Nest site selection in the Common Eider *Somateria mollissima*: differences between the archipelago zones

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The nest site selection and reproductive traits were studied in Eiders breeding in three zones of the Finnish archipelago. These differed in the degree of isolation (safety from terrestrial predators), the vegetation and human disturbance. The data were gathered in summer 1988 and comprised 52 islands and 1057 Eider nests.

Both the numbers of Eiders and their density were higher in the outer zone, where the birds bred on all the islands. In the inner zone, they preferred the smaller and most isolated islands. The nests were located further from the water and more of them were covered in the outer zone than elsewhere. Outer zone Eiders bred earliest and were shyest, and their nests were least frequently robbed. These differences were probably due to the earlier break-up of the ice, better protection from terrestrial predators and weaker human disturbance in the outer zone. In general, covered nests contained more eggs than open ones. The Eiders laid later and more of their nests were robbed on disturbed than on undisturbed islands. On open (well-isolated and less disturbed) islands, the nest density was higher, breeding occurred earlier and fewer nests were robbed. In the principal component analysis, the first principal component (interpreted as safety from predators) accounted for 43% of the variation in nest density and 20% of the variation in the distance of the nest from the shore, the laying date and flushing distance. The second principal component (interpreted as island size) explained 40% of the variation in the distance of the nest from the shore and 10% of the variation in nest density. The third principal component (in terpreted as archipelago zone) explained 56% of the variation in clutch size and 20% of the variation in the laying date and flushing distance of female Eiders.

The Eiders preferred well-isolated islands that were not disturbed by humans and had enough vegetation to offer cover for the nest; the type of island (open vs. wooded) was not important, but the islands fulfilling these conditions were mostly open. Eiders were able to breed successfully in all zones, but the inner zone seemed to be a poorer breeding habitat, as human disturbance and terrestrial predators reduced the number of islands suitable for nesting.

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Introduction

The most numerous duck in the Baltic is the Eider (*Somateria mollissima*), its population having increased from about 300 000 pairs in 1970 to more than 600 000 pairs in the 1980s (Stjernberg 1982). When the population was smaller, Eiders were virtually absent from the inner archipelago (e.g. Bergman 1939, Andersson et al. 1978), but since the population increase, they have bred even on the inner islands (Grenquist 1965, Andersson et al. 1978, Stjernberg 1982). Theories on habitat selection predict that birds breed where they can maximize their reproductive output (Partridge 1978). This could indicate that the inner archipelago is a less suitable habitat for Eiders, as they have bred there only since their numbers increased.

All birds have nest site preferences, based on the vegetation and other factors, e.g. protection from predators (Hildén 1965). Incubating Eiders and their nests are especially vulnerable to predation because the nests are situated on the ground, often in quite open sites. During laying, the female leaves her nest for foraging and although she usually covers the eggs, avian predators (gulls and crows) can locate the nest and rob it, especially on open islands where the nests are visible. After laying, the female incubates virtually without leaving her nest (Korschgen 1977, Hario 1983). Avian predators cannot drive the female from the nest (Ahlén & Andersson 1970), but if she is flushed from the nest by humans or by terrestrial predators, it can be robbed by the disturbers or birds. Predation has been smaller when the nests are located on isolated islands, in dense colonies of Eiders or gulls or terns, or in sites with good cover, and these choices have been interpreted as strategies for avoiding predation (Hildén 1965, Ahlén & Andersson 1970, Bengtson 1970, Livezey 1981, Gerell 1985).

The aim of this study was to identify the factors influencing nest site selection in the Common Eider and to discover whether these include the probability of predation. I also wished to know whether the nest site selection or reproductive parameters of Eiders differ between different parts of the archipelago, and whether the inner archipelago can be considered a suboptimal habitat for these birds.

Material and methods

The study area

The study area, a 4–6-km-wide strip of archipelago extending about 20 km from the mainland to the open sea, is situated in the SE part of the Gulf of Finland, 20 km east of Helsinki (Fig. 1). Modifying the definitions of Häyrén (1900) and Luther (1951), I grouped the islands into three zones: the inner, the middle and the outer (Fig. 1). These zones differed from each other in vegetation, isolation (absence of terrestrial predators) and human disturbance.

The *inner zone* has most vegetation. The area of land exceeds that of water and the waters are sheltered (Fig. 1). The islands are mostly large and wooded and many of them harbour terrestrial predators. As the islands are near each other, the predators can swim from island to island. Nearly all of the largest islands have permanent human settlement and many islands have summer cottages. The boat traffic is heavy.

