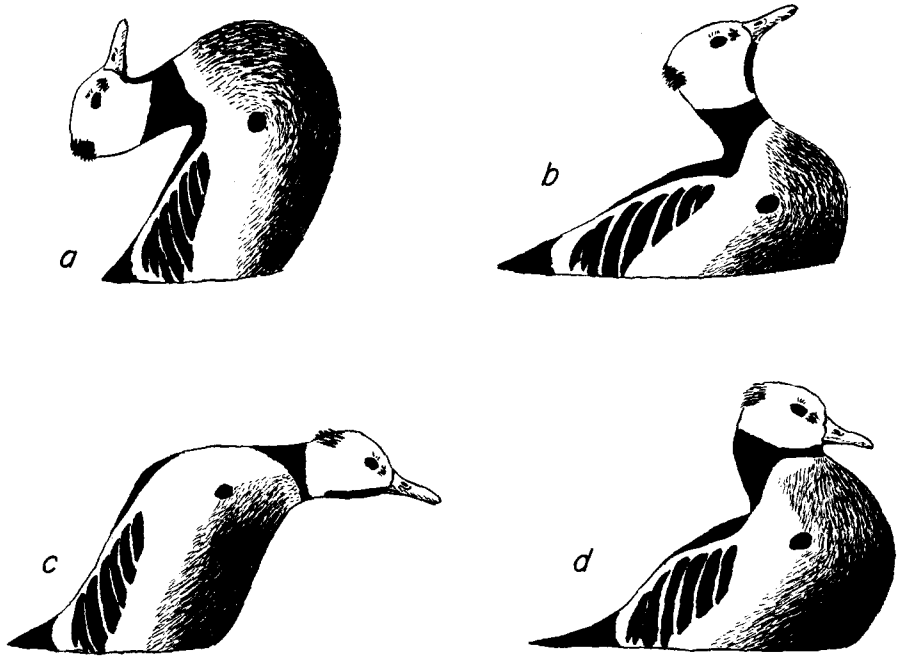

Fig. 2. Displays of male Steller Eider: a, Rearing; b, Head-toss; c, d, Shake.

the shallow water at the edge of the beach. In Izembek Bay, the large flocks fed mainly around the extensive beds of eelgrass (*Zostera*).

Food is also obtained by diving, the wings being opened as in the other eiders. I never saw food items brought to the surface. The small molluscs and crustaceans which make up a large part of the diet (Cottam, 1939) must be swallowed before the birds reach the surface.

When diving for food, there is a strong tendency for the members of a flock to submerge simultaneously, as described by Major Bendire (*in* Bannerman, 1958). The effect is very striking when a large number of birds is involved; at one moment perhaps a thousand birds are on the surface, a few seconds later none is in sight. The shower of spray thrown up by a raft of feeding birds is visible for a great distance.

Steller Eiders are agile on land. They walk and run rapidly with ease but with a pronounced waddle like that of the large eiders. They sleep on the water or on a sandbar or bed of exposed eelgrass.

DESCRIPTION OF THE DISPLAYS

Displays are given in the same situations as in the Common Eider (*Somateria mollissima*): in courting parties, before and after copulation, and during hostile encounters between pairs. The displays of the male and female will be described and then each situation will be discussed. I have used the same ethological terminology as in my paper on the European and Pacific races of the Common Eider, *Somateria mollissima mollissima* and *S. m. v. nigra* (McKinney, 1961), and the same names are used for displays which I consider homologous in the two species. Most of these names agree with those of Johnsgard (1964).

TABLE 1

THE NUMBER OF HEAD-DIPPING ACTIONS IN BATHE DISPLAYS OF THE STELLER EIDER AND THE PACIFIC EIDER

Number of head-dipping actions in each Bathe	Number of records	
	Steller Eider	Pacific Eider
1	–	6
2	4	10
3	8	8
4	1	5
5	6	11
6	7	6
7	8	6
8	5	1
9	4	–
10	4	–
11	1	–
12	1	–
13	1	–
14	2	–
15	1	–
16	1	–
17	1	–
Totals	55	53

DISPLAYS OF THE MALE

Rearing.—(Johnsgard, 1962.) This extremely rapid display was performed only by swimming birds. The head and body are suddenly moved backward so that the breast is lifted from the water. In the peak position, the long axes of head and body are almost vertical (fig. 2*a*). Then immediately the bird returns to a normal swimming posture. The whole body is involved, not just the head as in the "Head-throws" of goldeneyes (*Bucephala*) and pochards (*Aythya*). I never heard a call accompanying the movement. Blair (1936) and Williams (1941) recorded this display and emphasized that the tawny breast is conspicuously exposed.

Head-toss.—(= "Chin-lifting," Johnsgard, 1964.) The bill is tossed upward and backward very rapidly and returned immediately to the resting position (fig. 2*b*). There is variation in the degree to which the breast is raised and Head-toss can be confused with Rearing when the bird is distant. However, no true intermediates between the two displays were recorded on film. Head-toss is basically a movement of the head while Rearing involves the whole body. Head-toss is commonly performed on land as well as on the water. I never heard an accompanying call.

