Using any two of the three external characters should also be highly useful in revealing the sex ratio of sharptails at checking stations. On our sample of 257 birds, only 3 percent were incorrectly sexed, and the errors canceled each other to reflect the true sex ratio of the sample. This method of handling field data may furnish the most accurate population sex ratios for both species of prairie grouse.

We have found the use of crown feathers for sex determination to be valuable in saving time when counts of prairie grouse are being made on dancing grounds. Binoculars can be used to sex birds that are passive on the dancing ground. A quick visual check is much better than waiting to see whether the bird will display in the course of dancing activity. This is especially valuable late in the morning dancing-activity period of the males on a ground, when passive periods of the dancing males become more frequent and prolonged.

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*Received for publication February 27, 1967.*

# FACTORS INFLUENCING NESTING SUCCESS OF EIDERS IN PENOBSCOT BAY, MAINE[1]

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*Abstract:* Histories were recorded for 1,030 American eider (*Somateria mollissima dresseri*) nests on five islands during two breeding seasons in Penobscot Bay, Maine. Nesting success was 39 percent in 1964 and 36 percent in 1965. Predation by gulls was responsible for most nest losses. Five factors were found to be related to nesting success: nesting cover, clutch size, partial predation, gull populations, and human disturbance. Nests in hardwood shrubs and cow parsnip (*Heracleum maximum*) had relatively high success while those in grasses and nightshade (*Solanum dulcamara*) were much less successful. Nests with a complete clutch of fewer than four eggs were less successful than those with four or more eggs. When part of a clutch was lost to predators the chance of ultimate success of the remaining eggs was reduced. The number of nesting gulls per nesting eider on a given island was inversely related to the nesting success of the eiders on that island. Human disturbance was indirectly responsible for lowered nesting success.

During a study of the breeding biology of the American eider in Penobscot Bay, Maine, in the spring and summer of 1964 and 1965 (Choate 1966), data were collected on several factors believed to influence nesting success of the species. The objective of this paper is to point out these factors and the extent of their influence.

The author is grateful to Howard L. Mendall and Malcolm W. Coulter, Professors of Game Management, University of Maine, who assisted with field work and reviewed the manuscript. Professor Mendall also served as project supervisor. Credit is likewise due to many University students

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and staff members, and residents of the island of Islesboro, without whose aid in the field this project would have been impossible.

## THE STUDY AREA

Penobscot Bay is approximately 30 miles long, and, at its mouth, 28 miles wide. It primarily drains the Penobscot River and is located about midway between the easternmost and westernmost points on the Maine coast. Mean high tide is around 10 ft.

Eider nests were studied on five islands which range from approximately 0.25 to 4 acres in area. The islands are named Flat Island, Mouse Island, Goose Island, East Goose Rock, and Robinson Rock. All are rather long and narrow. Flat Island is low lying and very level. The others, especially Robinson Rock, are steep sided and rise abruptly out of the water. However, the central portions are more level and slope gently toward the steep edges.

Each island is composed of bed rock covered with a thin layer of soil. The rock is exposed at the edges and sometimes near the center of the islands. Wherever the soil has accumulated sufficiently it supports dense growths of vegetation.

Excluding Flat Island, the soils are mainly humus. Flat Island apparently has a layer of more sterile mineral soil as evidenced by its vegetation. Bayberry (*Myrica pensylvanica*), a shrub which grows on sterile soil (Fernald 1950), is abundant.

The major plant species present on the study islands are: cow parsnip (*Heracleum maximum*); several grasses—timothy (*Phleum pratense*), witch-grass (*Agropyron repens*), redtop (*Agrostis alba*), Kentucky bluegrass (*Poa pratensis*), and wild rye (*Elymus virginicus*); miscellaneous small herbs, primarily common ragweed (*Ambrosia artemisiifolia*) and pineapple weed (*Matricaria matricarioides*); nettle (*Urtica viridis*); nightshade (*Solanum dulcamara*); goldenrod (*Solidago rugosa*); and shrubs composed of rose (*Rosa* sp.), bayberry, and raspberry (*Rubus* sp.).

Nesting on the study islands are several other species of birds: black duck (*Anas rubripes*), great black-backed gull (*Larus marinus*), herring gull (*L. argentatus*), double-crested cormorant (*Phalacrocorax auritus*), black guillemot (*Cepphus grylle*), and song sparrow (*Melospiza melodia*). Meadow voles (*Microtus pennsylvanicus*), found in abundance on Flat Island, are the only small mammals known to inhabit the study area.

