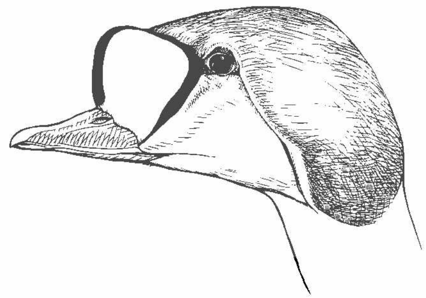
Effects of starvation on muscle and organ mass of King Eiders *Somateria spectabilis* and the ecological and management implications



MICHAEL A. FOURNIER and JAMES E. HINES

In the spring of 1990 we salvaged 21 carcasses of starved King Eiders from the Tuktoyaktuk and McKinley Bay areas of the Northwest Territories. The carcasses were dissected and muscle and organ masses were measured for comparison with shot birds obtained from the Inuit hunters of Holman, N. W. T. Most muscles and organs were significantly smaller in starved birds. The exception was the gizzard which was larger in starved birds. Average mass loss at death was approximately 45% of estimated initial body mass in males and 53% in females. This was reflected in the percent mass loss of individual muscles and organs. Starved females lost an estimated 4% more supracoracoideus mass, 4% more pectoralis mass, 5% more heart mass, 4% more gonad mass, 4% more liver mass, and 8% more intestine length than starved males when compared to their shot counterparts. The amounts and types of materials found in the gizzards of starved eiders varied considerably from that found in the gizzards of shot birds. Periods of starvation, either lethal or sublethal, during spring migration may have a severe impact on King Eider population dynamics.

Keywords: Canada, Ducks, Spring Migration, Cold Weather, Feeding, Populations, King Eider

King Eiders *Somateria spectabilis*, returning along the Beaufort Sea coast to breeding areas in the Canadian western arctic, use restricted areas of open water in the sea ice for resting and feeding. The open water leads of the Cape Bathurst polynya are well developed by April in most years (Stirling & Cleator 1981) and constitute the largest known spring staging area for King Eiders in the region (Barry 1986). Re-freezing of leads or closure due to ice movements may leave eiders unable to feed during critical periods of low temperature.

Starvation of western arctic eiders during spring migration has been recorded on a number of occasions over the past century (Palmer 1976). The phenomenon was first recorded in 1882 by Murdoch (1885) and was most recently observed in the spring of 1990 (this study). King Eiders often represent a large percentage of the carcasses observed during these starvation periods but detailed information has rarely been collected. Some carcass weights were recorded by Barry (1968) and some reconnaissance surveys were undertaken to estimate the number of dead birds (Barry 1968, Myres in Palmer 1976). In 1964 Barry (1968) estimated 100,000 eiders (mostly King Eiders) died, representing approximately 10% of the Canadian western arctic breeding population.

This study was undertaken opportunistically as the result of a natural event, and thus comprised a 'natural' experiment. The objective was to assess the effect of starvation on individual muscles and organs of King Eiders in comparison with samples of shot birds. Secondarily, it is an attempt to provide useful information concerning the ecological and management implications of a potentially catastrophic natural event.

Methods

King Eider carcasses were salvaged from the Tuktoyaktuk (69°27'N, 133°02'W) and McKinley Bay (69°56'N, 131°10'W) areas in the Northwest Territories. Starving eiders were first observed on approximately 7 May 1990 in open ditches in the community of Tuktoyaktuk and in open water surrounding the Canmar oil drilling rig at McKinley Bay (Forsyth pers. comm.).

Eiders are taken infrequently by native hunters in the Tuktoyaktuk-McKinley Bay area. Therefore, the samples of shot King Eiders were obtained from the Inuit hunters of the community of Holman

Table 1. Weights of spring migrant King Eiders from published accounts.

Location	Date	Mean wt. Males	n	Mean wt. Females	n	Source
Hooper Bay Alaska	4-15 May 1924	1832	16	1749	8	Brandt in Palmer 1976
Birnik Alaska	16-26 May 1949-51	1813	8	1653	5	Rausch & Schiller in Palmer 1976
Unknown	Spring	1814	14	1633	9	Nelson & Martin 1953 in Johnsgard 1975
USSR	Spring	1831	?	1748	?	Dement'ev & Gladkov 1967
Birnik Alaska	10-11 May 1958	1765	45	1610	35	Myres in Palmer 1976
Wainwright Alaska	26 May 1958	1908	36	1830	15	Myres in Palmer 1976
Birnik Alaska	10-11 June 1958	1912	27	1836	25	Myres in Palmer 1976
Holman N.W.T.	May-June 1990	1731	14	1828	15	This Study
Holman	May-June 1991	1895	13	1876	15	This Study
Holman	May-June 1992	1801	15	1916	15	This Study

(70°44'N, 117°45'W) approximately 500 km to the east. These samples, assumed to represent normal spring migrants in the Beaufort Sea region (**Table 1**), consisted of 15 males and 15 females per year, collected in 1990, 1991 and 1992. These birds were shot during the traditional spring harvest which occurs during late May and early June.

