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COMPARATIVE REPRODUCTIVE ECOLOGY OF FEMALE BUFFLEHEADS (*Bucephala albeola*) AND BARROW'S GOLDENEYES (*Bucephala islandica*) IN CENTRAL BRITISH COLUMBIA

by

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Submitted in partial fulfilment
of the requirements for the degree of
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ABSTRACT

Waterfowl (Anseriformes) generally have high energetic costs for reproduction because they lay large, energy-rich eggs. Consequently, many temperate nesting ducks (Anatinae) occupy seasonally productive environments to meet nutritional requirements for egg production. However, ducks in the genus *Bucephala* often breed in unproductive boreal and montane regions. This study was conducted to investigate nutritional aspects of reproduction in female Buffleheads (*Bucephala albeola*) and Barrow's Goldeneyes (*Bucephala islandica*) breeding in central British Columbia.

Diet composition of breeding female Buffleheads and Barrow's Goldeneyes, which consisted primarily of benthic insects, was similar, providing support for the food defense hypothesis as an explanation for evolution of fixed space territoriality in the genus *Bucephala*.

Mean egg laying interval (± SE) for Buffleheads was 48.36 ± 2.35 hr, which was similar to that of Barrow's Goldeneyes that laid, on average, every 45.32 ± 1.40 hr. As a consequence of slower rates of egg production, daily energetic costs of reproduction in female Buffleheads and Barrow's Goldeneyes, evaluated relative to their basal metabolic requirements, are among the lowest documented for ducks.

Patterns of lipogenesis differed between female Buffleheads and Barrow's Goldeneyes, but both species catabolized somatic fat for egg production. Buffleheads maintained stable body protein during reproduction, and thus relied exclusively on dietary protein for clutch formation, whereas Goldeneyes catabolized small amounts of somatic protein to produce egg protein in 1993. Use of body protein by a primarily carnivorous duck suggests that protein availability, i.e. invertebrate abundance, in breeding habitats used by Goldeneyes was periodically deficient. Somatic mineral supplied approximately 8% of clutch minerals in Buffleheads and 3% of clutch minerals in Goldeneyes during the

1993 breeding season, but neither species used endogenous minerals for eggshell production in 1994.

Size of lipid and protein reserves did not limit clutch size in either Buffleheads or Barrow's Goldeneyes. Furthermore, clutch size was negatively related to somatic mineral mass in Buffleheads, but positively related to clutch size in Barrow's Goldeneyes. Thus, from a nutritional perspective, only mineral availability limited clutch size in Barrow' Goldeneyes, whereas relatively low rates of somatic tissue catabolism suggested that nutrient availability may not constrain clutch size in Buffleheads.

Keywords: reproductive ecology, nutritional ecology, diet composition, egg laying interval, clutch size, nutrient reserves, Bufflehead, *Bucephala albeola*, Barrow's Goldeneyes, *Bucephala islandica*

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CHAPTER 1. GENERAL INTRODUCTION

1.1 COSTS OF REPRODUCTION IN WATERFOWL

Waterfowl (Anseriformes) are nidifugous birds that have relatively high nutritional costs for reproduction compared to altricial and other precocial birds (King 1973, Ricklefs 1974, Walsberg 1983, Alisauskas and Ankney 1992). The concept of "higher costs" for reproduction in waterfowl originates primarily from characteristics associated with their eggs, including their high energy density (kJ/g) and large size relative to the body mass of females producing them (Lack 1967, 1968). Furthermore, many species of ducks (Anatinae) produce these large, energy-rich eggs on a daily basis (Drobney 1980, Alisauskas and Ankney 1994). To meet nutritional requirements for clutch formation, however, many species of waterfowl store nutrients (i.e., lipids, protein, and mineral) as somatic tissue and catabolize them when demands for these substrates exceed dietary intake (see review in Alisauskas and Ankney 1992). Furthermore, many species of waterfowl breed in highly productive habitats (e.g., prairie wetlands and northern river deltas) increasing exogenous nutrient availability to laying females.

There are, however, several genera of waterfowl, including Mergansers (*Mergus* spp.), Goldeneyes (*Bucephala* spp.), and Scoters (*Melanitta* spp.) adapted to breed in less productive boreal and montane regions. Perhaps, the most significant adaptation to lower exogenous nutrient availability in these species has been to lengthen the time required for clutch formation, thereby extending egg laying intervals and reducing daily nutritional requirements. Furthermore, species in the genus *Bucephala* defend spatially distinct breeding and brood rearing territories, which may maintain high quality foraging sites in otherwise unproductive habitats. Clutch size in waterfowl nesting in environments with low nutrient availability may be strongly influenced by tradeoffs with other energy demanding activities such as incubation or territorial defence of brood rearing areas. Therefore, these species may curtail energy investment in their clutch to maintain sufficient energy reserves for incubation (see Ankney and MacInnes 1978) or to defend exclusive foraging areas for their young.

This study was conducted to investigate the nutritional tactics for reproduction in female *Bucephala* and to determine factors that may proximately constrain clutch size in ducks nesting in unproductive montane environments. Adaptive significance of diet composition, nutrient reserves, and habitat quality to breeding female Buffleheads (*Bucephala albeola*) and Barrow's Goldeneyes (*Bucephala islandica*) were studied in central British Columbia in 1993 and 1994. Egg laying intervals and their effect on the energetic costs of reproduction in these species were studied during the 1995 breeding season.

1.2 REPRODUCTIVE ECOLOGY OF THE *BUCEPHALA*

1.2.1 *Species in the genus Bucephala*

The genus *Bucephala* consists of only three species, including Bufflehead, Common Goldeneyes (*B. clangula*), and Barrow's Goldeneyes. Body mass varies considerably among these species with nonbreeding Barrow's Goldeneye females ($\bar{x}$ = 799 g, *n* = 16; Chapter 4) being approximately 2.5 times heavier than nonbreeding female Buffleheads ($\bar{x}$ = 328 g, *n* = 18; Chapter 4). Female Common Goldeneyes from central Canada have an intermediate mean body mass ($\bar{x}$ = 659 g, *n* = 34; Eadie et al. 1995), but average mass of this species varies widely over its broad geographic range (Cramp and Simmons 1977, Eadie et al. 1995).

1.2.2 *Distribution and populations of species in the genus Bucephala*

All species in the genus *Bucephala* breed in North America, but the breeding distribution of both species of Goldeneyes extend into the Palearctic (Palmer 1976, Bellrose 1980, Cramp and Simmons 1977). Buffleheads are restricted to the Nearctic (Palmer 1976, Bellrose 1980), with only accidental records from western Europe (Cramp and Simmons 1977). The continental population of Buffleheads is estimated at 1 - 1.4 million birds (Gauthier 1993), but this estimate is likely conservative given that much of this species' breeding range is not covered by the May North American Waterfowl Survey conducted annually by the United States Fish and Wildlife Service and the Canadian Wildlife Service (CWS). Barrow's Goldeneyes have a discontinuous range in North America with northeastern (Atlantic) and northwestern (Pacific) populations isolated from one another by several thousand kilometers (Palmer 1976, Bellrose 1980). The Pacific population of Barrow's Goldeneyes, which breeds primarily in British Columbia, the Yukon, Alaska, and the Pacific northwestern states, is estimated at approximately 180,000 birds (Savard 1987a), whereas the Atlantic population, which consists of eastern Quebec (Reed and Bourget 1977) and Icelandic (Bengston 1972, Gardarsson 1979) subpopulations, numbers slightly < 5000 birds. Common Goldeneyes have a Holarctic distribution and generally breed in forested habitats at latitudes >50° N (Cramp and Simmons 1977, Eadie et al. 1995). Bellrose (1980) estimated that the North American Common Goldeneye population consisted of approximately 1.25 million birds, but this estimate likely suffers from the same bias in estimating the continental population of Buffleheads, namely that much of the boreal habitat used by these species is not adequately surveyed (Eadie et al. 1995).

The breeding distribution of *Bucephala* in North America is principally confined to forested areas in boreal and northern montane ecosystems. Buffleheads breed throughout the aspen parklands in the Northern Great Plains, but predominantly nest in boreal and lower altitude montane forests in Canada and Alaska (Gauthier 1993). Buffleheads apparently reach their highest breeding density (3.3 - 10 birds/sq. mile) in the Cariboo and Chilcotin districts of central British Columbia (Munro 1942, Bellrose 1980). Over 60% of the world's population of Barrow's Goldeneye breed in British Columbia (Savard 1987a), and though few area-specific density estimates exist, breeding pair counts suggest that similar to Buffleheads, they reach their maximum breeding density in the aspen parklands of British Columbia. Densities of breeding Common Goldeneyes are generally low over most of their range (1 - 17 pairs/100 km^2; see review in Eadie et al. 1995), but are apparently highest in the Athabasca River Delta of the Northwest Territories (Bellrose 1980).

Although the breeding ranges of Barrow's and Common Goldeneyes have considerable overlap, interspecific differences in habitat use typically separate these species during reproduction. In central British Columbia, for instance, Barrow's Goldeneyes typically breed on wetlands with higher alkalinity and salinity (Munro 1918, 1939, Savard 1984) than those used by breeding Common Goldeneyes. Moderately alkaline and saline wetlands tend to be more productive than other montane wetlands (Rawson and Moore 1944, Cannings and Scudder 1978) and often lack fish, which compete with female *Bucephala* for aquatic invertebrates (Savard 1987a); thus, these habitats likely represent higher quality foraging sites for female Goldeneyes (Eriksson 1978, 1983, Eadie and Keast 1982). Therefore, it is possible that the larger Barrow's Goldeneyes exclude Common Goldeneyes from fishless wetlands in British Columbia, particularly given the aggressive interspecific territoriality exhibited by this species toward its congeners (see below).