In the *middle zone* the area of water exceeds that of land (Fig. 1). The islands are mainly wooded and some of the largest have terrestrial predators, but as they are further apart, many of them are well isolated (Fig. 1). There are few permanent inhabitants or summer cottages, but some of the islands are used extensively for recreation. The boat traffic is intensive, but not as heavy as in the inner zone.

In the *outer zone* the water area clearly exceeds that of land. The islets are virtually treeless and fairly small (Fig. 1). Except for occassional visits by American minks (*Mustela vison*), there are no terrestrial predators, and the islands are well isolated. Human disturbance is minimal, as the islands are protected by law and visited only by researchers 1–3 times during

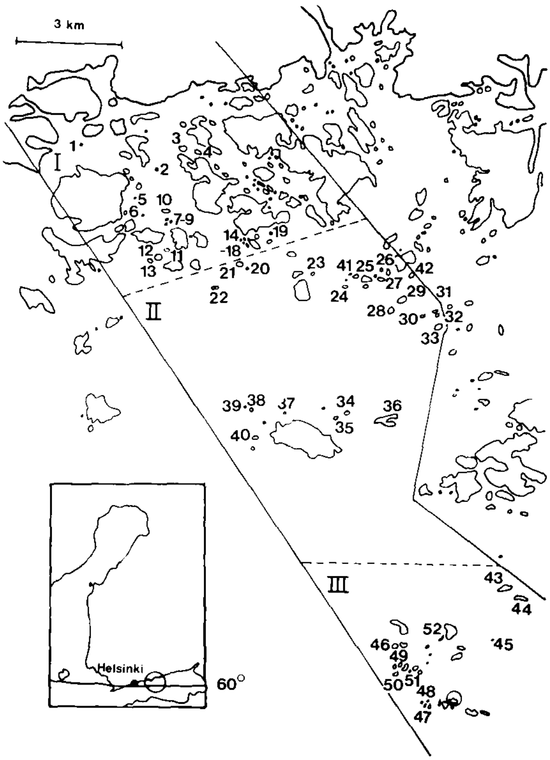

Fig. 1. The study area and its location in the SE Gulf of Finland. Numbers indicate censused islands, the open dot the Game Research Station of Söderskär. I inner archipelago zone, II middle archipelago zone, III outer archipelago zone.
Islands:

1. Fästningen, 2. Bässen, 3. Klovaholmen, 4. Peliholmen, 5. Alören, 6. Tallören, 7. Alörarna 1, 8. Alörarna 2, 9. Alörarna 3, 10. Bärholmen, 11. Björkholmen, 12. Björnholmen, 13. Björnungen, 14. Raterna 1, 15. Raterna 2, 16. Raterna 3, 17. Raterna 4, 18. Raterna 5, 19. Lilla Kooören, 20. Träskörskobben, 21. Träskören, 22. Rönn, 23. Korpungen, 24. Torrvedshällarna, 25. Kitiskari, 26. Lilla Granholmen, 27. Västra Byholmen, 28. Lilla Högholmen, 29. Stora Högholmen, 30. Högholmsören, 31. Trädgårdsholmen, 32. Lilla Trädgårdsholmen, 33. Vitholmen, 34. Lillkobben, 35. Storkobben, 36. Kajholmen, 37. Skomakaren, 38. Musborstan, 39. Borstören, 40. Stenören, 41. Alratet, 42. Södra Byholmen, 43. Inre Kittelskär, 44. Yttre Kittelskär, 45. Bisapallen, 46. V. Satamasaari, 47. Reevit 1, 48. Reevit 2, 49. Barkholmit 1, 50. Barkholmit 2, 51. Barkholmit 3, 52. Jussikariören.

the Eiders incubating period. The boat traffic is moderate.

Material and field methods

Data were gathered during the summer of 1988. In the inner archipelago, the ice broke up on 2 May. Male Eiders were counted from a boat from 2 May to 16 May in the inner and middle zones, to obtain an estimate of the breeding population and its distribution. The counts were mainly made in the morning or evening. In the outer zone, Eiders were known to breed on all the islands and the population was estimated by nest counts (Hario & Selin 1988).

On the basis of these counts, I chose 52 islands and from 18 May to 26 May recorded all the Eider nests I could find, noting their distance from the shore, the amount of cover, and the laying date, clutch size and flushing distance of the female. The frequency of robbed nests was also established. The censuses were finished on 26 May, when some of the clutches had hatched, as I wished to concentrate on first clutches. The success of breeding was checked by counting females with young from a boat in the inner and middle zones on 6–8 June, when the young were approximately one week old and the females remained near their breeding islands. Young were not counted in the outer zone, as the population was too large.

In the inner and middle zones, practically all islands with breeding Eiders were censused. In the outer zone, where Eiders bred on all the islands, half of the islands were censused, five of the largest in cooperation with the Game Research Station at Söderskär.

