An Inferred Sex Differential in Copper Metabolism in Ross' Geese (*Anser rossii*): Biogeochemical and Physiological Considerations

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ABSTRACT. The geology and the levels of various minerals in the nutrient chain of the ecosystems of the breeding grounds of most populations of wild geese are distinctive. Hence minerals that become incorporated in the keratin of the primary feathers grown on the breeding grounds can be used as biological tracers to determine origins of migrants. Hormones indirectly affect the levels of some minerals in the feather keratin. Estrogen is presumed to account for higher levels of copper found in the primary feathers of adult female, as compared with adult male, Ross' geese (*Anser rossii*).

RÉSUMÉ. *Sur une différence selon le sexe dans le métabolisme du cuivre chez l'oie de Ross* (Anser rossii): *considérations biogéochimiques et physiologiques*. Dans la chaîne alimentaire des écosystèmes des terrains de reproduction de la plupart des peuplements d'oies sauvages, la géologie et les niveaux des divers minéraux sont distinctifs. Les minéraux incorporés dans la kératine des premières plumes qui poussent sur ces terrains peuvent donc servir de "traceurs" biologiques pour déterminer l'origine des migrants. Les hormones affectent indirectement les niveaux de certains minéraux dans la kératine des plumes. On suppose que l'estrogène explique les niveaux plus élevés de cuivre trouvés dans les premières plumes de la femelle adulte, en comparaison avec le mâle adulte, chez l'oie de Ross (*Anser rossii*).

РЕЗЮМЕ. *Половые отличия в метаболизме гуся Росса* (Anser rossii): *биогеохимический и физиологический подход*. Содержание различных минералов в цепи питания большинства популяций диких гусей имеет характерные особенности. Следовательно, анализ минералов, входящих в состав кератина маховых перьев первого порядка, может быть использован как биологический индикатор для определения происхождения мигрантов. Гормоны могут косвенно воздействовать на содержание ряда минералов в кератине перьев. У самок гуся Росса (Anser rossii) обнаружено более высокое, чем у самцов, содержание меди в маховых перьях первого порядка, что очевидно обусловлено эстрогеном.

INTRODUCTION

The capacity of keratins, particularly hair and wool, to reflect variations in dietary intake of trace elements is well known (Schwartz 1960; Underwood 1971; Weiss, Whitten and Leddy 1972); perhaps less widely realized is the sensitivity of feather keratin in reflecting the minerals in the ecosystem in which a bird lives. On the basis of a report that variations in the mineral content of the feathers of ruffed grouse *(Bonasa umbellus)* in New Hampshire reflected major geological provinces in the state (McCullough and Grant 1951), we initiated an extensive study of the mineral content of the primary feathers of the wings of North American wild

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geese for the purposes of determining the origins of migrant and wintering populations (Hanson and Jones 1968). Since the inception of our studies in 1965, the primaries of over 3,000 wild geese have been analysed. However, data on sex were available only for the samples of Ross' geese discussed here, and only these were from a sufficiently restricted area as to permit valid comparison of the sexes.

Wild waterfowl lend themselves particularly well to the determination of origins from the mineral patterns of feathers, because the flight feathers of these birds are almost wholly grown while they are on their breeding grounds; in this respect, blue and snow geese *(Anser caerulescens)* and Ross' geese *(Anser rossii)* are especially advantageous populations to study, as the great majority of individuals nest in discrete colonies in widely separated areas of the North American Arctic. Although some of the colonies are located on areas underlain by similar limestones of Palaeozoic age, each of these breeding grounds has been subjected to glacial and drainage influences from adjacent areas of Precambrian rock, and some by marine inundation during recent time with resultant differences in the mineral profile of their soils and plants. These differences in the nutrient chain are in turn reflected in the mineral profile of the flight feathers, making it possible to determine the origins of the various populations. Excepted from this statement are male ducks of many species and the yearlings and nonbreeding segments of some populations of geese which may make a moult migration to points distant from breeding grounds.

Most of the known populations of Ross' geese nest in a 185-mile wide and 84-mile deep zone south of Queen Maud Gulf on the Canadian mainland (Ryder 1969) which is indicated in Fig. 1.