Displays involving a rapid upward and backward movement of the bill occur in all species and in both sexes of eiders (Johnsgard, 1964), and superficially similar head movements occur also in *Aythya* and *Bucephala*. Confident decisions on homologies of these movements are readily made within each of the latter genera, but several interpretations are possible in the eiders. Therefore I have given a distinctive name (Head-toss) to one of the commonest displays of the male Steller Eider rather than including it with the "Chin-lifting" of other species as Johnsgard (1964) has done.

Shake.—("Upward-stretch," Johnsgard, 1964.) I have not detected any differences in form between this display and the comfort movement used to shake water

Fig. 3. Erect posture of male Steller Eider.

from the plumage. There is a slight, but very noticeable, difference from the Shake of the Common Eider. During the rotary head movements, the head is flicked forward instead of upward (fig. 2*c*), then the head is jerked back very quickly before the chest sinks forward to the water (fig. 2*d*). Similar components give an "exaggerated" appearance to the shakes of several other distantly related members of the Anatidae, for example, the Common Sheldrake, *Tadorna tadorna*, the Crested Duck, *Lophonetta specularioides*, the Black Scoter, *Melanitta nigra* (McKinney, 1965).

Head-turn.—The bill is moved mechanically from side-to-side a variable number of times, the movements being more rapid than in the corresponding display of the Common Eider. In its most striking form, Head-turn is performed with the head held erect as the male swims away from the female. Less conspicuous Head-turns are given with the head in a resting position.

Preen-dorsally (shortened to "Preen" in the text).—The head is turned around and the bird nibbles with the bill on the back or shoulder areas.

Bill-dip.—The head is moved forward so that the bill touches or almost touches the water.

Bathe.—Head-dipping movements similar to those used in normal bathing are performed. In the Steller Eider, Bathe often includes a long, continuous series of head-dipping actions; up to 17 have been recorded. No long series were recorded in the Pacific Eider (table 1).

Head-roll.—The head is briefly turned back and the cheek is rubbed on the shoulder.

Head-shake.—The head is shaken laterally very rapidly.

Erect Posture.—("Alert posture," Johnsgard, 1964.) The head is held erect and the tail may be cocked to a varying degree (fig. 3). This appears to be a preflight posture probably functioning in both males and females as a signal indicating readiness to fly. It is very frequently seen in the males of a courting party and is often adopted, by the male especially, after postcopulatory Rearing (p. 282).

Short Flight.—From an Erect Posture, the male rises steeply with rapid wing-beats, flies a short distance (perhaps six feet), and alights with a conspicuous splash. There is considerable variation in the length of the flight.

Calling.—I was never able to detect any male call, but Johnsgard (personal communication) has heard captives giving calls, similar in tone to those of the female, in hostile situations.