Birds were frozen and then stored for several months before dissection. After thawing, the carcasses were weighed and the skin and feathers were removed from the abdominal section of the bird. Amounts of subcutaneous and abdominal fat were assessed visually and categorized as none, low, moderate, or high. Pectoralis and supracoracoideus muscles were removed first, followed by the entire gastrointestinal tract, and finally the gonads and kidneys. All fat and connective tissue was removed from organs which were then rinsed clean and patted dry prior to weighing. Gizzards were weighed with and without contents. Large vessels were removed from the heart before weighing. Body mass was measured (1 g) on a beam balance (5 kg capacity). Mass of individual muscles and organs was measured (0.1 g) on a small beam balance (300 g capacity). Intestinal mesenteries were cut and the excised intestines were laid uncoiled on a table and their length was measured (1.0 cm).

Sample sizes for several parameters are not equal among shot samples due to destruction of tissues in some carcasses. However, with the exception of kidney tissue in males shot in 1990 (n=5) all sample sizes of muscles and organs for shot birds range between 13 and 15. Sample sizes of all muscles and organs in starved birds equal 13 for females and eight for males with the exception of the testes (n=7).

Approximate average mass loss at death of the carcass and individual muscles and organs was calculated by averaging the percent differences observed between shot and starved samples. For example, starved males were 43%, 48%, and 45% lighter than males shot in 1990, 1991, and 1992 respectively. The average of these values, 45%, is our reported approximate average mass loss at death for starved males.

Means were compared using an Analysis of Variance (ANOVA) and Duncan's Multiple Range Test (SAS Institute 1985) with P<0.05 level of significance. Means are presented with the corresponding standard error (SE).

Table 2. Weights of starved King Eiders from published accounts.

Location	Date	Mean wt. Males	n	Mean wt. Females	n	Source
Banks Island N.W.T.	1956	1000	1	----	-	Manning et al. 1956
Birnik Alaska	1958	1020	1	----	-	Myres in Palmer 1976
Anderson River N.W.T.	1961	975	4	----	-	Barry 1968
Tuktoyaktuk N.W.T.	1990	992	8	881	13	This Study

Results

Mean mass of starved male King Eiders from this study was similar to other reports, but we found no data on starved females (**Table 2**).

None of the starved birds had any subcutaneous or abdominal fat. Our subjective assessment of fat deposits of shot King Eiders indicated higher levels of fat reserves in both sexes but also an apparent difference between the sexes. In females, 89% were assessed as having high levels of subcutaneous and abdominal fat and 11% were assessed as moderate. In males fat deposits were assessed as high in 58%, mod-

Table 3. Results of Duncan's Multiple Range Test comparisons of muscle and organ measurements of shot and starved male King Eiders.

	Starved Male 1990 Mean±SE	Duncan Grouping	Shot Male 1990 Mean±SE	Duncan Grouping	Shot Male 1991 Mean±SE	Duncan Grouping	Shot Male 1992 Mean±SE	Duncan Grouping
Carcass	992±24	C	1731±41	B	1895±39	A	1801±30	AB
Heart	9.2±0.3	C	15.7±0.4	B	17.1±0.3	A	16.1±0.3	B
Gizzard	38.1±1.4	A	35.1±2.2	AB	31.6±1.2	B	32.1±1.5	B
Liver	19.5±1.5	C	39.6±2.4	A	33.0±1.4	B	34.2±1.1	B
Supracoracoideus	20.2±1.3	B	40.3±1.0	A	41.1±0.8	A	42.8±0.7	A
Pectoralis	111.5±8.2	C	261.2±7.5	B	284.6±5.4	A	288.0±5.5	A
Testes	0.3±0.1	B	3.3±0.5	A	3.5±0.3	A	3.2±0.3	A
Kidney	12.5±0.4	B	15.9±0.6	A	15.9±0.6	A	17.3±0.6	A
Intestine (cm)	145.8±3.8	C	182.9±4.4	A	168.0±3.3	B	165.3±3.0	B

Similar Duncan Groupings indicate no significant difference between means. All indicated differences are significant at $P<0.05$.