The competitive exclusion hypothesis is supported by habitat use of breeding Common Goldeneyes in eastern Canada, which preferentially nest on fishless wetlands in the absence of Barrow's Goldeneyes. Interestingly, Common Goldeneyes have actually benefitted from wetland acidification in boreal habitats, which has reduced or eliminated insectivorous fish populations in some wetlands (McNicol and Wayland 1992, Mallory et al. 1994). This also suggests that Common Goldeneyes are perhaps better adapted to more acidic wetlands than those typically used by Barrow's Goldeneyes. Buffleheads nest in a broad range of wetland types (Erskine 1972) and breed sympatrically with one or both species of Goldeneyes over most of their range.

1.2.3 *Nest site characteristics*

The *Bucephala* are primarily arboreal cavity nesters in North America, but Barrow's Goldeneyes breeding in Iceland generally nest on the ground (Scott 1952) or in rock crevices (Cramp and Simmons 1977). Similarly, Common Goldeneyes nesting in the northernmost limits of their distribution are reported to use ground cavities created by boulders or rocks (Palmer 1976, Bellrose 1980), but they generally nest in tree cavities throughout most of their range. Arboreal nest cavities used by Buffleheads are typically created by Northern Flickers (*Colaptes auratus*), whereas those used by Common and Barrow's Goldeneyes are generally excavated by Pileated Woodpeckers (*Dryocopus pileatus*). Other natural cavities used by female *Bucephala* originate from weathered holes created by fallen tree limbs and hollowed out areas in the tops of broken off trees. Buffleheads and both species of Goldeneyes also use nest boxes (Savard 1988a, Gauthier 1988, Lumsden et. al. 1980, 1986), which is a characteristic often exploited by biologists to facilitate research on the breeding biology of these species (see below). Goldeneyes consistently use a larger proportion of suitable nest boxes than Buffleheads (Savard 1988a, Gauthier 1988, Lumsden et. al. 1980, 1986, see below), suggesting that Goldeneyes are more nest site limited than are Buffleheads.

1.2.4 *Alternative reproductive tactics*

An alternative reproductive tactic that has evolved in the *Bucephala*, possibly as a result of nest site limitation, is intraspecific brood parasitism (i.e., one female laying her eggs in the nest of another female or host). Consistent with the possibility of nest site limitation, brood parasitism occurs much more frequently in Goldeneyes than in Buffleheads. Furthermore, both species of Goldeneyes are interspecific brood parasites, commonly parasitizing each other (Eadie 1989) and occasionally Buffleheads when their nest sites are large enough for Goldeneyes to enter (Erskine 1959, 1990, J. Thompson, pers. observ.). Bufflehead eggs have been found in the nests of Golden.yes, but this probably represents displacement of the former species rather than interspecific brood parasitism, particularly because female Goldeneyes are reported to kill Buffleheads if they encounter them in larger nest cavities (Erskine 1959).

Generally, most female *Bucephala* do not lay parasitically, but a fraction of the population are seasonally obligate or facultative brood parasites (Eadie 1989). Why these females adopt this alternative reproductive tactic is not clear, but it has been theorized that parasitic females are young or lower quality birds that have not secured their own nest sites. It is unclear what proportion of these parasitically laid eggs result in birds recruited to the breeding population, so the ultimate consequences of this behavior remain unknown.

1.2.5 *Territoriality in breeding Bucephala*

Species in the genus *Bucephala* are the only North American Ducks in which males and females defend spatially and temporally stable territories during breeding (Savard 1984). This differs from most other ducks, wherein males defend a revolving territory around their female (e.g., Mallards [*Anas platyrhynchos*], Titman 1983) or no territory at all (e.g. Northern Pintails [*Anas acuta*], Derrickson 1978). Territorial defence in the *Bucephala* results in frequent aggressive behaviors that appear most developed in Barrow's Goldeneye. In interspecific territorial disputes, paired Goldeneyes always dominate Buffleheads, but Barrow's Goldeneyes are not consistently dominant to Common Goldeneyes (Savard 1984). Despite their smaller size, paired Buffleheads tend to dominate and successfully exclude unpaired and subadult Goldeneyes (Savard 1984).

Fixed breeding territories are defended by paired male Buffleheads against conspecifics, congeners, and other species of diving ducks (Donaghey 1975, Savard 1982, 1984, Gauthier 1987a, 1987b), but the function of these territories is not completely understood. There is little dispute that they serve as an exclusive foraging area wherein females spend up to 60 - 80% of their time feeding for aquatic invertebrates during egg laying (Savard 1987a, Gauthier 1993). Thus, Donaghey (1975) hypothesized that Buffleheads established breeding territories to defend foods required by laying females. However, Gauthier (1987b) argued against this hypothesis and suggested that mate-guarding was the primary function of breeding territories in Buffleheads, and that this secondarily evolved into defence of a specific area so that pairs could maintain vigilance over their nest site. Thus, he considered that females, rather than food for females, were the resource defended by males. There are several flaws in Gauthier's argument, which are presented in the discussion of Chapter 2.

Barrow's Goldeneyes also aggressively defend breeding territories and paired males in this species are the only duck in North America known to establish and defend fixed winter territories. Savard and Smith (1987) indicated that Barrow's Goldeneyes were most aggressive toward species with similar diets in both spring and winter, and thus speculated that one of the primary functions of territorial behavior in this species was to protect their food supply. Subsequently, Savard (1988b) suggested that breeding territories may be defended by males to reduce interference competition between their females and species with similar diets, thus indicating that space, rather than food, was the resource defended by male Goldeneyes.

Male *Bucephala* generally abandon their females by the second week of incubation. Female Buffleheads and Barrow's Goldeneyes that successfully hatch young defend spatially and temporally distinct brood rearing territories that are often twice the size of breeding territories (Donaghey 1975, Gauthier 1987a, Savard 1982, 1988b, Einarsson 1988, 1990). These females aggressively defend brood rearing areas against conspecifics, congeners, and other species with similar diets, in decreasing order of magnitude. Aggressive actions by brood-tending females are typically limited to threats, chases, or attacks, but they also occasionally kill the young of conspecifics (Savard 1987b) and in the case of Goldeneyes, kill the young of congeners and other species that are potential food competitors (Andrew 1960, Sugden 1960, Robertson and Stelfox 1969, Savard 1982, J. Thompson, pers. observ.).

Territories defended by brood females are typically not the same area previously defended by males (Savard 1988b), but are often closer to the nest site except in late hatched broods, which may be forced to move considerable distances to locate an unoccupied and suitable territory (Gauthier 1987a). Brood territories may also be established in locations other than the original breeding territory because of seasonal changes in food distribution (Savard 1988b, Einarsson 1990), and possibly greater selectivity in the diets of foraging ducklings (Eriksson 1976, 1978). There seems to be general agreement among all studies that brood territories are established to provide young with a dependable source of food for rapid growth and enhanced survival (Savard and Smith 1987, Gauthier 1987a). This hypothesis is supported by a negative correlation between density of food and brood territory size (Gauthier 1987a). and establishment of initial brood territories in the areas where food density is highest (Einarsson 1990).

1.3 STUDY OBJECTIVES AND HYPOTHESES

This study focused specifically on the nutritional ecology of reproduction in sympatrically breeding female Buffleheads and Barrow's Goldeneyes. Because most palustrine wetlands on the Fraser Plateau of central British Columbia have relatively high alkalinity and high occupancy rates by Barrow's Goldeneyes (see study area description below), breeding Common Goldeneyes were rare and not included in this study. Because current evidence suggests that clutch size in waterfowl has a low heritability (Findlay and Cooke 1987, Lessells et al. 1989), I investigated potential proximate constraints on clutch size in female *Bucephala*. Buffleheads and Barrow's Goldeneyes were selected as the study species because unlike most species of prairie nesting ducks. they (1) nest in relatively less productive montane environments, (2) have extended egg laying intervals, (3) defend spatially and temporally stable breeding and brood rearing territories,

(4) are sympatrically breeding cavity nesters, and (5) are congeners that differ markedly in body size. The comparative nature of this study provides one of the best approaches for evolutionary insights into the reproductive adaptations of birds (Lack 1968).

I hypothesized that because female Buffleheads and Barrow's Goldeneyes have primarily carnivorous diets (i.e., high protein) during reproduction, that their clutch size would be proximately constrained by lipid requirements to produce eggs. Because nearly all temperate nesting waterfowl investigated can catabolize endogenous nutrients (typically lipid) to produce eggs (Alisauskas and Ankney 1992), I monitored body composition of females from arrival on breeding areas through clutch formation. I predicted that somatic lipid mass of female *Bucephala* would be negatively related to their cumulative lipid investment in egg lipids, whereas body protein and mineral mass would be unrelated to levels of commitment of these nutrients in the clutch. Furthermore, because of variation in productivity in montane wetlands, I predicted that habitat quality, as indexed by several limnological variables (e.g., alkalinity, pH, total phosphorous, and chlorophyll A), could directly effect body condition of birds and corresponding rates of somatic nutrient investment in their clutch. Finally, I hypothesized that smaller body size in Buffleheads placed greater restrictions on somatic nutrient contribution to clutch formation than in Barrow's Goldeneyes. I predicted that greater reliance on exogenous nutrients by Buffleheads would be reflected in lower rates of body fat loss than observed in Goldeneyes during egg production, but would also result in more pronounced changes in diet composition of breeding female Buffleheads than in female Goldeneyes.

1.4 STUDY AREA

The study area (52°07'N 122°27'W) encompassed approximately 250 km^2 in the Cariboo Parklands of central British Columbia. Elevations in this region of the Fraser Plateau range from 1380 m above sea level in the western portion of the study area to 910 m in the eastern sector. The climate ranges from warm, dry summers to cold winters with light to moderate snowfall. Average monthly temperatures range from a high of 13.7° C in July to a low of -11.6° C in January (Topping and Scudder 1977). Mean annual precipitation is relatively low, averaging only 434 mm in eastern regions of the study area (Steen and Roberts 1988). Snow cover generally persists from November into early April. Forest habitats in this region are part of the Interior Douglas Fir (*Pseudotsuga menziesii*) zone (Krajina 1969), characterized by rolling grassland interspersed with mixed stands of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), Douglas fir, and black spruce (*Picea mariana*). Forest composition corresponds to a moisture gradient, with Douglas fir and lodgepole pine occurring in more xeric areas, while aspen and black spruce predominate in wetter sites.