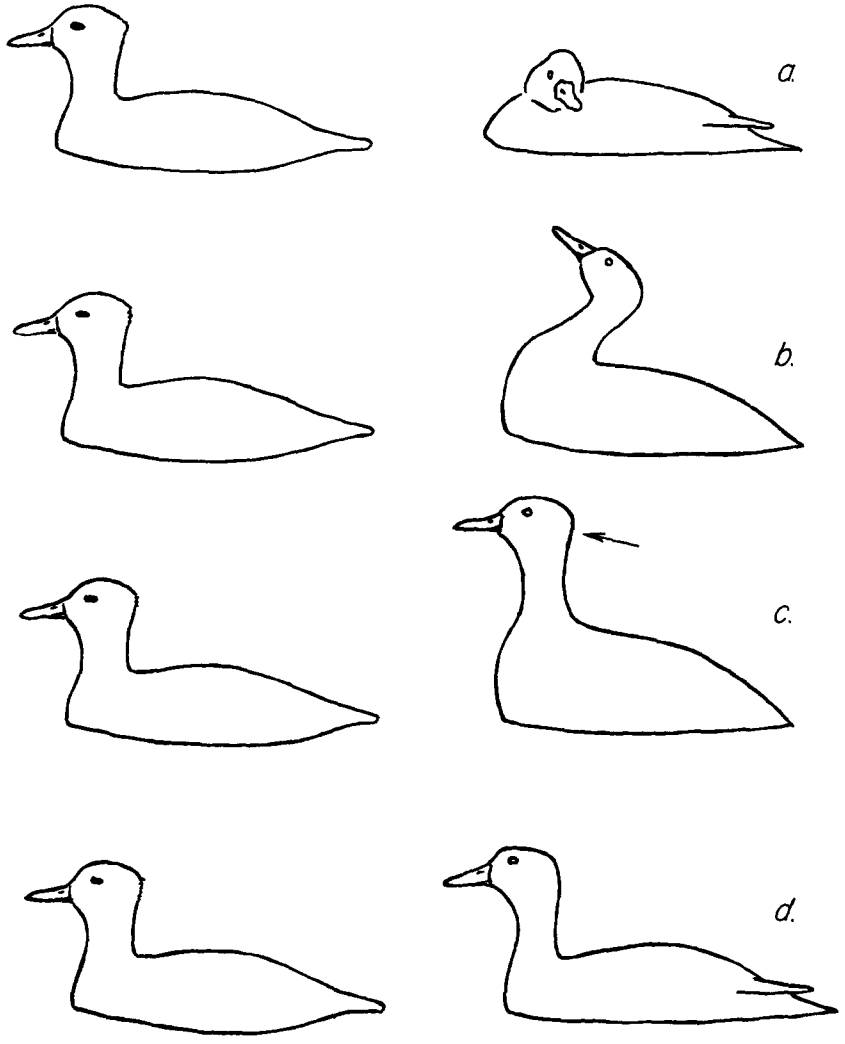

Fig. 4. Consecutive postures adopted by a female Steller Eider Inciting while swimming behind her mate. a, sideways threatening directed at another bird; b, bill up posture with the breast raised slightly from the water; c, the head is swung forward; d, the bird has returned to a normal swimming posture. Drawn from frames 1, 6, 10, and 14 of a film exposed at 24 frames per second.

Displays of the Female

Inciting.—As in the Common Eider and in many other species of ducks, this display has two components; threatening movements toward another bird alternate with upward movements of the head. In the Steller Eider, the upward lifting of the head is similar to the Head-toss of the male. The head is moved very rapidly and smoothly from the threat posture to a bill-up position, in which the breast is raised slightly out of the water, and then swung forward, with neck erect, to the original position (fig. 4). The upward motion of the head is accompanied by a loud *coooay* call.

In the Common Eider, the threatening component of Inciting alternates with a series of Chin-lifting movements which are accompanied by *gog-gog* calls. The second phase of Inciting in the Steller Eider is much more rapid and less complicated.

Rippling Call.—Females are very vocal and a constant chatter is heard from flocks. The calls are harsh and guttural, consisting of a rapid, stuttering series of notes *a-a-a-a-a-ar*, rising in pitch to give a rippling effect.

Prone Posture.—The female stretches her head forward along the surface of the water in a posture similar to that of the Common Eider.

Bathe and Preen-dorsally.—These displays, typical of the male, were recorded on two occasions in females.

BEHAVIOR IN COURTING PARTIES

Courting parties of the Steller Eider are much more difficult to study than those of the Common Eider. On the water, the parties take essentially the same form in both species; a number of males crowd around a female, frequently chasing one another and performing displays. In the Steller Eider, however, the males appear to have a constant urge to take to the air, and courting flights similar to those of species of *Anas* and *Aythya* are very common. At Izembek Bay, I was seldom able to watch a courting party at close range and because of the aerial pursuits it was impossible to follow an individual male for more than a few minutes. Furthermore, all the actions are faster than those of the Common Eider. The following general account is based on 23 dictated records of activities of courting parties and several short film sequences. Detailed analysis of this phase of the behavior will be impossible without the aid of long sequences of good quality movie films.

Most courting parties contained from three to seven males, but the size of the group often changed rapidly. New males flew in to join parties on the water, and males frequently dropped out from courting flights. Almost all flights were of short duration (less than 30 seconds); others were timed at 40 seconds, one minute, and about three minutes. The distance between takeoff point and landing place was usually only a few hundred yards, but the birds often changed direction, circling and swerving over one area. The longest flight I saw, lasting about three minutes, was estimated to maneuver over an area one-half mile in diameter, but the total distance traveled must have been close to two miles.

In many courting flights, one "preferred male" flew close to the female and remained with her when other males dropped out. After the party alighted, one male was usually conspicuously aggressive, making repeated rushes at the other males. Similar behavior occurs in courting parties of other species of ducks; presumably the most attentive and aggressive male has already formed a pair bond of some strength with the female. Loud, raucous calls were sometimes heard from a courting flight and I suspect that these were given by the female as she made Inciting movements.

Immediately after alighting, the males began chasing one another and performing Shake, Head-toss, and Head-turn displays. Brief fighting between two males was recorded on three occasions.

In five different courting parties I saw one male make repeated dashes across the water toward the female. In all cases, these chases were closely associated with attacks by the same male on other males in the party. Similar behavior occurs in the Common Eider.

Males frequently assumed Erect Postures and gave Shakes, Head-shakes, and

TABLE 2

THE OUTCOME OF 31 SEQUENCES OF COPULATORY BEHAVIOR

A. Copulation occurred		18[1]
B. Copulation did not occur, apparently because:		
(1) Pair interrupted by the approach of other birds	4	
(2) Pair disturbed; alert, then flew	4	
(3) Female's precopulatory behavior low-intensity	1	
(4) Male's precopulatory behavior low-intensity	1	
(5) Male was a subadult	3	
		13
Total		31

[1] In 4 cases, the pair was first seen when the male had already mounted.

other movements typical of anatid preflight behavior (bathing, wing-flapping, both-wings-stretch). Usually when the female joined the males in these activities the whole party would take off on a courting flight. If the female did not show a tendency to fly, however, the males continued to adopt Erect Postures, giving preflight movements and from time-to-time one would perform a Short Flight.

