Use of Serum Biochemistry to Evaluate Nutritional Status and Health of Incubating Common Eiders (*Somateria mollissima*) in Finland

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Accepted 11/28/00

ABSTRACT

During 1997–1999, we collected serum samples from 156 common eider (*Somateria mollissima*) females incubating eggs in the Finnish archipelago of the Baltic Sea. We used serum chemistry profiles to evaluate metabolic changes in eiders during incubation and to compare the health and nutritional status of birds nesting at a breeding area where the eider population has declined by over 50% during the past decade, with birds nesting at two areas with stable populations. Several changes in serum chemistries were observed during incubation, including (1) decreases in serum glucose, total protein, albumin, β-globulin, and γ-globulin concentrations and (2) increases in serum uric acid, creatine kinase, and β-hydroxybutyrate concentrations. However, these changes were not consistent throughout the 3-yr period, suggesting differences among years in the rate of carbohydrate, lipid, and protein utilization during incubation. The mean serum concentrations of free fatty acids, glycerol, and albumin were lowest and the serum α- and γ-globulin levels were highest in the area where the eider population has declined, suggesting a role for nutrition and diseases in the population dynamics of Baltic eiders.

Introduction

The number of common eiders (*Somateria mollissima*) in several of their nesting areas in the Gulf of Finland has declined by over 50% during the past decade, while the number of eiders elsewhere in the Finnish archipelago of the Baltic Sea has increased or remained stable (Hario 1998). The population decline has been primarily caused by low (1%–5%) duckling survival (Hario 1998), but significant mortality of adult females has also been observed during some years (Hario et al. 1992). Ducklings die at an early age, and females are usually found dead in poor body condition within 5–10 d after they have completed incubation (Hario et al. 1992; Hario 1998; Hollmén et al. 1998).

Reasons for the mortality and poor reproductive success of eiders in the Gulf of Finland are not well understood. Avian cholera has been implicated in mortalities of nesting common eiders in several of their breeding areas (Korschgen et al. 1978; Swennen and Smit 1991; Christensen et al. 1997), but the disease has not been diagnosed in eiders in Finland. However, recent studies suggest that other infectious and parasitic diseases and contaminants affect the health of the breeding eiders as well as duckling survival in Finland (Hario et al. 1992; Hollmén et al. 1996, 1998, 2000; Franson et al. 2000), and interactions between diseases and physiological condition of eiders have been considered potentially significant.

Diminished food resources have been recently implicated in the eider population changes in the Finnish archipelago. The common eiders seldom leave their nest to feed during the approximately 26 d of incubation but, instead, rely energetically on the body reserves acquired during the prebreeding season (Milne 1976; Parker and Holm 1990; Hario et al. 1999). Consequently, female eiders lose approximately 30% of their body weight during incubation, and the weight of the female eider is at its lowest at the time when the young are hatching (Milne 1976; Hario 1983; Parker and Holm 1990). The end of incubation also coincides with the depletion of fat reserves (Milne 1976), suggesting that eider females are nearing their limit of natural fasting even when food resources are abundant. Studies of the Baltic blue mussel (*Mytilus edulis*), the preferred food of the common eider (Öst and Kilpi 1998), have revealed sig-

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Physiological and Biochemical Zoology 74(3):333–342. 2001. 1522-2152/2001/7403-0060$03.00

nificant differences in mussel size and density among different eider breeding areas along coastal Finland. Mussels are less abundant and smaller in the central and eastern Gulf of Finland, where numbers of eiders have declined, and it has been suggested that eiders breeding in areas with decreased mussel biomasses are not capable of building and maintaining adequate body reserves during the prebreeding season to successfully complete their nesting cycle. However, during a short-term study, the temporal variations in eider breeding success were not directly associated with blue mussel abundance and size (Hario et al. 1999), and the association between food resources, female body condition, and breeding outcome remains obscure.

Serum chemistry and enzyme activities are valuable tools for monitoring the health and nutritional status of animals (Lumeij 1997). Serum chemistry analyses also have been used to experimentally characterize the three metabolic phases associated with long-term fasting in geese and penguins (Robin et al. 1987, 1988; Boismenu et al. 1992; Stevens 1996). During the adaptation phase 1, protein catabolism decreases and lipid mobilization increases. During phase 2, lipids are used as a primary source of energy, and in phase 3 protein reserves of the body can no longer be preserved and protein catabolism increases. Changes in certain blood chemistry variables have been used as indicators of differences in the type of energy reserves utilized during these three phases. Uric acid concentration has been used as an index of protein catabolism because uric acid is the main end product of nitrogen excretion in birds (Robin et al. 1987; Boismenu et al. 1992). β-hydroxybutyrate is a ketone body produced in liver by partial fatty acid oxidation, and blood levels have been related to the rate of lipid metabolism (Le Maho et al. 1981; Cherel et al. 1988). Serum protein concentrations reflect protein synthesis and degradation and were found to decline in greater snow geese during prolonged fasting (Boismenu et al. 1992). Serum chemistry variables also can be used to evaluate organopathies or infectious diseases in birds (Hochleithner 1994). Inflammatory processes, such as aspergillosis, psittacosis, and tuberculosis, cause increases in serum globulin concentrations that can be detected by serum protein electrophoresis (Hochleithner 1994). Acanthocephalans, the most common intestinal parasites of eiders in Finland, affected serum protein concentrations of experimentally infected eider ducklings (Hollmén et al. 1999).