There is a high density of small (< 1 ha) to moderate sized (1 to 50 ha) palustrine wetlands on the Fraser Plateau that are generally too alkaline and/or too shallow to support fish, but most basins have well developed and diverse invertebrate communities (Boyd and Smith 1989). With the exception of Lesser Scaup (*Aythya affinis*), Barrow's Goldeneyes and Buffleheads are the most common and widespread breeding ducks in this region (Boyd et al. 1989). During this study, wetlands were at average to above average water levels, which maintained good populations of Goldeneyes and Buffleheads (CWS, unpubl. data) and a strong reproductive effort during all three years.

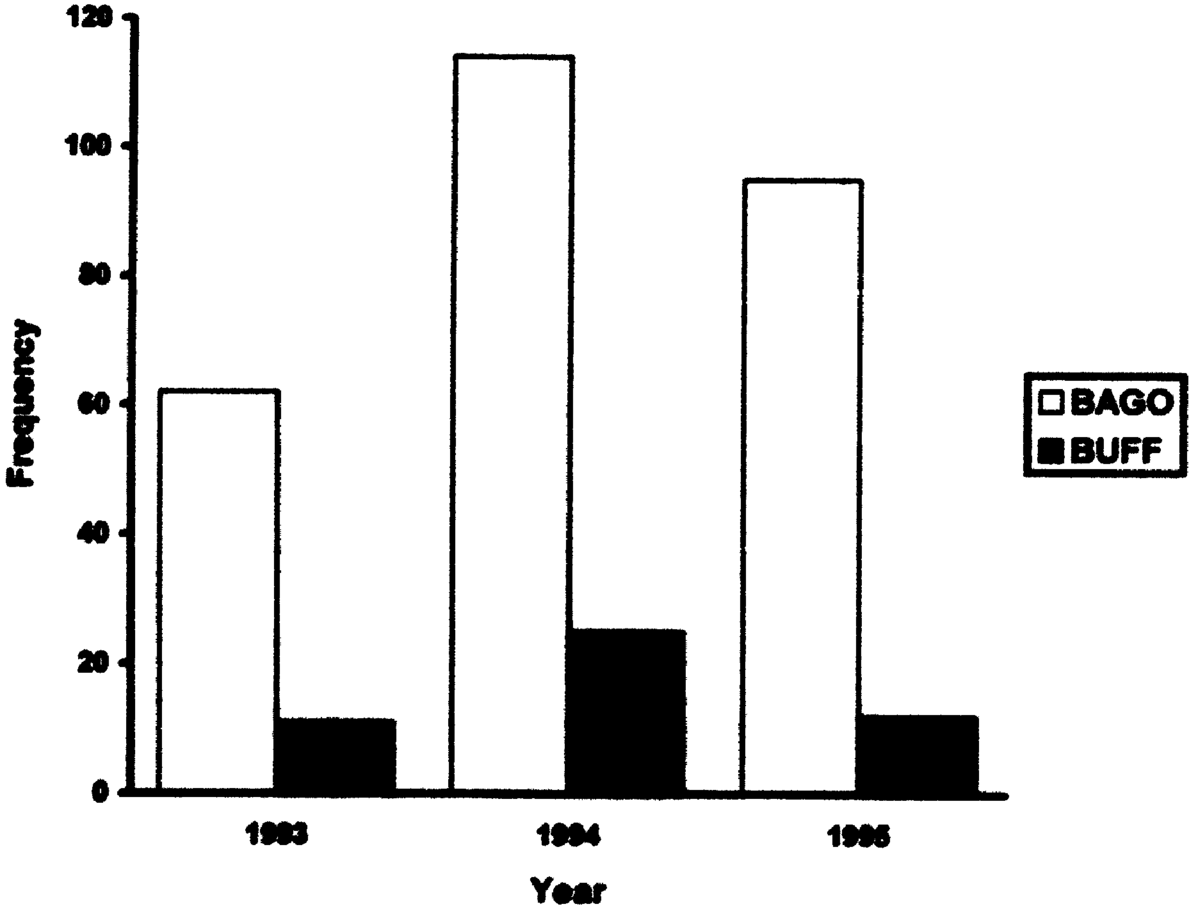
Wetlands used by breeding Barrow's Goldeneyes in central British Columbia are relatively deeper, with less emergent vegetation, and higher pH and total dissolved nitrogen than unused wetlands (Savard et al. 1994). Buffleheads also use relatively deeper ponds with less emergent cover, but avoid wetlands with high turbidity and extremely high alkalinity (Savard et al. 1994). Notably, all wetlands used by breeding female *Bucephala* in this study were devoid of fish, indicating that birds actively avoided wetlands where they had to compete with fish for aquatic invertebrates. Further details on habitat use and populations of breeding waterfowl in the Cariboo Parkland region can be found in Boyd et al. (1989), Savard (1991), and Savard et al. (1994). Additional information on the limnology of wetlands in this area can be found in Boyd and Savard (1987) and Boyd and Smith (1989).

1.5 NEST BOX PROGRAM

High breeding densities of Barrow's Goldeneyes on my study area were at least partially attributable to establishment of approximately 350 nest boxes during a previous study (Savard 1986). Large numbers of breeding Buffleheads were supported by good interspersion of grassland and forest habitats, which in turn attracted large numbers of breeding Northern Flickers. This woodpecker is the primary cavity excavator of natural nest sites used by Buffleheads (Erskine 1972, Gauthier 1993).

To improve access to nests and maintain good populations of breeding Barrow's Goldeneyes and Buffleheads, I repaired and maintained 42 of Savard's Goldeneye nest boxes and 26 of his Bufflehead nest boxes. All other nest boxes from Savard's study had been destroyed by weather or black bears (*Ursus americanus*). In addition to these remaining structures, I erected 175 new Goldeneye nest boxes in September 1992 and 59 new Bufflehead boxes in early April 1993. Nest boxes were regularly monitored from late April - July in 1993 - 1995 (see Appendices 1 & 2), to investigate various aspects of egg laying and incubation in female *Bucephala*. Because most Goldeneyes and Buffleheads select their nest site during the summer before they are used (Eadie and Gauthier 1985), use rates were fairly low in nest boxes during the first year (Figure 1.1). However, despite collecting many nesting female Buffleheads and Goldeneyes using nest boxes, the number of birds using these structures increased from 1993 to 1994, and the number of birds using boxes in 1995 was at least equivalent to or higher than the number of birds using these nest sites in 1993 (Figure 1.1). Notably, nest box use by Goldeneyes was considerably greater than by Buffleheads in all years of this study, presumably because there were fewer suitable natural nest sites for Goldeneyes.

Fig. 1.1. Frequency of nest box use by female Buffleheads and Barrow's Goldeneyes in central British Columbia from 1993 - 1995. The number of Bufflehead nests include those in Bufflehead and Goldeneye nest boxes (See Appendices 1 & 2). Because of small entrances (7 x 7 cm) in Bufflehead boxes and their larger body size, Goldeneyes were excluded from these nest sites.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1.6 SCOPE OF THE DISSERTATION

Most data presented in this thesis concern only those aspects of reproduction associated with egg production in female *Bucephala*. I also collected extensive data on incubation energetics and nest attentiveness in female *Bucephala*, but these data will be presented in separate papers that will follow publication of the diet and egg production studies presented herein. This thesis has been organized into this introductory chapter followed by three chapters that correspond to intended publications. The first (and present) chapter discusses costs of reproduction in waterfowl and basic reproductive ecology of species in the genus *Bucephala*. Chapter one also describes the study area and nest box program, and outlines the questions and hypotheses investigated in this project. Chapter two investigates diet and digestive tract morphology of female Barrow's Goldeneyes and Buffleheads relative to nutritional requirements for egg production and incubation. Chapter three reports egg laying intervals in Buffleheads and Barrow's Goldeneyes and models the energetic costs of egg formation in both species. Chapter four concludes by investigating nutrient reserve dynamics of female Buffleheads and Barrow's Goldeneyes during clutch formation. Additionally, I have included several appendices that report use of Goldeneye nest boxes (Appendix 1), use of Bufflehead nest boxes (Appendix 2), morphological measurements of female Buffleheads and Barrow's Goldeneyes (Appendix 3), and morphology of Bufflehead and Barrow's Goldeneye eggs (Appendix 4).

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CHAPTER 2. DIET COMPOSITION AND DIGESTIVE TRACT MORPHOLOGY OF BREEDING FEMALE BUFFLEHEADS AND BARROW'S GOLDENEYES

2.1 INTRODUCTION

Female waterfowl (Anseriformes) generally have high nutritional requirements during reproduction because they lay large eggs relative to their body mass (Lack 1968) and their eggs have a high energy density (kJ/g) compared to altricial and most other precocial birds (Alisauskas and Ankney 1992). However, prebreeding waterfowl can store nutrients, including lipid, protein, and mineral, as somatic tissue that can be used to meet daily nutrient requirements when physiological demands exceed dietary intake. Generally, temperate nesting ducks use a "mixed strategy" whereby both endogenous and exogenous nutrients are incorporated into their clutch. Omnivorous ducks often rely on their diet to acquire much of the protein and mineral content deposited in their clutch, whereas a considerable fraction of the lipid content in at least their initial clutch is acquired during spring migration when birds routinely consume high carbohydrate plant foods (e.g., seeds, submergent macrophyte tubers) to facilitate somatic fat storage (Krapu and Reinecke 1992). As a consequence of relying on exogenous protein and minerals during egg production, diet composition in breeding ducks, particularly the fraction of the diet represented by animal foods, often varies with reproductive stage and nutrient reserve use (see review in Krapu and Reinecke 1992).