Short Flights were related in three different ways to the other members of the courting party. Sometimes the male flew from behind the group, the flight bringing him up to the other birds. Other Short Flights were performed beside the party and parallel to its direction of movement. In some cases the male flew away from the party, alighting ahead of the other birds. I saw about thirty of these flights and although these three patterns were distinguishable I cannot say which is most common. On several occasions I thought a male gave a display (presumably either Rearing or Head-toss) immediately after alighting from a Short Flight.

Rearing, Head-toss, Shake, and Head-turn were all closely associated with overt hostility between males. The following sequences were recorded:

Head-turn + Rearing (2)
Head-turn + Rearing + Head-turn (1)
Rearing + Head-turn (3)
Rearing/Head-toss + chases another male (4)
Rearing + is chased by another male (2)
Shake + Rearing (2)
Shake + Head-turn + Rearing + Head-turn (1)
Head-turn + Shake + Head-turn (1)
Head-turn as male is chased by female (1)

Johnsgard (1964) observed that Rearing normally occurs in the following sequence: Erect Posture + Shake + Head-turn (as male Steams toward female) + Rearing + Head-turn (as male Steams away from female).

BEHAVIOR ASSOCIATED WITH COPULATION

Records were made of 31 copulatory behavior sequences, mostly between April 16 and April 28 at Izembek Bay. Of these sequences, 18 led to apparently successful copulation. In the other cases, precopulatory behavior came to an end for a variety of reasons (table 2). Most of these observations were made under poor conditions and while the main features of the behavior could be discerned only nine records are detailed enough for full analysis.

TABLE 3

MALE DISPLAYS RECORDED IN NINE PRECOPULATORY SEQUENCES[1]

Sequence number:	1	2	3	4	5	6	7	8	9	Total	Per cent
Preen	7	10	23	26	50	30	20	18	17	201	40.7
Bathe	3	5	4	2	12	5	14	8	2	55	11.1
Bill-dip	4	4	29	35	70	34	6	12	14	208	42.1
Head-shake	–	–	2	1	1	3	3	3	3	16	3.2
Head-roll	–	–	–	–	1	–	3	1	–	5	1.0
Head-turn	–	–	–	–	–	6	–	1	2	9	1.8
Total:	14	19	58	64	134	78	46	43	38	494	
Duration in seconds:	?	45	80	65	210	130	105	90	50		

[1] The beginning of most sequences was not seen, but the records probably give a good sample of the relative frequency of displays. Sequences 1 to 5 ended with a Shake, followed by mounting and apparently successful copulation; sequences 6 to 9 were interrupted by other birds or by an alert.

Pairs had a strong tendency to move away from the flock to copulate. Four precopulatory sequences were interrupted by the approach of other birds and clearly some degree of isolation is necessary. Sometimes pairs would become separated from the flock by a slow process of drifting away as they fed. More often, pairs made deliberate flights out from the flock, alighting several hundred yards away.

The general pattern of copulation is similar to that found in the Common Eider, the female remaining relatively inactive in the Prone Posture while the male swims around her performing a continuous series of displays. The commonest male displays are Preen, Bill-dip, and Bathe; Head-shake, Head-roll, and Head-turn are much less frequent (table 3). After giving a series of these displays for a variable length of time (up to three and one-half minutes recorded), the male performs a single Shake and then rushes rapidly across the water with head high and mounts the female. On a few occasions I noted that the male gave Head-turns as he approached the female and/or as he mounted and sat on her back, but these movements were difficult to detect, and I cannot say if they occur regularly.

The order of the male's precopulatory displays is not random (table 4 and fig. 5), the following two-movement sequences occurring more frequently than expected: Preen + Bathe, Preen + Bill-dip, Bathe + Preen, Bathe + Head-roll, Bill-dip + Preen. Other sequences occur less often than expected: Preen + Preen, Bathe + Bill-dip, Bill-dip + Bathe. The only displays which were repeated more than once in series were Preen (three recorded on one occasion) and Bill-dip (three recorded on six occasions). A typical example of precopulatory behavior, including the three commonest displays, would be: Bathe + Preen + Bill-dip + Preen + Bill-dip + Bill-dip + Preen + Bill-dip + Preen + Bathe + . . .

In the sequences which ended in mounting there were no tendencies for any of these displays to become more or less frequent toward the end of the sequence. The last display before the final Shake was Preen (twice) and Bill-dip (twice).

On two occasions, a female lifted her head from the Prone Posture and performed a few Bathe and Preen displays which looked exactly like those of the male. Johnsgard (1964) once recorded Bill-dipping and Preen-dorsally in a female before she assumed the Prone Posture.