In order to avoid a phenological bias, I first censused half of the inner and middle zones, then the outer zone, and finally the rest of the inner and middle zones.

I thus obtained data on 19 islands and 81 nests from the inner, on 23 islands and 373 nests from the middle and on 10 islands and 603 nests from the outer zone. The whole material comprised 52 islands and 1057 nests.

The flushing distance of the female and the distance of the nest from the shore were measured by eye. Small differences in these variables should therefore not be accorded too much attention.

The laying date was estimated by floating eggs in water, measuring the area of the egg emerging above the surface (e.g. Väisänen 1974), and converting the area to days (Merilä et al. 1975). The method is not absolutely accurate, but valid for comparisons. All the eggs found on small islands were examined in this way, but on large islands, or islands with dense Eider populations, only those of every second or third nest were floated. With the exception of the four largest islands, the visits did not exceed one hour. As a rule all nests were covered after the visit.

Statistical methods

The size and type of islands, occurrence of gulls, degree of human disturbance, and cover of the nest were treated as ranked variables in the ANOVAs, being coded as follows:

Size of island
1. Very small, 1 ha
2. Small, 1–1.9 ha
3. Medium, ≥2 ha

Type of island
1. Open
   1.1. Only herbs
   1.2. Herbs and some bushes
   1.3. Bushes and some trees
2. Wooded
   2.1. Forest mixed with open areas
   2.2. Totally covered with forest.

Gulls
1. No breeding gulls
2. A few gulls (≤10 pairs, usually *Larus canus*) nesting on the island
3. A gull colony (>10 pairs, usually *L. argentatus*, in a few cases *L. canus* or *L. ridibundus*).

Degree of disturbance by humans
1. Low (protected islands and islands with summer cottages not occupied during the Eider breeding period)
2. Moderate (islands visited a few times during the breeding period)
3. High (islands visited frequently during the breeding period)

Nest cover
1. Poor (nest visible from above)
2. Good (nest covered from above)

The continuous variables chosen were the distance of the nest from the shore, date of laying, clutch size, flushing distance of the female, percentage of robbed nests, density of Eider nests on the island and in some

Table 1. Means and standard deviations of variables related with the breeding ecology of female Eiders, nest density and percentage of robbed nests in the three archipelago zones. (Number of islands or nests in parenthesis.)

	Zone						
	Inner		Middle		Outer		P
Size of censused islands, ha	0.8±0.9	(19)	1.4±1.7	(23)	1.6±1.4	(10)	ns
Distance of nest from shore, m	11.2±9.2	(81)	27.8±19.8	(373)	41.1±17.0	(603)	<0.001
Flushing distance, m	3.3±2.9	(75)	4.2±7.4	(328)	15.7±17.9	(523)	<0.001
Date of laying (1= 18 April)	21±5	(62)	19±5	(191)	17±5	(195)	<0.001
Clutch size	4.7±1.3	(75)	4.7±1.0	(331)	4.5±1.2	(582)	ns
Density, nests/ha	5		12		38		–
Robbed nests, %	14		13		5		<0.001

cases also the size of the island. One-way analysis of variance (ANOVA) was used to estimate the effects of the ranked variables on the continuous variables. Differences between the means were tested with F-tests. The differences between the percentages of robbed nests were tested with the χ^2 -test. The analyses were performed (1) keeping the three zones separate and (2) combining the inner and middle zones.

The principal component analysis was made on the whole data set, being based on the correlation matrix. Unrotated factor loadings were used to estimate what percentage of the variation in variables related with the breeding ecology of Eiders was accounted for by each principal component.

Results

Differences between the archipelago zones

The density of nesting Eiders, location of the nest and the reproductive variables of the Eider females differed between the zones (Table 1). The Eiders evidently preferred the outer zone; the density of their nests was considerably higher there than in the other zones (Table 1). In the inner zone the Eiders preferred small islands (Fig. 1), in the outer zone they bred on all the islands, irrespective of their size.

More nests were covered in the outer zone (51%) than in the middle (29%) or inner (17%) zones, although the outer islands had sparser vegetation. Covered nests and nests on large islands were placed further from the shore than nests visible from above (Table 2) or nests on small islands (island size — distance of nest from shore, r=0.38, N=434). Irrespective of the size of the island, the nests were located further from the shore in the outer zone (Table 1).

Eiders in the outer zone bred significantly earlier and were shyer than those in the middle and inner zone (Table 1). There were no statistically significant differences in the mean clutch sizes between the zones, but the frequency of robbed nests was lowest in the outer zone (Table 1).

Effect of nest site characteristics on density and reproduction

Size type of island

The size of the island had a statistically significant effect only on the distance of the nest from the shore. As the size of the island did not influence the reproductive traits, the results are not shown in a separate table.