Table 4. Results of Duncan's Multiple Range Test comparisons of muscle and organ measurements of shot and starved female King Eiders.

	Starved Female 1990 Mean±SE	Duncan Grouping	Shot Female 1990 Mean±SE	Duncan Grouping	Shot Female 1991 Mean±SE	Duncan Grouping	Shot Female 1992 Mean±SE	Duncan Grouping
Carcass	881±12	C	1828±39	B	1876±18	AB	1916±25	A
Heart	8.1±0.3	C	14.9±0.4	B	15.9±0.3	AB	16.5±0.4	A
Gizzard	31.3±1.0	A	23.1±1.3	C	25.0±0.9	BC	26.2±0.9	B
Liver	18.0±0.6	C	35.4±1.2	A	32.3±0.9	B	35.7±1.2	A
Supracoracoideus	17.6±0.4	C	40.8±0.8	A	37.8±1.0	B	40.9±0.8	A
Pectoralis	96.9±3.2	C	267.9±4.5	B	257.4±4.9	B	282.6±4.5	A
Ova	0.5±0.03	B	10.4±1.4	A	9.3±1.7	A	10.2±1.7	A
Kidney	11.4±0.4	C	14.9±0.6	B	13.7±0.5	B	16.6±0.6	A
Intestine (cm)	136.1±2.4	C	194.1±4.7	A	174.0±4.2	B	166.5±3.3	B

Similar Duncan Groupings indicate no significant difference between means. All indicated differences are significant at $P<0.05$.

Table 5. Frequency of occurrence of gizzard contents in shot (all years) and starved King Eiders.

Gizzard Contents	Starved Males (*n*=8)	%	Shot Males (*n*=45)	%	Starved Females (*n*=13)	%	Shot Females (*n*=45)	%
Sand	8	100	2	4	12	92	1	2
Pebbles	6	75	16	36	13	100	12	27
Plant Material	4	50	0	0	8	62	2	4
Shell Fragments	0	0	40	89	0	0	34	76
Unidentified	0	0	1	2	2	15	2	4
None	0	0	3	7	0	0	9	20

erate in 29%, low in 7% and none in 7%. All of the males with no fat deposits and two of the three males with low fat deposits were shot in 1990. Some of these birds may have experienced a period of starvation.

There were significant differences between shot samples in all measured parameters in at least one comparison (i.e. in at least one sex in one year) (**Tables 3** and **4**). Differences in muscle and organ masses as well as fat deposits may be indicative of significant yearly variation in the body condition of King Eiders arriving at the breeding grounds.

Differences among years in shot birds produced only one significant change in the magnitude of trends observed between shot and starved birds. The gizzard mass of starved males was similar to that of the 1990 shot males (P=0.08) but was higher than that of the 1991 and 1992 shot males (P<0.05).

All muscles and organs measured were significantly smaller in the starved birds with the exception of the gizzards, which were larger in starved birds (**Tables 3** and **4**).

Differences between starved and shot birds were generally greater in females than males. Our results indicate an approximate average mass loss at death of 45% of the average body mass of shot birds in starved King Eider males and 53% in starved females. Starved females, on average, lost 5% more heart mass, 4% more supracoracoideus mass, 4% more pectoralis mass, 4% more gonad mass, 4% more liver mass, and 8% more intestine length than starved males when compared to their shot counterparts. The apparent increase in gizzard mass of starved females was, on average, 10% greater than that observed in starved males.

Gizzard contents differed considerably between starved and shot birds (**Table 5**) both in volume and type of material present. The mean mass of gizzard contents was not different (P=0.67) between starved males and males shot in 1990 but was different between starved males and males shot in 1991 and 1992 (P<0.05). Overall mean mass of contents was 6.2±1.6 g for starved males (n=8) versus 2.5±0.6 g for shot males (n=45). Mean mass of gizzard contents in females was significantly different between starved birds and all shot samples (P<0.01 in all cases) with overall mean masses of 5.5±0.7 g for starved birds (n=13) versus 1.0±0.2 g for shot birds (n=45).