TABLE 4

THE ORDER OF MALE PRECOPULATORY DISPLAYS AS SHOWN BY AN ANALYSIS OF NINE SEQUENCES[1]

↓ PRECEDES / FOLLOWS →	Preen	Bathe	Bill-dip	Head-shake	Head-roll	Head-turn	Total
Preen	12*	44	131	3	–	6	196
	81.2	19.8	83.4	6.5	2.0	3.4	
Bathe	41	–	5*	3	5	1	55
	23.0	5.6	23.6	1.8	0.6	0.9	
Bill-dip	129	5*	63	9	–	–	206
	85.4	20.8	87.5	6.8	2.1	3.6	
Head-shake	14	–	1	–	–	1	16
	6.6	1.6	6.8	0.5	0.2	0.3	
Head-roll	3	–	1	1	–	–	5
	2.1	0.5	2.1	0.2	0.1	0.1	
Head-turn	2	–	5	–	–	–	7
	3.1	0.7	3.2	0.2	0.1	0.1	
Total	201	49	206	16	5	8	485

[1] The upper figure in each cell is the observed frequency; the lower figure is the expectation. Underlined pairs of figures indicate statistically significant positive associations; asterisks indicate significant negative associations (by the method of Andrew, 1956).

It was very difficult to tell whether precopulatory behavior was initiated by the male or by the female. Several times I had the impression that the male began giving displays before the female adopted the Prone Posture.

The rate of performing precopulatory displays is much higher (25 to 59 displays per minute) than in the Pacific Eider (11 to 20 displays per minute). This is largely caused by differences in the duration of certain displays. For example, Bill-dip is a very brief action in both species but Wing-flap of the Pacific Eider and Bathe of the Steller Eider take much longer to perform. The main factor causing the wide variation in rates recorded in the Steller Eider appears to be the frequency of Bathe. When a male gives many Bathes, the rate for total displays is reduced (table 5).

Precopulatory behavior in subadult males was seen on three occasions. Preen, Bathe, Bill-dip, and Shake were recorded, and one male made several rushes toward the female. None of these males mounted.

The act of copulation is brief and similar in form to that of the Common Eider.

The behavior of male and female after copulation was recorded in some detail on 18 occasions (table 6) and similar patterns were noted after about a dozen other copulations. Immediately on dismounting, the male performs a single Rearing display, then adopts an Erect Posture and at least sometimes gives Head-turns. The female may make Inciting movements while swimming close behind the male, and she usually bathes briefly. Then, often within 15 to 30 seconds after dismounting, the male makes one or more Short Flights away from the female (2 to 15 yards in length) or both members of the pair take off and fly back to join a flock.

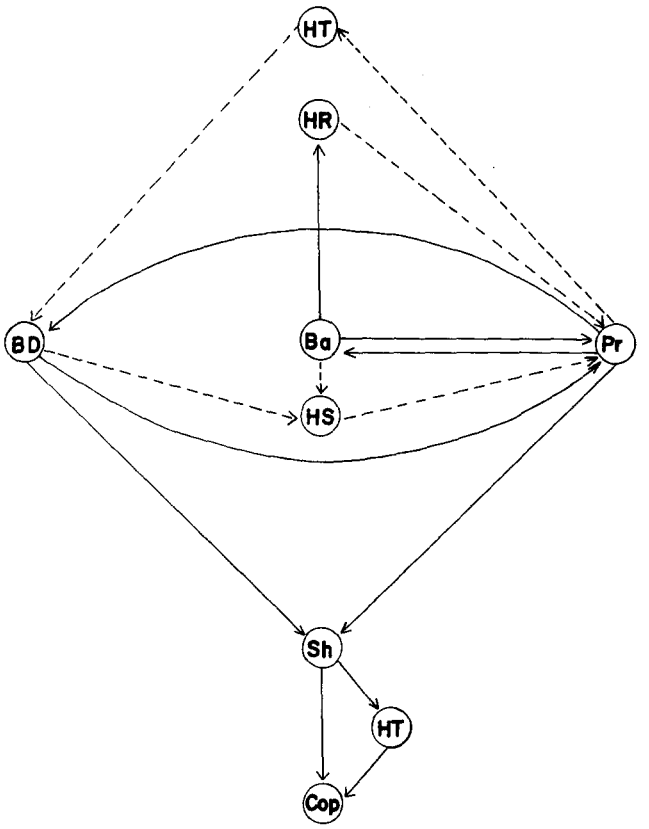

Fig. 5. The order of precopulatory displays of male Steller Eider. For explanation, see text. Ba = Bathe, Pr = Preen, HR = Head-roll, HS = Head-shake, BD = Bill-dip, HT = Head-turn, Sh = Shake, Cop = copulation.

BEHAVIOR DURING ENCOUNTERS BETWEEN PAIRS

When pairs swam close together there was often a brief outburst of displays and some signs of overt hostility. I saw Rearing, Head-toss, Shake, and Erect Postures in males, while females gave Inciting. Usually it was impossible to identify pairs for more than a few moments at a time in the dense flocks, and I have no quantitative data on the displays occurring in this situation.