Barrow's Goldeneyes (*Bucephala islandica*) and Buffleheads (*B. albeola*), similar to most other species in the anatid tribe Mergini (sea ducks), typically nest in unproductive wetland habitats where foraging opportunities are poor compared to the fertile wetlands of the Northern Great Plains. The few species of sea ducks that have been studied thus far show remarkable variation in their nutrient acquisition patterns for clutch formation. Female Common Eiders (*Somateria mollissima*), in a manner typical of

Arctic nesting geese (Anserinae), rely almost exclusively on endogenous reserves accumulated before laying to provide the nutrients needed for egg production (Milne 1976, Korschgen 1977). Reliance on endogenous reserves in this species has presumably evolved in response to constraints imposed by high rates of nest loss to gulls (Laridae) and other avian predators, thus necessitating close nest attendance. Conversely, female White-winged Scoters (*Melinitta fusca*) breeding on saline wetlands in the Northern Great Plains acquire all nutrients incorporated in their clutch directly from their diet and defer nutrient reserve use until incubation (Dobush 1986). Buffleheads and Goldeneyes, and probably other sea ducks, may also reduce daily nutrient demands of egg production by extending time for completion of rapid ovarian follicle growth and thereby increasing egg laying intervals (Chapter 4). These adaptations apparently evolved to minimize disparity between daily nutrient requirements for egg production and daily nutrient intake, suggesting that these species rely to some extent on exogenous nutrients for egg production.

There is little unbiased information on foods consumed by Buffleheads and Barrow's Goldeneyes during reproduction (see below) and no understanding of food use relative to the nutritional requirements during breeding. Our present knowledge of foods used by breeding Buffleheads is based on examination of gizzard contents by Cottam (1939), Munro (1942), and Erskine (1972). Information about food habits of Barrow's Goldeneyes breeding in North America is from studies of gizzard contents published in the early 1900's (Munro 1918, 1939, Cottam 1939). Unfortunately, these early studies often combined birds from different habitats, seasons, and sexes making inferences about the diet's ability to meet the requirements of nutrient demanding events, such as egg laying and incubation, impossible. Furthermore, most of these studies were based on gizzard contents or combined esophageal and gizzard contents, which can bias diet composition by overestimating importance of foods with slower passage rates (e.g., seeds, mollusks) (Swanson and Bartonek 1970).

Food choice by breeding ducks (anatids) has evolved in response to many factors including habitat use, bill morphology, nutritional requirements, and intra- and interspecific competition (Krapu and Reinecke 1992). This study was designed to 1) investigate how the nutritional demands of reproduction affect diets of female Buffleheads and Barrow's Goldeneyes, 2) evaluate interspecific differences in diets of these sympatrically breeding congeners, and 3) interpret intraspecific variation in digestive tract morphology relative to diet in both species. Comparative studies on congeneric species with markedly different body masses provide an opportunity to evaluate evolutionary consequences of body size on nutritional tactics of birds. Because smaller species of birds can store absolutely less nutrient reserves, they should show greater modification in their diet during egg laying than do larger species that can rely more on somatic nutrients. Thus, I hypothesized that diet shifts between reproductive periods would be more pronounced in Buffleheads than in Barrow's Goldeneyes in response to the nutritional requirements of reproduction. This research was carried out as part of a larger project investigating proximate constraints on reproduction of sympatrically breeding *Bucephala* in mesotrophic montane wetlands.

2.2 METHODS

2.2.1 *Specimen collection and reproductive status*

Female Buffleheads ($n = 98$) and Barrow's Goldeneyes ($n = 97$) were shot at foraging sites or captured on their nests throughout the breeding season in 1993 and 1994 (Canadian Wildlife Service permits PC BK 93/15 & 94/12). Birds that were shot were typically observed foraging for ≥ 10 minutes before they were collected to ensure that there was food in the upper digestive tract. Also, birds were collected over a broad range of times (04:30 to 23:00 h) to make sure that foods consumed throughout the diel cycle were represented. Generally, no more than two birds of each species were collected from any particular wetland. To relate diet to nutritional requirements throughout reproduction, specimens were categorized into one of the following reproductive periods: Non-Rapid Follicular Growth (Non-RFG), Prelayers (≥ 1 rapidly developing ovarian follicle, but lacking post-ovulatory follicles), Early Layers (>number of rapidly developing ovarian follicles than post-ovulatory follicles), Late Layers (> number of post-ovulatory follicles than rapidly developing ovarian follicles), Early Incubation (≤ 15 days incubation), and Late Incubation (>15 days incubation). Rapid Follicular Growth (RFG) was indicated by ≥ 1 developing follicle weighing ≥ 0.14 g (dry mass) in Buffleheads and ≥ 0.17 g (dry mass) in Goldeneyes. Non-RFG birds were primarily prebreeders (i.e., birds collected before most birds had initiated RFG) and a few nonbreeders (i.e., birds with no ovarian growth collected after most birds had initiated RFG). Early and late incubation periods were pooled into a single category in diet composition analyses because few incubating birds contained food items in their upper digestive tract.

2.2.2 *Diet assessment*

Immediately following collection, 2 - 3 ml of 80% ethanol was injected gently into the esophagus of each specimen to minimize post-mortem digestion of food items (Swanson and Bartonek 1970). Esophageal and proventricular contents were removed within 3-4 hours and placed into individually labeled vials containing additional 80% ethanol. Gizzard contents were not examined because their inclusion typically underestimates the importance of foods less resistant to mechanical processing (e.g. soft-bodied invertebrates) (Swanson and Bartonek 1970).

In the laboratory, foods were identified, sorted, and oven-dried to constant mass at 65°C. I identified most invertebrate foods to family and plant foods to genus. References used in classification of food items included Martin and Uhler (1939) and Fassett (1957) for plant material, and Merritt and Cummins (1984) and Clifford (1991) for invertebrates. Dried foods were weighed to the nearest 0.0001 g on a Sartorius digital scale. Dry mass was selected in lieu of volumetric measures of food consumption to facilitate nutritional interpretation of the diet (Reinecke and Owen 1980).

2.2.3 *Digestive tract morphology*

The digestive tract, including the liver and pancreas, was removed from each specimen and dissected into the upper digestive tract (including the esophagus and proventriculus), gizzard, small intestine, ceca, and large intestine. Lengths (1 mm) of the upper digestive tract, small intestine, ceca, and large intestine were measured using a meter stick. Gizzard length (0.01 mm) was measured from the proventricular junction to the most distal point using digital calipers. To reduce variation in measurements associated with elasticity of these organs, all measurements were made on unstretched components and before removal of ingesta. Total digestive tract length was derived by summing lengths of the upper digestive tract, gizzard, small intestine, ceca, and large intestine.

Ingesta and adhering visceral fat were removed from wet digestive organs before they were weighed. Total digestive tract mass was derived by summing masses of emptied upper digestive tract, gizzard, small intestine, ceca, and large intestine. The liver was cut into small pieces, placed in an aluminum drying pan, oven-dried to constant mass at 80° C, and then ground into a fine homogenate using a Moulinex coffee grinder. Dried cellulose thimbles were filled with approximately 10 g of dried liver homogenate and subsequently washed with petroleum ether in a modified Soxhlet apparatus to extract lipids (Dobush et al. 1985). Lean liver and liver fat mass were determined by extrapolating samples values back to the original dry mass.

2.2.4 *Statistical analysis*

Diets of breeding Barrow's Goldeneyes and Buffleheads were summarized as aggregate percent dry mass and frequency of occurrence for each food consumed (see

Swanson et al. 1974, Reinecke and Owen 1980). Sample sizes in several reproductive periods were too small to investigate annual differences in diet given the large variances associated with food habits data. Furthermore, based on similar habitat conditions (i.e. water levels) over the course of this study and my personal observations while processing food samples, I had no evidence to suggest that diets differed between years for either species. Because food habits data were converted to proportions and were not normally distributed, I analyzed the data using nonparametric statistics. Differences in consumption of plant and animal material and changes in use of specific food items relative to stage of reproduction within each species were investigated using Kruskal-Wallis one-way analysis of variance tests (PROC NPAR1WAY; SAS Institute Inc. 1985). If differences in use of a specific food or dietary component were detected in the overall model, contrasting reproductive periods were determined using Dunn's multiple comparisons test (Daniel 1990). Interspecific comparisons of proportional use of invertebrate taxa and specific plant components were done using Mann-Whitney U-tests (PROC NPAR1WAY; SAS Institute Inc. 1985).

Variation in digestive tract morphology between reproductive periods and years were investigated using two-way analysis of variance (PROC GLM; SAS Institute Inc. 1985). For digestive tract components that differed ($P < 0.05$) by reproductive status in the overall model, Tukey - Kramer multiple comparisons tests were used to determine which means were different. Separate means and their corresponding standard errors were presented for each year when a significant annual effect was found in the overall model.

2.3 RESULTS

2.3.1 *Diet composition of female Buffleheads relative to stage of reproduction*

Seventy-seven of 98 Buffleheads that I collected contained food in their upper digestive tracts, and thus were included in diet composition analyses (Tables 2.1 & 2.2). Diets of breeding female Buffleheads were diverse and included foods from > 20 invertebrate families and 9 plant genera. Buffleheads were primarily carnivorous as animal foods occurred in all birds (Table 2.1) and represented ≥ 75% of the diet throughout reproduction (Table 2.2). Furthermore, animal foods became increasingly important ($P = 0.0455$) from prelaying through incubation, while consumption of plant foods declined ($P = 0.0455$) compared to non-RFG birds (Table 2.2).