The density of Eider nests was higher, the laying was earlier and the frequency of robbed nests was lower on open than on wooded islands (Table 3), according to the whole data set and the data from the middle and inner zones.

Gulls

On islands with gull colonies, as compared with islands with few or no gulls, the density of Eider nests seemed to be higher and the frequency of robbed nests lower, while the Eiders evidently bred earlier and were shyer (Table 4). However, these trends seemed to be due to the location and to the type or degree of disturbance of gull islands rather than to the gulls themselves. When Eider nests on otherwise similar

Table 2. Means and standard deviations of variables related with the breeding ecology of Eider females having open and covered nests. (Number of nests in parenthesis.)

	Type of nest				
	Open		Covered		P
Distance of nest from shore, m					
whole material	27.0±17.2	(627)	44.4±18.9	(430)	<0.001
outer zone omitted	20.4±16.7	(331)	36.8±21.3	(123)	<0.001
Flushing distance, m					
whole material	9.4±14.1	(542)	12.3±16.8	(384)	<0.01
outer zone omitted	4.2±6.9	(290)	3.5±6.4	(113)	ns
Date of laying (1 = 18 April)					
whole material	18±5	(334)	18±5	(114)	ns
outer zone omitted	19±6	(207)	19±4	(46)	ns
Clutch size					
whole material	4.5±1.2	(577)	4.7±1.2	(411)	<0.01
outer zone omitted	4.6±1.1	(291)	4.9±1.0	(111)	<0.01

Table 3. Means and standard deviations of variables related with the breeding ecology of Eiders, nest density and percentage of robbed nests on open and wooded islands. (Number of islands or nests in parenthesis.)

	Type of island				
	Open		Wooded		P
Size of censused islands, ha					
whole material	1.0±1.0	(26)	1.5±1.6	(26)	ns
outer zone omitted	0.5±0.3	(16)	1.5±1.6	(26)	ns
Distance of nest from shore, m					
whole material	36.1±18.9	(735)	29.6±21.0	(322)	<0.001
outer zone omitted	13.2±5.9	(129)	29.6±21.0	(322)	<0.001
Flushing distance, m					
whole material	13.3±16.9	(653)	4.0±7.4	(273)	<0.001
outer zone omitted	4.1±5.4	(127)	4.0±7.4	(273)	ns
Date of laying (1 = 18 April)					
whole material	17±5	(285)	20±6	(163)	<0.001
outer zone omitted	18±5	(87)	20±6	(163)	<0.05
Clutch size					
whole material	4.6±1.2	(708)	4.7±1.1	(280)	ns
outer zone omitted	4.7±1.1	(122)	4.7±1.1	(280)	ns
Density, pairs/ha	33		8		–
outer zone omitted	19		8		–
Robbed nests, %	5		17		<0.001
outer zone omitted	3		17		<0.001

Table 4. Means and standard deviations of variables related with the breeding ecology of Eiders, nest density and percentage of robbed nests on islands with and without gull colonies. (Number of islands or nests in parenthesis.)

	Number of breeding gulls on island						
	None		Few (<10)		Colony		P
Size of censused islands, ha							
whole material	0.5±0.3	(10)	1.3±1.0	(27)	1.6±2.2	(15)	ns
outer zone omitted	0.6±0.3	(9)	1.3±1.0	(23)	1.2±2.4	(10)	ns
Distance of nest from shore, m							
whole material	16.8±12.6	(43)	26.0±19.2	(280)	38.2±18.8	(734)	<0.001
outer zone omitted	17.9±12.6	(39)	26.5±20.4	(235)	24.2±19.2	(180)	<0.05
Flushing distance, m							
whole material	2.7±3.0	(38)	3.9±6.1	(249)	13.7±17.2	(639)	<0.001
outer zone omitted	2.2±2.6	(34)	3.1±5.3	(211)	5.6±8.6	(158)	<0.001
Date of laying (1 = 18 April)							
whole material	21±5	(29)	20±6	(159)	17±5	(260)	<0.001
outer zone omitted	21±5	(29)	20±6	(130)	18±5	(94)	<0.001
Clutch size							
whole material	4.5±1.2	(37)	4.6±1.2	(249)	4.6±1.2	(702)	ns
outer zone omitted	4.5±1.2	(33)	4.7±1.1	(210)	4.8±1.1	(163)	ns
Density, nests/ha	9		8		31		–
outer zone omitted	7		8		15		–
Robbed nests, %	24		20		6		<0.001
outer zone omitted	24		19		18		ns

Table 5. Means and standard deviations of variables related with the breeding ecology of Eiders, nest density and percentage of robbed nests on four undisturbed islands of open type in the middle zone. (Number of nests in parenthesis.)