DISCUSSION

Duck displays probably serve a number of biological functions. Some are linked with hostility and appear to have threat function. Many are associated with pair formation and copulation, and probably have the functions of "courtship" listed by Tinbergen (1954): synchronization of mating activities, orientation, the suppression of nonsexual responses in the partner, and the maintenance of reproductive isolation. Recent discussions of the differences between the displays of closely related sympatric species of ducks (Sibley, 1957; Johnsgard, 1963, 1964) have stressed the role that these behavior patterns play as isolating mechanisms. Circumstantial evidence suggests

TABLE 5

THE RATE OF DISPLAYS IN EIGHT PRECOPULATORY SEQUENCES CORRELATED WITH THE FREQUENCY OF BATHE

Sequence number:	4	3	5	2	9	7	6	8
Total displays per minute:	25	26	29	36	38	44	46	59
Per cent bathe in sequence:	26	30	19	6	9	7	5	3

that distinctive differences between the display repertoire of sympatric species could play such a role, but it should not be assumed that all specific differences have evolved as a result of selection pressure for distinctiveness. Hinde (1959) has pointed out that physiological or ecological factors could be involved, while Tinbergen (1959*a*:327) cautions that "it is simply impossible to judge the part played by selection in the evolution of a certain character unless all its functional contexts, including its relations with other functional systems, have been investigated."

Cullen (1957) has shown how the behavior of the Kittiwake (*Rissa tridactyla*) is adapted to cliff nesting, and certain differences between its displays and those of other gulls can be interpreted as adaptations to the habitat. Influences of the breeding environment on the evolution of pair-formation patterns in ploceine weaver birds have been demonstrated by Crook (1962). In this group, differences in types of pairing behavior and the form of displays can be understood only in relation to food habits and habitat preferences. The possibility that specific differences in duck displays have been influenced by such factors seems to have been overlooked.

A comparison of the behavior of the Steller Eider and that of the Common Eider reveals differences in degree of sociability and readiness to take wing in the two species. I suggest that these characteristics are correlated with specific differences in habitat and vulnerability to predators and that the threat of attack by birds of prey has been an important factor influencing many aspects of the behavior of the Steller Eider, including the displays (see table 7).

Sociability.—In almost all their springtime activities, Steller Eiders are intensely social, individuals seldom straying far from the large flocks. This characteristic may be advantageous to the species in several ways. Congregating in densely-packed rafts when diving for food may ensure feeding efficiency; a flock attracts other birds and localized sources of food are advertised and exploited to the full. Also, the individuals in a flock are probably less vulnerable to attack by birds of prey; there are more birds to react to the sight of a predator and alerts are contagious.

The strength of the social tendency is especially obvious when pairs leave the flock to copulate. They move away only a short distance and often fly straight back to the flock immediately after copulation.

TABLE 6

POSTCOPULATORY BEHAVIOR[1]

Male				Female			
Rearing	Erect Posture	Head-turn	Short Flight	Bathing	Inciting	Pair flies	Total records
14	9	2–4	6	10	7–9	9	18

[1] Many records were incomplete because of poor conditions for observation and some patterns may be of more regular occurrence than the figures indicate.

TABLE 7

SOME DIFFERENCES BETWEEN THE BEHAVIOR OF THE STELLER EIDER AND THE COMMON EIDER

STELLER EIDER	EUROPEAN/PACIFIC EIDER
A. General behavior	A. General behavior
1. Often feeds in shallow water by dabbling on the surface, with head under water, or by upending.	1. Feeds mostly by diving in deep water; large items often brought to the surface.
2. Diving flocks densely packed.	2. Diving flocks not densely packed.
3. Strong tendency to synchronize dives.	3. No strong tendency to synchronize dives.
4. Rises steeply at takeoff.	4. Cannot rise steeply at takeoff.
5. Flies up at approach of Bald Eagle or Gyrfalcon.	5. Responses to birds of prey in spring not observed; dives, and is vulnerable to Bald Eagle during breeding season.
B. Copulatory behavior	B. Copulatory behavior
1. Pairs often fly out from flock to copulate, returning quickly.	1. Flights away from flock not recorded.
2. Male has no Wing-flap display.	2. Male has conspicuous Wing-flap.
3. Male gives only one Shake.	3. Male gives many Shakes.
4. Final precopulatory display (Shake) invariable.	4. Final precopulatory display variable.
5. Male silent.	5. Male European Eider gives some calls during precopulatory behavior; postcopulatory call in both races.
C. Behavior in courting parties	C. Behavior in courting parties
1. Males frequently show preflight behavior.	1. Males do not show preflight behavior.
2. Courting flights very common; underwater pursuits absent.	2. Courting flights absent; underwater pursuits occur.
3. Short Flights common.	3. Short Flights absent.
4. Display movements rapid and brief; compound movements absent.	4. Display movements slower; compound movements in European race.
5. No loud calls accompanying male display movements.	5. Loud cooing calls accompany main male display movements.

Synchronous diving by the members of a feeding flock is probably a further reflection of the social tendency and of the reluctance of individuals to be left alone on the surface. Similar synchronized diving occurs in flocks and pairs of the Harlequin Duck (*Histrionicus histrionicus*) and in pairs of the Common Goldeneye (*Bucephala clangula*). Bretherton (1896) has described how hunters take advantage of this characteristic of flocks of the Harlequin Duck, which often feed close to rocky shores. Each time the birds dive, the hunter rises from his hiding place and advances to a closer shelter. The procedure is repeated until the birds are within shotgun range. This technique could not have been used with the Steller Eiders I watched since diving flocks were always far away from the shore. Under these conditions it is unlikely that submerged flocks could be taken by surprise by an approaching bird of prey.