The occurrence of grit (pebbles) in the gizzard was more frequent in starved birds. In addition, the gizzards of a large number of starved birds contained small quantities of fibrous plant material and sand which was uncommon among shot birds (**Table 5**). In two cases the gizzards of starved female eiders contained traces of what appeared to be flakes of marine paint.

Discussion

It is possible that differences in collection dates and locations may have exaggerated or diminished the magnitude of the observed differences between starved and shot birds. Despite this, we believe our comparisons are valid.

Reduction of organ and muscle mass in starving birds may result from direct use of protein and lipid fractions to supply metabolic needs, depletion of stored nutrients such as glycogen, atrophy resulting from reduced use, or some combination of the above.

Differences in muscle mass between shot

and starved birds were large and, on a percentage basis, were exceeded only by differences in gonad mass. The comparatively large muscle mass required for flight provides birds with a large, labile source of readily available nutrients (Kendall *et al.* 1973). In fasting Willow Grouse *Lagopus lagopus* pectoralis muscle is the main organ depleted during starvation, supplying as much as 40% of energy requirements and exceeding mass loss from fat catabolism (Grammeltvedt 1978).

The gizzard was the only organ which showed an increase in mass in starved birds when compared with shot birds. Korschgen (1977) observed a linear increase in the protein content of the gizzards of Common Eiders *Somateria mollissima* with increases in wet weight. Thus, starving King Eiders appear to have directed essential protein to the gizzard, increasing its size and (presumably) its effectiveness at a time when all other organs were being depleted. The only logical explanation for this situation is that birds were attempting to survive on a nutritionally deficient 'starvation' diet consisting of coarse materials. Changes in gizzard mass and the use of grit may result from changes in the texture and fibre content of the diet (Leopold 1953, Lewin 1963, Gardarsson 1971, Moss 1972, Ziswiler & Farner 1972, Pendergast & Boag 1973, Miller 1975, Savory & Gentle 1976, Krapu 1981, Drobney 1977 in Drobney 1982, Kehoe & Ankney 1985, Robel *et al.* 1990) as well as from changes in nutrient storage (Ankney 1977).

Our comparison of gizzard contents between starved and shot birds indicates differences in ingestion of several materials. In general, the gizzards of starved birds contained a higher frequency of sand, pebbles, and plant material while those of shot birds showed a comparatively high frequency of shell fragments. Higher occurrence of plant material in the gizzards of starved birds may or may not be significant. Some studies suggest that King Eiders make use of a mixed diet or a diet of predominantly plant material, when the birds are found in fresh water habitats near nesting areas (Salomonsen 1950-51 and Hanson *et al.* 1956 in Bellrose 1976, Lamothe 1973). Sand, which also had a high rate of occurrence in starved eiders, has been previously observed in the alimentary tracts of American Coots *Fulica americana* and ducks that died of starvation (Trautman *et al.* 1939). However, there is no evidence to suggest that it was present as the result of deliberate ingestion rather than as a byproduct of ingestion of other materials (i.e. potential food items or grit).

Shorter intestine length of starved eiders may appear inconsistent with an attempt to derive nutrients from nutritionally inadequate food items and subsequent increases in gizzard mass. Although some low quality food items were consumed by starving eiders, availability of even these inadequate resources may have been severely limited. Reduced gut lengths in starved eiders are probably a result of reduced levels of feeding, as well as active catabolism of lipid and protein components. Parker & Holm (1990) observed declines of 43% to 64% in intestine weight of Common Eider females during periods of reduced feeding. Fisher (1954) considered intestinal protein to be highly labile during periods of starvation.

Significant differences were observed in the heart muscle of starved King Eiders. Changes in the mass of the heart may result from factors similar to those affecting skeletal muscle, the removal of stored materials and/or atrophy due to reduced activity (Braun 1971, Pendergast & Boag 1973). Starving eiders may have been confronted with a combination of these factors. Nutrients may have been withdrawn necessarily from heart muscle in an attempt to sustain life. A concomitant reduction in skeletal muscle may have left birds with reduced capabilities of diving and flight and thus reduced activity rates.