The first objective of our study was to evaluate the intermediary metabolism and nutritional status of common eider females during natural incubation fast over a 3-yr period in the Gulf of Finland by using serum chemistry analyses. We hypothesized that metabolic shifts similar to what have been described in fasting geese and penguins could be observed in fasting eiders, and that annual differences in the body condition of females could be associated with their breeding success. Our second objective was to compare female health and body condition between a nesting area in the central Gulf of Finland, where reproduction has been poor since the mid-1980s, with sites located farther west, where eider populations have remained relatively stable over the same time period and where blue mussel biomasses are greater (Hario et al. 1999; M. Kilpi, unpublished observation). Our hypothesis was that if nutrition and diseases were involved with the observed eider declines, serum chemistries would show evidence of poorer energy reserves and a higher prevalence of inflammatory conditions in birds nesting in the central Gulf of Finland. To test these hypotheses, we collected blood from eiders during their natural incubation fast in areas with stable (Hanko West and Tvärminne) and declining (Söderskär) populations and measured serum concentrations of variables associated with lipid metabolism (free fatty acids, glycerol, triacylglycerol, and β-hydroxybutyrate), protein metabolism (total protein, albumin, uric acid), carbohydrate metabolism (glucose), muscle degradation (creatine kinase), dehydration (urea, sodium, potassium, chlorides), and inflammatory conditions (α-, β-, and γ-globulins) (Hochleithner 1994).

Material and Methods

Study Areas

Study sites consisted of three common eider breeding areas in the Finnish archipelago of the Baltic Sea: Hanko West (59°50′N, 22°50′E), Tvärminne (59°50′N, 23°15′E), and Söderskär (60°06′N, 25°25′E). The Söderskär breeding area is located in the central Gulf of Finland, an area where the eider population has declined by over 50% during 1987–1996 as a result of low duckling survival rates (Hario 1998). Hanko West and Tvärminne are located farther west in the Baltic proper and the western edge of the Gulf of Finland, and there the survival rates of eider ducklings have been higher and the breeding populations have remained relatively stable. Most of the eiders in the study areas nest on rocky islands partly covered with low shrubby vegetation, such as juniper bushes, and occasional trees, but in Tvärminne and Söderskär part of the population nests on wooded islands.

Sample Collection

Using long-handled dip nets, a total of 63 common eider females were captured on their nests during May and June 1997 at the three study locations: Hanko West ($n = 12$), Tvärminne ($n = 16$), and Söderskär ($n = 35$). At Söderskär, an additional 49 and 44 females were captured during May and June of 1998 and 1999, respectively. The median start of incubation at Söderskär was calculated as described by Laurila and Hario (1988). The hens were weighed to the nearest 10 g with a spring scale, and the incubation stage of the nest was determined by calculation of egg densities (Hario 1983) or by flotation of eggs in water (Kilpi and Lindström 1997). Blood samples were collected from the eider females via jugular venipuncture with plastic syringes equipped with 21-ga needles and transferred to plastic tubes without anticoagulant. The handling time from capture until bleeding was less than 5 min for all hens. Blood samples were allowed to clot at approximately 4°C for 2 h and centrifuged at 1,500 *g* for 10 min. Serum was separated and stored at −80°C until the laboratory analyses.

