MOULT CHARACTERISTICS AND HABITAT SELECTION OF POSTBREEDING MALE BARROW'S GOLDENEYE *(BUCEPHALA ISLANDICA)* IN NORTHERN YUKON

by

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ABSTRACT

I investigated the moult characteristics and habitat selection of postbreeding male Barrow's Goldeneye on the Old Crow Flats, Yukon Territory, during the summers of 1995 and 1996. A total of 438 birds were captured and measured during remigial moult in 1995; 61 birds were recaptured and remeasured to determine body weight changes and remigial growth rates. Philopatry to the Old Crow Flats and to individual lakes was observed. Growth rates of the ninth primary were similar for adult and immature birds, remained constant, and were not affected by the date remigial moult began. In general, adult and immature birds maintained or gained body weight during the early stage of remigial moult, then lost body weight as moult advanced. The body weight of adults decreased significantly during remigial growth. Change in body weight was not affected by a bird's age or by differences between lakes. Heavier birds had significantly greater ninth primary growth rates and declines in body weight than lighter birds suggesting that body reserves may be used to increase the rate of moult and, as a result, decrease the flightless period. The flightless period lasted 27 - 34 days, excluding the preshedding interval. Remigial moult extended from early July to mid-September, with the peak of moult occurring between 20 July and 23 August.

Barrow's Goldeneye did not favor large lakes over small lakes but a significant positive relationship between number of birds and lake productivity was observed. Two explanations for this relationship are proposed: (1) goldeneye choose productive lakes to obtain abundant food, and/or (2) high densities of goldeneye enhance lake productivity via nutrient recycling. Results of this study support the theory that loss of body weight during remigial moult is an adaptive strategy used to regain flight sooner: I propose that

Barrow's Goldeneye migrate to the Old Crow Flats to obtain abundant food and to avoid predators and disturbance (macro-habitat strategy) and select lakes that satisfy food requirements (micro-habitat strategy).

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INTRODUCTION

Feathers are an attribute unique to birds and serve many functions. Their chief functions are to protect the body from temperature changes and to provide flight (Welty and Baptista 1990). Flight allows birds to migrate, exploit resources and escape life-threatening situations. Plumage can provide cryptic colouration for protection against predators and distinctive colouration for species recognition and courtship. However, feathers become worn and damaged and must be periodically replaced (a process referred to as 'moult'). Moult is a productive process which requires substantial energy and nutrients for the synthesis of new feathers and other associated products (Murphy 1996).

Determining the energetic cost of feather synthesis has been difficult partly because the process of moult interacts with other metabolic processes. For example, loss of feathers can decrease the insulative ability of the plumage and thus increase thermoregulatory costs but these costs can differ depending on the intensity of moult. Schieltz and Murphy (1997) found that air temperatures below a lower critical temperature did not increase thermoregulatory costs for White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) unless they were replacing more than 24% of their plumage. The nitrogen content of the plumage does not appear to vary greatly among species (Hohman et al. 1992) thus the energy content of avian plumage may be estimated to be 22 kJ/g dry mass, based on studies of the White-crowned Sparrow (Murphy and King 1982). Energy and nutrient demands required for feather synthesis and other metabolic process associated with moult may be met by (1) foods consumed in the diet, (2) endogenous reserves, (3) alteration in the timing, rate and/or pattern of moult so that requirements match nutrient availability, or (4) a combination of the above adjustments (Murphy and King 1982). As well, changes in behavior, such as reduced time spent active, can reduce daily energy expenditure and thus partially compensate for the energy demands of moult (Murphy 1996). Thompson (1979) determined that Canvasbacks (*Aythya valisineria*) spend more time resting during wing moult than at other times during the postbreeding period. Similarly, Brown and Bryant (1996) found that the mean daily energy expenditure of dippers (*Cinclus cinclus*) was lower during moult than at any other time during the annual cycle.

Knowledge of the extent, rate, duration and timing of moult in a species can help to evaluate the nutritional challenge of moult on a bird (Murphy 1996). Because moult generally does not overlap with other energetically demanding events such as reproduction and migration, some researchers suggest that moult may be nutritionally too costly to be compatible with other events in the annual cycle ("staggered costs" hypothesis; Lovvorn and Barzen 1988). However, some birds do overlap moult with either reproduction or migration which indicates that these events can be energetically compatible (see Payne 1972). Even if moult is separated from other events in the annual cycle this does not necessarily indicate that the events are not energetically compatible. For instance, Brown and Bryant (1996) determined that moult did not elevate basal metabolic rate or daily energy expenditure in dippers and suggested that the timing of moult was not constrained by the energetic costs of feather synthesis. Departures from the separation of events may be attributed to pressures of time, shortages of energy, or may originate from differences in mating or social systems (King 1974). Variability in the relationships between moult, breeding and migration among species suggests that each species has evolved a moult strategy that is best suited to its own annual cycle and the environmental conditions in which it lives.

Feather development

Each feather grows from a region of actively growing cells (papilla) at the base of a feather follicle. When it emerges from the follicle, the new feather is enclosed in a protective waxy sheath and is referred to as being 'in pin' (Ginn and Melville 1983). As the feather continues to grow its tip ruptures the end of the sheath and the barbs spread out to form the vane. The sheath remains around the lower part of the feather until it stops growing, the feather during this stage is described as 'in sheath' (Ginn and Melville 1983). The protective sheath then splits open and flakes away or is preened off, releasing the mature feather. A small remnant of the papilla remains at the base of the follicle after the feather has matured (Welty and Baptista 1990). If a feather is accidentally removed the follicle will regenerate a new one to replace it, but otherwise the follicle remains inactive until the next normal moult. At the proper time for moulting, the reactivated follicle grows a new feather that pushes out the older feather above it (Welty and Baptista 1990).

Moult in waterfowl

Birds use flight to find food and escape predators so the moult of flight feathers must not severely impair flight capabilities. Thus, most birds moult their flight feathers sequentially so that they are not rendered flightless. In contrast, waterfowl can find food and escape predators without flying and have evolved a simultaneous wing moult

(Hohman et a. 1992) which involves a period of flightlessness. Waterfowl make various adjustments to minimize the energetic and nutritional costs associated with moult, and to decrease the risks associated with flightlessness.

In general, the wing moult occurs during the postbreeding period (defined as "that segment of the annual cycle ... bracketed by the reproductive and fall migration periods"; Hohman et al. 1992). In this way, the energy demands of wing moult are not added to the energy demands of reproduction, and birds have new flight feathers before the fall migration. Variability in moult strategies can often be attributed to different mating and social systems. In geese, biparental care of the young has resulted in different strategies for breeding and non-breeding birds. Breeding adult male and female geese moult on the breeding grounds where they remain to care for their young. Immature and non-breeding geese typically migrate north from breeding areas to traditionally used moult sites (Salomonsen 1968, Owen and Black 1990). Male ducks do not help care for their young and characteristically leave their mates during incubation and migrate to a milder climate, often in the direction of their wintering areas (Salomonsen 1968) or to permanent wetlands near breeding areas (Hochbaum 1944). In contrast, female ducks tend to remain on breeding grounds and moult after the young have fledged (Hohman et al. 1992) but some females may abandon their young and migrate to moulting sites (Common Goldeneye *Bucephala clangula*; Eadie et al. 1995). Populations which breed in the south show less tendency to move to moult and there are no known substantial moult migrations in tropical waterfowl (Owen and Black 1990).

The evolution of a special moult migration suggests that there is a fitness advantage for individuals that participate. Moult migration has likely evolved in relation to environmental factors such as food availability and climatic conditions (Johnson and Herter 1990). Salomonsen (1968) proposed that moult migrations of waterfowl are undertaken to secure special resources, principally; abundant food, protection from predators, and seclusion from disturbance. Owen and Ogilvie (1979) proposed that, because plants are at an earlier stage of growth in the Arctic, geese that migrate north have access to highly digestible, protein-rich food. Long days and relative absence of predators are also possible advantages of moulting in the Arctic (Welty and Baptista 1990). There are, however, potential costs associated with northward migration for moult. In general, there is a progressive shortening of the duration of moult towards higher latitudes which is correlated with the shorter summer season (King 1974). Thus, waterfowl that moult at high latitudes may have higher daily energetic and nutritional demands than birds moulting further south because, (1) birds may replace feathers more rapidly, (2) birds may have further to travel on fall migration and therefore less time available for premigratory fattening (King 1974), and (3) temperatures are more likely to fall below a minimum critical level (Schieltz and Murphy 1997).

The postbreeding period is an important part of the annual cycle of waterfowl, requiring substantial investments of energy and nutrients for feather synthesis and associated metabolic changes (Schieltz and Murphy 1997) and the accumulation of energy reserves to meet the costs of fall migration (Hohman et al. 1992). As well, birds experience a period of flightlessness which makes them vulnerable to predators and to changes in food availability. Although, physiologically, moult may not be a great strain on the energy or nutritional resources of a bird, the timing, duration, pattern and rate of moult need to be known to evaluate the ecological significance of moult in a species.

Objectives

Despite the importance of moult, it remains the part of the life cycle that is least understood for some species. One reason why we know so little about moult of free-living birds is due to their secretive nature during this vulnerable time. In fact, the study of some species has not been possible because the location of moult sites are not known or are so remote that field studies are difficult for logistic reasons. For example, over 60% of the world's population of Barrow's Goldeneye breed and winter in British Columbia (Savard 1987) but the moulting locations of these birds are unknown. Male Barrow's Goldeneye leave breeding areas in the interior of B.C. during late June and 'disappear' until late October (S. Boyd, pers. comm.) when they reappear at wintering areas off the coast of B.C. Two moult sites for this species have been found in the Arctic. Although immature and non-breeding geese typically moult in Arctic areas, this behavior is less common among ducks (Owen and Black 1990).

In this study, I investigate the moult ecology of male Barrow's Goldeneye on the Old Crow Flats in northern Yukon. In Chapter 1, I examine the characteristics of wing ("remigial") moult including the timing and duration of the flightless period, remigial growth rates, and body weight changes. In Chapter 2, I examine habitat selection in relation to both predation risk and food supply. In the 'General Discussion', I summarize the information from Chapters 1 and 2, highlight management considerations regarding postbreeding Barrow's Goldeneye, and in particular the population moulting on the Old Crow Flats, and suggest research that should be conducted.

STUDY SPECIES

Description

Barrow's Goldeneye are a large, sexually dimorphic diving duck in the tribe Mergini (sea ducks). Males are larger than females. The mean weight of the male and female is 1100 g and 800 g, respectively (Madge and Burn 1988).

Pair-formation begins in late winter and continues on the breeding grounds. This species begin spring migration to breeding areas in early April, either alone or in pairs. Females breed at 2 years of age or older and return to the general area where they fledged (Savard 1987). They usually return to the same breeding territory and tend to use the same nest site from year to year (Savard 1986). Tree cavities are the preferred nest site but ground cavities are occasionally used. In Iceland, typical nesting habitat does not exist so females nest in rock crevices and among dense vegetation (Madge and Burn 1988). Barrow's Goldeneye are sociable, although highly territorial during the breeding season. The typical clutch size in British Columbia is 9-10 eggs (Savard 1986).

Once clutches are complete and incubation has started, males leave their mates for postbreeding areas. In western North America, postbreeding areas may be near breeding areas, although very little is known of the whereabouts of adult and immature males from June through to October. In Alaska and eastern North America, movements north of breeding areas occur (Palmer 1976). Most females move to larger lakes within breeding areas to moult and remain nearby until fall migration. Fall migration begins when lakes start to freeze (Palmer 1976, Savard 1987). Banding returns from breeding areas in Alaska and British Columbia indicate that Barrow's Goldeneye winter in coastal areas close to breeding areas (Bellrose 1976, Savard 1987). Large aggregations sometimes occur near extensive mussel beds. Pairs that re-unite during winter may separate from wintering flocks and establish territories which they defend from conspecifics as well as other diving ducks (Savard 1986).

Distribution and abundance

Over 90% of the world's population of Barrow's Goldeneye are believed to breed and winter in western North America. They breed west of the Rocky Mountains from southern Alaska to northern California and winter along adjacent coastal lowlands (Madge and Burn 1988). Small numbers winter inland on open rivers and lakes. A small population of Barrow's Goldeneye winters along the Atlantic coast of North America from Gulf of St Lawrence south to Maine, with small numbers in the Maritime provinces (Daury and Bateman 1996). With only three records of possible breeding Barrow's Goldeneye in eastern Canada (Daury and Bateman 1996), the breeding distribution in the east remains unknown. There is a small, but stable, resident population in Iceland and a small wintering population in Greenland.

The entire world's population of Barrow's Goldeneye is estimated at ca. 200,000 birds (Madge and Burn 1988). Savard (1987) suggests that the Pacific and Atlantic populations are 180,000 and 5,000 birds, respectively. Daury and Bateman (1996) recently estimated the Atlantic Canada and Maine population at 400 birds.