Mollusks were consumed by female Buffleheads in all reproductive periods except during non-RFG (Table 2.1). Consumption of planorbid snails and unidentified gastropod shell fragments increased markedly ($P \leq 0.05$) during laying when birds incurred calcium requirements for eggshell formation. Possibly to acquire additional minerals for eggshell synthesis, several late laying Buffleheads had ingested fragments of avian eggshell and small bones (Table 2.1). Incubating birds consumed gastropods less frequently than did birds undergoing RFG (Table 2.1), but over 4% of their diet was still composed of gastropod shell fragments.

Crustaceans were uncommon in the diet of breeding Buffleheads. Fairy shrimp (Anostraca) were only consumed during non-RFG and prelaying, and never represented > 4.1% of the aggregate dry mass of the diet (Table 2.2). Cladocerans, principally *Daphnia*, were the most frequently eaten crustaceans (Table 2.1), but due to their low body mass they never represented a large fraction of the total diet (Table 2.2). Amphipods, including *Hyallela* and *Stygobromus*, were consumed by only two birds during late laying and represented only 1% of all foods eaten during this period (Table 2.2).

Table 2.1. Percent occurrence of foods consumed by breeding female Buffleheads in south-central British Columbia, 1993 - 94. Diets are presented relative to stage of reproduction.

	Reproductive Periods[a]				
Food item	Non-RFG (18)[b]	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Total animal material	100	100	100	100	100
Mollusca (Gastropoda only)					
Lymnaeidae (Pond snails)	0	0	12.50	8.33	8.33
Planorbidae (Orb snails)	0	0	25.00	12.50	0
Unidentified shell fragments	0	22.22	62.50	62.50	8.33
Arachnida					
Hydrachnidia (Water mites)	0	11.11	25.00	8.33	16.67
Crustacea					
Cladocera (Water fleas)	16.67	0	25.00	12.50	0
Amphipoda (Scuds)					
Hyallela	0	0	0	4.17	0
Stygobromus	0	0	0	4.17	0
Anostraca (Fairy shrimp)	11.11	11.11	0	0	0
Insecta					
Ephemeroptera (Mayflies)[d]	5.56	11.11	12.50	20.83	16.67
Odonata					
Anisoptera (dragonflies)[d]	5.56	0	12.50	0	0
Zygoptera (damselflies)[d]	16.67	55.56	31.25	33.33	75.00

Table 2.1. Continued

Food item	Reproductive Periods[a]				
	Non-RFG (18)	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Hemiptera					
Corixidae (Water boatmen)					
Adults	5.56	0	6.25	0	16.67
Larvae	0	0	0	0	8.33
Notonectidae (Backswimmers)[c]	0	0	6.25	0	0
Unidentified hemiptera[c]	0	0	0	8.33	0
Trichoptera (Caddisflies)					
Adults	0	0	6.25	0	16.67
Larvae	5.56	11.11	18.75	8.33	33.33
Coleoptera					
Curculionidae (Aquatic weevils)[c]	0	0	12.50	0	0
Dytiscidae (Predaceous water beetles)					
Adults	22.22	0	18.75	20.83	8.33
Larvae	16.67	11.11	18.75	16.67	33.33
Haliplidae (Crawling water beetles)[c]	5.56	11.11	12.50	16.67	16.67
Hydrophilidae (Water scavenger beetles)[c]	0	0	6.25	0	0
Unidentified coleoptera[c]	0	11.11	18.75	8.33	8.33
Diptera					
Chaoborinae (Phantom midges)					
Pupae	16.67	11.11	56.25	37.50	33.33
Larvae	44.44	44.44	68.75	50.00	41.67
Chironomidae (Nonbiting midges)					
Pupae	11.11	11.11	18.75	33.33	16.67
Larvae	61.11	33.33	43.75	41.67	33.33
Culicidae (Mosquitoes)[d]	0	0	18.75	8.33	0
Tabanidae (Deer flies)[d]	11.11	0	6.25	0	0
Stratiomyidae (Soldier flies)[d]	16.67	0	12.50	0	0

Table 2.1. Continued.

Food item	Reproductive Periods[a]				
	Non-RFG (18)	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Vetebrate material					
Animal bones	0	0	0	4.17	0
Avian eggshell	0	0	0	4.17	0
Total plant material	55.56	55.56	81.25	37.50	16.67
Tubers and rootstalks:					
Potamogeton spp. (Pondweeds)	5.56	11.11	6.25	8.33	0
Cyperus spp. (Chufa)	5.56	11.11	31.25	4.17	0
Seeds:					
Carex spp. (Sedges)	0	22.22	25.00	0	8.33
Cyperus spp. (Chufa)	5.56	0	6.25	0	0
Eleocharis spp. (Spike rushes)	5.56	11.11	0	0	0
Glyceria spp. (Manna-grass)	0	0	6.25	0	0
Hippurus spp. (Marestail)	16.67	11.11	31.25	16.67	0
Myriophyllum spp. (Water milfoil)	0	0	25.00	0	0
Potamogeton spp. (Pondweeds)	22.22	22.22	25.00	16.67	0
Ruppia spp. (Wigeongrass)	5.56	0	0	8.33	0
Scirpus spp. (Bulrushes)	27.78	11.11	25.00	20.83	0

[a] See methods for definitions of reproductive periods.
[b] Sample size.
[c] Exclusively adults.
[d] Exclusively larvae.

Table 2.2. Aggregate percent dry mass of foods consumed by breeding female Buffleheads in south-central British Columbia, 1993 - 94. Diets are presented relative to stage of reproduction.

			Reproductive Periods[a]				
Food item	*H* [b]	*P* [c]	Non-RFG (18)[d]	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Total animal material	9.72	0.0455	87.06	75.43	92.24	91.44	97.60
Mollusca (Gastropoda only)							
Lymnaeidae (Pond snails)	3.03	NS	0	0	0.72	3.73	0.03
Planorbidae (Orb snails)	9.36	0.0527	0	0	5.33	1.00	0
Unidentified shell fragments	16.12	0.0029	0	1.69	13.60	21.49	4.19
Arachnida							
Hydrachnidia (Water mites)	6.04	NS	0	1.11	2.63	0.01	8.38
Crustacea							
Cladocera (Water fleas)	5.38	NS	0.08	0	0.20	0.20	0
Amphipoda (Scuds)							
Hyallela	2.29	NS	0	0	0	0.73	0
Stygobromus	2.29	NS	0	0	0	0.34	0
Anostraca (Fairy shrimp)	5.93	NS	4.11	1.88	0	0	0
Insecta							
Ephemeroptera (Mayflies)[f]	2.27	NS	0.05	0.04	0.12	2.04	0.77
Odonata							
Anisoptera (dragonflies)[f]	5.08	NS	4.31	0	0.58	0	0
Zygoptera (damselflies)[f]	13.22	0.0103	2.11	23.61	2.15	10.65	24.81
Hemiptera							
Corixidae (Water boatmen)							
Adults	5.01	NS	0.63	0	3.40	0	1.29
Larvae	5.58	NS	0	0	0	0	0.01
Notonectidae (Backswimmers)[e]	3.94	NS	0	0	1.06	0	0
Unidentified hemiptera[e]	4.64	NS	0	0	0	3.72	0

Table 2.2. Continued.

			Reproductive Periods[a]				
Food item	H[b]	P[c]	Non-RFG (18)[d]	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Trichoptera (Caddisflies)							
Adults	7.62	NS	0	0	0.27	0	1.55
Larvae	5.54	NS	0.39	8.17	7.12	0.25	7.57
Coleoptera							
Curculionidae (Aquatic weevils)[e]	7.98	NS	0	0	0.13	0	0
Dytiscidae (Predaceous water beetles)							
Adults	2.94	NS	10.34	0	1.81	3.14	8.33
Larvae	1.94	NS	2.89	4.55	0.28	1.44	5.96
Haliplidae (Crawling water beetles)[e]	1.68	NS	0.13	0.10	1.39	2.96	3.83
Hydrophilidae (Water scavenger beetles)[e]	3.94	NS	0	0	0.07	0	0
Unidentified coleoptera[e]	3.76	NS	0	11.11	6.13	1.12	4.69
Diptera							
Chaoborinae (Phantom midges)							
Pupae	6.04	NS	7.05	0.94	6.79	7.54	15.12
Larvae	2.51	NS	14.42	7.94	13.27	6.84	2.64
Chironomidae (Nonbiting midges)							
Pupae	5.43	NS	0.20	0.29	0.50	8.49	1.96
Larvae	6.53	NS	37.44	14.00	19.79	10.77	6.47
Culicidae (Mosquitoes)[f]	6.86	NS	0	0	4.16	2.22	0
Tabanidae (Deer flies)[f]	4.61	NS	0.27	0	0.16	0	0
Stratiomyidae (Soldier flies)[f]	7.25	NS	2.56	0	0.17	0	0
Unidentified insects	1.94	NS	0.08	0	0.41	0	0
Vetebrate material							
Animal bones	7.98	NS	0	0	0	0.15	0
Avian eggshell	4.94	NS	0	0	0	3.50	0

Table 2.2. Continued.

Food item	*H*[b]	*P*[c]	Reproductive Periods[a] Non-RFG (18)[d]	Prelaying (9)	Early Laying (16)	Late Laying (24)	Incubating (12)
Total plant material	9.72	0.0455	12.94	24.57	7.76	7.67	2.40
Tubers and rootstalks:							
Potamogeton spp. (Pondweeds)	2.89	NS	0	4.87	0.79	1.60	0
Cyperus spp. (Chufa)	9.89	0.0423	0.06	2.22	0.13	0.01	0
Seeds:							
Carex spp. (Sedges)	11.22	0.0242	0	3.38	0.15	0	0.01
Cyperus spp. (Chufa)	2.71	NS	0.02	0	0.05	0	0
Eleocharis spp. (Spike rushes)	4.70	NS	0.13	1.80	0	0	0
Glyceria spp. (Manna-grass)	3.94	NS	0	0	0.01	0	0
Hippurus spp. (Marestail)	4.84	NS	3.58	0.04	1.97	1.98	0
Myriophyllum spp. (Water milfoil)	16.37	0.0026	0	0	0.79	0	0
Potamogeton spp. (Pondweeds)	3.63	NS	4.59	4.86	0.84	1.09	0
Ruppia spp. (Wigeongrass)	2.93	NS	0.42	0	0	0.40	0
Scirpus spp. (Bulrushes)	4.06	NS	2.07	7.39	3.03	2.59	0
Unidentified vegetation	2.51	NS	2.07	0.10	0	0	2.39

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[a] See methods for definitions of reproductive periods.
[b] Kruskal - Wallis test statistic.
[c] Probability value from Kruskal - Wallis Test. NS = Not significant ($P < 0.05$).
[d] Sample size.
[e] Exclusively adults.
[f] Exclusively larvae.