MATERIALS AND METHODS

The 20 sets of primary feathers of Ross' geese from Karrak Lake (67° 14′ N., 100° 14′ W.) analysed for the present study were taken from a series of adults collected between 15 June and 9 July, 1968, on their return to their nesting islands. In addition to the above sample, flight feathers of 11 adult Ross' geese were collected by Hanson in November 1969 at Tule Lake National Wildlife Refuge, California, from birds shot by hunters.

With respect to their nutritional experience the previous summer while growing flight feathers, the sample of Ross' geese from Karrak Lake can be regarded as unusually homogeneous. This assessment is attributed to the fact that geese tend to return with exceptional fidelity to their birth places or breeding areas; some females may even use their same nest scrapes of the previous year. After the eggs hatch, the adults and broods spread out over the surrounding tundra, although their movements may tend to be in a direction downstream towards the coast.

Analytical procedures have been described elsewhere (Hanson and Jones 1968). In brief, only the vane portions of primary feathers were analysed, about one gram of oven-dried sample being adequate. Prior to weighing and trimming off the vane portions, transverse clippings of the whole feathers were washed by shaking in 250 ml. conical flasks three times for one-hour in distilled water with intervening

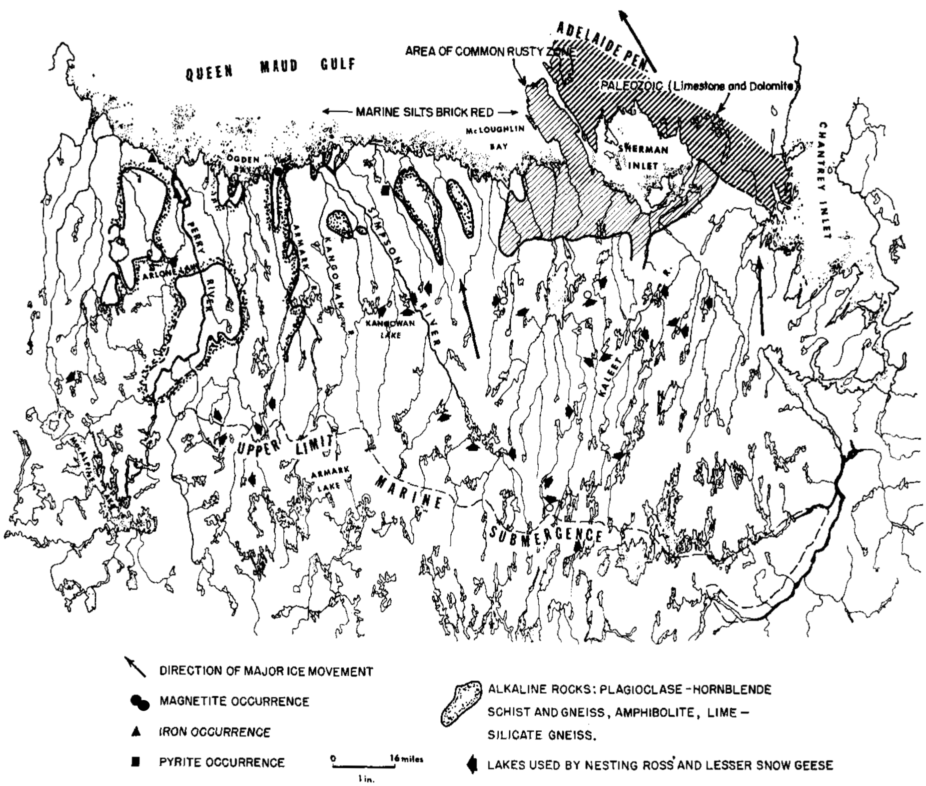

FIG. 1. Geological setting of the colonies of nesting Ross' geese in the Queen Maud Gulf Lowlands (after Ryder 1969). Karrak Lake is named Kangowan Lake on this map. Acid rocks, mostly granites, occupy the area not indicated by the stipple convention for alkaline rocks (i.e., not shown completely between contacts). Geology drawn from Craig (1961), Heywood (1961) and Fraser (1964).

rinses, and the flasks and contents then drained of excess water and dried in an oven held at 60° C for at least 24 hours. The vane portions were ashed at 500° C in a muffle furnace, and then analysed with a direct-reading Jarrell-Ash optical emission spectrograph. Contents of copper were estimated from plant standards, the matrix or composition of which was similar to that of feathers.