Moult sites

The only recorded moult sites where large numbers of male Barrow's Goldeneye gather are the Old Crow Flats in northwest Yukon (Savard 1987) and the Yukon Flats in northeast Alaska (King 1963). The estimated number of goldeneye moulting on the Old Crow Flats varies widely. Pre-moult population estimates of goldeneye (*B. islandica and B. clangula*) range from a low of 395 in 1981 to a high of 18,941 in 1980, with a 10 year mean of 7,165 ± 4507 (SD) (Hawkings et al. 1995). Mossop and Hayes (1977) estimated 1,700 to 7,000 moulting Barrow's Goldeneye on the Old Crow Flats in late July of 1977. Since the mid 1970's, over 2000 Barrow's Goldeneye have been banded on the Old Crow Flats (Mossop 1990, CWS unpublished data) and 38 banded birds have been recovered. All band recoveries were from Alaska, most of them near Kodiak Island in southeastern Alaska, between September and January. Barrow's Goldeneye arrive near Kodiak Island beginning in early fall and remain throughout the winter (D. Zwiefelhofer pers. comm.). Based on these banding records, it appears that Barrow's Goldeneye moulting on the Old Crow Flats winter along the coast of Alaska. Small numbers of moulting male and female Barrow's Goldeneye have been observed on inlets along the west coast of Kodiak Island in the Gulf of Alaska (D. Zwiefelhofer pers. comm.) which suggests that this species may moult either inland or on coastal waters.

The moulting location of Barrow's Goldeneye from breeding areas in British Columbia is unknown. In the Atlantic region, groups of moulting goldeneye (*B. islandica* and *B. clangula*) have been observed in inlets on the coast of northern Labrador (Daury and Bateman 1996).

STUDY AREA

Biophysical description

The Old Crow Flats (Figure 1) is a 518,000 ha (5,000 km^2) lacustrine plain in the northern Yukon (68° N, 140°W) that contains over 388,600 ha of wetland suitable for waterfowl (Russell et al. 1978).

The following biophysical description of the Old Crow Flats ecoregion is taken from Oswald and Senyk (1977) and Posten et al. (1973). The area has a cold dry climate. The mean July temperature is 12°C with an average annual temperature of -10° C. The average annual precipitation varies from 170 to 250 mm, half of which falls as snow (Posten et al. 1973). Lakes range in size from <1 km^2 to 42 km^2 and are uniformly shallow (average less than 2 m), but vary in configuration, shoreline relief, and shoreline cover types. Permafrost underlies the area and forms the lake margins, which sometimes erode causing sudden changes in water level. Where drainage occurs, sedge stands develop and provide nesting habitat for waterfowl (IUCN 1987).

Shoreline vegetation is birch (*Betula glandulosa*), willow (*Salix* spp.), alder (*Alnus* spp.), and black spruce (*Picea mariana*). Density and composition of emergent and submergent plant communities vary greatly between lakes and probably depend on lake characteristics such as water depth, type of substrate, exposure, and water level fluctuations (Posten et al. 1973). Submergent vegetation, predominantly *Potomogeton* and *Myriophyllum* spp., occurs in most lakes but is most dense in deep water. Emergent vegetation occurs in shallow waters and is dominated by horsetail (*Equisetum* spp.) and sedges (*Carex* spp.).

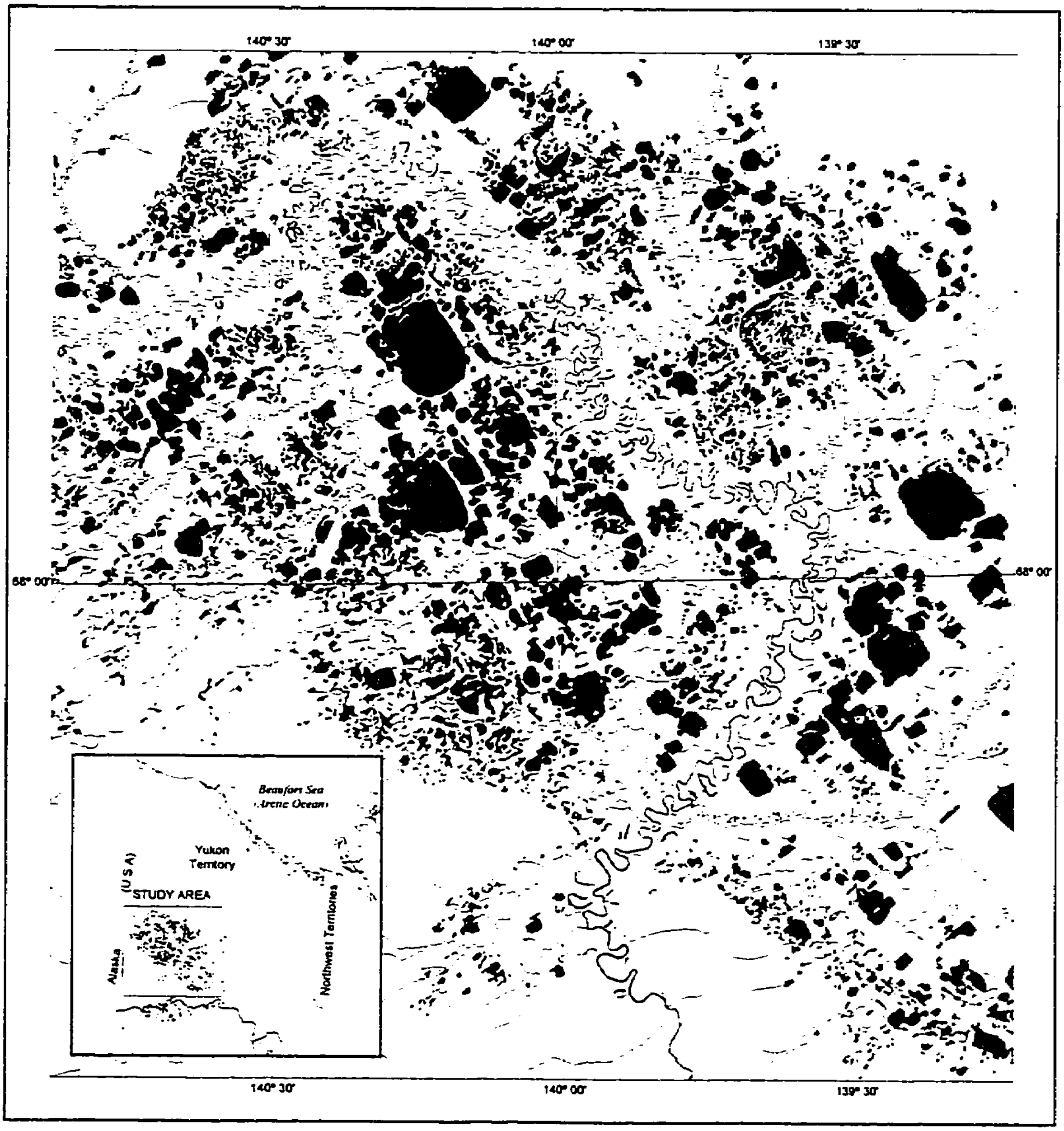


Figure 1. Location of the Old Crow Flats study area in northern Yukon.

Wildlife

Lakes of the Old Crow Flats are highly productive and contain a rich invertebrate fauna for such a high latitude (IUCN 1987). The area is an important breeding, moulting, and pre-migration staging area for some 500,000 waterfowl, including scoters (*Melanitta fusca* and *M. perspicillata*), scaup (*Aythya marila* and *A. affinis*), American Wigeon (*Anas americana*), Northern Pintails (*Anas acuta*), Canvasbacks (*Aythya valisineria*), Oldsquaw (*Clangula hyemalis*), goldeneye (*Bucephala iclandica* and *B. clangula*), Tundra Swans (*Cygnus columbianus)*, Greater White-fronted Geese (*Anser albifrons*), and loons (*Gavia* sp.) (Hawkings and Hughes 1995). Densities of ducks on the Old Crow Flats are up to 3 times higher than in 11 other primary waterfowl breeding grounds in nearby Alaska (Conant and Groves 1995). Muskrats (*Ondatra zibethicus*) are abundant, as are moose (*Alces alces*) in summer and barren ground caribou (*Rangifer tarandus granti)* in spring and fall.

CHAPTER 1: CHARACTERISTICS OF REMIGIAL MOULT OF MALE BARROW'S GOLDENEYE IN NORTHERN YUKON

Introduction

The main function of moult is to replace worn and damaged feathers. Most birds have one complete moult per year in which all of the feathers are replaced. In waterfowl, this moult generally occurs during the postbreeding period. Geese and swans have 1 plumage cycle per year and thus one complete moult (body, wing and tail feathers) per year. In contrast, ducks have two plumage cycles per year (non-breeding or "basic" plumage, and breeding or "alternate" plumage). Males acquire alternate plumage during the fall and retain it until the end of the breeding season. When the female begins incubation the male starts to moult into basic plumage which is followed by wing and tail feather moult. Towards the end of this moult, males begin to acquire alternate plumage (which may or may not be completed before fall migration) and retain it until the end of the next breeding season.

The synthesis of new feathers requires nutrients and energy (Murphy 1996). Species which moult most of their feathers over a short period, such as ducks, may have larger increases in daily energy requirements (Payne 1972) than birds which spread moult over a long period. Hence, moult may be a nutritionally stressful event ("stress" defined as "a situation in which [a bird's] nutrient demands exceed its nutrient ingestion, resulting in net catabolism of body tissues to the extent that one or more vital physiological functions are impaired"; King and Murphy 1985) in the annual cycle of waterfowl.

Knowing the daily cost of moult is important in determining the nutritional challenge that moult imposes on a bird (Murphy 1996). However, determining the energetic cost of feather synthesis is difficult partly because the process of moult interacts with other metabolic processes (Schieltz and Murphy 1997). The intensity of moult can influence thermoregulatory costs when air temperature is below the lower critical temperature (Payne 1972, Schieltz and Murphy 1997), and changes in behavior, such as less time feeding and more time resting (Bowman 1987, Thompson 1992) can compensate for energy costs of moult (Murphy 1996). The minimum requirements of moult can be derived from a knowledge of the composition of the plumage. The main nutritional requirements of moult are energy and protein. Plumage is approximately 90% protein by dry mass, may range from 4% -12% of a bird's body mass, and can be 25% of the total body protein content (Murphy 1996).

Waterfowl meet the energy and nutrient demands of moult from either foods consumed during the moult period (Lesser Snow Geese *Chen caerulescens caerulescens*; Ankney 1979, Brant *Branta bernicla*; Ankney 1984, Canvasback *Aythya valisineria*; Thompson 1992, Blue-winged Teal *Anas discors*; Hohman et al. 1997), by catabolizing endogenous nutrients (Redheads *Aythya americana*; Baily 1985, Black Ducks *Anas rubripes*; Bowman 1987), or a combination of the above. Weight loss commonly associated with moult (see Hohman et al. 1992; Table 5-2) has often been interpreted as an adaptive strategy that permits these birds to regain flight before primary feathers are fully re-grown (Douthwaite 1976, Ankney 1979, Owen and Ogilvie 1979, Young and Boag 1982, Sjoberg 1988, Thompson 1992) rather than as evidence of nutritional stress. Panek and Majewski (1990) suggest that decreased body mass of Mallards (*Anas* *platyrhynchos*) is related to their secretive behavior which reduces both foraging time and exposure to predators.

Understanding of the physical changes that a bird undergoes during moult and the timing, duration and speed of moult relative to the annual life cycle can help predict the energetic significance of moult (Murphy 1996) as it relates to physiological status, habitat requirements and fitness of the individual (Lovvorn and Barzen 1988).

The purpose of this study was to investigate the moult of Barrow's Goldeneye on the Old Crow Flats in northern Yukon. The specific objectives were: (1) to determine the timing, duration and intensity of remigial moult, (2) to investigate body weight change during remigial moult, and (3) to discuss observed relationships in regard to current ideas about the energetic and nutritional demands of moult. I predicted that body weight would decrease with increasing primary growth and that birds moulting late would have faster feather growth rates than birds moulting early. I also predicted that rates of feather growth and body weight loss would be greater for birds at this Arctic site than rates found for birds moulting further south.

Methods

Capture and measurement of birds

Barrow's Goldeneye were drive-trapped, banded and measured on 5 lakes in July and again in August 1995. Birds were aged using wing plumage characteristics (Carney 1992). Adult males were defined as those older than 2 years of age (ASY) and immature males were those in their second year (SY). Each bird was weighed (g), sexed (by feather characteristics and, if necessary, cloacal exam), and banded, and the length of the ninth primary (mm), total tarsus (mm) and culmen 1 (mm) were measured (Dzubin and Cooch 1992).