The liver mass of starved birds was considerably lower than that of shot birds. The liver responds rapidly to dietary changes (Magnan 1913, Hanson 1962, Hazelwood 1972, Pendergast & Boag 1973, Tome 1984). Fisher (1954) reported that the liver provides the most labile protein available during periods of starvation. Parker & Holm (1990) reported a 63% decrease in liver weight between pre-laying and post-laying groups of Common Eider females over only a 4.6 day period. A decrease in liver weight between the egg-laying and incubation periods (a period of fasting) has been observed in a number of species of waterfowl including Lesser Snow Geese *Anser caerulescens* (Ankney 1977), Brant *Branta bernicla* (Ankney 1984), Canada Geese *Branta canadensis* (Raveling 1979), Wood Ducks *Aix sponsa* (Drobney 1982) and

Ruddy Ducks *Oxyura jamaicensis* (Tome 1984).

Differences in the size of the kidneys of starved eiders were of the lowest magnitude observed in any muscle or organ. Jordan (1953) also observed that the kidneys of starving Mallards *Anas platyrhynchos* appeared to be the most resistant to atrophy of all organs measured. These results may be related to the increased functional importance of the kidneys during periods of starvation. Cahill (1978) observed that although, under normal circumstances, the kidney of man provides less than 10% of glucose production, in prolonged starvation the component provided by the kidney increases.

In all cases differences in mass of gonadal tissue between starved and shot birds were higher than in any other organ. Gonadal tissue represents a highly mobile nutrient source for the starving organism (Barry 1962, Grammeltvedt 1978). Alternatively, gonadal development requires an adequate level of nutrient reserves (Korschgen 1977). Thus, either starvation precluded the development of gonadal tissue or nutrients originally utilized for gonad development were removed and directed to another purpose during starvation.

Our data suggest a difference between male and female King Eiders in resistance to starvation. At death, females showed a larger decline from assumed initial body weight than males. Jordan (1953) observed increased resistance to starvation in wild female Mallards with overall mortality rate of males double that of females. Average weight loss of dead male Mallards was 53% of initial body weight while that of females was 56% (Jordan 1953). We observed a larger difference between the sexes with an approximate average mass loss at death of 45% in males and 53% in females. As well, weights of the heart, supracoracoideus, pectoralis, gonads, and liver, and length of the intestine all indicated a proportionally larger decline in King Eider females. Comparison of organ weights lead Jordan (1953) to believe there were differences between the sexes in resistance of organs to weight loss. Higher starvation survival rates of females have been reported for domestic Mallards, Ring-necked Pheasants *Phasianus colchicus*, Ruffed Grouse *Bonasa umbellus* and Wild Turkeys *Meleagris gallopavo* (Latham 1947).

We speculate that larger reserves of nutrients initially, and possibly an enhanced ability to make use of these reserves via physiological mechanisms allows females to withstand food deprivation better than males. Hanson (1962) stated that female Canada Geese probably more readily survive periods of starvation because of superior fat reserves, a result of the lipogenic effect of estrogens. Common Eider females have been observed to go through a period of hyperphagia in the spring, in preparation for breeding, which may result in hypertrophy of organs and hyperlipogenesis (Gorman & Milne 1971, Korschgen 1977). In Greater Snow Geese *Anser caerulescens atlantica*, Boismenu *et al.* (1992) found that the length of time a bird could fast and total mass lost during the fast were correlated with initial fat reserves.

Breeding females of most North American waterfowl decline to their lowest annual mass at or shortly after the hatching period (Alisauskas & Ankney 1992). Extended periods of fasting are experienced annually during incubation and represent a normal phase of the nutritional cycle of females. This may result in sex specific adaptation in ability to withstand starvation.

Ecological considerations and management implications

Freezing temperatures and/or adverse winds, coincident with the spring migration of eiders in the Beaufort Sea region, may present a compound threat to their survival. Decreasing temperatures may increase nutrient requirements to meet metabolic needs while reducing food availability due to re-freezing of open water feeding areas. The length of time King Eiders can survive such conditions is likely directly related to levels of nutrient reserves as well as ambient temperature (Jordan 1953).

The potential impact of lethal periods of food deprivation on King Eider populations is obvious. Unfortunately, data on the numbers of birds involved in this and previous 'starvation events' are largely inadequate. However, Barry's (1968) estimates indicate that the impact can be large and widespread. The low overall fecundity of eiders suggests that such events could not be sustained on a regular basis (Goudie *et al.* in press).