## METHODS

During the 1964 season eider nests were studied on Mouse Island, Goose Island, East Goose Rock, and Robinson Rock. In 1965, Flat Island was substituted for Robinson Rock in order to determine differences in nesting success in shrubby vegetation on Flat Island as contrasted to success in herbaceous vegetation on the other islands.

Commencing in the early spring of both seasons, visits were made at least once a week to each island to search for eider nests, except when adverse weather prevented. Searches were limited to a maximum of 3 hours in an attempt to prevent overexposure of eggs to adverse temperatures when unattended by females.

This procedure was altered somewhat in 1965 to test the effect of human disturbance on nesting success. Goose Island and East Goose Rock, which had about the same success and same number of visits in 1964, were checked an unequal number of times in 1965. Goose Island was visited 27 times spaced throughout the season and East Goose Rock 12 times. On the basis of 1964 data, I assume that if there had been no human disturbance in 1965 nesting success would have been about equal on the two islands.

Eider nests were marked with numbered wooden stakes, and pertinent data were recorded for each nest on every visit, including: date, island, number of eggs, nesting cover, and concealment. Nesting cover was recorded as the type of vegetation immediately surrounding the nest and included the following: cow parsnip, grass, nettle, miscellaneous herbs, nightshade, barren rock,[3] goldenrod, nettle–grass, and shrubs. If two or more plant species surrounded a nest, the one that provided the most cover was recorded. In the case of the nettle–grass type there were enough nests where neither grass nor nettle predominated to justify the use of this mixed-cover type.

Concealment was evaluated by looking directly down on the nest from a standing position and estimating what percent of the nest area was blocked from view by the vegetation. The four concealment classes used were poor, fair, good, and excellent, representing respectively 0–25, 26–50, 51–75, and 76–100 percent of the nest hidden.

Fecal matter was wiped off the eggs if the female had defecated on them when she flushed. The clutch was then covered with down to insulate the eggs and to help camouflage them from predators.

Nests were periodically rechecked until the eggs hatched, were destroyed, or were deserted. Nest fate was ascertained by Girard's (1939) method of looking for shell membranes in recently abandoned sites. A nest was considered successful when one or more membranes could be found in or near it. If there were no signs of success or there was evidence of disturbance, the nest fate was recorded as destroyed. If there was no indication of recent activity at a nest containing eggs, it was considered deserted. Eggs were recorded as infertile when the female incubated them much beyond 4 weeks and, when the eggs were subsequently opened, there was no apparent embryo development. A partially developed embryo was interpreted as having died from overexposure to adverse weather or some other factor which was not determined.

[3] Arbitrarily included as a cover type.

Eider and gull populations were estimated from nest counts made throughout the study except at Flat Island. Since the extent of renesting was unknown, only approximations of the breeding populations could be made. Since both sexes of gulls incubate the eggs it was assumed that two gulls occupied a nest. Male eiders left the islands when nesting began and only one eider was considered to occupy a nest.

When feasible, birds were observed from a blind, so that predatory activities of gulls on eider nests could be viewed.

In order to determine nesting densities, each island except Flat Island was mapped, using a plane table and alidade.

## RESULTS

Histories were recorded for 1,030 eider nests (569 in 1964 and 461 in 1965). Of this total the fate was determined in 963 cases. Overall success was quite similar in the two years. In 1964, 39 percent of the nests produced one or more young and 39 percent of the eggs hatched. The corresponding figures for 1965 were 36 percent nest success and 39 percent hatching success.

Predation caused the greatest proportion of nest losses (Table 1). Crows (*Corvus brachyrhynchos*) often visited the study islands, but it is believed that gulls were the chief predators. Whenever crows were

Table 1. Fate of 963 eider nests in the Penobscot Bay study area, 1964 and 1965, expressed in percentages.

| Year | Percent of Nests | | | | |
|---|---|---|---|---|---|
| | Hatched | De-stroyed | De-serted | Infertile or Ex-posed to Heat | Total |
| 1964 (515 nests) | 39 | 52 | 8 | 1 | 100 |
| 1965 (448 nests) | 36 | 58 | 3 | 3 | 100 |

Table 2. Hatching success of 946* eider nests, by cover types.

| Cover Type | 1964 | | 1965 | |
|---|---|---|---|---|
| | No. of Nests | Percent Hatched | No. of Nests | Percent Hatched |
| Cow parsnip | 222 | 48 | 204 | 39 |
| Grass | 133 | 33 | 88 | 19 |
| Nettle | 32 | 41 | — | — |
| Miscellaneous herbs | 25 | 32 | 12 | 17 |
| Nightshade | 23 | 26 | 22 | 14 |
| Rock | 24 | 25 | 35 | 26 |
| Goldenrod | 15 | 40 | 21 | 33 |
| Nettle–Grass | 32 | 31 | — | — |
| Shrubs | — | — | 58 | 74 |
| Total | 506 | 39 | 440 | 36 |