Analysis

Birds were considered to be in active remigial moult if they had any new ninth primary growth. Mean ninth primary growth rate (mm/day ± SE) and mean change in body mass (g/day ± SE) were calculated for recaptured individuals in active remigial moult by dividing the difference between the first and second capture measurements by the capture interval. Relationships between variables were evaluated using analysis of variance (T-TEST and GLM, SAS Institute Inc. 1989). Multiple comparisons were performed using Bonferroni adjusted t-tests (SAS Institute Inc. 1989) at the 5% level of significance. The relationship between ninth primary growth rate and body mass change of birds was examined using linear regression and correlation analyses (REG and CORR, SAS Institute Inc. 1989). Unless stated otherwise, a 5% level of significance was used for all tests.

To estimate the length of the flightless period, I used the following equation and assumed that ninth primary growth remained constant: [(average length of a full ninth primary x estimated % re-growth needed to regain flight) / average ninth primary growth rate]. The timing of moult was estimated from ninth primary lengths obtained at banding.

Banding records were investigated for evidence of moult site fidelity. First, I estimated the number of birds banded in 1994 that could be expected to be alive in 1995 based on a survival rate of 70% (Savard 1987). I multiplied this number by the proportion (estimated) of birds captured to determine the number of birds that I would expect to have captured (assuming a random distribution) if all surviving birds returned to the same lake. Finally, the actual number of birds recaptured on the same lake was divided by the expected value to determine percent fidelity to individual lakes.

Results

Capture of birds

We captured 284 Barrow's Goldeneye on 5 lakes between 18 and 28 July 1995 and 215 birds between 6 and 11 August 1995, including 61 recaptured birds. Of the 438 birds banded, most (90%, n = 396) were adult males (ASY) while less than 10% (n = 37) were immature males (SY) (Table 1). Five individuals could not be accurately aged and were excluded from the analysis. Birds with damaged ninth primaries were excluded from growth rate analyses.

Ninth primary growth rate

Adult males in different stages of active remigial moult (based on ninth primary length at first capture) had similar mean ninth primary growth rates (mm/day ± SE) (Table 2; 4.10 ± 0.07 for moult stage 1 and 3.97 ± 0.08 for moult stage 2), suggesting that the growth rate of primary feathers remains constant during most of the remigial moult. The mean ninth primary growth rate of birds that had no ninth primary when first captured was significantly slower ($P < 0.001$, df = 38) than those in active remigial moult, which was

Table 1. The number of male Barrow's Goldeneye captured, banded and measured (and recaptured and remeasured) during remigial moult on the Old Crow Flats, 1995.

Lake Number	Capture Dates	Adult Males (ASY)[a]	Immature Males (SY)[a]	Age Unknown (AHY)[a]	Total
2	21 July; 6 August	32 (12)	4	1	37 (12)
3	26 July; 7, 8 August	69 (27)	12 (8)	1	82 (35)
26	28, 29 July; 12 August	110 (13)	5	2	117 (13)
39	18 July; 10 August	160 (1)	15	1	176 (1)
41	27 July; 14 August	25	1	0	26
Total		396 (53)	37 (8)	5	438 (61)

[a] ASY = after second year, SY = second year, AHY = after hatch year

Table 2. Mean ninth primary growth rate ± SE (and sample size) of male Barrow's Goldeneye in different stages of remigial moult on the Old Crow Flats, 1995.

Moult Stage[2] at first capture	Adult Male (ASY)[1]	Immature Male (SY)[1]
0	3.30 ± 0.16 (19)[a] range: 2.35 - 4.99	3.69 ± 0.33 (3) range: 3.03 - 4.08
1	4.10 ± 0.07 (11)[b] range: 3.68 - 4.35	4.01 ± 0.08 (3) range: 3.85 - 4.11
2	3.97 ± 0.08 (11)[b] range: 3.65 - 4.62	4.56 (1)

[1] ASY = after second year, SY = second year

[2] Moult Stage (0) no new ninth primary when first captured, (1) 0 mm < ninth primary < 30 mm, (2) ninth primary ≥ 30 mm

[a] Means in the same column with the same letter are not significantly different (alpha = 0.05).

expected because the new feather does not appear immediately after the old feather drops out. Mean ninth primary growth rates of birds in active remigial moult were not significantly different between adult and immature males or among lakes (Table 3). The combined mean ninth primary growth rate (mm/day ± SE) of adult and immature males ($n = 26$) was 4.05 ± 0.05. Thus, the average daily percent change in feather length over the period of development (mean length of full ninth primary = 155 mm ± 2 (SE), $n = 9$) was 2.6% (range: 2.4% to 3.0%). Ninth primary growth rates were not significantly influenced by date but were significantly related to initial body weight. Heavier birds had faster rates of ninth primary growth (Figure 2; $P < 0.004$, $r^2 = 0.30$, $n = 26$) than lighter birds.

Weight change

The mean body weight of adult males decreased significantly during remigial moult (Figure 3); a similar, although not significant, trend was observed in immature males. Approximately 6% of mean initial body weight was lost between moult stages 0 and 4. Adult males in different stages of active moult (based on ninth primary length at first capture) had a similar mean rate (g/day ± SE) of weight loss (Table 4; -1.18 ± 0.52 for moult stage 1 and -2.75 ± 0.76 for moult stage 2), but those just beginning remigial moult had a mean weight gain (0.95 ± 0.67, $n = 19$). The change in body weight of immature birds had a trend similar to adult birds, however sample sizes were too small to be meaningful statistically. Individuals that had no ninth primaries when initially captured (moult stage 0) tended to gain weight slightly between captures, while those in active moult tended to maintain or lose weight (Figure 4). Change in body weight

Table 3. Mean ninth primary growth rate (mm/day) ± SE (and sample size) of male Barrow's Goldeneye during active* remigial moult on the Old Crow Flats, 1995.

Lake Number	Adult Male (ASY)[a]	Immature Male (SY)[a]
2	4.04 ± 0.12 (6)	4.14 ± 0.15 (4)
3	4.05 ± 0.10 (9)	no data
26	4.02 ± 0.08 (7)	no data
All Lakes	4.04 ± 0.05 (22)	4.14 ± 0.15 (4)

* birds with new ninth primary growth > 0 when first captured

[a] ASY = after second year, SY = second year

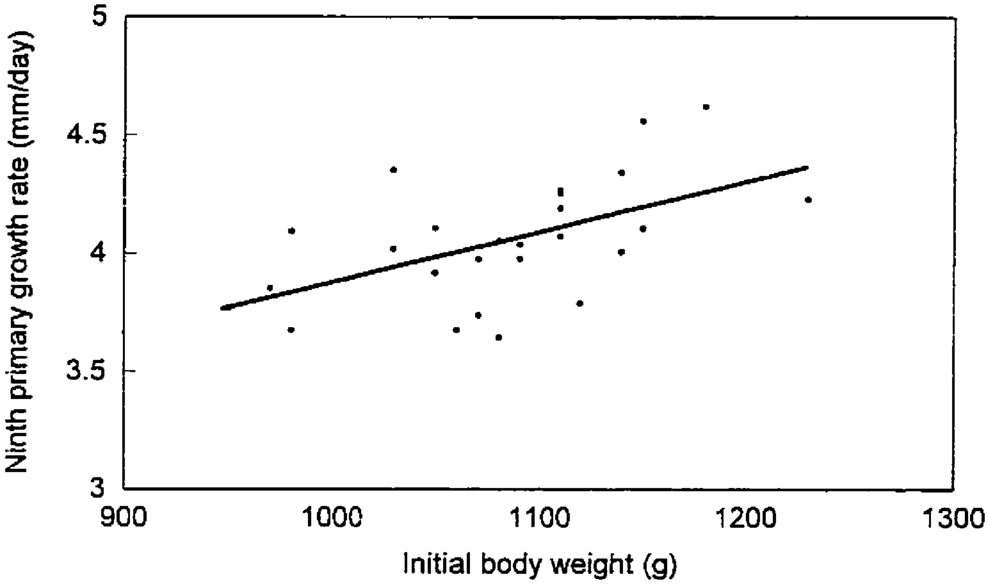


Figure 2. Relationship between ninth primary growth rate (mm/day) and initial body weight (g) of male Barrow's Goldeneye (ASY and SY) during remigial moult on the Old Crow Flats, 1995 ($n = 26$, $y = 1.74 + 0.002x$, $P < 0.004$, $r^2 = 0.30$).

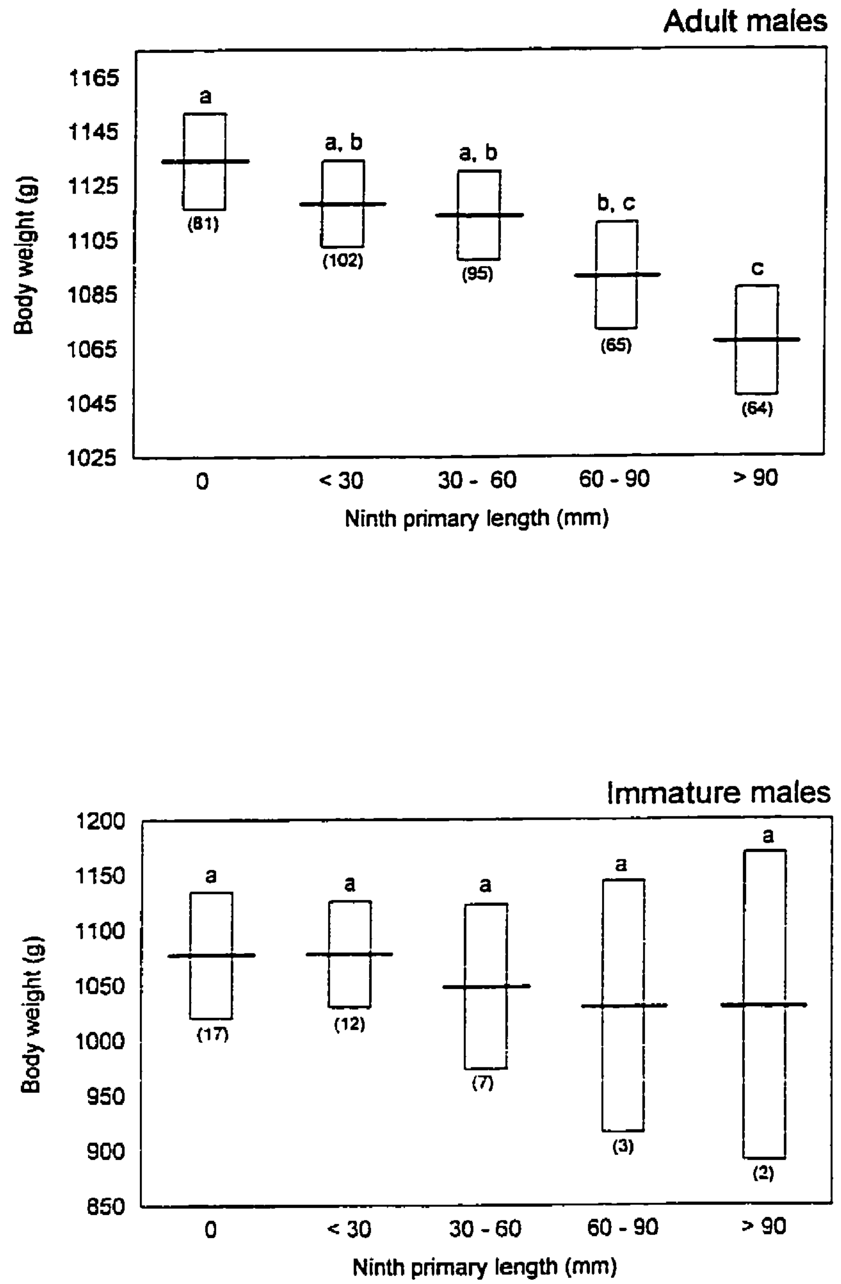


Figure 3. Mean body weight (g) and 95% confidence interval (and sample size) of male Barrow's Goldeneye (ASY and SY) in different stages of remigial moult (based on ninth primary length) on the Old Crow Flats, 1995. Means with the same letter are not significantly different.

Table 4. Mean daily change in body weight ± SE (and sample size) of male Barrow's Goldeneye (ASY and SY) during different stages of remigial moult on the Old Crow Flats, 1995.

Moult Stage[2] at first capture	Adult Males (ASY)[1]	Immature Males (SY)[1, 3]
0	0.95 ± 0.67[a] (19) range: -5.71 - 5.38	3.74 ± 1.24 (3) range: 1.54 - 5.83
1	-1.18 ± 0.52[b] (15) range: -5.38 - 2.31	0.96 ± 0.73 (4) range: 0 - 3.08
2	-2.75 ± 0.76[b] (11) range: -6.43 - 1.33	-4.62 (1)

[1] ASY = after second year, SY = second year

[2] Moult Stage: (0) no new ninth primary, (1) 0 mm < ninth primary < 30 mm, (2) ninth primary ≥ 30mm

[3] Statistics not applied due to small sample sizes.