Serum Chemistry Analyses

Serum chemistry analyses were performed at the Central Laboratory of the Faculty of Veterinary Medicine (University of Helsinki, Helsinki, Finland). Total protein was determined with the biuret method (Weichselbaum 1946) using human protein (Precimat Protein, Boehringer Mannheim, Mannheim, Germany) as standard (Lumeij 1997) and reagents from Boehringer Mannheim. Enzymatic methods were used to determine free fatty acids (Shimizu et al. 1980) with standards and reagents from Wako Chemicals (Neuss, Germany). Glycerol was measured with a direct enzymatic, colorimetric procedure, which utilizes a quinonamine chromogen system in the presence of glycerol kinase, glycerol phosphate oxidase, and peroxidase (Randox Laboratories, Crumlin, U.K.). For the analysis of β-hydroxybutyrate, the serum proteins were precipitated with cold 0.6 M perchloric acid. The acidified serum was centrifuged and the supernatant was neutralized with a solution of 3 M potassium hydroxide and 2 M potassium chloride before the enzymatic analysis of β-hydroxybutyrate concentration (Hansen and Freier 1978). Serum sodium, potassium, and chloride concentrations were measured directly by ion-selective electrodes using manufacturer's standards for calibration (Kone Microlyte 2+3, Konelab Corp., Espoo, Finland). Standards for the glucose, triacylglycerol, urea, uric acid, and creatine kinase (CK, EC 2.7.3.2) measurements were bovine serum-based calibration material provided for the Kone Specific analyzer by Konelab. Enzymatic, colorimetric methods were used for the determination of glucose (Trinder 1969) and triacylglycerols (Wahlefeld 1974). An enzymatic method was used to determine urea (Gutmann and Bergmeyer 1974), and a spectrophotometric method was used to measure uric acid (Fossati et al. 1980). Creatine kinase activity was measured according to the recommendations of the Scandinavian Society for Clinical Chemistry and Clinical Physiology (1979). Serum protein electrophoresis was performed on agarose films according to manufacturer's instructions (Beckman Instruments, Application Manual, Brea, Calif.), and films were scanned at 600 nm in a Beckman Appraise densitometer to determine prealbumin, albumin, α-globulin, β-globulin, and γ-globulin concentrations in the samples.

Statistical Analyses

During 1997–1999 the relationship between serum chemistry variables and the incubation stage was examined at Söderskär using a regression analysis. The relationship between the serum CK and total protein concentration was examined with a correlation analysis. The serum chemistry variables at the end of incubation were compared among the years with an ANOVA (Sokal and Rohlf 1995). The frequency of birds with serum β-hydroxybutyrate concentration <1 mmol/L during the last week of incubation was determined. In 1997, the mean incubation stages among the study sites were compared with ANOVA, and the serum chemistry variables that showed no relationship with the incubation stage were compared among the breeding areas using ANOVA. Serum chemistry variables that were normally distributed after log transformation were tested using a parametric ANOVA, while the other variables were tested using a nonparametric ANOVA (Kruskal-Wallis test). Those variables that showed a clear relationship with the incubation stage were compared among the years and areas using a parametric ANCOVA with the incubation stage as a covariate (Sokal and Rohlf 1995). When the regression slopes for the different breeding years and areas were homogenous, as assessed by the lack of interaction between the covariate and the site, the effect of the covariate was examined. Statistical significance was determined at 0.05.

Results

Serum Chemistry at Söderskär during 1997–1999

A total of 128 eider females were captured during days 1–27 of incubation at Söderskär. The females lost weight during incubation (Fig. 1) to mean (±SD) weights of 1,535 (±138), 1,488 (±104), and 1,533 (±92) g in 1997, 1998, and 1999, respectively, at the time when their ducklings were hatching. The median dates for the start of incubation were May 2, May 5, and May 2 in 1997, 1998, and 1999, respectively. In 1997, a negative relationship was detected between incubation stage and serum γ-globulin concentration, and a positive relationship was found between incubation stage and serum uric acid con-

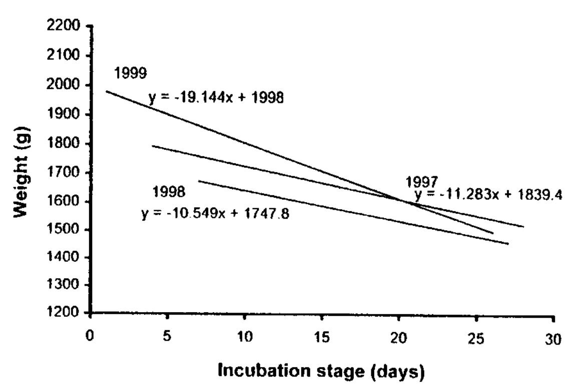

Figure 1. Regression of weight on incubation stage of common eider females at Söderskär, 1997–1999.

centration (Fig. 2*A*). In 1998, a positive relationship was detected between incubation stage and serum uric acid and CK concentrations, and an inverse relationship was detected between incubation stage and serum glucose, total protein, albumin, β-globulin, and γ-globulin concentrations (Fig. 2*A*–2*C*). During the last week of incubation, 14% and 12% of birds had a β-hydroxybutyrate concentration of <1 mmol/L in 1997 and 1998, respectively. In 1999, a negative relationship was detected between incubation stage and serum β-globulin concentration, and a positive relationship existed between incubation stage and serum β-hydroxybutyrate concentration (Fig. 2*D*). No relationships were detected between incubation stage and serum free fatty acid, glycerol, triacylglycerol, urea, sodium, potassium, chloride, and α-globulin concentrations. A negative correlation was found between serum CK and total protein concentrations (Spearman's $r = -0.323$, $P = 0.0002$).