* This number differs by 17 from the number of nests included in Table 1 because 17 nests did not fit any of the cover categories, being in driftwood, seaweed, etc.

observed on an island they were feeding along the shoreline and were not near active eider nests. On the other hand, personnel who aided in field work observed gulls preying upon eider nests. As shown in Table 1, some clutches did not hatch because they were infertile, deserted by the female, or possibly were overheated (see Rolnik 1943:157) by exposure to direct sunlight.

There is disagreement as to the effect of avian predators on eider production. According to Cooch (1966) such effect is negligible when an eider population is maintaining itself at carrying capacity. If the population is depressed, however, predation may be important in maintaining low numbers. In the Grand Manan Archipelago, New Brunswick, Pimlott (1952) found little evidence that gulls preyed on eider eggs. On the other hand, Belopol'skii (1957:269) analyzed 25 stomachs of the glaucous gull (*Larus hyperboreus*) and found that eider ducklings and eggs made up 12 percent of the contents. On many occasions Reed (1964) observed herring and black-backed gulls preying on eider nests.

Since production was limited primarily by nest predation, several factors were examined which might have a bearing on predation.

## Nesting Cover

Percent success in the various cover types was considered (Table 2). Success for nests in a given type was compared to success in all other types combined. Chi-square values showed that in 1964 nesting success was significantly higher for nests in cow parsnip than for those in the other types ($P < 0.005$) while nests in grass had lower success ($P < 0.10$). The 1965 data showed nests in grass and nightshade to have significantly lower nesting success ($P < 0.005$ for grass and 0.025 for nightshade) than nests in the other types. Success of nests in shrubs was much higher ($P < 0.005$) than in the other types.

Apparently these differences in predation were directly related to the physical characteristics of the plant species. The broad leaves of cow parsnip provided more concealment than any other cover plant. Although the relationship was not precise, data collected on concealment of nests in the herbaceous cover types indicated greater success for those better concealed. Shrubs provided little concealment until nesting was near completion. However, the thick barrier produced by the stems and branches of the shrubs apparently discouraged gulls from preying upon eider nests by hindering their movement through the vegetation.

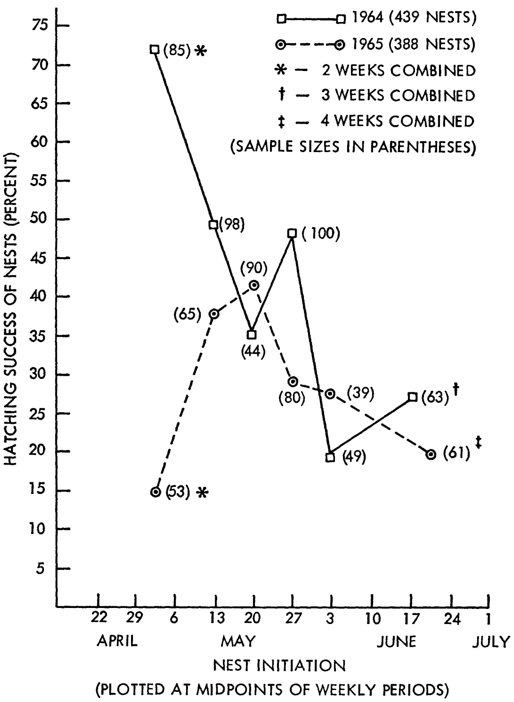


Fig. 1. Hatching success of eider nests in relation to date of nest initiation, Penobscot Bay, Maine.

Other studies have shown cover type and degree of concealment to be related to nesting success. Lewis (1959) observed sheltered and concealed eider nests on wooded islands, and there was practically no predation, but on treeless islands about 20 percent of the nests were destroyed. Belopol'skii (1957:272) and Grenquist (1959) also found higher success in sheltered as opposed to open sites.

The effect of dense cover (such as the shrub type of the present study) in reducing predation is also pointed out by Reed (1964) in a study of black ducks; nests in dense cover were protected from gulls because the gulls' long wings appeared to hinder their movement in such cover.

Nesting success might be expected to increase as the season progressed and vegetation developed. However, this held true only for the early part of the 1965 season (Fig. 1). Success increased in nests initiated up to the last part of May, after which it declined. In 1964, nesting success was at its height early in the season and dropped as the season progressed. There is no satisfactory explanation for this decrease later in the season.