[a] Means with the same letter are not significantly different (alpha = 0.05).

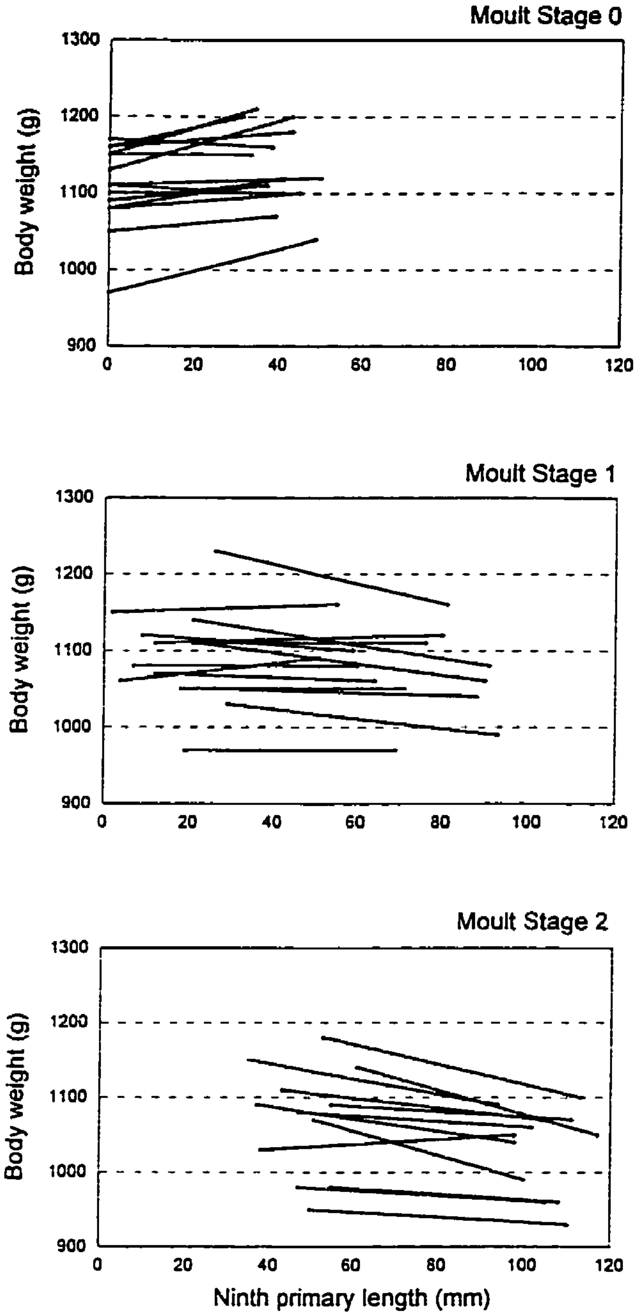


Figure 4. Change in body weight (g) of male Barrow's Goldeneye (ASY and SY) during 3 stages of remigial moult (based on ninth primary length at first capture: (0) no new ninth primary, (1) 0 mm < ninth primary < 30 mm, (2) ninth primary ≥ 30 mm).

between captures was not significantly influenced by age, lake, or date of capture but was significantly correlated with initial body weight. Heavy birds lost a greater percentage of their body weight per day than did lighter birds (Figure 5; $P < 0.01$, $r^2 = 0.22$, $n = 32$).

Relationship between weight change and ninth primary growth rate

The mean initial weight (g ± SE) of recaptured birds was 1082 ± 13 ($n = 26$). The structural size (based on tarsus and culmen length), date of capture (Julian day), and stage of moult (initial ninth primary length) were not significantly different between individuals above and below the mean initial weight (Table 5), however individuals above the mean lost significantly more weight (g/day) and had greater ninth primary growth rates (mm/day) than individuals below the mean. A marginally significant relationship was found between ninth primary growth rate and change in body weight (Figure 6; $P < 0.06$, $r^2 = 0.15$, $n = 26$).

Length of the flightless period

I estimated that males could fly when their primaries reached 80% of their final length. Nine adult birds captured with old primaries had a mean ninth primary length of 155 ± 2 (SE) mm. Using this mean to approximate the final ninth primary length of recaptured birds, only 4 recaptured birds had ninth primaries over 80% of their final length. Assuming the mean ninth primary growth rate remained constant until the end of moult, the average length of the flightless period, excluding the pre-shedding interval, of male Barrow's Goldeneye on the Old Crow Flats was ~ 31 days (range: 27 - 34 days).

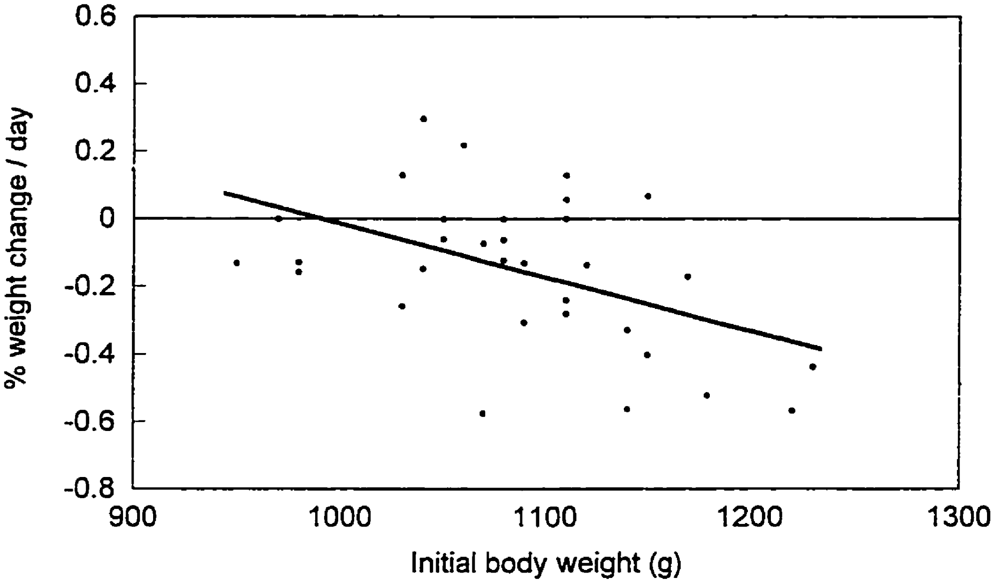
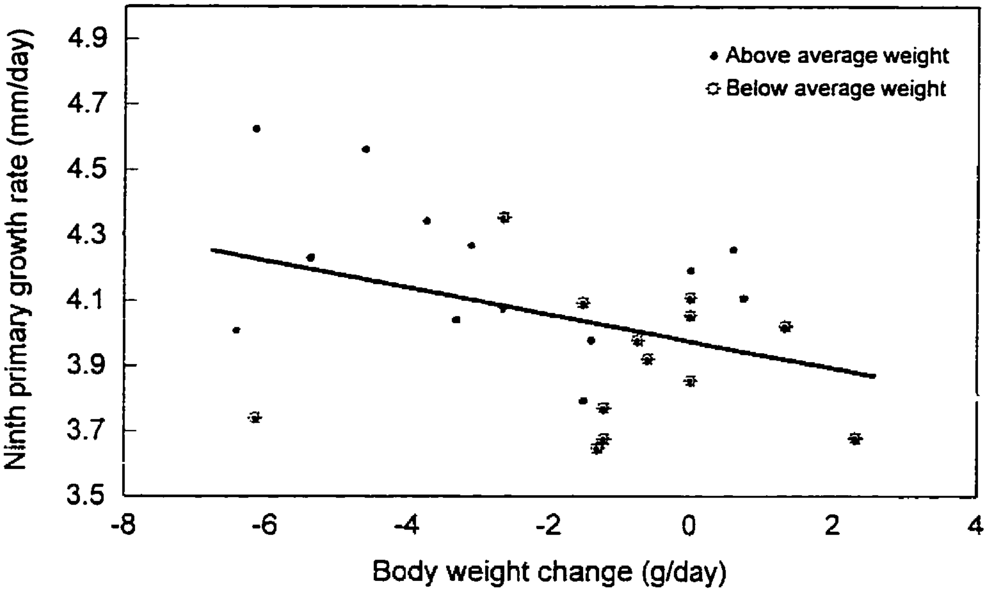


Figure 5. Relationship between percent body weight change per day and initial body weight (g) of male Barrow's Goldeneye (ASY and SY) during remigial moult on the Old Crow Flats, 1995 ($n = 32$, $y = 1.57 + -0.0016x$, $P < 0.01$, $r^2 = 0.22$).

Table 5. Comparison of moult characteristics between male Barrow's Goldeneye (ASY and SY) with initial body weight (g) heavier and lighter than the mean initial weight (1082 ± 13 (SE) g) of recaptured birds (n = 26) on the Old Crow Flats, 1995.

	Heavier than initial mean weight (n = 13)	Lighter than initial mean weight (n = 13)	Prob > |T|
Change in body weight (g/day)	-2.85 ± 0.68	-0.92 ±0.56	0.04
Ninth primary growth rate (Marbled Murrelet/day)	4.19 ± 0.06	3.91 ± 0.06	0.004
Tarsus length (mm)	51.25 ± 0.35	51.28 ±0.29	0.95
Culmen length (mm)	34.37 ± 0.25	34.61 ± 0.25	0.50
Julian day	206.6 ± 0.80	206.3 ± 0.72	0.78
Initial ninth primary length (mm)	30.56 ± 5.16	30.92 ± 5.02	0.96



* average weight of all birds (n = 26) at the time of inital capture.

Figure 6. Relationship between ninth primary growth rate (mm/day) and body weight change (g/day) of male Barrow's Goldeneye (ASY and SY) during remigial moult on the Old Crow Flats, 1995 ($P < 0.06$, $r^2 = 0.15$, $n = 26$).

Timing of remigial moult

I used the mean ninth primary growth rate to extrapolate the start and end dates of remigial moult for each bird and determined that remigial moult of male Barrow's Goldeneye on the Old Crow Flats in 1995 extended from early July to mid September, with the peak of moult occurring between 20 July and 23 August.

Moult site fidelity and moult migration

Fifty-six of 410 (13.7%) moulting Barrow's Goldeneye banded by the Canadian Wildlife Service (CWS, unpublished data) on 3 lakes on the Old Crow Flats in 1994 were recaptured during moult in 1995 (Table 6). Lake 26 and Lake 2 had estimated moult site fidelities of 55% and 21%, respectively (Table 7). The fidelity rate on Lake 2 was probably higher than 21% because birds capable of flight flew off the lake and may not have returned. About half of the birds on Lake 2 flew away when banding occurred on 21 July, 1995, whereas no birds were observed capable of flight by 28 July, 1995 when we trapped on Lake 26.

Discussion

Weight change

Weight gain prior to moult has been recorded in waterfowl (Lesser Snow Goose; Ankney 1979, Brant; Ankney 1984, Mallard; Young and Boag 1982, Pehrsson 1987). Endogenous nutrient reserves may be used during flightlessness to maintain feather production if malnutrition occurs (Murphy 1996). Thus, weight gain prior to moult may be a strategy used as security against unpredictable feeding conditions. Alternatively,

Table 6. Location of moulting male Barrow's Goldeneye banded on the Old Crow Flats in 1994 and recapture location in 1995.

Number and location of birds banded in 1994		Location of birds recaptured in 1995					
Lake	Number of birds banded	Lake 2	Lake 3	Lake 26	Lake 39	Lake 41	Total
2	69	7	4	4	-	4	19
26	312	1	-	30	3	1	35
41	29	-	-	2	-	-	2
Total	410	8	4	36	3	5	56

Table 7. Estimated moult site fidelity of male Barrow's Goldeneye to specific lakes on the Old Crow Flats based on banding records from 1994 and 1995. Formula: number of birds recaptured in 1995 / [(number banded in 1994) * (est. survival rate of 0.70) * (est. proportion of lake population captured in 1995)].