Readiness to fly.—A strong tendency to take wing is apparent in courting parties, even when there is no immediate threat of attack by birds of prey. Males constantly adopt Erect Postures and make preflight movements. Short Flights by individual males are frequent. Courting flights by the whole party replace the underwater pursuits characteristic of the Common Eider. This emphasis on readiness to fly may have survival value in facilitating a quick reaction to birds of prey. The birds in a courting party must be preoccupied with one another to a large extent: every individual is reacting constantly to the other members of the group—chasing, retreating, following, performing displays. At the same time, conspicuous displays of the males presumably serve such functions as advertising readiness to pair, attracting the attention of the female, and discouraging rivals. Perhaps the incorporation of preflight and aerial behavior patterns reflects a "compromise" between conflicting selective forces, the increased vulnerability resulting from the preoccupation of pairing birds and their conspicuousness being offset by constant readiness to flee from danger.

Undoubtedly many other factors also influence the degree to which a species uses aerial displays. With increasing body size, power production becomes relatively less while the power required for flight increases (Wilkie, 1959). Thus, within a group of birds having a certain type of wing structure and correlated flying technique we might expect the larger species to spend less time flying. Trends in this direction have been noted in the North American herons (Meyerriecks, 1960) and the gulls (Moynihan, 1959; Tinbergen, 1959*b*), the smaller species having more aerial displays. Although the Common Eider is a strong flier it is possible that the absence of courting flights and Short Flights in this species is correlated with the amount of energy which would be consumed by such activities.

Aerial pursuits and Short Flights do occur in many duck species of small or medium size, but they are not performed by all small ducks. For example, the Laysan Duck (*Anas laysanensis*) is adapted to a sedentary and largely terrestrial way of life in which flight is seldom necessary (Warner, 1963), whereas the Ruddy Duck (*Oxyura jamaicensis*) is specialized for diving and life among emergent vegetation having little need to fly except during the migration season. Aerial displays and pursuit flights appear to be absent in both species. The Steller Eider has specialized in flying as a method of escape (as opposed to diving or sheltering in vegetation), and this characteristic has apparently favored the evolution of aerial displays.

Conspicuousness of the displays.—Several features of the copulatory behavior may have survival value in reducing the conspicuousness of the isolated pair. Two of the most obvious precopulatory displays of the Common Eider are Wing-flap and Shake. The absence of Wing-flap in the Steller Eider is unexpected in view of the presence of Bathe. The precopulatory sequence Bathe + Wing-flap of the Common Eider has obviously been derived from the normal comfort movement sequence of bathing followed by wing-flapping. Apparently, there has been selection against the inclusion of Wing-flap in the Steller Eider.

While Common Eiders perform many Shakes during precopulatory behavior Steller Eiders give only one Shake in each sequence, immediately before the male mounts. This could have special significance in shortening the period during which the pair is most vulnerable to attack. I saw several precopulatory sequences break off during the preliminary stage as a result of a disturbance. Apparently the birds are not so preoccupied with sexual behavior at this stage that they will not respond to danger. The final, rigid sequence (Shake + rush to the female + copulation + post-copulatory behavior) occupied less than 30 seconds in seven timed sequences. This

must be the most dangerous period, when the pair is fully occupied with the act of copulation. Perhaps the single final Shake display has evolved as a clear signal to the female that the male is about to mount, thus enabling the female to remain alert for predators until the last moment before copulation. European and Pacific eiders have no final, stereotyped sequence of displays immediately before mounting.

Furthermore, male Steller Eiders give no loud calls during copulatory behavior. Some cooing calls are given by European Eiders before copulation, while both European and Pacific eiders have a postcopulatory call.

The rapidity and brevity of the display movements of the Steller Eider may also be adaptive in rendering this species less vulnerable to a surprise attack. The European Eider, King Eider (*Somateria spectabilis*), and Spectacled Eider (*Lampronetta fischeri*) all have compound display movements involving continuous sequences of two or more head movements (see Johnsgard, 1964). These compound displays take considerably longer to perform than the Bridling and Head-toss displays of Steller Eiders. Of course, the speed of display movements is also correlated with body size. As Lorenz (1953) describes, the social courtship of the Common Teal (*Anas crecca*) resembles a movie film of the Mallard (*Anas platyrhynchos*) projected at high speed. But this factor does not explain the absence of compound displays in Steller Eiders and their presence in other eiders.