Greater nest loss late in the season indicated a lack of success in renests (nests with little down and small clutches in the last part of the season indicated that renesting occurred). Thus, renesting may not have made up to any great extent for nests lost earlier in the season.

In contrast to the present study, Lewis (1939:73) found that egg destruction decreased to almost none about the middle of June. He attributed the decline to two factors: (1) vegetation development provided more shelter and (2) large schools of small fish arrived, supplying readily available food to nest predators. Paynter (1951: 505), on the other hand, concluded that early and late nests were equally successful in producing young.

## Nest Densities

Considering entire islands, nest densities ranged from 3.8 per 1,000 square ft (166 nests/acre)[4] on Mouse Island in 1965 to 8.9 per 1,000 square ft (389 nests/acre) on East Goose Rock in 1964. No relationship was found between nest density on an island and success of the nests on that island. Nest densities on small, arbitrarily chosen areas of each island ranged from 4.3 to 136.4 per 1,000 square ft (187 to 5,940 nests/acre). In these areas also, no

[4] Most of the nest densities expressed in nests per acre are based on an area of less than 1 acre and are therefore unreal figures. They are presented merely to provide comparison with other waterfowl species where densities are usually measured in nests per acre.

Table 3. Success of eider nests by clutch size* (complete clutches only).

| | Less than Four Eggs | | Four or More Eggs | | All Complete Clutches | |
|---|---|---|---|---|---|---|
| Year | No. of Nests | Percent Success | No. of Nests | Percent Success | No. of Nests | Percent Success |
| 1964 | 129 | 53 | 190 | 67 | 319 | 62 |
| 1965 | 107 | 50 | 159 | 66 | 266 | 60 |

* See text explanation for apparent discrepancy with Tables 1 and 2.

relation could be found between nest density and nest success.

In contrast to the present study, Belopol'skii (1957:272, 294) found higher nesting success in a large, densely populated eider colony than on islands where eider nests were sparse. A larger sample of islands with like vegetation and a greater range of nest densities might have shown a similar relationship in the present study.

## Clutch Size

In both years, those nests with an above-average clutch size (four or more eggs) were more successful than those with below-average clutch size (Table 3). A Chi-square test showed the differences in success to be significant ($P < 0.025$). Possible reasons for these differences are: (1) the larger clutches were laid by older birds which had more capability and/or desire to bring off a brood successfully; (2) eiders, regardless of age, were more strongly attached to nests with larger clutches.

At Kent Island, New Brunswick, Paynter (1951:504) showed that the size of complete clutches of eider eggs was not related to the survival rate. Paynter (1949:152) found a contrasting situation, however, for herring gulls where success was higher in three-egg clutches than in two-egg clutches. He believed that in two-egg nests the female lacked the full measure of stimulation provided by a full clutch which causes broodiness and parental care, so that the nests were poorly guarded and more susceptible to predation.

The figures for nesting success in Table 3 are considerably higher than overall nesting success. This difference results because Table 3 includes only complete clutches, and rate of success in nests where clutches were completed was greater than for all nests. Of those nests destroyed in 1965, 66 percent were lost before the clutch was complete. (The nature of the data tabulation prevented calculation of the corresponding figure for 1964.) Thus, once a full clutch of eggs was laid there was less chance the nest would be destroyed. A lower rate of destruction after completion is to be expected since the female is more attentive to the nest when incubation begins.

## Partial Predation

In some nests only part of the clutch was lost to predators. In 1964, partial predation was recorded in 13 percent of the nests; in 1965 it was noted in 9 percent. Once a gull located a nest and took part of the eggs, it might be expected that the nest would more likely be lost on subsequent visits by the same gull. Partial predation was recorded for nests only after incubation started. Thus, success for partially destroyed clutches was compared to success among incubated clutches where either no eggs or all eggs were destroyed (Table 4). In 1964, success was significantly lower ($P < 0.01$) in the partially destroyed clutches. Although success was also lower in 1965, the difference was not significant ($P > 0.01$).

Milne (1963) found in Scotland that some partial predation occurred without nest desertion but the subsequent success of these nests is not known. No other studies are known of eider nesting where partial predation has been considered in relation to nesting success.

## Gull Populations

It was suspected that the numerical ratio of gulls to eiders might influence nesting success. It appears that this was the case in 1964 (Table 5) when success decreased as the gull : eider ratio increased. Although this did not hold true in 1965, the differential effects that year of human disturbance (discussed in next section) probably overshadowed any effects of the gull : eider ratios.