Lake	Lake area (km^2)	# of birds banded in 1994	Proportion of birds captured in 1995	# of birds recaptured on the same lake in 1995	Estimated fidelity to same lake
2	1.25	69	.70	7	21%
26	7.65	312	.25	30	55%
41	32.50	29	< .05	0	-

pre-moult weight gain may be a strategy that allows a bird to reduce foraging time during flightlessness, and thus decrease exposure to predators (Panek and Majewski 1990). Adult male Barrow's Goldeneye in early remigial moult on the Old Crow Flats had similar weights to adults during the breeding season in British Columbia (mean weight (g ± SD) of 1132 ± 56.7 in 1995 and 1097 ± 89.8 in 1996; S. Boyd personal communication) and to published weights in species accounts (mean 1100 g ; Madge and Burn 1988, mean 1090 g (n = 3) cited in Palmer 1976) suggesting that individuals did not gain substantial body reserves prior to moult. However, recaptured birds just beginning moult (moult stage 0 in Figure 4) experienced weight gains. In Canvasback, carcass composition could not explain the difference in body weight between early and late pre-flightless birds so it was suggested increased blood volume associated with engorged feather follicles was the cause (Thompson 1992). Increased blood volume may explain the weight difference between birds in early and advanced moult in this study, or birds may have been building body reserves (perhaps those lost during migration). A small weight gain due to increasing feather mass may be expected as remigial feathers grow, however, estimating this weight gain would be difficult because body and tail feathers are shed and re-grown during the same period as flight feathers.

Weight loss as an adaptive strategy

Body mass of waterfowl during remigial moult tends to decline or remain unchanged (see Hohman et al. 1992: Table 5-7). Seasonal body weight loss can indicate a period of stress or be an adaptive strategy. Many studies have rejected the suggestion that moult is a nutritionally stressful event in the annual life cycle of waterfowl (Lesser Snow Geese; Ankney 1979, Ruddy Ducks; Hohman 1993, Blue-winged Teal; Hohman et al. 1997). Thompson (1992) determined that moulting male canvasbacks easily met the nutritional requirements of moult from dietary intake despite the fact that they lost weight during the moult period. He suggests that body fat metabolism during remigial moult allows birds to occupy open-water habitats that reduce their risk of predation and permits birds to regain flight at an earlier stage. Other studies have also suggested that loss of body weight during moult is an adaptive strategy that allows birds to regain flight sooner (Douthwaite 1976, Owen and Ogilvie 1979, Sjoberg 1988). The logic is that reduced wing-loading allows lighter birds to fly sooner than heavier birds with the same feather length (Owen and Ogilvie 1979). Possible advantages of regaining flight quickly include (1) decreased risk of predation, (2) increased ability to find food and shelter, (3) longer time to rebuild body reserves for fall migration, and (4) early migration and arrival on wintering areas and thus increased chance of obtaining a mate or a territory. Costs associated with using body reserves to increase the speed of feather growth would likely be associated with decreased body reserves, which are used to ensure uninterrupted feather growth (Douthwaite 1976) and/or body maintenance in the event of food limitation.

In my study, the mean body weight of adult birds was significantly less at the end of moult than at the beginning of moult. There was an average loss of 6% of body weight between birds just beginning moult and those more than half way finished. If the same rate of loss was experienced until moult was complete, birds would have lost 10-12% of their body weight. This weight loss is similar to that recorded for male teal (10% - 19%

for *Anas crecca*; Sjoberg 1988, 11% for *Anas erythrorhyncha*; Douthwaite 1976). Was this weight loss the result of nutritional stress? Some birds were able to maintain, and even gain weight, while maintaining above average ninth primary growth rates which suggests that the nutritional and energy demands of moult could be met through dietary intake. Heavier males had greater ninth primary growth rates and greater percent loss of body weight than lighter males. That heavy and light birds had similar tarsus and culmen lengths suggests that heavy birds were not structurally larger than light birds and thus body mass may indicate physical condition (defined here as the amount of stored fat reserves). Douthwaite (1976) dissected moulting Red-billed Teal and found that fat reserves reflected seasonal changes in body weight and thus heavy birds were 'fat' birds and light birds were 'thin' birds. Assuming that body weight in this study reflected physical condition, this would suggest that birds in the best condition used body reserves to increase feather growth rates. Lighter birds in this study tended to have smaller percent loss of body weight and lower ninth primary growth rates which suggests that either there was no advantage for them to use body reserves to increase the rate of feather growth (they were already light) or that there would be a survival disadvantage if they did. Thus, the data appear to favor weight loss as an adaptive strategy used to regain flight quickly. In contrast to the present study, Hohman (1993) found no depletion of fat reserves in moulting Ruddy Ducks (*Oxyura jamaicensis*) and suggested the advantages of weight loss may be reduced in diving ducks that use open-water habitats during the flightless period and dive to feed and escape from predators.

What would be the potential benefits of rapid remigial moult for Barrow's Goldeneye on the Old Crow Flats? It has been suggested that diving ducks, which spend most of the flightless period in open water, likely have lower predation risks during the flightless period relative to dabbling ducks (Hohman et al. 1992). Even so, mortality risks during periods of flightlessness are likely greater than during periods of flight so selection should favor rapid moult.

Rapid moult also may be beneficial for birds moulting in highly seasonal environments such as the Arctic (Hohman et al. 1992). Winter conditions on the Old Crow Flats can occur in August. In 1996, below freezing temperatures caused ice to form on lakes by 22 August. Early ice cover on lakes would likely be detrimental to flightless diving ducks as the areas accessible for feeding would be diminished, cold temperatures could reduce the availability of food, and birds could become entrapped in ice (King 1974, S. Boyd, pers. comm.). Weather records for Old Crow indicate that ice formation on lakes, in August, could have occurred in 6 years between 1969-1995 (Environment Canada, unpubl. data). Perrins and McCleery (1995) found that late-moulting Mute Swans in sub-Arctic areas were less likely to survive than those which started moult earlier. The disadvantage was presumed to be delayed fall migration which subjected late-moulters to bad autumn weather. However, it also was suggested that late moulting birds may have been in poor condition. Birds on the Old Crow Flats would likely benefit from rapid moult because they would be able to leave a lake or migrate from an area if necessary to avoid poor weather and/or feeding conditions.

Barrow's Goldeneye delay returning to wintering areas even after flight is regained (Palmer 1976, Savard 1987, S. Boyd pers. comm., D. Zwiefelhofer pers. comm.), and pairing generally does not occur until mid-winter (Savard 1987). It is, therefore, unlikely that birds moult rapidly to return to wintering areas early to find a mate. My results did not find a relationship between the rate of moult and the date of moult initiation. However, I did not recapture birds which initiated moult in August. These individuals would be the ones most likely to have rapid moult if environmental factors were important.

Rate of moult may be an indirect indicator of the condition, and therefore quality, of a bird. Robertson et al. (unpubl. manuscript) show that wild male Harlequin Ducks (*Histrionicus histrionicus*) which moult (includes wing and body plumage) relatively quickly have an advantage when trying to obtain a mate in the subsequent winter. They postulate that males in good condition moult rapidly to establish themselves in the dominance hierarchy which will later help them attract females. If rate of moult is correlated with qualities that favor females choosing a male, then selection should favor rapid moult.

Feather growth rates and the timing and duration of moult

Ninth primary growth rates of male Barrow's Goldeneye on the Old Crow Flats were similar for both adult and immature birds, appeared to remain constant, and were not related to the date moult was initiated. Owen and Ogilvie (1979) also found that feather growth rates of wild Barnacle Geese were similar irrespective of age or sex and that feather growth rates remained constant throughout the flightless period. In contrast, the feather growth rates of captive Bullfinch (*Pyrrhula pyrrhula)* and Greenfinch (*Carduelis chloris*) (Newton 1967) and Mallard (Panek and Majewski 1990) slowed towards the end of moult. I was unable to determine remigial growth rates near the completion of moult because birds were capable of flight before their primaries reached full length. However, Newton (1967) suggests that the most accurate estimates of the timing and duration of moult in individual birds are obtained if the estimates are not made from birds caught while the ninth primary is in its last stage of growth. The slower growth rate that I observed for birds captured with no re-growth present was likely due to a delay in the emergence of the new feather. The time elapsed between the loss of an old flight feather and the emergence of a new one was 1 to 3 days for 2 species of captive finch (Newton 1967).

The timing of moult is related to the timing of breeding (Hohman et al. 1992) and is possibly influenced by distances traveled from breeding areas. Birds which moult at high latitudes may have more rapid moult than birds further south due to a reduced time for completion of moult prior to departing for wintering areas (King 1974). Mewaldt and King (1978) found that the duration of post-nuptial moult of the White-crowned Sparrow decreased northward by an average of 2.6 days per degree of latitude between the southern most and northern most limits of its breeding range. The daily percent change in remigial feather length of birds in this study (range: 2.4% to 3.0%), located at 68° N, was the same as the most common values reported for other species of waterfowl (2-3%, Hohman et al. 1992), and was less than what has been recorded for male Teal (*Anas crecca*) in northern Sweden (4.6%, 63° N, Sjoberg 1988) but similar to data for male Brant in N.W.T., Canada (2.73%, 77° N, Boyd and Maltby 1980). The duration of flightlessness of males in my study, 27-34 days (excluding the pre-shedding interval) was longer than the period of flightlessness reported for species further south (21-28 days for Mallards in California; Young and Boag 1981, 21-28 days for Canvasback in central

Alberta; Thompson 1992). Peak remigial moult of Canvasback in central Alberta occurs in early August (Thompson 1992) which is similar to the peak of remigial moult found in my study (20 July - 23 August). These findings are opposite to what I had predicted. I predicted that birds in the Arctic would initiate remigial moult earlier and have faster remigial growth rates, and therefore a shorter flightless period, due to the time constraint imposed by a short summer and reduced time available for pre-migratory fattening.

Site fidelity

In waterfowl species, female philopatry to natal breeding areas and traditional use of wintering areas and staging sites on migration are well documented (Bellrose 1976, Palmer 1976). This behavior could enhance individual survival and breeding success (Erskine 1971, Owen and Black 1990). High survival at familiar sites may contribute to moult site fidelity (Bowman 1987, Bowman and Longcore 1989). Postbreeding waterfowl would likely benefit from accumulated experience at local moulting sites, although the extent to which individuals return to postbreeding areas is unknown for most species (Hohman et al. 1992). Fifty-two percent of 29 recaptured postbreeding male Black Ducks were on the same wetland in 2 consecutive years of study and over 71% were within 2 km of their initial capture site (Bowman and Brown 1992). In my study, the recapture rate, adjusted for survival (Savard 1987) but not for capture effort, was 19.5%. True fidelity rates are probably higher because it is unlikely we captured all of the birds that returned (only 5 lakes were trapped). The data indicate strong fidelity to specific lakes, especially because less than a hundred meters separate these lakes from many others with Barrow's Goldeneye. Fidelity rates, adjusted for survival and capture effort, on two lakes within the study area were 21% (Lake 2) and 55% (Lake 26). I believe the fidelity rate for Lake 2 is a minimum value for reasons already given.

Data quality and limitations

Because birds do not feed during the drive-trapping and handling process and are subjected to hours of swimming when they would most likely be resting, it is likely that they would experience some weight loss and possibly reduced ninth primary growth as a result of the capture and handling process. The magnitude and duration of effects due to the capture process of birds in this study are not known. Newton's (1967) study of captive finches found that disturbance could delay the progression of moult (shedding of feathers) but did not affect the growth of feathers already in moult. The fact that; (1) many recaptured birds in my study gained weight between captures, and (2) the mean weight of all birds in the study (those that were only captured once) decreased during moult, reassures me that the observed changes in body weight were due to the moult process and not due to effects of capture.

Significant yearly variation in the body mass and ninth primary length of moulting Lesser Snow Geese have been recorded (Williams et al. 1994) as have yearly variations in the percentage of weight lost during moult for male Teal (Sjoberg 1988). I investigated moult characteristics of Barrow's Goldeneye during the summer of 1995. Whether birds would exhibit similar change in body mass and ninth primary growth rates in years when environmental conditions are substantially different is open to speculation.

Four people identified, sexed, aged and banded birds during this study, and 2 people collected all the weights and measures. Some of the unexplained variability may have been due to misidentified birds, either age, species (Barrow's Goldeneye and Common Goldeneye can look very similar during moult), or sex (males look like females), or to biases between the individuals who weighed and measured birds. I believe errors in measurements due to different handlers would be minimal as sample sizes are large and birds were passed to handlers in a random fashion. However, misidentified birds could have contributed fairly large errors. Females are smaller than males and Common Goldeneye are smaller than Barrow's Goldeneye (Madge and Burn 1988). Fortunately, there are few Common Goldeneye and even fewer females on the Old Crow Flats (% of capture during 1994 and 1995, n = 1226: Barrow's Goldeneye, male = 95.6% female = 0.8%; Common Goldeneye, male = 2.6% female = 1.0%; CWS unpubl. data) so the chance of making a mistake were not large.

Conclusions

Rates of primary feather growth and weight change of moulting male Barrow's Goldeneye on the Old Crow Flats were consistent with average rates reported for other waterfowl species, and appeared unaffected by location (lake) or by the date remigial moult was initiated. There was a significant reduction in the body weight of adult males during the moult period. Loss of body weight to increase ninth primary growth rate, and thus reduce the flightless period, may have been a strategy used primarily by birds in good condition. I propose that selection favors a rapid moult period because survival risks during this vulnerable period are likely higher than during other periods of the annual cycle. Birds in good condition may be able to moult more quickly than birds in poor condition by using their nutrient/energy reserves to increase feather growth rates.