Our data provide some evidence that

sublethal exposure to starvation may also have a significant negative impact upon King Eider populations via its influence on body condition of birds arriving at the breeding grounds. Differences between shot samples suggest that male King Eiders, in the spring of 1990, were in worse body condition than in other years as evidenced by lower levels of abdominal fat and significantly lower total body mass, heart mass, and pectoral muscle mass. A number of factors could account for such differences, including a sublethal period of food deprivation or interrupted migration to breeding areas. Although our data are equivocal for females (there is some indication of superior body condition in the 1992 shot sample but not in the 1991 shot sample, when compared to 1990) it is likely that females could be affected in a similar manner.

Depletion of nutrient reserves in breeding females may produce a significant decline in reproductive performance. There are a number of mechanisms via which this may result, including delayed egg-laying leading to increased susceptibility to predation (Spurr & Milne 1976) or early fall freeze-up (e.g. Barry 1968), reduced clutch size (Milne 1976), reduced nest attendance (Thompson & Raveling 1987, Gloutney & Clark 1991) leading to increased predation, nest desertion (Harvey 1971, Mallory & Weatherhead 1993), death during incubation (Ankney & MacInnes 1978) or death following incubation (Hepp *et al.* 1990). Sea ducks may frequently defer breeding (Bengtson & Ulfstrand 1971, Coulson 1984).

The short arctic summer is unlikely to provide enough time for a bird with significantly depleted nutrient stores to regain the level of body condition necessary to survive the rigors of successful reproduction. Boismenu *et al.* (1992) observed that Greater Snow Geese, after a period of fasting, ate 2.3 times as much food as prior to the fast and recovered only 58% of mass loss after two weeks. Protein requirements for egg-laying by Common Eiders (and presumably also King Eiders) are quite high in comparison with other anatidae which use stored protein reserves (Korschgen 1977, Ankney 1984). Cantin *et al.* (1974) observed a maximum loss of 45% of body mass among incubating Common Eiders. Ankney & MacInnes (1978) observed an 85% and 24% decrease in fat and protein reserves, respectively, in female Lesser Snow Geese during incubation. The costs of reproduction are undoubtedly similar in King Eider females which are believed to feed little, if at all, during the incubation period (Freuchen & Salmonsen in Lamothe 1973, Lamothe 1973).

Starvation of low numbers of King Eiders may be a relatively regular feature of the annual cycle of the species, with long-term population stability maintained by high adult survival. In contrast, en masse starvation may be an irregular and cataclysmic event with severe repercussions on populations for decades. Several consecutive late seasons or a combination of late seasons and a disaster such as a major oil spill could produce a devastating effect upon the Canadian western arctic population of the King Eider. The fact that yearlings tend to migrate later and to different areas than adults and all adults do not arrive simultaneously (Palmer 1977) may reduce the risk of complete devastation. However, other factors such as the low apparent productivity of eiders, the use of restricted areas of open water during migration, and the ever present threat of early fall freeze-up leave this species in a vulnerable position.

It is important that agencies responsible for waterfowl management in North America expend some effort to improve our knowledge of population levels and productivity of this species, as present information is inadequate. Additionally, should another starvation period occur, waterfowl managers should be prepared to initiate surveys to estimate the extent of the die-off and monitor its effects upon reproductive effort and success. Recent declines in other species of eider ducks in the Pacific Northwest (Kertell 1991, Stehn *et al.* 1993) should make us aware of the crucial need for baseline data and on-going monitoring of King Eider populations.

The authors wish to express their sincere thanks to the members of the Hunters and Trappers Association of Holman for their efficiency in providing shot birds. Thanks are also due Dr Ray Alisauskas, Dr Bob Bromley and Dr Ian Goudie for providing valuable comments on drafts of the manuscript.

References

Alisauskas, R.T. & Ankney, C.D. The cost of egg laying and its relationship to nutrient reserves in waterfowl. pp. 30-61 in: B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu. (Eds.). 1992. *Ecology and management of breeding waterfowl.* Univ. of Minnesota Press, Minneapolis.

Ankney, C.D. 1977. Feeding and digestive organ size in breeding Lesser Snow Geese. *Auk* 94:275-282.

Ankney, C.D. 1984. Nutrient reserve dynamics of breeding and moulting Brant. *Auk* 101:361-370.

Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459- 471.

Barry, T.W. 1962. Effects of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19-26.

Barry, T.W. 1968. Observations on natural mortality and native use of Eider Ducks along the Beaufort Sea Coast. *Can. Field-Nat.* 82:140-144.

Barry, T.W. 1986. Eiders of the western Canadian Arctic. pp. 74-80 in: A. Reed (Ed.). *Eider ducks in Canada.* Can. Wildl. Serv. Rept. Ser. No. 47.