Based on a small number of observations, it is believed that black-backed gulls preyed more heavily than herring gulls on eider nests. There was an apparent relation between all gull : eider ratios and nesting success, but it may well be that most nest destruction was by black-backed gulls even though, based on rough estimates, they made up only about a fourth of the total gull population.

## Human Disturbance

In many waterfowl production studies human influence is a factor, although its importance is often hard to measure. In the present study, human disturbance appeared to influence nesting success to a great extent. Observations from a blind showed that after an investigator left an island, the gulls returned much sooner than the eiders. Of course, before the eiders returned, the nests were highly vulnerable to predation by the gulls.

Table 4. Eider nest success in relation to loss of part of the clutch during incubation (complete clutches only).

| | Clutches with Partial Predation | | Clutches without Partial Predation | |
|---|---|---|---|---|
| Year | No. of Records | Percent Success | No. of Records | Percent Success |
| 1964 | 52 | 44 | 260 | 65 |
| 1965 | 40 | 50 | 224 | 61 |

Observations during a nest-trapping and banding operation on Robinson Rock in 1965 also indicated the effect of human disturbance. When the island was revisited one or more times on the same day, after setting nets or banding eiders, many newly destroyed nests were evident. Gulls were seen flying back to the island as soon as the workers left, and they no doubt destroyed many nests before the eiders returned. Grenquist (1959) also believed that flushing a female eider from her nest gave crows a chance to destroy the nest. Black-backed gulls were observed by Todd (1963) to break up an eider nest after a man flushed the female.

Human disturbance did not appear to cause much nest desertion. Only a small percentage of nests was considered deserted (Table 1) and it is not known how many of these were actually the result of human disturbance. It should be pointed out that nests could have been abandoned and subsequently destroyed before they were labeled deserted. Thus, the actual percentage of abandoned nests could have been somewhat higher than shown in Table 1.

There is disagreement as to the effect of human disturbance on nest desertion. Paludan (1962), who captured breeding female eiders on the nest and banded them, noted that few abandoned. Usually the females returned to the nests in a short time. However, Hildén (1964) studied

Table 5. Eider nest success related to the ratio of gulls (including both herring and black-backed) to eiders.

| Island | 1964 | | | 1965 | | |
|---|---|---|---|---|---|---|
| | | Eider Nests | | | Eider Nests | |
| | Gull : Eider | No. | % success | Gull : Eider | No. | % success |
| Mouse Island | 1.3 : 1 | 247 | 47 | 1.5 : 1 | 223 | 29 |
| Goose Island | 1.9 : 1 | 86 | 36 | 2.0 : 1 | 113 | 27 |
| East Goose Rock | 2.0 : 1 | 64 | 34 | 3.5 : 1 | 52 | 40 |
| Robinson Rock | 2.2 : 1 | 118 | 28 | — | — | — |

several species of ducks and observed that the eider was the species most apt to desert its nest. In a number of cases the nest was abandoned after the female was flushed only once.

A few clutches apparently were lost because of overexposure to heat when nests were checked on hot, sunny days. Several cases of partially developed embryos were suspected to be the result of this exposure. Overheating occurred when many eiders were flushed from their nests and it was 2 hours or more before the observer could cover all the eggs.

During artificial incubation of eider eggs, a temperature of 42 C or higher may kill all the embryos (Rolnik 1943:157). This temperature was occasionally exceeded in the present study. Overheating occurred primarily in sparse cover where the eggs were not sufficiently shaded from the direct sunlight. There was no evidence that any losses were caused by excessive cooling of the eggs.

As with desertion, losses to overexposure may have been greater than indicated in Table 1. Embryos could have died and the eggs been eaten by predators before it was known that the embryos had perished. In such cases the nests would have been included in the predation category.

As mentioned in Methods, there was differential human disturbance on two islands in 1965. Goose Island, with more than twice as many visits, had 27 percent nest success—about two-thirds that for East Goose Rock (40 percent). Chi-square showed the difference to be significant ($P < 0.10$). Thus, with greater human disturbance on Goose Island, nesting success was significantly lower.

In the Cape Dorset Area, Northwest Territories, egg loss was heavier than normal when the eiders were frequently disturbed (Cooch 1966). Paynter (1951) believed that an observer's presence contributed to decreased eider nesting success.

Milne (1963) attempted to measure the effect of disturbance on success in a manner similar to that of the present study. A study area that was visited daily was compared with a relatively undisturbed control area. Although success was somewhat lower (3 percent) in the disturbed area, the difference was not significant.

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*Received for publication October 17, 1966.*

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