CHAPTER 2: HABITAT SELECTION BY MOULTING MALE BARROW'S GOLDENEYE IN NORTHERN YUKON

Introduction

During the flightless period of remigial moult, waterfowl require food and protection from predators. Because the energy and nutrient demands of moult are generally met through the diet at the time of feather synthesis (Ankney 1984, Thompson 1992, Hohman et al. 1997), a flightless bird is dependent on local food availability. Flightlessness also increases a bird's vulnerability to predation. The common observation that flightless birds are highly secretive and easily disturbed during moult (Hochbaum 1944, Bowman 1987, Thompson 1992, Panek and Majewski 1990) suggests that moult is a potentially risky undertaking. To minimize the costs associated with simultaneous wing moult, waterfowl should chose habitats that both provide abundant food and reduce predation risks (Hohman et al. 1992).

Many waterfowl species make long migrations to specific areas where they undergo remigial moult. Salomonsen (1968) suggests that moulting areas provide requirements not met on breeding areas; principally, seclusion from disturbance, low risk of predation, and abundant food. Non-breeding and failed nesting geese commonly leave breeding areas and migrate north to Arctic moulting sites (Salomonsen 1968). Owen and Ogilvie (1979) suggest that by migrating north geese can take advantage of abundant protein-rich food due to later spring growth. Johnson and Herter (1990) believe this "food hypothesis" best explains Arctic moult migrations. Long days and the relative absence of predators also are believed to be advantageous for geese moulting in the north

(Welty and Baptista 1990). Potential costs are a very short season, harsh climatic conditions and increased energy required for migration (Johnson and Herter 1990).

Although less common than in geese, some duck species also migrate north to traditionally used moult sites in the Arctic. In western North America, scientists have specifically targeted moult sites to band large numbers of moulting waterfowl (Yukon Flats, Alaska; King 1973, Old Crow Flats, Yukon; Mossop and Hayes 1977, Hawkings et al. 1995) but habitat selection by postbreeding waterfowl at these sites had not been investigated.

In this study, I investigate habitat selection by flightless male Barrow's Goldeneye on the Old Crow Flats in northern Yukon. I attempt to determine the factors influencing their selection of habitat at the local scale and, in particular, to test the hypotheses that moult habitats (lakes) are selected to 1) minimize the risk of predation, and 2) ensure abundant food resources. To test the influence of predation risk on habitat selection, I assumed that large lakes provided more protection from predators than small lakes and predicted that the density of Barrow's Goldeneye would be greater on large lakes (indicating selection of habitats based on predation risk). To test the influence of food on habitat selection, I assumed that total phosphorus, total nitrogen and/or chlorophyll would be good indicators of lake productivity and predicted that the density of Barrow's Goldeneye would be greater on productive lakes (indicating selection of habitats based on food availability).

Methods

Lakes with moulting Barrow's Goldeneye were selected randomly with the following exceptions: (1) 2 very large lakes >30 km^2 were not surveyed because it was difficult to obtain an accurate waterfowl estimate, and (2) lakes < 1 km^2 were not surveyed because they were too difficult to access by float plane. To compare physical and chemical characteristics of lakes, a sample of lakes without moulting Barrow's Goldeneye were selected based on their similarity (size, shape, color, submerged vegetation) to lakes already included in the survey.

When a lake with Barrow's Goldeneye (>1) was found, I did an intensive survey of the lake. The aircraft speed, altitude and flight path varied as required to provide the best coverage of each lake. In general, we flew the perimeter of the lake first and then across the middle, if necessary. Two crew members helped spot waterfowl and I estimated the number of birds present and marked their general location on a map. When a group of birds was very large or contained a mix of species, we landed on the lake and I surveyed the group using binoculars.

Physical and chemical characteristics were determined on each lake immediately following the waterfowl survey. A lake depth profile was obtained from the float plane using a Lorance X-16 Chart Recording Depth Sounder. The location and length of the transect was chosen so that it provided a general profile of the lake bottom, usually from the shore to the middle of the lake. The meter probe was suspended in the water while the plane taxied along the transect. An average lake depth was estimated from each profile chart. Lake area was determined from 1:50,000 topographical maps using a Sokkisha Compensation Planimeter.

I sampled lake water from the float plane near the middle of each lake. Temperature, conductivity, pH, dissolved oxygen and turbidity were measured with an Applied Micro Systems Aquamate 1000 multi-probe with internal datalogging set at 10 second intervals for approximately 15 minutes per site. At the end of each day, the data were downloaded and compiled on a Toshiba Laptop computer. Average values for each component were determined from the last 10 minutes of each session.

Two one-litre water samples were collected from each lake. Sterilized plastic bottles were rinsed twice with lake water, turned upside down, submerged roughly 30 cm, turned upright and filled. One water sample was refrigerated and the other was processed for future analysis of chlorophyll-a. The water sample was filtered through Watman 4.25cm GF/C (glass microfibre filter) in a 250 ml capacity filter holder. An electric and/or hand vacuum pump was used to facilitate the filtering process. The filters were folded in half, wrapped in aluminum foil and frozen. When the lake survey data collection was finished, the samples were packed on ice and sent to the Pacific Environmental Science Center Laboratory (North Vancouver, B.C.) to determine concentrations of total nitrogen, total phosphorus, sulphate, alkalinity, chlorophyll-a and total dissolved solids. Three replicate water samples and one replicate chlorophyll sample were included for data verification.

1995 water chemistry

During Barrow's Goldeneye captures in 1995 (Chapter 1), water chemistry was determined for 15 lakes of various size, including the five lakes where birds were trapped and measured. Methods were the same as previously described for the summer of 1996, except that separate instruments were used to measure conductivity and pH rather than an AMS Aquamate 1000. Equipment problems and poor weather hampered the data collection and delayed the processing of many samples. I have included only the data that I feel were of high quality (water samples sent to the Pacific Environmental Science Centre Laboratory, North Vancouver, B.C.).

Analysis

It is important that the unit used to express the density of birds on a lake be biologically relevant (Savard et al. 1994). Lakes on the Old Crow Flats were uniformly shallow (mean 1.67 m ± 0.09 SE) therefore, I assumed the entire lake bottom was accessible to feeding diving ducks and used the total lake surface area to express the density of Barrow's Goldeneye on each lake.

Variables which were not normally distributed (total nitrogen, sulphate, chlorophyll, lake area and duck density) were transformed using $\log(x + 1)$, except total phosphorus which was $-1/x$ transformed. Relationships between duck density and lake characteristics were examined by producing scatter plots and Pearson correlations (CORR, SAS Institute Inc. 1989). I examined the relationship between Barrow's Goldeneye density and the variables most likely to be good indicators of lake productivity (chlorophyll-a, total nitrogen, total phosphorus) using multiple linear regression analysis (REG, SAS Institute Inc. 1989). The t-test statistic (TTEST, SAS Institute Inc. 1989) was used to compare physical and chemical characteristics of lakes with and without Barrow's Goldeneye. I used a 5% level of significance for all tests. Unless otherwise stated, all analyses are based on data collected in 1996.

Results

A total of 29 lakes were surveyed between 29 July and 4 August, 1996: 21 lakes with Barrow's Goldeneye and 8 lakes without. Duck density on lakes with Barrow's Goldeneye was not significantly correlated with lake area (Table 8; $r = 0.10$, $P = 0.67$, $n = 21$), the physical lake characteristic used to test the hypothesis concerning predator avoidance. Duck density on lakes with Barrow's Goldeneye was significantly correlated with both total phosphorus and chlorophyll (Table 8; $P < 0.05$, $n = 21$, $r = 0.69$ and 0.51, respectively). A significant linear regression was found between duck density and total phosphorus concentration on lakes with Barrow's Goldeneye (Figure 7; $r^2=0.48$, $P < 0.001$, $df = 19$). Lake area was not significantly correlated with any of the chemical variables most likely to indicate lake productivity (chlorophyll, total nitrogen, total phosphorus) (Table 8).

Nitrogen-phosphorus (N:P) ratios of lakes in 1996 ranged from 56:1 to 12:1 (Table 9; mean ratio 32:1). In 1995, N:P ratios ranged from 55:1 to 15:1 (Table 10; mean ratio 33:1). There was a significant relationship between total nitrogen and total phosphorus (Table 8; $r = 0.52$, $n = 21$) and between chlorophyll and total phosphorus in

Table 8. Matrix of significant correlations between physical and chemical variables of lakes with moulting Barrow's Goldeneye (n = 21) on the Old Crow Flats, 1996. The first row is the Pearson correlation coefficient, the second row is the probability value.

	Duck density	Lake area	Lake depth	Nitrogen	Total Phosphorus	Chlorophyll	Alkalinity	pH	Conduct-ivity	Sulphate
Duck density	-									
Lake area	0.098 0.672	-								
Lake depth	-	-	-							
Nitrogen	-	-	-	-						
Total Phosphorus	0.6948 0.0005	-	-	0.5293 0.0136	-					
Chlorophyll	0.5143 0.0171	-	-	0.5272 0.0140	0.8401 0.0001	-				
Alkalinity	-	-	-	-0.5270 0.0141	-	-	-			
pH	-	-	-0.5256 0.0144	0.4628 0.0347	-	-	-0.5671 0.0073	-		
Conductivity	-	-	-	-0.6183 0.0028	-	-	0.8942 0.0001	-0.7585 0.0001	-	
Sulphate	-	-	-	-	-	-	-	-0.4782 0.0283	0.6179 0.0028	-

Table 9: Physical and chemical characteristics of 29 lakes on the Old Crow Flats collected July 29 - August 4, 1996.

Lake No.	Duck Density (#/km2)	Lake Area (km2)	Depth (m)	Nitrogen (ppm)	Total Phosphorus (ppm)	N/P	Chloro-phyll (ug/l)	pH	Conduct-ivity (um/s)	Alka-linity (ppm)	Sulphate (ppm)
2	84	1.25	1.6	0.64	0.026	25	3.2	9.4	145.04	78.1	5.8
3	78	3.20	2.4	0.57	0.018	32	1.8	9.1	172.39	98.1	4.7
10	23	2.60	2.2	0.68	0.017	40	1.7	8.6	165.87	92.0	4.5
22	0	2.03	2.5	0.64	0.017	38	3.8	9.1	172.55	106.0	4.6
26	98	7.65	1.5	0.70	0.022	32	4.6	10.1	98.45	63.2	3.2
28	21	1.40	2.3	0.79	0.022	36	4.7	8.4	174.24	99.8	6.3
32	369	2.25	2.0	0.91	0.034	27	2.6	9.0	86.11	55.8	2.3
39	171	5.50	1.8	0.83	0.020	42	3.2	9.9	110.64	65.6	5.0
42	0	8.15	1.2	0.73	0.015	49	1.7	9.2	120.00	64.7	24.0
46	36	1.25	1.5	0.73	0.022	33	3.9	9.4	135.69	79.1	5.2
47	0	1.60	2.4	0.70	0.018	39	4.8	9.0	150.53	87.9	5.7
66	0	0.88	1.4	0.78	0.015	52	2.2	9.3	110.00	67.2	5.5
68	0	3.28	0.7	0.66	0.023	29	2.0	9.3	88.00	81.7	5.5
80	19	3.17	1.6	0.73	0.016	46	3.0	10.4	95.20	71.0	2.8
81	121	7.65	1.6	0.88	0.025	35	5.8	9.9	102.55	52.3	6.3
82	0	5.18	1.5	1.00	0.024	42	8.8	8.9	159.30	85.0	13.0
83	77	3.00	1.0	0.75	0.023	33	3.5	9.3	140.90	82.0	5.4

Table 9, cont.