	Islands with gull colonies		Islands with few gulls		P
Islands	2		2		–
Size of island, ha	0.8		0.6		–
Distance of nest from shore, m	12.0±2.9	(24)	11.6±3.5	(39)	ns
Flushing distance, m	4.9±3.6	(24)	2.5±2.2	(39)	<0.01
Date of laying (1 = 18 April)	18±4	(17)	15±4	(20)	ns
Clutch size	4.8±0.8	(24)	4.6±1.0	(35)	ns
Density, pairs/ha	15		33		–
Robbed nests, %	0		0		–

islands (same zone, same type and same degree of human disturbance) with and without gull colonies were compared, none of these relationships emerged, except that of the flushing distance (Table 5).

Degree of human disturbance

On frequently disturbed islands, the density of Eider nests was lower, the frequency of robbed nests was higher, the females laid later and were less shy and

Table 6. Means and standard deviations of variables related with the breeding ecology of Eiders, nest density and percentage of robbed nests on disturbed and undisturbed islands. (Number of islands or nests in parenthesis.)

	Degree of disturbance			
	Low	Moderate	High	P
Size of censused islands, ha				
whole material	1.1±1.1 (23)	1.5±1.7 (23)	1.0±0.8 (6)	ns
outer zone omitted	0.7±0.6 (18)	1.6±1.9 (18)	1.0±0.8 (6)	ns
Distance of nest from shore, m				
whole material	36.4±19.4 (704)	30.4±19.9 (309)	23.4±17.6 (44)	<0.001
outer zone omitted	17.1±11.8 (187)	31.6±22.3 (223)	23.4±17.6 (44)	<0.001
Flushing distance, m				
whole material	13.1±17.0 (633)	5.9±8.9 (259)	0.8±1.2 (34)	<0.001
outer zone omitted	3.7±4.7 (184)	4.9±8.7 (185)	0.8±1.2 (34)	<0.01
Date of laying (1 = 18 April)				
whole material	17±5 (267)	19±6 (156)	22±6 (25)	<0.001
outer zone omitted	19±5 (120)	19±6 (108)	22±6 (25)	<0.05
Clutch size				
whole material	4.6±1.2 (687)	4.7±1.2 (267)	4.3±1.1 (34)	ns
outer zone omitted	4.7±1.2 (180)	4.8±1.1 (192)	4.3±1.1 (34)	<0.05
Density, pairs/ha	28	9	7	–
outer zone omitted	15	8	7	–
Robbed nests, %	2	19	27	<0.001
outer zone omitted	4	17	27	<0.001

Table 7. Means and standard deviations of variables related with the breeding ecology of Eiders, nest density and percentage of robbed nests on disturbed and undisturbed islands of the same type (wooded) situated in the same archipelago zone (middle). (Number of nests in parenthesis.)

	Degree of disturbance			
	Low	Moderate	High	P
Islands	2	6	2	
Size of island, ha	1.9	1.6	1.5	–
Distance of nest from shore, m	35.6±14.9 (32)	35.2±22.5 (98)	30.3±22.6 (17)	ns
Flushing distance, m	2.2±1.8 (31)	3.9±7.8 (86)	1.4±1.8 (10)	ns
Date of laying (1 = 18 April)	20±4 (31)	19±5 (52)	23±7 (9)	ns
Clutch size	5.0±0.9 (31)	4.7±1.2 (88)	4.1±1.4 (10)	ns
Density, pairs/ha	8	11	6	–
Robbed nests, %	3	16	41	<0.05

had smaller clutches than on undisturbed islands (Table 6). As disturbed and undisturbed islands differed with respect to both type and location, I compared islands of the same type (wooded) in the same zone (middle); the trends in the date of laying, clutch size and frequency of robbed nests were as before, though (due to the small data set) only the last trend was statistically significant (Table 7).