Bellrose, F.C. 1976. *Ducks, geese and swans of North America.* Stackpole Books, Harrisburg, PA, and Wildlife Management Institute, Washington, DC, USA.

Bengston, S.A. & Ulfstrand, S. 1971. Food resources and breeding frequency of the Harlequin Duck *Histrionicus histrionicus* in Iceland. *Oikos* 22:235-239.

Boismenu, C. Gauthier, G. & Larochelle, J. 1992. Physiology of prolonged starvation in Greater Snow Geese (*Anser caerulescens atlantica*). *Auk* 109:511-521.

Braun, C.E. 1971. Seasonal trends in body fat of White-tailed Ptarmigan. *Env. Ecol. Soc. Amer.* 52:44.

Cahill, G.F., Jr. 1978. Famine symposium - physiology of acute starvation in man. *Ecol. Food Nutr.* 6:221-230.

Cantin, M., Bedard, J. & Milne, H. 1974. The food and feeding of Common Eiders in the St. Lawrence estuary in summer. *Can. J. Zool.* 52:319-334.

Cherel, Y., Robin, J.P. & LeMaho, Y. 1988. Physiology and biochemistry of long-term fasting in birds. *Can. J. Zool.* 66:159- 166.

Coulson, J.C. 1984. The population dynamics of the Eider Duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis* 126:525-543.

Dement'ev, G.P., & Gladkov, N.A. (Eds.). 1967. *Birds of the Soviet Union.* Vol. IV. Israeli Program for Scientific Translation. Jerusalem.

Drobney, R.D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. *Condor* 84:300-305.

Fisher, R.B. 1954. *Protein metabolism.* Methuen and Co. London. 198 pp.

Gardarsson, A. 1971. *Food ecology and spacing behavior of Rock Ptarmigan (Lagopus mutus) in Iceland.* Ph.D. dissertation, Univ. Calif., Berkley. 382 pp.

Gloutney, M.L. & Clark, R.G. 1991. The significance of body mass to female dabbling ducks during late incubation. *Condor* 93:811-816.

Gorman, M.L. & Milne, H. 1971. Seasonal changes in the adrenal steroid tissue of the Common Eider *Somateria mollissima* and its relation to organic metabolism in normal and oil-polluted birds. *Ibis* 113:218-228.

Goudie, R.I., Conant, B., Kondratev, A.V., Petersen, M. & Vermeer, K. 1994 (in press). The status of sea ducks in the north Pacific Rim: toward their conservation and protection. *Trans. North Am. Wildl. Nat. Res. Conf.* 59.

Grammeltvedt, R. 1978. Atrophy of a breast muscle with a single fibre type (*M. pectoralis*) in fasting Willow Grouse *Lagopus lagopus L. J. Exp. Zool.* 205:195-204.

Hanson, H.C. 1962. The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arct. Inst. Tech. Pap.* 12. 68 pp.

Harvey, J.M. 1971. Factors affecting Blue Goose nesting success. *Can. J. Zool.* 49:223-234.

Hazelwood, R.L. 1972. The intermediary metabolism of birds. in: D.S. Farner & J.R. King (Eds.). *Avian Biology.* Vol. 2. Academic Press, New York. 612 pp.

Hepp, G.R., Kennamer, R.A. & Harvey, W.F. 1990. Incubation as a reproductive cost in female Wood Ducks. *Auk* 107:756-764.

Johnsgard, P.A. 1975. *Waterfowl of North America.* Indiana Univ. Press, Bloomington. 575 pp.

Jordan, J.S. 1953. Effects of starvation on wild Mallards. *J. Wildl. Manage.* 17:304-311.

Kehoe, F.P. & Ankney, C.D. 1985. Variation in digestive organ size among five species of diving ducks (*Aythya* spp.). *Can. J. Zool.* 63:2339-2342.

Kendall, M.D., Ward, P. & Bacchus, S. 1973. A protein reserve in the pectoralis major flight muscle of *Quelea quelea. Ibis* 115:600-601.

Kertell, K. 1991. Disappearance of the Steller's Eider from the Yukon-Kuskokwim Delta, Alaska. *Arctic* 44:177-187.

Korschgen, C.E. 1977. Breeding stress of female Eiders in Maine. *J. Wildl. Manage.* 41:360-373.

Krapu, G.L. 1981. The role of nutrient reserves in Mallard reproduction. *Auk* 98:29-38.