RESULTS

The findings of the copper content of two samples of primary feathers of Ross' geese are summarized in Table 1. The sex differential in mean copper levels of the Karrak Lake birds is highly significant ($P<.001$) and significant at the five per cent level for the California sample. The exact origin of the random sample of Ross' geese shot in California is unknown; however, it is highly probable that they summered in the Queen Maud Gulf lowlands. Inasmuch as this extensive breeding-ground varies considerably geologically, it is notable that this second sample of primaries of Ross' geese also exhibits a significant sex differential in copper content.

TABLE 1. Copper content of the vanes of primary feathers of adult Ross' geese collected at Karrak Lake, N.W.T., and at Tule Lake National Wildlife Refuge, California.

Area of collection	Sex	No.	Mean (p.p.m.)	SD	Range	P
Karrak Lake, N.W.T.	M	10	17.8 ± 0.7	2.1	13 - 20	< .001
Karrak Lake, N.W.T.	F	10	27.1 ± 2.1	6.6	18 - 39	
Tule Lake, N.W.R., California	M	5	10.2 ± 1.2	2.6	7 - 13	< .05
Tule Lake, N.W.R., California	F	6	14.2 ± 1.3	3.2	11 - 18	

DISCUSSION

Our findings on blue and lesser snow geese have indicated that as high as 85 per cent of samples of these geese of unknown origin can be identified by means of the discriminate function test and the aid of a computer, using as reference the mineral patterns of wing feathers of geese banded on their breeding grounds. In the case of Canada geese (*Branta canadensis*) 92 per cent of 388 individuals representing 17 races were correctly identified on the basis of the mineral patterns of their flight feathers (Hanson and Jones 1974). It is therefore evident that the pattern of minerals in feathers of geese reflects the nutrient chain in the ecosystem in which they grew their flight feathers. Because comparison of the mineral profile from feathers of adult and immature blue and lesser snow geese from the same area revealed few important basic differences, it can also be concluded that adult birds returning from their wintering grounds do not carry over a labile pool of mineral elements that distorts or masks the pattern of intake of minerals obtained on the breeding grounds. Evidently the 40-50 day period spent on the breeding grounds prior to the moult (in the case of Ross' geese) is sufficient time for a turnover of any labile component of body minerals ingested south of the breeding grounds, and this "transported metabolic pool" has only a trivial effect, or none at all, on the feather mineral profile.

Geology and soils

No account of the soils or detailed description of the bedrock geology exists for the immediate Karrak Lake area. The geology of the Queen Maud Gulf area has been described briefly by Queneau (in Hanson *et al.* 1956), Heywood (1961) and Fraser (1964). The latter two reports are reconnaissance reports of the Canadian Geological Survey that are accompanied by geologic maps based on observations made along transects spaced at 6-mile intervals. The surficial geology of the northern portion of the Keewatin District has been described by Craig (1961).

The bedrock of the area to the south of Queen Maud Gulf is composed chiefly of massive crystalline rocks of the Canadian Shield, particularly granite and gneissic granite (Heywood 1961), but includes scattered pods and zones of calcium-rich metamorphic rocks ranging from plagioclase-hornblende gneisses and schists to amphibolites (see Fig. 1). Outcrops of limestones and dolomites of Ordovician and Silurian ages, and perhaps Cambrian age, occur to the east on

Adelaide Peninsula. Copper-bearing rock was first reported from the region by Queneau (in Hanson *et al.* 1956) and at the present time the general region is undergoing active mineral exploration.

The zone of lakes used by nesting Ross' geese falls within the area of marine submergence which extends 80 miles inland from the coast (see Fig. 1). Old beach ridges are prominent on coastal hills. The sediments of the region are silty or clay-rich and contain pebbles and, locally, range in thickness up to 300 feet along the Arrowsmith River south of Pelly Bay.

The soils fall within the general and rather nondescript classification of Arctic soils (Ellis 1960). These soils exhibit little development in the sense that horizons typical of temperate regions are practically absent except for the accumulation of a thin organic horizon. Where the plant cover is well developed, vegetation serves to insulate the soil and permafrost occurs near the soil surface. Sometimes in soils developed in unconsolidated fine-textured parent materials a thin zone of grey colour occurs overlying the permafrost; the colour reflects the occurrence of reducing conditions.