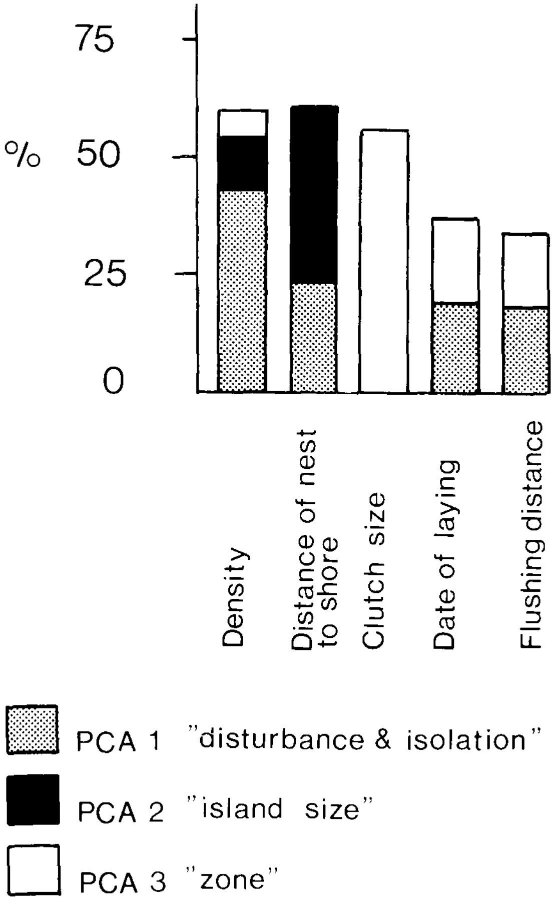

Fig. 2. Percentage of variation in nest density and reproductive traits of Eiders explained by the first three principal components (PCA).

Table 8. Rotated factor loadings on the first three principal components (PCA). Loadings <|0.3| are not shown.

Trait	PCA 1	PCA 2	PCA 3
Zone	0.466	–0.436	0.504
Size of island		0.742	
Type of island	0.664	0.334	0.366
Gulls	–0.732		
Degree of disturbance	0.758		
Nest cover		0.748	
Density	–0.770		
Distance of nest from shore		0.771	
Date of laying	0.492		
Flushing distance			–0.498
Clutch size			0.719

Nest cover

In all the zones open nests contained fewer eggs than covered nests (Table 2). The difference was most pronounced in the outer zone. Open nests were also more often subject to predation (79% of the robbed nests lacked cover).

Relative effect of nest site characteristics on reproduction

The principal component analysis gave three main components which together explained 34–61% of the variation in density and reproductive parameters (Fig. 2). The first principal component had the strongest loadings on island type, occurrence of gulls and degree of human disturbance (Table 8). It arranged the nests from those on open, undisturbed islands with gull colonies to those on wooded and disturbed islands without gulls. As the open gull islands were located in the outer zone, or on the edges of the archipelago, they were also well isolated from terrestrial predators. I called the first factor "safety from predators"/"disturbance and isolation". It explained a large part (43%) of the variation in nest density and about 20% of the variation in the distance of the nest from the shore, date of laying and flushing distance (Fig. 2).

The second principal component had the strongest loadings on island size and nest cover (Table 8). It arranged the nests from open nests on small islands to covered nests on large islands. As more nests (52%) were concealed on large islands than on small islands (9%), I called this factor "island size". It explained 38% of the variation in the distance of the nest from the shore and 11% of the nest density variation (Fig. 2). Both trends can be considered mathematical, as no nest can be very far from the shore on a small island, and island size influences nest density, giving large densities for small islands (Haila 1988).

The third principal component had the strongest loadings on zone and type of island, arranging the nests from those on wooded islands in the inner zone to those on open islands in the outer zone (Table 8). I called this factor "zone". It explained 56% of the clutch size variation and nearly 20% of the variation in the date of laying and flushing distance (Fig. 2). Besides differences on vegetation, the zone factor includes the better overall cover offered by forest and the greater diffuse disturbance (boat traffic, summer cottages) in the inner zone.

Discussion

Nest site selection

Judging from the results of this study, Eiders do not avoid islands with taller vegetation (bushes and/or forest). The principal component analysis showed that both the isolated location of an island (safety from terrestrial predators) and a low degree of human disturbance attract Eiders and lead to high densities. Thus the main factor behind nest site selection seems to be avoidance of predation.

Theoretically, if the life of the female is in danger, as is the case with terrestrial predators, Eiders should avoid nesting altogether. Many researchers have reported that Eiders avoid breeding on the mainland or islands with terrestrial predators (Ahlén & Andersson 1970, Bengtsson 1970, Schamel 1977), but prefer isolated islands which are difficult for terrestrial predators to reach. If disturbed by predators, female Eiders seem to change their breeding island (Valste & Palmgren 1984).

In this study the largest islands inhabited by humans and several terrestrial predators were not used by breeding Eiders. Larger islands attracted Eiders only when they were well isolated. In the inner zone Eiders bred on small islets, probably because these were most isolated. In the middle and outer zones Eiders bred even on large islands.

Theoretically, Eiders can react in two ways to human disturbance (not actually threatening the life of the female): change the breeding island (Bergman 1939) or become tame and reluctant to leave the nest (Hildén 1965). The latter strategy is supposed to be more common in cases where Eiders are often confronted with humans but are not flushed from the nest.