Twelve, 16, and 15 females were captured at Söderskär in 1997, 1998, and 1999, respectively, when their ducklings were hatching (days 25–27 of incubation). The mean glucose concentration in the serum of females was lowest in 1997 and highest in 1999. The mean serum α-globulin concentration was highest in 1997. The mean serum uric acid and CK concentrations were highest in 1998 (Table 1). No differences were detected among years in other serum chemistries of female eiders at the end of incubation, and the results were combined (Table 2).

Site Comparisons

A total of 51 common eiders were captured on their nests during the third and early in the fourth week of incubation (days 14–24) in May and June 1997 at the three study locations: Hanko West ($n = 12$), Tvärminne ($n = 16$), and Söderskär ($n = 23$). The mean incubation stage of captured females did not differ among sites. The mean serum concentration of free fatty acids was lower in birds incubating at Söderskär than in those incubating at Hanko West (Fig. 3*A*), and the mean serum concentration of glycerol was lower in birds at Söderskär than in those at Hanko West and Tvärminne (Fig. 3*B*). The mean serum albumin concentration was lower at Söderskär than at Hanko West (Fig. 3*C*), and the mean serum α-globulin and γ-globulin concentrations were higher at Söderskär than at Hanko West and Tvärminne (Fig. 3*D*, 3*E*). No differences were detected among the study sites in other serum chemistries.

Discussion

Serum Chemistry during Incubation: Do Eiders Enter Phase 3?

Effects of long-term fasting on avian metabolism have been extensively studied in geese and penguins, and fasting has been divided into three phases (Stevens 1996). During phase 1, birds adapt to using stored lipids as their primary source of energy and in phase 2 the stored lipids are used almost exclusively for

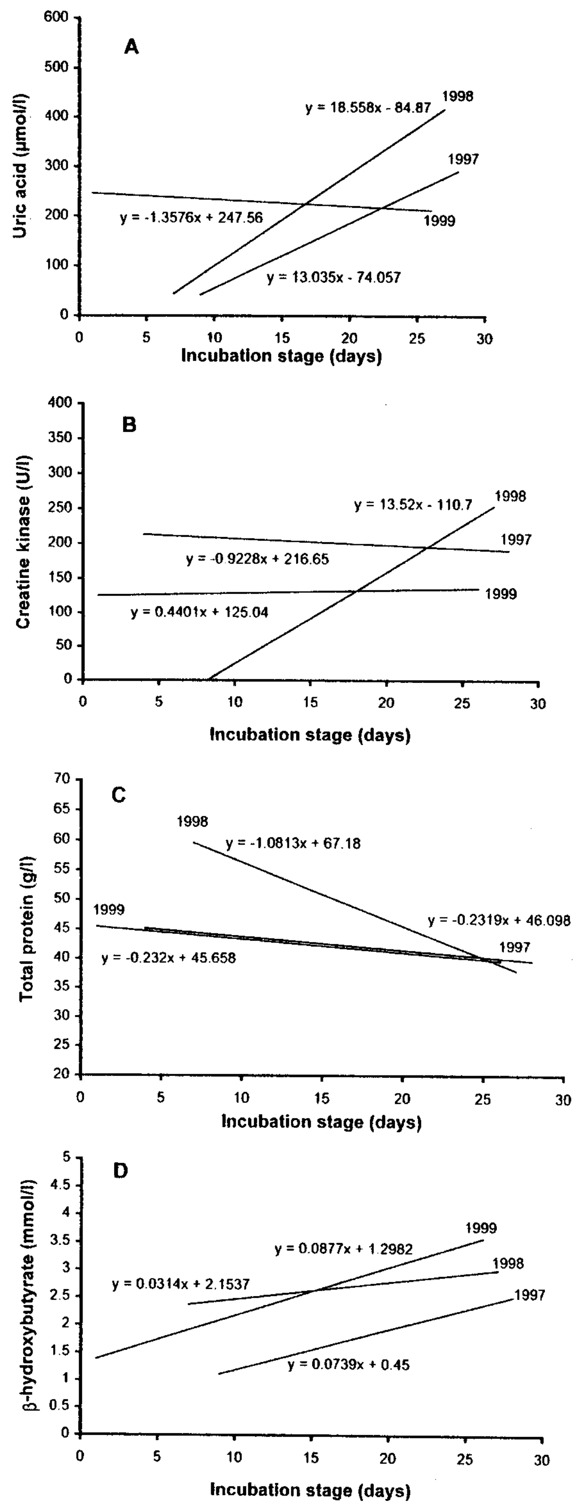

Figure 2. Regressions of serum uric acid (*A*), creatine kinase (*B*), total protein (*C*), and β-hydroxybutyrate (*D*) concentrations on incubation stage of common eider females at Söderskär, 1997–1999.

energy. Triglycerides form the largest portion of stored lipids in avian adipose tissue and liver, and mobilization of triglycerides releases glycerol and free (nonesterified) fatty acids (Hochleithner 1994). Free fatty acids are hydrolyzed from triglycerides and released directly from the adipose tissue into plasma, but in liver they are partially oxidized into β-hydroxybutyrate and these ketone bodies are released into circulation. Korschgen (1976) found that plasma free fatty acid level increased and remained high in incubating eider hens in Maine and attributed this finding to adequate fat reserves throughout the incubation fast in those birds. We also found that serum free fatty acid levels remained constant in eiders nesting in Finland, suggesting that their fat reserves were not completely depleted during incubation.