Aquatic insects were most of the food mass consumed by breeding Buffleheads. The principal insect taxa found in the upper digestive tracts were midge (Chironomidae) and phantom midge (Chaoborinae) larvae and pupae, and damselfly larvae (Zygoptera) (Table 2.2). Despite the overall importance of insects in the diet of breeding female Buffleheads, only the proportion of Zygoptera larvae in the diet differed ($P = 0.0103$) between reproductive periods. These insects were consumed most frequently during prelaying and incubation (Table 2.1) and comprised nearly 25% of the diet during these periods.

Several other insect foods showed trends (i.e., $P < 0.1$) in dietary importance. Chironomid larvae comprised nearly 40% of the diet during non-RFG, but declined to 6.5% of the diet in incubating birds. Similarly, phantom midge larvae went from approximately 14 % of the diet during non-RFG to < 3% of the diet during incubation. Phantom midge pupae showed a corollary pattern representing a larger proportion of the diet during incubation than in earlier reproductive periods. Adult dytiscid beetles represented > 8 % of the diet before and after RFG, but were generally less utilized during egg formation. A variety of other insects occurred in the food contents of breeding Buffleheads but few taxa represented > 5 % of the diet during any reproductive period.

Plant foods represented < 25% of overall diet composition during reproduction (Table 2.2). Seeds were the most frequently consumed vegetable matter and represented a larger fraction of the diet ($P \leq 0.05$) during non-RFG and prelaying than in subsequent periods. More specifically, seeds from pondweeds (*Potamogeton* spp.), marestail (*Hippurus vulgaris*), and bulrushes (*Scirpus* spp.) were among the most frequently consumed plant foods. Tubers and rootstalks of sago pondweed (*Potamogeton pectinatus*) and chufa (*Cyperus esculentus*) represented the only other plant components ingested during reproduction.

2.3.2 *Diet composition of female Barrow's Goldeneyes relative to stage of reproduction*

A total of 53 of 97 Barrow's Goldeneyes that I collected contained food in their upper digestive tracts, and were subsequently included in diet composition analyses (Tables 2.3 & 2.4). Diets of female Barrow's Goldeneyes were less diverse than those of Buffleheads. The total proportion of the diet represented by animal material was > 83% throughout the breeding season and did not vary among reproductive periods (P = 0.1253). Plant foods were less utilized than animal foods ($P \leq 0.05$), and comprised < 10% of the diet during non-RFG, early laying, and late laying, and < 20% of the diet during prelaying and incubation (Table 2.4). Use of most food items did not change ($P >$ 0.05) between reproductive periods in female goldeneyes, but some trends in food use were apparent.

Aquatic insects were most of the diet in all reproductive periods (Table 2.4). Zygoptera larvae typically comprised the largest fraction of the diet (Table 2.4) and were the most frequently consumed food by birds during prelaying, late laying, and incubation (Table 2.3). Other insect foods that were large components in the aggregate dry mass of the diet included pupae and larvae of non-biting midges and phantom midges. Chironomid larvae represented the largest proportion of the diet for non-RFG birds (≈ 30% of the aggregate diet), but generally represented a smaller proportion of the diet during RFG and incubation. Phantom midge larvae, which were probably erroneously included with Chironomids in previous diet studies (see below), represented 7 - 10.5% of the diet of birds during non-RFG, early laying, and incubation. Furthermore, phantom midge pupae comprised up to 28% of diet during early laying. Other aquatic insects were consumed, but typically were lower proportions of the overall diet (Table 2.4).

Mollusks, exclusively represented by gastropods, were consumed during all reproductive stages except non-RFG (Table 2.3). In most instances, birds consumed fragments of empty gastropod shells rather than living organisms, although live

Table 2.3. Percent occurrence of foods consumed by breeding female Barrow's Goldeneyes in south-central British Columbia, 1993 - 94. Diets are presented relative to stage of reproduction.

Food item	Non-RFG (11)[b]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
	Reproductive Periods[a]				
Total animal material	100	88.89	100	100	87.50
Mollusca (Gastropoda only)					
Planorbidae (Orb snails)	0	0	0	7.14	0
Gastropod shell fragments	0	11.11	15.38	35.71	25.00
Arachnida					
Hydrachnidia (Water mites)	0	0	7.69	7.14	25.00
Crustacea					
Cladocera (Water fleas)	9.09	0	0	7.14	0
Amphipoda (Scuds)					
Gammarus	0	0	0	7.14	0
Hyallela	0	0	15.38	0	0
Insecta					
Ephemeroptera (Mayflies)[d]	27.27	11.11	30.77	7.14	0
Odonata					
Anisoptera (dragonflies)[d]	9.09	11.11	15.38	0	25.00
Zygoptera (damselflies)[d]	45.45	55.56	53.85	64.29	62.50
Hemiptera					
Corixidae (Water boatmen)[c]	18.18	11.11	23.08	21.43	25.00
Notonectidae (Back swimmers)[c]	0	0	0	14.29	0
Trichoptera (Caddisflies)[d]	18.18	11.11	0	14.29	12.50

Table 2.3. Continued.

	Reproductive Periods[a]				
Food item	Non-RFG (11)[b]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
Coleoptera					
Dytiscidae (Predaceous water beetles)					
Adults	0	0	23.08	21.43	12.50
Larvae	0	22.22	15.38	14.29	12.50
Haliplidae (Crawling water beetles)[d]	0	0	0	0	12.50
Unidentified coleoptera[c]	9.09	0	0	0	12.50
Diptera					
Chaoborinae (Phantom midges)					
Pupae	27.27	11.11	46.15	42.86	50.00
Larvae	36.36	11.11	46.15	7.14	37.50
Chironomidae (Midges)					
Adults	0	0	7.69	0	0
Pupae	9.09	11.11	30.77	35.71	25.00
Larvae	54.55	33.33	76.92	50.00	37.50
Ceratopogonidae (Biting midges)[d]	0	11.11	7.69	7.14	0
Stratiomyidae (Soldier flies)[d]	0	0	7.69	0	0
Tabanidae (Deer flies)[d]	0	0	0	7.14	0
Syrphidae (Flower flies)[d]	0	0	7.69	0	0
Total plant material	27.27	44.44	38.46	57.14	87.50
Tubers and rootstalks from:					
Potamogeton spp. (Pondweeds)	0	22.22	0	21.43	25.00
Cyperus (Chufa)	0	0	0	0	25.00

Table 2.3. Continued.

Food item	Reproductive Periods[a]				
	Non-RFG (11)[b]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
Seeds from:					
Carex spp. (Sedges)	9.09	0	0	7.14	12.50
Eleocharis spp. (Spike rushes)	0	0	0	7.14	0
Hippurus spp. (Marestail)	0	0	0	21.43	25.00
Potamogeton spp. (Pondweeds)	18.18	11.11	7.69	14.29	25.00
Ruppia spp. (Wigeongrass)	0	0	0	14.29	12.50
Scirpus spp. (Bulrushes)	9.09	11.11	23.08	35.71	37.50

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[a] See methods for definitions of reproductive periods.

[b] Sample size.

[c] Exclusively adults.

[d] Exclusively larvae.

Table 2.4. Aggregate percent dry mass of foods consumed by breeding female Barrow's Goldeneyes in south-central British Columbia, 1993 - 94. Diets are presented relative to stage of reproduction.

			Reproductive periods				
Food item	H [b]	P [c]	Non-RFG (11)[d]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
Total animal material	6.43	NS	92.70	83.06	96.83	91.92	90.20
Mollusca (Gastropoda only)							
Planorbidae (Orb snails)	2.93	NS	0	0	0	1.33	0
Unidentified Gastropod shells	5.60	NS	0	0.14	0.21	8.72	15.97
Arachnida							
Hydrachnidia (Water mites)	2.17	NS	0	0	2.99	0.01	7.00
Crustacea							
Cladocera (Water fleas)	4.05	NS	0.05	0	0	3.63	0
Amphipoda (Scuds)							
Gammarus	2.93	NS	0	0	0	3.52	0
Hyallela	6.58	NS	0	0	0.13	0	0
Insecta							
Ephemeroptera (Mayflies)[f]	5.45	NS	1.57	2.30	2.72	0.04	0
Odonata							
Anisoptera (dragonflies)[f]	3.35	NS	1.81	3.60	2.52	0	0.50
Zygoptera (damselflies)[f]	0.71	NS	19.32	29.55	31.99	28.25	30.67
Hemiptera							
Corixidae (Water boatmen)[e]	0.45	NS	12.92	0.53	0.55	0.70	0.62
Notonectidae (Back swimmers)[e]	5.97	NS	0	0	0	0.21	0
Trichoptera (Caddisflies)[f]	2.33	NS	4.93	0.12	0	0.33	0.33

Table 2.4. Continued.