In this study, the outer zone females were caught by researchers, so they did not benefit from staying on the nest. In the inner and middle zones, where females were not flushed from the nest if unobserved by human visitors, the females were significantly tamer on disturbed than on undisturbed islands. Actually, many females on the disturbed islands refused to leave their nests altogether, and I was able to check the clutch size by gently tipping the bird to one side. The flushing distance was also generally shorter in the inner and middle zones, probably because Eiders were not methodically flushed from their nests, as in the outer zone, and they were more used to humans, due to the heavy boat traffic and the many summer cottages. The shorter flushing distance in these zones was not due to the lower density, as flushing distance was not found to be correlated with density.

The reaction of Eiders to avian predation, threatening only the eggs, seems to be to place their nests in cover (Livezey 1981, but see also Gerell 1985). In this study more nests were covered in the outer zone, where the islands were open and the nests easy to discover.

Although avoidance of predators seemed to be a very important factor in the nest site selection of Eiders, the data of this study did not corroborate the hypothesis that Eiders breed in gull colonies in order to avoid terrestrial predators, as has been suggested by, e.g., Hildén (1965) and Gerell (1985). I will return to this below.

Effect of nest site on reproduction and nest density

In this study the location, size and type of the island, the number of gulls breeding on it and the degree of human disturbance were correlated. Islands situated near the open sea (the outer zone islands and other islands on the edge of the archipelago) were open, as were all the small islets, whereas wooded islands were larger with a more sheltered location. Open islands were preferred by gulls, which seldom form colonies on wooded islands. Unlike the gulls, humans prefer wooded islands with cliffs and a good anchoring place, which results in the open gull islands being less disturbed than the wooded ones. None of the most disturbed islands were open or had gull colonies.

As open islands are mostly located on the edges of the archipelago, facing the open sea, they become free of ice sooner than the more sheltered wooded islands. This could explain why Eiders bred earlier on open than on wooded islands. Open islands were also less disturbed, which probably accounts for the lower frequency of robbed nests and the higher nest density on open than on wooded islands.

In this study, gulls did not influence the reproductive success of the Eiders. Eiders in gull colonies have been reported to breed earlier (Gerell 1985), and to have larger clutches and fewer robbed nests (Gerell 1985, Götmark & Åhlund 1988) than Eiders breeding elsewhere. These trends were observed in this study, but they were not due to the gulls, but to the location of the gull islands and the weaker human disturbance, as they were not observed when islands of the same type were compared. Thus the Eiders' preference for nesting in gull colonies is probably not due to the protection given by the gulls, but because the two species prefer the same type of islands (e.g. Nordberg 1950, Gerell 1985).

Differences between the zones

The differences in the location of islands and the liability of the nest to predation seemed to result in the Eiders having slightly different breeding strategies in the inner and outer archipelago. The islands of the outer zone are exposed to the sea and winds and have little vegetation. Eiders breed there early, probably because the ice breaks up early. Due to the wave action, the nests are placed further from the shore than in the more sheltered inner and middle zones. In the absence of terrestrial predators, Eiders breed on all islands irrespective of their size. During laying, when the females leave their nests for foraging, the uncovered nests are easily discovered, and some of the first-laid eggs are probably stolen. This is indicated by the fact that in the outer zone the mean clutch size of nests on very open islands was smaller than on open islands with bushes, a trend that was not seen in other zones. The Eiders in the outer zone also preferred to nest in cover. During incubation, the nests are safe, as the females no longer leave them and are not flushed from them by people.

In the inner and middle zones Eiders prefer the most isolated and least disturbed islands, which are mostly very small. As the ice breaks up later, the Eiders breed later than in the outer zone. During laying, the risk of predation is fairly low as the boating season has not yet begun. Moreover, most Eider nests were found in forest and were not easily detected by aerial predators. During incubation, human disturbance is severe on certain islands. Here the Eiders try to minimize predation by staying on the nest as long as possible. Still, considerably more nests are robbed in the inner and middle zones than in the outer zone.

According to this study, the ideal nesting place for an Eider is an undisturbed island, well isolated from terrestrial predators and with enough vegetation to give cover for the nest. When these conditions are fulfilled, the type of island seems to be of less importance (30% of all the nests and 70% of the nests in the inner and middle zones — where Eiders were able to choose between open and wooded islands — were located on wooded islands). Many other studies have confirmed that Eiders are able to breed successfully on totally open, bushy and wooded islands (Bergman 1939, Nordberg 1950, Ahlén & Andersson 1970, Milne & Reed 1974, Valste & Palmgren 1984).

Is the inner zone a suboptimal breeding habitat for Eiders?