In geese and penguins, β-hydroxybutyrate levels have been shown to increase during phase 2 and decrease rapidly in phase 3 of fasting (Le Maho et al. 1981; Groscolas 1986), when birds convert from stored lipids to proteins as their major source of energy. Serum β-hydroxybutyrate levels increased during incubation in 1999, and if the lipid metabolism of eiders is similar to that of geese and penguins, our results suggest that in 1999 eiders completed their incubation while still using lipids as their major source of energy. However, in 1997 and 1998, the serum β-hydroxybutyrate levels did not increase progressively throughout the incubation period, and 14% and 12% of birds, respectively, had low concentrations (<1 mmol/L) in their blood during the last week of incubation, suggesting a metabolic shift toward protein utilization (Groscolas 1986; Boismenu et al. 1992). Le Maho et al. (1981) showed that the variations in serum β-hydroxybutyrate levels were a mirror image of daily change in body mass and rate of nitrogen excretion in fasting geese and suggested a key role for β-hydroxybutyrate in regulation of body mass and sparing of protein reserves during fasting. Thus, the differences in the behavior of β-hydroxybutyrate during incubation that were observed among the years at Söderskär may reflect annual differences in the ability of birds to control weight and protein loss during the incubation fast.

The intake and metabolism of essential amino acids from the diet are required to maintain nitrogen balance in animals (Kaneko 1997), and during starvation, protein limits survival more than fats or carbohydrates (Felig 1979). Boismenu et al. (1992) found that in greater snow geese (*Chen caerulensis atlantica*) total plasma protein levels started to fall in phase 3 of fasting, indicating utilization of body proteins. In eiders, serum total protein and albumin concentrations remained stable during incubation, except in 1998, when both total protein and albumin levels decreased during incubation. The observed declines may indicate transition of eiders to phase 3 and protein utilization or hepatic, renal, or gastrointestinal disease such as parasitism during incubation (Kaneko 1997).

Alpha globulins consist mainly of acute-phase proteins and lipoproteins, β-globulins consist of complement, transferrin, ferritin, plasminogen, fibrinogen, and some lipoproteins and immunoglobulins, and γ-globulins consist mainly of immunoglobulins (Hochleithner 1994; Kaneko 1997). Serum α-globulin levels increase with acute inflammation (Hochleithner 1994), and the higher mean α-globulin level in 1997 may be associated with a higher prevalence of inflammatory diseases. In 1998 and 1999, serum β-globulin concentrations decreased in eiders during incubation, but the levels remained constant

Table 2: Mean (±SD) concentrations of serum chemistry variables in common eider females ($n = 43$) at the end of incubation at Söderskär, years 1997–1999 combined

	Mean	SD	Min–Max[a]
Free fatty acids (μmol/L)	.98	.47	.19–1.84
Glycerol (μmol/L)	288	124	32.0–591
Triacylglycerol (mmol/L)	1.02	.37	.06–2.00
β-hydroxybutyrate (mmol/L)	3.20	1.92	.36–10.0
Total protein (g/L)	39.4	7.24	25.7–56.6
Prealbumin (g/L)	.49	.15	.25–.86
Albumin (g/L)	18.1	4.43	9.39–28.1
β-globulins (g/L)	10.5	2.97	5.49–18.9
γ-globulins (g/L)	3.49	1.15	1.46–5.78
Urea (mmol/L)	.40	.33	0–1.80
Sodium (mmol/L)	151	11.5	110–170
Potassium (mmol/L)	3.00	.94	1.80–7.40
Chloride (mmol/L)	109	8.44	80.0–122

[a] Minimum and maximum values expressed as a range.

Table 1: Mean (±SD) concentrations of serum chemistry variables in common eider females at the end of incubation, Söderskär, 1997–1999

	1997 ($n = 12$)		1998 ($n = 16$)		1999 ($n = 15$)	
	Mean ± SD	Min–Max[a]	Mean ± SD	Min–Max[a]	Mean ± SD	Min–Max[a]
Glucose (mmol/L)	9.98 ± 1.46	7.00–12.4	11.51 ± 1.52	9.40–13.9	13.24 ± 2.49	10.0–17.4
Uric acid (μmol/L)	291 ± 143	162–642	418 ± 287	147–1,220	170 ± 59.2	108–330
Creatine kinase (U/L)	220 ± 136	89.0–511	271 ± 164	91.0–672	146 ± 33.2	82.0–201
α-globulins (g/L)	8.02 ± 2.57	4.33–12.7	5.72 ± 2.05	1.87–8.37	7.07 ± 1.78	3.59–9.76

[a] Minimum and maximum values expressed as a range.