Food item	H [b]	P [c]	Reproductive periods Non-RFG (11)[d]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
Insecta (continued)							
Coleoptera							
Dytiscidae (Predaceous water beetles)							
Adults	4.94	NS	0	0	1.14	0.72	0.42
Larvae	2.45	NS	0	10.82	0.14	0.23	0.05
Haliplidae (Crawling water beetles)[f]	5.88	NS	0	0	0	0	0.27
Unidentified coleoptera[e]	4.05	NS	0.08	5.00	0	0	0.42
Diptera							
Chaoborinae (Phantom midges)							
Pupae	4.51	NS	10.52	0.19	28.04	9.22	11.74
Larvae	6.58	NS	10.47	2.88	8.78	0.20	7.54
Chironomidae (Midges)							
Adults	3.23	NS	0	0	0.03	0	0
Pupae	3.70	NS	0.72	0.03	2.43	3.31	3.33
Larvae	3.09	NS	28.93	19.74	14.19	21.51	11.34
Ceratopogonidae (Biting midges)[f]	1.87	NS	0	0.37	0.01	0.01	0
Stratiomyidae (Soldier flies)[f]	3.23	NS	0	0	0.34	0	0
Tabanidae (Deer flies)[f]	2.93	NS	0	0	0	5.84	0
Syrphidae (Flower flies)[f]	3.23	NS	0	0	0.61	0	0
Unidentified insects	4.94	NS	1.37	7.79	0.01	4.14	0
Total plant material	6.43	NS	7.30	16.94	3.17	8.08	9.80
Tubers and rootstalks from:							
Potamogeton spp. (Pondweeds)	0.01	NS	0	0	0	0	0.08
Cyperus (Chufa)	11.97	0.0176	0	0	0	0	0.86

Table 2.4. Continued.

Food item	H[b]	P[c]	Reproductive periods Non-RFG (11)[d]	Prelaying (9)	Early Laying (13)	Late Laying (14)	Incubating (8)
Seeds from:							
Carex spp. (Sedges)	2.31	NS	0.54	0	0	0.15	0.14
Eleocharis spp. (Spike rushes)	2.93	NS	0	0	0	1.35	0
Hippurus spp. (Marestail)	8.23	NS	0	0	0	1.34	4.57
Potamogeton spp. (Pondweeds)	3.53	NS	5.86	4.34	0.09	2.29	1.90
Ruppia spp. (Wigeongrass)	4.73	NS	0	0	0	1.27	0.03
Scirpus spp. (Bulrushes)	3.59	NS	0.90	11.11	3.06	1.18	2.21
Unidentified plant material	4.72	NS	0	1.49	0.02	0.50	0.01

[a] See methods for definitions of reproductive periods.
[b] Kruskal - Wallis test statistic.
[c] Probability value from Kruskal - Wallis Test. NS = Not signficant ($P < 0.05$).
[d] Sample size.
[e] Exclusively adults.
[f] Exclusively larvae.

Planorbid snails were eaten occasionally. Gastropod shell fragments were approximately 16% of the diet in incubating birds.

Crustaceans, notably amphipods, were unimportant in the diet of breeding Barrow's Goldeneyes (Table 2.4). Moreover, I found that even birds collected on wetlands "teeming" with amphipods had rarely consumed these organisms. Amphipods, including the genera *Gammarus* and *Hyallela*, were only found in diets of laying female Goldeneyes, but even then were consumed by ≤ 15% of the birds that I collected (Table 2.3). Furthermore, crustaceans never comprised > 7.5% of the dry mass of the diet in any reproductive period.

Seeds of submergent and emergent macrophytes, particularly pondweeds, marestail, and bulrushes were the majority of plant dry mass in the diet of Goldeneyes (Table 2.4). Seeds were most frequently eaten by Goldeneyes during late laying and incubation (Table 2.3), but represented larger proportions in the diets of prelaying and incubating birds. The only other plant foods in the diet of breeding Goldeneyes were tubers and rootstalks from sago pondweed and chufa, but they accounted for < 1% of the total diet throughout the breeding season.

2.3.3 *Comparative feeding ecology of female Buffleheads and Barrow's Goldeneyes*

The overall diet composition of breeding female Buffleheads and Barrow's Goldeneyes was similar (Table 2.5). Furthermore, there were no differences ($P > 0.5$) between the total proportions of plant and animal foods consumed by female Buffleheads and Goldeneyes (Table 2.5). However, when reproductive periods were evaluated separately there were two important differences that warrant mentioning. During prelaying, the diet of Goldeneyes contained a larger proportion of animal material ($P \leq 0.05$) than did the diet of Buffleheads. Conversely, during incubation the diet of Buffleheads contained a larger fraction of animal material ($P \leq 0.01$) than did the diet of Goldeneyes.

Table 2.5. Comparison of mean aggregate % dry mass in the diets of breeding female Buffleheads and Barrow's Goldeneyes represented by higher taxonomic groups of invertebrates and specific vegetative components.

Food item	Buffleheads (n= 77)	P^a	Barrow's Goldeneyes (n = 53)
Total animal matter	89.10	0.7981	89.24
Gastropoda	13.12	0.0011	5.14
Arachnida	1.98	0.2636	1.79
Crustacea	1.63	0.2876	1.93
Diptera	40.33	0.7691	39.83
Ephemeroptera	0.80	0.8592	1.12
Odonata	12.01	0.0088	29.74
Trichoptera	4.08	0.4209	1.18
Coleoptera	12.10	0.0018	2.57
Hemiptera	2.43	0.0853	2.38
Total plant matter	10.90	0.7981	10.76
Tubers & rootstalks	1.69	0.9499	0.52
Seeds	8.44	0.8440	10.22

[a] P value from Mann-Whitney U test.

There was also interspecific variation in consumption of particular invertebrate groups and plant components by breeding female Buffleheads and Barrow's Goldeneyes (Table 2.5). In this analysis, unless otherwise stated, I combined reproductive periods to investigate overall differences in food use between species. The diet of Buffleheads contained a larger proportion of gastropods ($P = 0.0011$) than did the diet of Goldeneyes; this pattern was most evident during RFG. Overall reliance on dipterans (i.e., the cumulative fraction of the diet represented by all dipteran families) was similar between species, but when dipteran families were evaluated separately Buffleheads consumed proportionately more phantom midge larvae ($P \leq 0.01$) than did Goldeneyes. Odonates, principally damselfly larvae, were a larger proportion of the diet ($P \leq 0.01$) in Goldeneyes than in Buffleheads; this difference was most apparent during non-RFG ($P \leq 0.05$) and early laying ($P \leq 0.05$). Coleopterans were relatively more important in the diet of Buffleheads ($P = 0.0018$) than in Goldeneyes, particularly during late laying ($P \leq 0.05$). Consumption of hemipterans and plant tubers and rootstalks was similar between species when reproductive periods were combined, but were most important in the diet of Buffleheads during late laying ($P \leq 0.05$) when reproductive periods were analyzed separately. Seeds were utilized equally by both species over the entire reproductive period, but were more prominent in the diet of Buffleheads during prelaying ($P \leq 0.05$) and conversely more important in the diet ($P \leq 0.01$) of Goldeneyes during incubation. In particular, Buffleheads ate proportionately more sedge seeds ($P \leq 0.05$) during prelaying than did Goldeneyes, while incubating Goldeneyes ingested proportionately more pondweed and bulrush seeds ($P \leq 0.05$) than did Buffleheads.

2.3.4 *Digestive tract morphology*

The effects of reproductive status and year on digestive tract morphology of female Buffleheads and Barrow's Goldeneyes are presented in Table 2.6. There was no

Table 2.6. Results from two-way ANOVA investigating the effects of reproductive status and year on digestive organs of breeding Buffleheads and Barrow' Goldeneyes.

Variable	Species^c	Year^d	Reproductive Status^a						Effects^b	
			Non-RFG	Prelayers	Early laying	Late Laying	Early incubation	Late incubation	Status	Year
Mass:										
Total digestive tract	BH	Pooled^e	13.09^g (0.45)	11.59 (0.38)	11.16 (0.31)	12.12 (0.33)	11.50 (0.44)	11.00 (0.28)	0.0006	NS
	BG	Pooled^f	45.03 (2.98)	38.88 (1.66)	35.52 (1.08)	36.24 (1.13)	33.34 (1.18)	31.55 (1.07)	0.0001	NS
Upper digestive tract	BH	Pooled	2.40 (0.10)	2.30 (0.09)	2.72 (0.07)	2.68 (0.06)	2.61 (0.11)	2.43 (0.07)	0.0017	NS
	BG	Pooled	6.64 (0.27)	6.65 (0.17)	6.85 (0.18)	7.27 (0.18)	6.30 (0.21)	6.32 (0.20)	0.0147	NS
Gizzard	BH	Pooled	5.70 (0.26)	4.72 (0.26)	4.17 (0.15)	4.39 (0.14)	4.71 (0.26)	4.55 (0.19)	0.0001	NS
	BG	Pooled	22.09 (1.86)	18.08 (0.95)	15.72 (0.61)	15.04 (0.62)	15.44 (0.77)	15.19 (0.58)	0.0001	NS
Small intestine	BH	Pooled	4.49 (0.14)	4.13 (0.21)	3.81 (0.15)	4.53 (0.18)	3.68 (0.17)	3.50 (0.13)	0.0001	NS
	BG	Pooled	14.46 (0.97)	12.39 (0.73)	11.34 (0.58)	12.18 (0.49)	9.97 (0.41)	8.71 (0.53)	0.0002	NS
Ceca	BH	Pooled	0.17 (0.01)	0.13 (0.01)	0.14 (0.01)	0.17 (0.01)	0.16 (0.01)	0.18 (0.01)	0.0566	NS
	BG	Pooled	0.38 (0.01)	0.32 (0.02)	0.32 (0.01)	0.34 (0.01)	0.39 (0.01)	0.39 (0.02)	0.0003	NS

Table 2.6. Continued.