Habitat, food habits, and predators.—In contrast to the Steller Eider which feeds largely in shallow water on small crustaceans, Common Eiders obtain most of their food by diving in deep water, often bringing crabs, razor shells, and mussels to the surface before swallowing them. In general, these differences in feeding habits probably entail greater risk of a surprise attack by a bird of prey in the case of the Steller Eider, and in shallow water there would be less chance of successful escape by diving. At Izembek Bay, the flocks of Steller Eiders were able to stay well away from shore, the shallow lagoon providing suitable feeding grounds with an unobstructed view of the horizon in all directions. On this area, responses to an approaching eagle or falcon were made while the bird of prey was a long distance away. At Nelson Lagoon, flocks spent much time along the shore of a peninsula, and I was able to watch them at close range from the shelter of a nearby bank. In this type of habitat, they would be more vulnerable to a surprise attack. I saw no attacks made, but by their immediate response of taking wing on the appearance of Bald Eagles and Gyrfalcons (both of which were commonly seen at Izembek Bay) it was clear that these predators are feared. Both raptors are known to take ducks, although other sources of food are often more easily obtained (Bent, 1937, 1938; Munro, 1938; Murie, 1940; Wright, 1953; Southern, 1963; Hancock, 1964).

According to the observations of Brooks (1922:557–558) on the duck-hunting behavior of Bald Eagles on the coast of British Columbia "the only chance a Duck has is to get on the wing at all costs." A bird which dives in an attempt to escape is hounded each time it surfaces until exhausted, when the eagle picks it off the water. On Okanagan Lake, in interior British Columbia, Brooks noted that the Bald Eagle preys largely on the American Coot (*Fulica americana*) during the winter when these birds are in large flocks on open water. The coots (p. 559) react to an approaching eagle by massing together; "standing up in the water all flap their wings below the outstretched feet of the attacker." Brooks noted that the eagle does not take a bird from such a tight flock, but if a coot leaves the flock and tries to escape by diving, it is soon tired out and captured.

Mr. Robert D. Jones (*in litt.*) reports that during the breeding season Bald

Eagles can be successful in taking Pacific Eiders. The ducks "dive and are very vulnerable. Predation by the Bald Eagle at Amchitka, where we have closely watched the process, is heavy. I think it is the chief factor limiting the population, and is most effective on the ducklings. Very large hatches of ducklings are reduced in two or three days to small aggregates of ducklings and hens. We find skeletal remains of adults (identifiable by the purple pigment—echinochrome from sea urchins—in the bones) common in the eagle nests." I have no evidence of eagle predation on this species at other seasons, but it seems likely that the large eiders are less vulnerable while wintering in deep water habitats.

Conclusion.—Many of the differences between the behavior of the Steller Eider and the Common Eider appear to be reflections of a stronger social tendency and greater readiness to fly in the former species. These characteristics of the Steller Eider have probably evolved as adaptations minimizing the risk of surprise attack by an aerial predator, although other factors may also have been involved. Certain features of the displays of the Steller Eider can be interpreted as adaptations tending to reduce the conspicuousness and vulnerability of the birds. The validity of these arguments could be checked by a thorough study of the ecology of the species in different habitats and at all seasons of the year.

SUMMARY

The behavior of the Steller Eider (*Polysticta stelleri*) was observed during April and May at two wintering areas on the Alaska Peninsula. Flocks of several thousand individuals included adult pairs, courting parties, and subadults. The birds were highly social when feeding and resting, often massing in tightly-packed rafts. They flew up at the approach of a Bald Eagle (*Haliaeetus leucocephalus*) or Gyrfalcon (*Falco rusticolus*).

Much food is obtained in shallow water by dabbling, up-ending, or feeding with the head under the surface. When diving for food, the members of a flock tend to submerge almost simultaneously.

Most courting parties contained from three to seven males and one female. On the water, the males performed Shake, Rearing, Head-toss, and Head-turn displays, all in close association with overt hostility. Chases of the female across the water by one male in the group were recorded. Males frequently assumed Erect Postures and made preflight movements and Short Flights. Parties constantly took to the air in brief courting flights.

Pairs usually moved away from the flock to copulate, often by making a deliberate flight of several hundred yards. The general pattern of copulatory behavior is similar to that of the Common Eider (*Somateria mollissima*): the female adopts the Prone Posture while the male swims nearby performing a continuous series of displays before mounting. The commonest male displays (totaling 95 per cent) are Preen-dorsally, Bill-dip, and Bathe. Head-shake, Head-roll, and Head-turn occur infrequently. These displays are not interspersed randomly, certain sequences being stereotyped. Bathe often includes more head-dipping actions than the corresponding display of the Common Eider.

Immediately before mounting the male gives a single Shake, then rushes toward the female, at least sometimes giving Head-turns. After copulation the male performs a Rearing display, then adopts an Erect Posture and may give Head-turns. The female may give Inciting. Often, within 15 to 30 seconds after dismounting, the male makes one or more Short Flights and/or the pair flies, returning to the flock.

During hostile encounters between pairs, males gave Rearing, Head-toss, Shake, and Erect Posture while females gave Inciting.

Much of the behavior at this time of year appears to be influenced by the threat of attack by birds of prey, especially the Bald Eagle. Strong tendencies to flock densely and to fly readily probably have survival value against predators and these tendencies appear to have affected feeding, pairing, and copulatory behavior patterns. It is suggested that some of the differences between the displays of the Steller Eider and Common Eider have resulted from selection pressure tending to reduce conspicuousness in the former species.

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