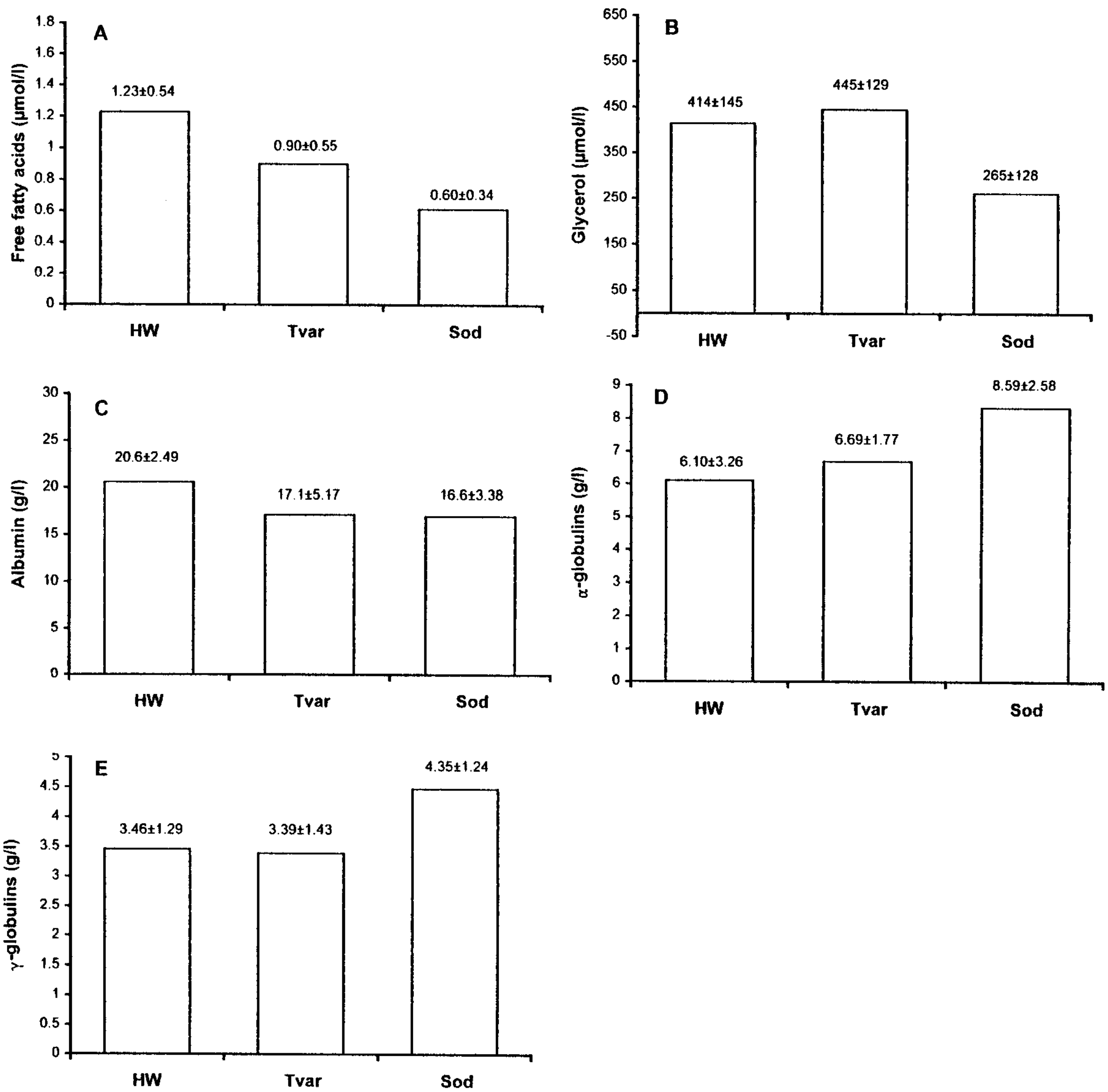

Figure 3. Significant differences of mean (±SD) serum concentrations of free fatty acids (*A*), glycerol (*B*), albumin (*C*), α-globulins (*D*), and γ-globulins (*E*) in incubating common eider females in 1997 among three study sites: Hanko West (*HW*), Tvärminne (*Tvar*), and Söderskär (*Sod*).

in 1997. Gamma globulins declined during incubation in 1997 and 1998 but remained stable in 1999. These differences in globulin concentrations may be associated with variation among the years in the prevalence of and responses to inflammatory diseases in eiders during the incubation fast.