Lake No.	Duck Density (#/km2)	Lake Area (km2)	Depth (m)	Total Nitrogen (ppm)	Total Phosphorus (ppm)	N/P	Chlorophyll (ug/l)	pH	Conductivity (um/s)	Alkalinity (ppm)	Sulphate (ppm)
84	159	0.88	1.2	0.94	0.027	35	4.9	10.2	116.72	88.4	0.9
85	0	1.70	0.7	1.09	0.073	15	8.1	7.6	51.01	26.3	13.0
86	12	2.15	1.5	0.78	0.014	56	0.9	10.4	107.50	74.1	1.9
87	25	1.63	1.2	0.91	0.039	23	6.2	9.2	114.29	76.9	2.6
88	315	4.13	2.0	0.93	0.055	17	11.0	9.5	119.18	70.6	3.4
89	0	8.23	1.5	0.74	0.028	26	4.4	9.7	103.28	56.8	6.3
90	68	12.93	2.2	0.55	0.025	22	3.8	8.6	147.20	88.7	3.0
91	307	2.28	1.6	0.63	0.031	20	4.9	9.0	168.87	103.0	6.7
92	136	2.73	1.5	0.71	0.028	25	3.7	8.9	167.57	99.7	6.4
94	57	5.43	2.2	0.62	0.022	28	3.5	8.8	188.05	110.0	8.3
95	26	3.43	2.0	0.66	0.022	30	3.0	9.9	112.80	83.9	1.6
96	264	1.38	1.5	1.09	0.090	12	8.7	10.4	102.40	76.5	4.5
Mean	85	3.69	1.7	0.77	0.028	32	4.3	9.3	128.49	78.8	5.8
± SE	± 19.76	± 0.53	± 0.09	± 0.03	± 0.003	± 2	± 0.44	± 0.12	± 6.24	± 3.41	± 0.83

Table 10. Physical and chemical characteristics of 15 lakes on the Old Crow Flats collected August 3-4, 1995.

Lake	pH (rel.U)	Nitrogen (ppm)	Phosphorus (ppm)	N:P ratio	Sulphate (ppm)
1	8.2	0.63	0.014	45:1	9.80
2	8.8	0.75	0.031	24:1	5.70
3	8.4	0.54	0.018	30:1	4.90
8	7.8	0.93	0.017	55:1	4.70
11	9.1	0.74	0.020	37:1	4.10
22	8.3	0.70	0.016	44:1	3.80
24	9.1	0.77	0.022	35:1	2.50
26	8.6	0.76	0.025	30:1	5.10
33	7.6	0.79	0.052	15:1	5.80
39	9.0	1.08	0.038	28:1	4.20
41	9.2	0.62	0.026	24:1	8.80
42	9.6	0.70	0.020	35:1	21.70
46	8.8	0.64	0.018	36:1	5.30
47	8.2	0.73	0.015	47:1	4.90
68	8.4	0.76	0.049	16:1	6.00
Mean(±SE)	8.6 ± 0.1	0.74 ± 0.03	0.025 ± 0.003	33:1	6.49 ± 1.18

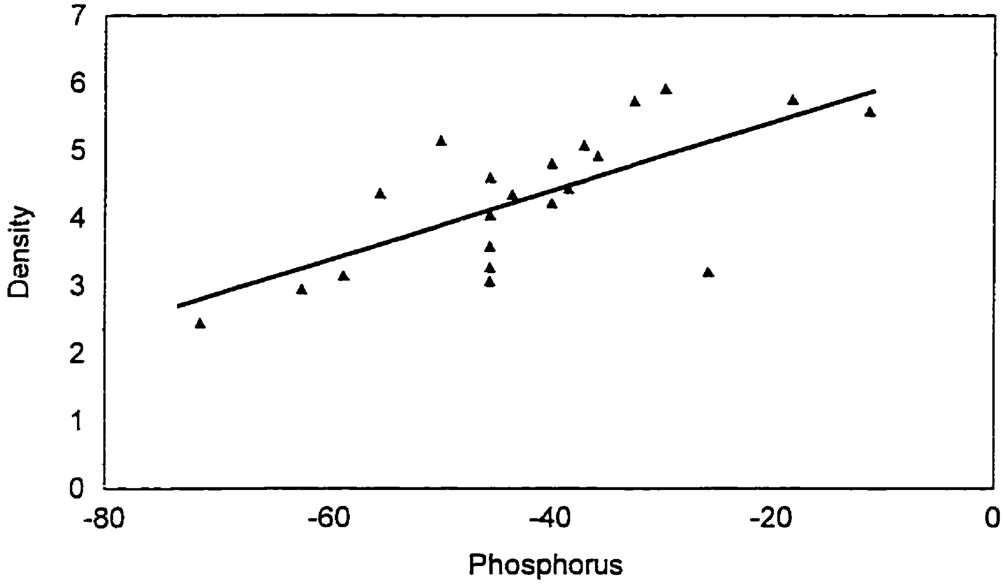


Figure 7. Relationship between duck density and total phosphorus for lakes with flightless male Barrow's Goldeneye (n = 21) on the Old Crow Flats, 1996 (n = 21, y = 6.43 + 0.05x, P < 0.001, r^2 = 0.48). Values are transformed: density = log(x +1), phosphorus = -1/x.

lakes with Barrow's Goldeneye (Figure 8; $r^2 = 0.71$, $P < .001$, df = 19). Physical and chemical characteristics of lakes used by Barrow's Goldeneye (n = 21) on the Old Crow Flats were not significantly different than those of lakes not used (n = 8) (Table 11). There was a marginally significant difference in the concentration of sulphate between lakes with and without moulting male Barrow's Goldeneye (Table 11; $P > |T| = 0.058$, df = 27). Lakes with Barrow's Goldeneye were alkaline (pH: mean 9.45 ppm ± 0.14 (SE)), had an average depth of 1.7 m ± 0.09 (SE), and ranged in size from 0.88 km^2 to 13 km^2 (mean 3.61 km^2 ± 0.63 (SE)).

Discussion

Distribution of Barrow's Goldeneye in relation to lake productivity

Phosphorus is generally considered to be the most common growth-limiting element in fresh water (Horne and Goldman 1994). In most lakes, there is a direct relationship between the concentration of the growth-limiting element and the maximum crop of phytoplankton, as expressed by chlorophyll-a (Horne and Goldman 1994). The regression coefficient in this study suggests that 71% of the variation in chlorophyll-a was explained by total phosphorus (Figure 8). Hence, phosphorus may be limiting phytoplankton production. Further evidence is found in the nitrogen-phosphorus ratios (N:P). A common lake N:P ratio is 10:1, with higher ratios indicating a deficiency of phosphorus (Horne and Goldman 1994). In the lakes studied, the average N:P ratio was 32:1 with a minimum ratio of 12:1 (Table 9). The similarity between N:P ratios in 1995 and 1996 (Tables 10 and 11) may suggest that phosphorus limitation is an annual event

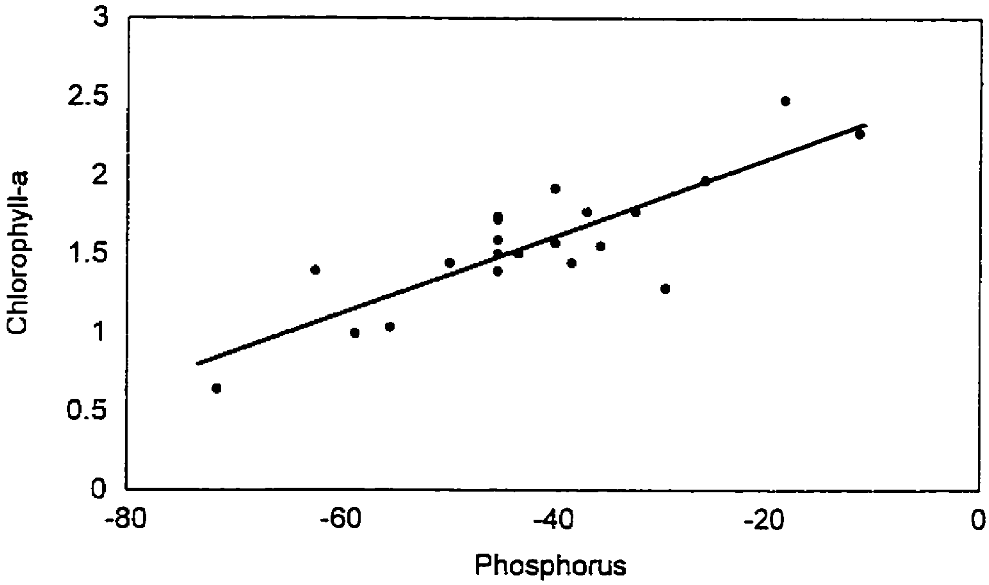


Figure 8. Relationship between total phosphorus and chlorophyll for lakes with flightless male Barrow's Goldeneye on the Old Crow Flats, 1996 ($n = 21$, $y = 2.60 + 0.02x$, $P < 0.001$, $r^2 = 0.71$). Values are transformed: phosphorus = $-1/x$, chlorophyll = $\log(x + 1)$.

Table 11. Mean (±SE) physical and chemical values for lakes with (n = 21) and without (n = 8) flightless male Barrow's Goldeneye on the Old Crow Flats, 1996.

		Lakes with Barrow's Goldeneye (n = 21)			Lakes without Barrow's Goldeneye (n = 8)		
Variable	Unit	Mean ± SE	Min	Max	Mean ± SE	Min	Max
ALKALINITY	ppm	81.37 ± 3.41	52.30	110.00	71.95 ± 8.52	26.30	106.00
CHLOROPHYLL	ug/l	4.22 ± 0.50	0.90	11.00	4.48 ± 0.96	1.70	8.80
CONDUCTIVITY	um/s	131.98 ± 6.78	86.11	188.05	119.33 ± 14.27	51.01	172.55
DEPTH	m	1.73 ± 0.09	1.00	2.40	1.49 ± 0.24	0.70	2.50
LAKE AREA	km^2	3.61 ± 0.63	0.88	12.93	3.88 ± 1.05	0.88	8.23
NITROGEN	ppm	0.76 ± 0.03	0.55	1.09	0.79 ± 0.06	0.64	1.09
PH	rel.U	9.45 ± 0.14	8.43	10.44	9.02 ± 0.22	7.59	9.67
PHOSPHORUS	ppm	0.028 ± 0.004	0.014	0.090	0.027 ± 0.007	0.015	0.073
TDS	ppm	114.76 ± 5.55	80.00	170.00	108.75 ± 13.29	70.00	170.00
SALINITY	ppm	0.08 ± 0.00	0.05	0.12	0.08 ± 0.01	0.03	0.11
SULPHATE*	ppm	4.32 ± 0.43	0.90	8.30	9.70 ± 2.37	4.60	24.00

* marginally significant P > |T| = 0.058 at alpha 0.05

and not just a phenomenon of 1996. Both the total phosphorus-chlorophyll relationship and N:P ratios suggest that phosphorus is limiting production in the lakes studied and therefore total phosphorus should be a good index of lake productivity. I found that Barrow's Goldeneye density and total phosphorus were positively related. A similar relationship between waterfowl densities and total phosphorus was found by Nilsson and Nilsson (1978). The positive relationship between Barrow's Goldeneye density and total phosphorus supports the food hypothesis which predicted that Barrow's Goldeneye chose lakes to secure abundant food resources.

An alternative explanation for the observed relationship between duck density and total phosphorus is that duck foraging and excrement deposited in lakes may have facilitated the turnover rate of nutrients, such as nitrogen and phosphorus, thus sustaining or enhancing net primary productivity. Gere and Andrikovics (1994) suggest that the trophic states of small lakes can be easily changed by a dense duck population due to consumption of food items and deposition of excrement. The trophic states of lakes with low water flows are particularly susceptible (Marion et al. 1994), as are phosphorus limited lakes (Manny et al. 1994). Lake eutrophication has been demonstrated to occur with fish. High predation pressure from fish can make plankton communities develop towards a composition of species with high turn-over rates of nutrients and result in a change in lake trophic status in the absence of changes in external nutrient loading (Andersson et al. 1978, Henrikson et al. 1980). Increased turn-over rates of nutrients could be particularly beneficial in summer, when all or nearly all the soluble (biologically available) phosphorus in fresh water lakes can become bound in living biomass or bottom sediments (Moyle 1946). Lakes in my study were generally small, shallow, with little or no inflow or outflow, and were phosphorus-limited. Hence, lakes may have been influenced by duck foraging and excrement. Unlike geese, dabbling ducks and colonial nesters that obtain nutrients from sites on shore (Gere and Andrikovics 1994, Marion et al. 1994, Manny et al. 1994), moulting diving ducks on the Old Crow Flats were limited to feeding on lakes. Other than the initial nutrients brought to a lake on arrival and during pre-moult, they could not contribute additional phosphorus to the lake. If large densities of ducks increase the productivity of lakes via nutrient recycling then I would expect confounding factors to bias the data. For example, very large lakes may not respond to nutrient loading as quickly or as effectively as smaller lakes and individuals may benefit by choosing a lake with a high duck density.

Distribution of Barrow's Goldeneye in relation to predation risk

Large lakes were not significantly correlated with duck density so the data do not support my prediction that moulting Barrow's Goldeneye select large lakes to minimize the risk of predation. Apparently, either (1) habitats at the local level were not selected based on predation risk, or (2) predation risk was not significantly correlated with lake size (in which case, I chose a poor indicator). Although I did not directly investigate predation risk, evidence of predation on moulting waterfowl has been found in other studies. The remains of moulting geese have been found in Arctic fox dens (Owen and Ogilvie 1979). In a study of flightless Black Ducks, 2 of 23 radio-marked birds were killed by predators (Bowman and Longcore 1989). As well, shifts in habitat use suggest that predation risk influences habitat selection. Fox et al. (1994) observed that wintering White-headed Ducks fed singly but gathered into rafts to preen, rest and sleep. Rafting was a behavioral strategy used by moulting ducks to avoid predation and was not related to foraging efficiency. Thompson (1992) attributed the use of offshore sites by moulting Canvasbacks to avoidance of mammalian predators, particularly mink (*Mustela vison*).