In all the zones, the Eiders managed to produce young, and there were no significant differences in the mean clutch sizes between the zones. On the other hand, the frequency of robbed nests was lower in the outer zone. On the outer zone islands visited by researchers alone, 5% of the nests were robbed. In the inner and middle zones 14% of the nests were robbed, a common figure in the Baltic region (Nordberg 1950, Götmark & Åhlund 1984, Pahtamaa 1987). Thus the inner zone could be considered a suboptimal breeding habitat for Eiders, since terrestrial predators and the stronger human disturbance reduce the number of suitable islands and the probability of predation is greater for the nest or female. This probably makes the inner zone less attractive and leads to low densities. Some females may also change the breeding island after their nests have been robbed.

It could be assumed that in a growing population it is the young birds that are forced to breed in suboptimal conditions. Eider clutches laid early in the year are larger than late ones (Laurila & Hario 1988), and first breeders and young Eiders lay smaller clutches than old birds (Laurila & Hario 1988). Thus, if the inner zone had the majority of young birds, the clutch size of these Eiders should be smaller than that of the outer zone birds. However, this was not the case.

The Eiders seemed to be fairly flexible in their nest site selection, breeding on all types of islands and reproducing successfully even in the less suitable conditions of the inner zone islands. It is possible that this flexibility is one, though surely not the only, reason for the vast increase of the Eider in the Baltic. Successful species are more likely to be opportunistic in their nest site or food requirements (e.g. Kilpi 1988). Another feature which can contribute to the success of the Eiders is their tolerance of human disturbance, i.e. their tendency to become tame.

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Selostus: Haahkan pesäpaikan valinta: saaristovyöhykkeiden väliset erot

Tutkin haahkan pesäpaikan valintaan vaikuttavia tekijöitä ja sitä, eroavatko pesäpaikan valinta tai lisääntymisominaisuudet eri saaristovyöhykkeillä Helsingin itäpuolella. Tutkimusalue jaettiin sisä-, väli- ja ulkosaaristovyöhykkeeseen. Vyöhykkeet erosivat toisistaan kasvillisuuden, saarten eristyneisyyden (etäisyys mantereesta tai suuresta saaresta) ja häirinnän puolesta. Kesän 1988 aikana kerätty aineisto koostui 52 saaresta ja 1057 haahkanpesästä.

Haahkoja oli eniten ja tiheimmässä ulkosaaristossa. Ulkosaaristossa haahkat pesivät kaikilla saarilla, sisäsaaristossa sen sijaan pienillä saarilla. Ulkosaaristossa oli enemmän suojapesiä kuin sisäsaaristossa, ja pesät olivat kauempana rannasta. Ulkosaariston haahkat pesivät aikaisemmin, niillä oli pidempi pakoetäisyys ja vähemmän pesätuhoja kuin sisäsaariston haahkoilla. Vyöhykkeiden väliset erot johtuvat tässä tutkimuksessa siitä, että sisäsaaristossa jää lähti myöhemmin, saaret ovat maapedoilta huonommin eristettyjä ja ihmisen häirintä suurempaa kuin ulkosaaristossa.

Pesäpaikka vaikutti lisääntymisominaisuuksiin siten, että suojapesissä oli enemmän munia kuin avopesissä. Häirintä vaikutti pesinnän ajankohtaan ja pesätuhojen määrään, häirityillä saarilla pesätuhot olivat suuremmat. Avoimilla luodoilla haahkat pesivät aikaisemmin ja vähemmän pesiä tuhoutui kuin metsäisillä saarilla. Erot johtuivat tässä tutkimuksessa siitä, että veneilijät suosivat metsäsaaria, joita häirittiin enemmän kuin avoimia luotoja. Saaren "turvallisuus" (maapedoilta hyvin eristetty, vähän häirintää) selitti 40% haahkojen tiheyden ja 20% pesinnän ajankohdan ja pakoetäisyyden vaihtelusta. Saaren koko selitti 40% pesän etäisyydestä rannasta ja 10% tiheyden vaihtelusta. Vyöhyke (kasvillisuus ja epäsuora häirintä, ts. veneliikenne) selitti 56% pesyekoon ja 20% pesinnän ajankohdan ja pakoetäisyyden vaihtelusta.

Tutkimusalueella haahkat suosivat petojen ja ihmisen vähän häiritsemiä saaria, joilla oli pesän suojaksi kasvillisuutta. Haahkat eivät karttaneet metsäsaaria, mutta edellämainitut vaatimukset täyttävät saaret olivat usein avoimia. Haahkat saivat poikasia kaikilla vyöhykkeillä, mutta sisäsaaristo oli haahkoille huonompi pesimäympäristö kuin ulkosaaristo, koska pesätuhot olivat sisällä suuremmat ja ihmisasutuksen, veneilyn ja maapetojen takia sisäsaaristossa on vähemmän sopivia pesäsaaria tarjolla.

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