Uric acid is the main end product of protein catabolism and nitrogen metabolism in birds and constitutes 60%–80% of the excreted nitrogen (Lumeij 1997). Impaired renal function can lead to elevations of blood nonprotein nitrogen concentrations but only when renal function is below 30% of its original capacity (Lumeij 1997). During fasting, uric acid concentrations in the blood reflect the changes in protein utilization, and increasing serum concentrations in relation to its daily excretion have been observed during phase 3 of fasting in geese and penguins (Robin et al. 1987, 1988). Serum uric acid concentrations increased in eiders during incubation in 1997 and 1998, suggesting an increasing rate of protein catabolism toward the end of incubation. No such increases were detected in serum uric acid concentrations in 1999, suggesting a more effective protein sparing. Uric acid concentrations of up to 1,220 μmol/L and a higher mean concentration as compared to the other years were detected in the serum of hens at the end of incubation in 1998, further reflecting possible differences in protein utilization among years.

Ingested carbohydrates are digested and hydrolyzed in the gastrointestinal tract, and they function as a major source of energy for feeding animals. During starvation, the maintenance of serum glucose levels depends initially on the breakdown of hepatic glycogen and later on the hepatic and renal gluconeogenesis (Cherel et al. 1988). In fasting birds, glucose is also produced from glycerol and protein-derived amino acids and the blood glucose concentrations generally remain at a constant level (Langslow 1978). Except in 1998, serum glucose levels remained constant in eiders during incubation. Low glucose levels in birds after 24 h of fasting could be explained by inadequate gluconeogenesis or inadequate levels of circulating glycerol and amino acids, and the declining protein levels in eiders during incubation in 1998 may explain their inability to maintain constant serum glucose levels. The mean serum glucose concentrations at the end of incubation were lowest in 1997 and highest in 1999, indicating improvements in glucose balance toward the end of the study period

Mean serum CK activities increased in eiders during incubation in 1998. CK originates from skeletal muscle, cardiac muscle, and brain (Hochleithner 1994), and enzyme activities have also been reported in kidney and, to a small extent, in liver of ducks (Franson et al. 1985). Separation of tissue-specific isoenzymes has not been reported in birds, but muscle tissue is considered the most important source for elevated serum CK activity. Markedly increased CK activities in captured wild animals, including birds, have been attributed to exertional (capture) myopathy (Williams and Thorne 1996). Acute degeneration and lysis of striated muscle cells associated with this syndrome elevate serum CK concentrations in waterfowl to >1,000 IU/L (Bollinger et al. 1989). The mean enzyme activity in the serum of eider hens at the end of incubation at Söderskär was 213 IU/L, which is similar to values (50–200 IU/L) reported in normal captive waterfowl (Bollinger et al. 1989). Furthermore, the capture and handling procedures of eiders were similar each year, and it is unlikely that the elevations in 1998 were caused by capture myopathy. Exercise can elevate serum CK activities in animals, and if the birds were losing their body condition more rapidly during incubation in 1998 than in 1997 and 1999, they may have left their nests more frequently to feed. The increased serum CK activity also may be related to decreased ability to preserve protein, leading to increased muscle wasting during incubation. Serum total protein concentrations decreased during incubation in 1998 and were negatively correlated with CK activities, and muscle atrophy may have been the likely source of increasing enzyme activities in 1998.

Tubular reabsorption of urea in the avian kidney is dependent on the state of hydration, and serum urea concentration can be used as a sensitive indicator of dehydration (Hochleithner 1994). Hypernatremia, hyperkalemia, and hyperchloremia also can be used as indicators of dehydration in birds (Hochleithner 1994). Serum concentrations of urea, sodium, potassium, and chloride remained stable in eider females, suggesting that the birds are able to maintain their hydration level relatively well during incubation.

Site Comparisons: Are There Physiological Differences among the Nesting Habitats?

We found evidence of differences in the nutritional status of the incubating eiders among the study sites, especially between Söderskär and Hanko West, the westernmost site. Mean concentrations of circulating free fatty acids were lower in serum of eiders from Söderskär as compared to Hanko West, and glycerol was lower at Söderskär than at the other sites. These findings suggest that triglycerides were metabolized at a lower rate from stored lipids of birds nesting at Söderskär or that those birds had lower fat reserves. Lower serum albumin levels in eiders nesting at Söderskär may also indicate malnutrition or a higher prevalence of diseases in those birds as compared to the other study areas. Blue mussels are less abundant and smaller in size at Söderskär, and eiders there feed more heavily on clams, amphipods, small fish, and seaweed (Hario et al. 1999). Perhaps the nutrients acquired from the alternative food items are less ideal for foraging eiders.