The anomalous copper background values in the soils of the nesting area are most likely associated with basic rocks occurring in the granitic terrain of the region. Vinogradov (1959) gives an average value of 200 p.p.m. as an average content for copper in basic igneous rocks, in contrast to 10 to 100 p.p.m. in acid igneous rocks. He also points out the ability of copper to diffuse from ore bodies into overlying soils, although this characteristic would not appear important enough to account for the moderately high values in the ecosystem at Karrak Lake. It would seem more likely that a rich and local copper source at, or very near, the surface has been eroded by glacial ice and admixed in the till of the principal nesting area that is otherwise a reflection of glacial erosion of granitic rocks.

The chemistry of copper in soil is intimately associated with organic matter (Stevenson and Ardakani 1972). Copper has been consistently found to have the highest stability constant among the transition series elements, a commonly-determined sequence being copper, nickel, cobalt, zinc, iron and manganese. Insoluble copper-organic matter complexes tend to accumulate in the surface horizon, giving the organic horizon the largest content of copper of any of the soil's horizons. This high affinity of organic matter for copper can decrease the soil's supplying power of this element to the extent that the element is limiting for plant growth. Many northern areas where agricultural exploitation of peat or muck soils has been attempted need supplemental applications of copper in order to be made productive. These remarks are given to suggest that if cupriferous rocks occur in the Karrak Lake area, the overlying soils, largely organic in nature, would have elevated copper contents in their organic horizon. Although considerable competition between the plant root and soil organic ligands would exist for this copper, somewhat elevated levels of copper would be expected in the sedge and grass flora consumed by geese; however, Cannon (1960) in her review of biogeochemical prospecting recorded that relationships between copper content of vegetation and copper-bearing ore bodies were not consistent. In the case of geese their grazing and browsing habits also bring them in contact with soil and, on occasions, fairly large amounts are ingested.

Copper levels in plants

In plants, copper "occurs as neutral or anionic complexes that are absorbed more readily than ionic copper" (Van Campen 1971), being associated primarily with several enzyme systems (Epstein 1972). The copper content of the aerial parts of grasses is fairly constant, but may vary 30-fold (1-30 μg./gm.), differences being attributed in part to the content and availability of copper in soils (Adelstein and Vallee 1962).

Similarly, we have found a 28-fold variation in the copper content of the primary feathers of blue and snow geese (8-10 p.p.m. to 225 p.p.m.). However, variation in copper levels within most populations of wild geese seldom exceeds four-fold.

Bowen (1966) cites a value of 14 p.p.m. as average for land plants. We do not have plant samples from the area around Karrak Lake or from cupriferous soils in other Arctic settings. However, we have analysed plant samples from granitic terrains on the west coast of Hudson Bay at, or near, the mouths of the McConnell, Seal and Caribou rivers. Sedges (*Carex* sp.) growing in sediments of the flood plains of these rivers ranged from 5 to 10 p.p.m. and averaged 8.2 p.p.m. copper. A sample of cotton grass (*Eriophorum* sp.) and an unidentified sedge collected along Caribou River contained 6 p.p.m. copper. We assume that these levels fairly represent the dietary intake of geese throughout the Canadian Arctic where similar rocks occur. In this regard, 38 snow geese that had been banded around the mouth of the McConnell river and subsequently shot elsewhere had an average of 10.6 p.p.m. of copper in the vanes of primary feathers (Hanson and Jones 1974). This fact suggests that the copper content of the plants in the Karrak Lake area may be several times greater than that found in plants along the west coast of Hudson Bay. The vanes of the primaries of one wild goose studied contained 225 p.p.m. of copper. Copper concentrations in the nutrient chain of its breeding grounds can only be surmised.

Copper in hair

Arthur (1965) found that copper in guinea pig (*Cavia porcellus*) hair was indicative of copper levels adjusted in the diet. Petering *et al.* (1971) have recently observed distinctly higher contents of copper in human hair of females as compared to that of males in age classes above 30 years. They found that copper content in male hair increases annually between 2 and 10 years of age, but beyond about 12 years of age it declines until it is equal (20 p.p.m.) to that in female hair at about 30 years of age, whereas in female hair there is a small steady increase with age. Speculation was made regarding differential needs and availability of copper between sexes, and the apparent influence of puberty in the case of males, but no biochemical mechanism was identified.