Similarly, I observed moulting male Barrow's Goldeneye on the Old Crow Flats associated in large groups and in open water. On three occasions, I witnessed birds feeding and each time individuals fed singly while those resting were in loosely formed rafts, often in the company of moulting Canvasback and scaup (*A. marila* and *A. affinis* The slightest disturbance caused loose aggregations to form into tightly knit large groups. I never witnessed diving ducks feeding while in these tight groups so I suspect that groups were formed to reduce individual predation risk.

The only likely predators of moulting diving ducks on the Old Crow Flats are Bald Eagles (*Haliaeetus leucocephalus*) and mink. There are 7 known pairs of Bald Eagles on the Old Crow Flats (D. Mossop, pers. comm.), roughly 1 pair for every 700 km^2. I spent a total of 11 weeks on the Old Crow Flats during July and August of 1994-1996 and during that time, I observed a Bald Eagle on only three occasions. Each observation occurred in 1996 and each sighting was in an area of marsh frequented by dabbling ducks and geese. Thus, indirect evidence suggests that predation risk for diving ducks on the Old Crow Flats is likely small.

Relationships between bird abundance and pond features are complex (Savard et al. 1994) and in such a complex system it is highly unlikely that any one factor would determine habitat choice. For instance, lakes without Barrow's Goldeneye tended to have higher sulphate concentrations than lakes with Barrow's Goldeneye. Sulphate concentrations can affect the distribution and survival of large aquatic plants (Moyle

1946), and aquatic plants provide cover from predators as well as affect the species richness and abundance of invertebrates. Thus, aquatic plants could satisfy a need for both predator avoidance and food.

It is likely that a combination of factors influenced the abundance of moulting ducks on lakes (Savard et al. 1994) and that interactions between these factors contributed to the unexplained error in the relationships that I observed. Although habitat selection based on predation risk was not demonstrated in this study, indirect evidence suggests it is an important factor influencing anti-predator behavior. I speculate that ducks that migrate to the Old Crow Flats to moult may do so because the risk of predation there is low. Hence, once they arrive, it is important that they find a habitat (lake) that will provide abundant food. In this case, habitat selection on a 'macro' scale (migration to the Old Crow Flats) may be a predator avoidance strategy, while habitat selection on a 'micro' scale (selection of lake) satisfies the need for food.

Data quality and limitations

Generally, one would take replicate samples from various locations on one lake to ensure data quality. I sampled each lake from only one location on the assumption that one sample would be representative because; (1) all lakes were uniformly shallow and well mixed due to wind action, (2) lakes were sampled randomly, and (3) the sampling period was fairly short and weather conditions were consistent. My assumption was supported by consistent results among 3 samples taken from one lake (total phosphorus (ppm)- 0.13, 0.12, 0.13, total nitrogen (ppm)- 0.78, 0.78, 0.77, alkalinity (ppm)- 82.3, 82.3, 81.9, sulphate (ppm)- 12, 12, 11).

My interpretation of the data assumes that flightless birds were "captive" on their lake and did not walk overland to other lakes. I believe this assumption is valid because flightless diving ducks rarely are seen on shore; and because lakes on the Old Crow Flats tend to have very steep banks of willow and birch which would make it difficult for a diving duck to climb. As well, I never witnessed any flightless ducks attempt to avoid being captured by climbing the shore; rather, flightless diving ducks swam or dove to avoid capture.

I investigated only a few of the many possible factors affecting habitat selection by moulting Barrow's Goldeneye. Many other factors could influence lake choice. First, I determined the number of flightless Barrow's Goldeneye on each lake but did not quantify the number of dabbling duck or other flightless diving ducks. Social interactions could influence lake choice. However, Barrow's Goldeneye were often found in groups with Common Goldeneye, Canvasback, scaup and Oldsquaw which argues against the importance of social interactions affecting habitat choice. Second, I often found large groups of moulting ducks gathered along shore or in island bays seeking shelter from the wind. However, lakes in the study area tend to be oriented perpendicular to the prevailing wind and have similar shoreline vegetative cover so I feel the availability of shelter would be similar on most lakes. Third, the abundance of fish may influence habitat selection by ducks (Eriksson 1983). I did not determine the presence of fish or their possible influence on habitat selection by ducks. Fourth, aquatic plants provide habitat for invertebrates, and food and escape cover for ducks. I did not quantify the species, abundance or distribution of aquatic plants as, generally, lakes on the Old Crow Flats have abundant aquatic vegetation.

Conclusions

Limited phosphorus in relation to nitrogen and a strong correlation between phosphorus and chlorophyll concentration suggests that lakes on the Old Crow Flats are phosphorus limited during the remigial moult of male Barrow's Goldeneye. Significant correlation between duck density and total phosphorus supports the hypothesis that moulting ducks seek habitats that will provide abundant food. An alternative explanation which merits further study is that lake productivity may be positively influenced by duck density via nutrient recycling. No supporting evidence for the predator hypothesis was found on a 'micro' habitat scale (lake selection). I speculate, based on indirect evidence, that migration to the Old Crow Flats may be a predator avoidance strategy on a 'macro' habitat scale (moult site location).

GENERAL DISCUSSION

During the annual cycle, birds make physiological, metabolic, morphological, and behavioral adjustments to minimize discrepancies between nutrient intake and nutrient demand (King and Murphy 1985). The timing of moult generally does not overlap with other energetically expensive events in the annual life cycle (Lovvorn and Barzen 1988, Hohman et al. 1992) which reduces daily nutrient and energy demands. During moult, bird's may also reduce daily nutritional costs by, (1) maintaining low body mass to reduce maintenance costs (Ankney 1979), (2) decreasing the intensity of moult (Murphy 1996), (3) decreasing activities (Thompson 1992), or (4) some combination of the above adjustments. Even when sufficient exogenous nutrients are available, a bird may chose to use endogenous reserves if there is an advantage in doing so (Baily 1985); for example, to avoid predation (Panek and Majewski 1990) or regain flight sooner (Douthwaite 1976, Owen and Ogilvie 1979, Bowman 1987, Thompson 1992, Hohman et al. 1997). Thus, weight loss may be an adaptive adjustment birds use to minimize nutritional and non-nutritional strains in the annual cycle (Murphy 1996) and is not necessarily indicative of nutritional stress (King and Murphy 1985). My research supports the hypothesis that weight loss is an adaptive strategy that some flightless birds use to regain flight sooner, and suggests that birds with sufficient endogenous reserves may use them not simply to meet the energy demands of moult or to loss body mass, but also to increase the rate of moult.

Management implications and research needs

Traditional use of the Old Crow Flats by moulting Barrow's Goldeneye has long been known by the Vuntut Gwitchin people of Old Crow and has been documented previously (Mossop and Hayes 1977, Hawking et al. 1995). This study shows that individual birds are philopatric to the Old Crow Flats and to specific lakes within the area. Barrow's Goldeneye are also philopatric to wintering and breeding sites (Savard 1987) so it is possible that this species winters, breeds and moults entirely within Alaska and Yukon. Management of this species would be improved if the wintering, breeding and moulting locations of local populations were known. Such knowledge would allow managers to more easily assess threats and could lead to better population monitoring. For instance, Barrow's Goldeneye are flightless and highly concentrated on the Old Crow Flats so surveys during moult may be an effective and efficient way of monitoring population trends. Radio-marking birds on the Old Crow Flats and on wintering areas in Alaska may help determine the origin of these birds.

One common attribute of moulting sites is that they are secluded from human disturbance. Birds typically become less active during moult which has been suggested to have the advantage of decreasing daily energy requirements (Murphy 1996) and exposure to predators (Panek and Majewski 1990). Birds exposed to human disturbance have experienced temporary weight loss (capture effect; Owen and Ogilvie 1979, Panek and Majewski 1990), abandoned preferred habitats (capture effect; Bowman 1987, Panek and Majewski 1990, boating activity; Bergman 1973) and changed their behavior (Panek and Majewski 1990). Thus, disturbance which would increase the activity of moulting birds would likely increase daily energy expenditures, may increase exposure to predators, and may force birds out of preferred habitats. To improve management of postbreeding waterfowl, the effects of disturbance and the coping ability of birds, need to be quantified so that survival and fitness consequences of potential industrial developments and human activities can be estimated.

Further research is needed into the relationship between duck density and total phosphorus levels in lakes. Do duck densities influence lake productivity? If so, does this process promote moult site fidelity? As well, very little information exists regarding the diet of moulting diving ducks, this topic also requires further investigation.

Old Crow Flats

The traditional use of wetlands by postbreeding waterfowl suggests that these areas possess unique attributes that make them suitable for moult (Hohman et al. 1992). Ideally, these areas would be protected from development and from human activities which may disturb birds. Realistically, the conservation of these areas will depend on careful management of at least some level of human activity. There are currently no industrial developments on the Old Crow Flats. The people of Old Crow hunt caribou on the Old Crow Flats during the winter and trap muskrats during the spring. In general, no human activity occurs during the summer. However, interest in this area may increase in the future due to recent changes in land management.

In 1995, under the terms of the Vuntut Gwitchin Final Agreement, the northern portion of the Old Crow Flats (north of the Old Crow River) became Vuntut National Park. Most of the remainder is settlement land belonging to the Vuntut Gwitchin First Nation and some remains federal crown land. The entire area has been recognized as a

Special Management Area (SMA) under the land claim agreement and a management priority is the conservation of fish, wildlife and their habitats, in particular migratory birds (Hawkings et al. 1995). The management plan currently being drafted for the park and the SMA area can benefit from my study. I recommend minimal disturbance of birds during July and August because these are the months when most Barrow's Goldeneye (and possibly other moulting diving ducks such as Canvasback and scaup) are likely to be flightless. Managers may want to consider avoiding developments near lakes with high concentrations of moulting ducks because of the philopatry demonstrated by some individuals.

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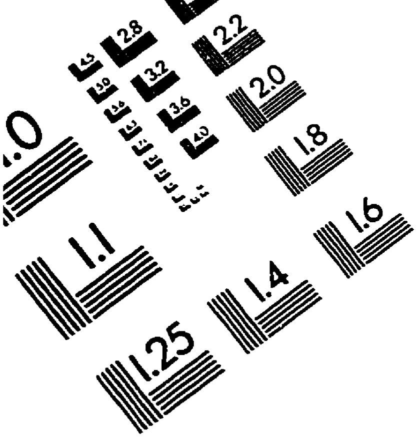

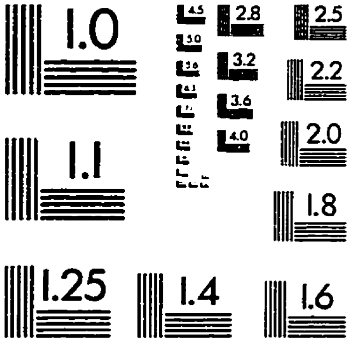

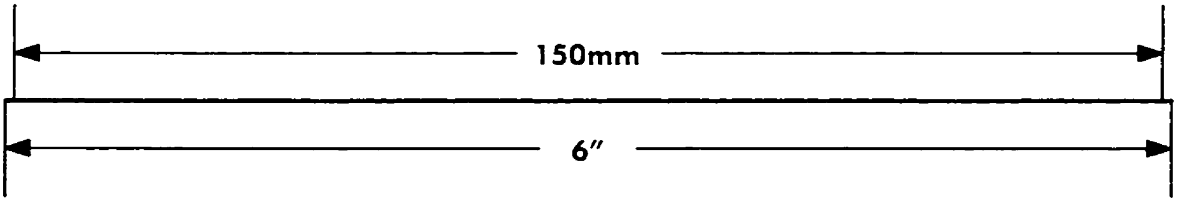

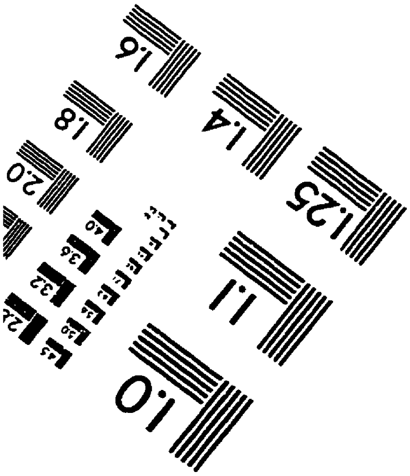

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