The finding of higher concentrations of α-globulins and γ-globulins in the blood of females that nest at Söderskär suggests a higher prevalence of inflammatory conditions and perhaps a higher frequency of exposure to infectious agents in this area (Kaneko 1997). Common eider females have been shown to be philopatric (Coulson 1984), an observation confirmed in Finland because the majority of hens return to the same breeding island where they hatched (M. Hario, unpublished observation). Thus, differences observed in γ-globulin levels could potentially reflect differences among the breeding habitats over the life span of the eiders that nest in the same location year after year. During the past decade, the mortality rates of breeding females and ducklings were higher at Söderskär as compared to the more western study sites, and the finding of high immunoglobulin concentrations there suggests that infectious diseases may have been involved.

Conclusions

It has been suggested that, in general, three metabolic phases of long-term fasting exist in mammals and birds (Le Maho 1983), and our results from common eider females during their incubation fast support this hypothesis. Our findings also show evidence of an annual variation in eider intermediary metabolism during incubation that was associated with annual differences in the breeding performance of eiders. During 1997–1999 at Söderskär, the mean clutch size was smallest in

1998, the mean incubation weight of females was lowest in 1998, and the percentage of females that abandoned their newly hatched ducklings was highest in 1998 (Hario et al. 1999; Hario and Kekkinen 2000), all suggesting that a larger portion of females were in poorer than average body condition during that nesting season. In 1998, serum concentrations of total protein, albumin, γ-globulin, and glucose declined, and serum concentrations of creatine kinase and uric acid increased significantly as incubation progressed, suggesting a decreased ability of nesting eiders to preserve proteins that year. The low serum β-hydroxybutyrate concentrations at the end of incubation in 14% and 12% of females in 1997 and 1998, respectively, and the progressive increase in serum concentrations through incubation in 1999 are evidence for annual differences in utilization of lipids. Parker and Holm (1990) estimated that eiders invest 33.8% of total prelaying energy into laying, and in the Gulf of Finland, poor body condition of eider hens in 1998 may have affected clutch sizes and later on their intermediary metabolism during incubation. Differences in the timing of the breeding season probably did not affect the body condition and intermediary metabolism of eider hens, as incubation started within a period of three calendar days in each year of our study. Differences among years at Söderskär cannot be explained by differences in numbers of renesting individuals, as eiders at our study site have not been found to start second clutches after predation (Hario 1983; Hario and Selin 1984). One possible explanation for the variation among years in the intermediary metabolism during incubation is that eiders were already in poorer body condition when arriving at the breeding grounds in 1998.

Serum chemistry analyses also revealed differences among stable and declining eider populations. Lower serum concentrations of free fatty acids, glycerol, and albumin were found in hens nesting in the central Gulf of Finland, where numbers of breeding eiders have declined since the mid-1980s (Hario et al. 1999). Inadequate food resources have been implicated in the decline, and our findings may be associated with an inability of eiders to maintain their fat reserves while feeding on their breeding grounds before egg laying. Furthermore, higher serum concentrations of α- and γ-globulins in eiders in the central Gulf of Finland indicated a higher prevalence of inflammatory diseases in this area. Interactions between nutrition and infectious diseases are highly important for the health of an individual and they generally operate through altered immunocompetence (Klasing 1997). Malnutrition increases susceptibility to infectious diseases, immune responses require energy, and pathology associated with infectious agents may influence the absorption and utilization of nutrients. The body weight of female eiders is at its lowest when their young are hatching (Milne 1976), and the female may then be most vulnerable to diseases, especially in areas such as Söderskär, where food resources may be inadequate for the restoration of body condition. At this time, the females also need to care intensively for the ducklings. In 1997, the breeding success of eiders was better than the average for the previous decade in the central Gulf of Finland. Jalanka (1986) measured serum chemistry variables in eider hens nesting in the same location in the mid-1980s, when the current decline started, and found lower albumin (14 ± 2 g/L) and triacylglycerol (0.72 ± 0.2 mmol/L) levels in eider serum than we found in late 1990s. These differences suggest that we may have found even larger differences among the study sites had we measured serum chemistries in eiders before 1997.

Our results suggest that poor health of eiders during incubation may be a predisposing factor to the female mortality observed in the Gulf of Finland. In addition, females in poor condition may lay poor-quality eggs, be forced to interrupt incubation to feed, be less able to defend their young from predators, and be more prone to transmit infections to their offspring. Thus, the physiological condition of the female may influence the survival of the ducklings, and studies of the health of the eider broods would be useful to better understand the losses of the downy eider young in the Finnish archipelago.

Acknowledgments

We thank P. Byholm, J. Kekkinen, J. T. Lehtonen, M. Öst, H. Selin, and K. Selin for field assistance, K. Selin for assistance with the field data, and T. Pankasalo for assistance with the laboratory analyses. This study was supported by research grants from the Maj and Tor Nessling Foundation and the American-Scandinavian Foundation.

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