Physiological considerations

In fowl (*Gallus domesticus*) copper becomes bound to a protein in the duodenal mucosa, the rate of binding there being five times greater than from the proventriculus (Hudson, Levin and Smith 1971). Similarly, in mammals, binding rates are most rapid in the duodenal section of the intestine (Van Campen 1971), and over 90 percent of the copper in mammalian plasma is associated with alpha-2 globulin ceroluplasmin (Adelstein and Vallee 1962), but the copper bound to serum albumin is believed to be the exchangeable copper transferable across cell membranes (Van Campen 1971). A third form of serum copper — that bound to amino acids — has been recognized (Sarkan and Kruck 1965). Presumably, it is from the latter two fractions of plasma copper that copper is transferred to the feather follicle — or possibly one or both molecules are bound to the forming keratin. It is of particular interest to note that Hoffman (1964) believes that, because copper is not easily removed from alpha-2 globulin, its function is "apparently not to transport copper, but rather to limit the amount of copper deposited in the tissues." In this respect feather keratin functions in a parallel, although perhaps an adventitious, way. In the case of Wilson's disease, however, alterations in copper homoeostasis are believed by Evans *et al.* (1973) to "result from the synthesis of an abnormal metal-binding protein with an increased affinity for copper."

According to Van Campen (1971), the mechanism that regulates copper absorption is not known: "There is little evidence that copper absorption from the intestine is regulated according to need as in the case of iron." Van Campen believes that absorption involves at least two mechanisms: "When copper concentrations in the gastrointestinal tract are low, absorption exceeds what should be expected on the basis of concentration; however, as the intestinal copper level is increased, absorption appears to become proportional to concentration." From these findings it must be concluded that excretion is the chief means of maintaining some semblance of homoeostasis for animals on a high dietary intake of copper. Although the liver and bile are probably the primary storage depot and excretion route for excess copper in the case of moulting geese, it appears that the feather keratin constitutes an additional disposal route of excess levels of dietary copper.

Underwood (1971) states: "There are no significant sex differences in whole blood or plasma copper in most species, but plasma copper is higher in human females than in males." This difference can, presumably, be attributed to the ability of estrogens to increase the copper binding capacity of the plasma albumins. In this connection it should be noted that scarcely significant amounts of estrogen (less than 5 picograms) are found in plasma samples from intact male white leghorn chickens as compared to less than 25 picograms per c.c. in the incubating hen and to over 700 picograms in some laying hens (Peterson and Common 1972).

Although gonadal tissues of geese of both sexes atrophy rapidly during the incubation period, the differentially higher levels of copper in the feathers of females must presumably reflect significantly higher levels of residual estrogens in adult females during the post-breeding moult as compared with other periods of the year (the period of the first half ovulatory cycle excepted). Differentially higher storage levels of copper in the livers of females at the onset of moult may also play a role in its availability during the moult. In humans, copper level in plasma increases during pregnancy. As might be expected, the administration of estrogen markedly increases serum copper and ceruloplasmin concentrations

(Adelstein and Vallee 1962; Underwood 1971; Van Campen 1971).

A more specific functional reason for higher copper levels in female Ross' geese is that copper has been implicated in shell membrane formation in fowl "by evidence that the mucosa of the isthmus contains much more copper than any other portion of the oviduct (Moo-Young *et al.* 1970). Such a heavy endowment of Cu^{++} reflects the activity of the isthmus mucosa in forming the keratin-like components of the shell membranes. Disulphide linkages are characteristic of keratin, and the oxidative closure of sulphhydral groups is regulated by cuproenzymes, much as elastin synthesis may be mediated by amine oxidase" (Hazelwood 1972).

CONCLUSIONS

We conclude that the sex differential observed in copper content of Ross' geese feathers results from unusually high levels of copper in the environment and the direct mediation of estrogens in increasing copper binding capacity of plasma proteins. This pool of copper is incorporated, to some degree, in feather keratin.

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