Lamothe, P. 1973. *Biology of King Eider* (Somateria spectabilis) *in a freshwater breeding area on Bathurst Island N.W.T.* MSc. Thesis, Univ. Alberta.

Latham, R.M. 1947. Differential ability of male and female game birds to withstand starvation and climatic extremes. *J. Wildl. Manage.* 11:139-149.

Leopold, A.S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. *J. Wildl. Manage.* 17:197-203.

Lewin, V. 1963. Reproduction and development of young in a population of California Quail. *Condor* 65:249-278.

Magnan, A. 1913. Variations experimentales en fonction du regime alimentaires. *Ann. Sci. Nat. Zool.* 19:115-225.

Mallory, M.L. & Weatherhead, P.J. 1993. Incubation rhythms and mass loss of Common Goldeneyes. *Condor* 95:849-859.

Maloney, S.K. & Dawson, T.J. 1993. Sexual dimorphism in basal metabolism and body temperature of a large bird, the Emu. *Condor* 95:1034-1037.

Manning, T.H., Hohn, E.O. & MacPherson, A.H. 1956. The birds of Banks Island. *Natl. Museum of Canada Bull.* 143. 144 pp.

Miller, M.R. 1975. Gut morphology of mallards in relation to diet quality. *J. Wildl. Manage.* 39:168-173.

Milne, H. 1976. Body weights and carcass composition of the Common Eider. *Wildfowl* 27:115-122.

Moss, R. 1972. Effects of captivity on gut lengths in Red Grouse. *J. Wildl. Manage.* 36:99-104.

Murdoch, J. 1885. Birds. in: P.H. Ray (Ed.). *Report of the international polar expedition to Point Barrow, Alaska.* Gov. Printing Off., Washington. 695 pp.

Palmer, R.S. 1976. *Handbook of North American birds.* Vol. 2, Waterfowl. Yale Univ. Press, New Haven Connecticut. 560 pp.

Palmer, R.S. 1977. King Eider studies. *Brit. Birds* 70:107-113.

Parker, H. & Holm, H. 1990. Patterns of nutrient and energy expenditure in female Common Eiders nesting in the high arctic. *Auk* 107:660-668.

Pendergast, B.A. & Boag, D.A. 1973. Seasonal changes in the internal anatomy of Spruce Grouse in Alberta. *Auk* 90:307-317.

Raveling, D.G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* 96:234-252.

Robel, R.J., Barnes, M.E., Kemp, K.E. & Zimmerman, J.L. 1990. Influences of time post-mortem, feeding activity and diet on digestive organ morphology of two emberizids. *Auk*:107:669-677.

SAS Institute Inc. 1985. *SAS/STAT guide for personal computers*. 6th ed. SAS Institute Inc., Cary, NC.

Savory, C.J. & Gentle, M.J. 1976. Changes in food intake and gut size in Japanese Quail in response to manipulation of dietary fibre content. *Br. Poult. Sci.* 17:571-580.

Spurr, E.B. & Milne, H. 1976. Factors affecting laying date in the Common Eider. *Wildfowl* 27:107-109.

Stehn, R.A., Dau, C.P., Conant, B. & Butler, W.I. Jr. 1993. Decline of Spectacled Eiders nesting in western Alaska. *Arctic* 46:264- 277.

Stirling, I. & Cleator, H. 1981. *Polynyas in the Canadian Arctic*. Can. Wildl. Serv. Occ. Pap. No. 45. 72 pp.

Thompson, S.C. & Raveling, D.G. 1987. Incubation behaviour of Emperor Geese compared with other geese: Interactions of predation, body size and energetics. *Auk* 104:707-716.

Tome, M.W. 1984. Changes in nutrient reserves and organ size of female Ruddy Ducks breeding in Manitoba. *Auk* 101:830-837.

Trautman, M.B., Trautman, B., Bills, W.E. & Wickliff, E.L. 1939. Winter losses from starvation and exposure of waterfowl and upland game birds in Ohio and other northern states. *Wilson Bulletin* 51:86-104.

Ziswiler, V. & Farner, D.S. 1972. Digestion and the digestive system. pp. 343-430 in: D.S. Farner and J.R. King (Eds.). *Avian Biology*. Vol. 2. Academic Press, New York.

Michael A. Fournier and Dr. James E. Hines, Canadian Wildlife Service, PO Box 637, Yellowknife, Northwest Territories, Canada. X1A 2N5.