Variable	Species[c]	Year[d]	Reproductive Status[a] Non-RFG	Prelayers	Early laying	Late Laying	Early incubation	Late incubation	Effects[b] Status	Year
Mass (continued):										
Large intestine	BH	Pooled	0.34	0.31	0.31	0.36	0.34	0.34	NS	NS
			(0.02)	(0.02)	(0.02)	(0.02)	(0.01)	(0.02)		
	BG	Pooled	1.46	1.44	1.28	1.41	1.25	0.95	NS	NS
			(0.10)	(0.16)	(0.11)	(0.07)	(0.15)	(0.09)		
Liver (Lipid-free)[h]	BH	1993[i]	3.34	3.29	3.38	3.26	3.08	2.83	0.0049	0.0035
			(0.22)	(0.16)	(0.13)	(0.15)	(0.23)	(-)		
		1994[j]	3.91	3.55	3.90	3.69	3.22	2.98		
			(0.52)	(0.20)	(0.45)	(0.11)	(0.14)	(0.10)		
	BG	Pooled	7.97	8.82	8.15	8.30	7.40	7.02	0.0012	NS
			(0.37)	(0.32)	(0.24)	(0.19)	(0.33)	(0.27)		
Liver lipid	BH	1993	0.42	0.32	0.30	0.27	0.30	0.12	0.0001	0.0450
			(0.07)	(0.04)	(0.02)	(0.07)	(0.08)	(-)		
		1994	0.56	0.33	0.46	0.42	0.16	0.15		
			(0.22)	(0.04)	(0.06)	(0.03)	(0.02)	(0.01)		
	BG	Pooled	1.05	1.22	0.82	0.79	0.46	0.38	0.0001	NS
			(0.18)	(0.14)	(0.08)	(0.05)	(0.04)	(0.02)		
Pancreas	BH	Pooled	1.56	1.40	1.71	1.67	1.41	1.34	0.0003	NS
			(0.11)	(0.11)	(0.08)	(0.05)	(0.05)	(0.04)		
	BG	Pooled	3.11	3.36	3.17	3.41	3.18	2.70	0.0054	NS
			(0.15)	(0.17)	(0.10)	(0.10)	(0.10)	(0.09)		

Table 2.6. Continued.

			Reproductive Status^a						Effects^b	
Variable	Species^c	Year^d	Non-RFG	Prelayers	Early laying	Late Laying	Early incubation	Late incubation	Status	Year
Lengths:										
Total digestive tract	BH	Pooled	1273.51	1232.05	1248.75	1285.49	1149.04	1105.13	0.0001	NS
			(25.66)	(30.58)	(21.83)	(0.33)	(18.47)	(16.20)		
	BG	Pooled	1742.58	1692.76	1708.81	1754.10	1615.06	1545.70	0.0091	NS
			(37.86)	(22.67)	(30.54)	(30.36)	(30.08)	(37.96)		
Upper digestive tract	BH	Pooled	170.11	168.00	168.31	166.74	172.29	172.36	NS	NS
			(1.65)	(1.45)	(1.55)	(1.46)	(1.42)	(1.47)		
	BG	Pooled	229.88	230.00	224.67	229.12	230.00	227.83	NS	NS
			(2.21)	(1.70)	(2.07)	(1.59)	(2.32)	(1.81)		
Gizzard	BH	Pooled	29.64	29.13	28.41	28.88	29.82	28.96	NS	NS
			(0.63)	(0.56)	(0.46)	(0.49)	(0.66)	(0.56)		
	BG	Pooled	42.17	40.50	40.88	41.09	41.54	40.61	NS	NS
			(0.72)	(0.80)	(0.74)	(0.62)	(0.92)	(0.48)		
Small intestine	BH	Pooled	940.00	903.44	911.06	933.48	811.93	769.50	0.0001	NS
			(22.67)	(27.92)	(16.54)	(18.38)	(14.96)	(14.51)		
	BG	Pooled	1284.25	1256.08	1251.06	1284.80	1148.79	1079.25	0.0005	NS
			(33.86)	(17.39)	(26.11)	(29.00)	(23.72)	(29.28)		
Ceca	BH	Pooled	87.78	88.50	102.54	108.39	91.27	91.28	0.0001	NS
			(2.22)	(4.20)	(3.93)	(3.18)	(4.15)	(3.64)		
	BG	Pooled	106.67	95.04	112.41	115.34	110.38	115.03	0.0020	NS
			(3.71)	(3.60)	(4.07)	(2.59)	(2.71)	(3.22)		

Table 2.6. Continued.

Variable	Species[c]	Year[d]	Reproductive Status[a] Non-RFG	Prelayers	Early laying	Late Laying	Early incubation	Late incubation	Effects[b] Status	Year
Large intestine	BH	Pooled	45.98	42.99	46.17	48.00	43.74	43.03	0.0570	NS
			(1.71)	(1.43)	(1.02)	(0.84)	(1.40)	(0.71)		
	BG	Pooled	79.62	71.13	79.80	83.75	70.13	64.82	0.0002	NS
			(3.55)	(4.14)	(3.61)	(2.26)	(3.82)	(2.63)		

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[a] See definitions in methods.

[b] No significant (P > 0.05) interactions, therefore data were reanalyzed using only main effects in the model. Probability values are presented for significant main effects. NS = Not significant (P > 0.0.5).

[c] BH = Bufflehead, BG = Barrow's Goldeneye.

[d] Separate means were presented for each year only when there were significant (P < 0.05) annual effects in the model.

[e] Pooled sample sizes for Bufflehead - Non-RFG = 18, Prelayers = 9, Early Layers = 16, Late Layers = 27, Early incubation = 14, Late incubation = 14

[f] Pooled sample sizes for Barrow's Goldeneye - Non-RFG = 16, Prelayers = 12, Early Layers = 18, Late Layers = 25, Early incubation = 14, Late incubation = 12.

[g] Mean with corresponding standard error below in parentheses.

[h] Lean dry mass.

[i] 1993 sample sizes for Bufflehead - Non-RFG = 13, Prelayers = 4, Early Layers = 12, Late Layers = 16, Early incubation = 4, Late incubation = 1.

[j] 1994 sample sizes for Bufflehead - Non-RFG = 5, Prelayers = 5, Early Layers = 4, Late Layers = 11,Early incubation = 10, Late incubation = 13.

annual variation in digestive tract morphology of Barrow's Goldeneyes (Table 2.6), whereas only lean liver ($P = 0.0035$) and liver fat ($P = 0.0450$) masses differed between years female Buffleheads (both were heavier in 1994 than in 1993). For the remaining digestive tract components, years were pooled and variation discussed only in relation to reproductive status (see below).

Total digestive tract mass differed between reproductive periods in Buffleheads ($P = 0.0006$) and Barrow's Goldeneyes ($P = 0.0001$). In both species, digestive tract mass was heaviest in non-RFG birds and declined ($P \leq 0.05$) as birds began ovarian growth (i.e., prelaying). Reduced mass was principally attributable to gizzard atrophy following arrival on breeding areas (Table 2.6) . Additionally, ceca mass declined ($P \leq 0.05$) between non-RFG and prelaying cohorts in both species and small intestine mass decreased ($P \leq 0.05$) between these periods in Barrow's Goldeneyes. Digestive tract mass remained similar throughout subsequent reproductive periods in Barrow's Goldeneyes (Table 2.6), but increased ($P \leq 0.05$) by approximately 1 g between early and late laying in Buffleheads (Table 2.6).

Considerable variation in mass of specific digestive tract components occurred between late laying and early incubation in Buffleheads and Barrow's Goldeneyes (Table 2.6), but these changes did not result in significant differences in total digestive mass between these periods in either species. Most notably, small intestine and lean liver mass (both years) decreased ($P \leq 0.05$) in both species after they began incubation. Liver fat also declined ($P \leq 0.05$) in both species during this period in 1994, but only in Barrow's Goldeneyes during 1993. Pancreas mass dropped ($P \leq 0.05$) between late laying and early incubation in Buffleheads, but did not decline ($P \leq 0.05$) in Goldeneyes until late incubation (Table 2.6). Only the upper digestive tract mass of Buffleheads declined ($P \leq 0.05$) during early incubation, whereas ceca mass of Barrow's Goldeneyes actually increased ($P \leq 0.05$).

Patterns in total digestive tract length were the same for both species (Table 2.6), being longest during late laying followed by a sharp decline in gut length ($P \leq 0.05$) as birds started incubation. Reduction in digestive tract length between late laying and early incubation resulted from declines in small and large intestine lengths ($P \leq 0.05$) in both species and additionally from reduced ceca length ($P < 0.05$) in Buffleheads. The only other significant difference in a digestive tract component that was common to both species was increased ceca mass ($P \leq 0.05$) between prelaying and early laying, but this change did not effect total digestive tract length.

2.4 DISCUSSION

2.4.1 *Bufflehead diet studies*

Aquatic insects. - The diet of breeding female Buffleheads was composed principally of aquatic insects. Insects from six different orders were eaten, but the most important were larvae of midges, phantom midges, and damselflies. Munro (1942) also found that Buffleheads breeding in the southern interior of British Columbia fed principally on aquatic insects, but indicated that odonate larvae and corixids comprised the majority of the diet. The importance of soft-bodied dipteran larvae was likely underestimated by Munro (1942) as his data were based largely on examination of gizzard contents (see Swanson and Bartonek 1970). Likewise, Erskine (1972) indicated that insects were the predominate component in the diet of adult Buffleheads during spring (66.5% total volume) and summer (71.5%). He also reported that birds using habitats in British Columbia and Alberta fed principally on chironomid larvae (13.6%) during spring, but shifted toward greater consumption of odonates (13.3%) and corixids (14.4%) during summer. Based on combined esophageal and gizzard contents, Erskine (1972) did suggest that corixids were the most frequently consumed food in the spring (i.e., 36.1% of birds) and summer (65.1%) diets of Buffleheads. Based exclusively on esophageal contents, I found that Hemipterans, including both corixids and notonectids, were found in the upper digestive tract contents of < 17% of the Buffleheads breeding on the Chilcotin Plateau (Table 2.1). All studies of food habits of breeding Buffleheads (Munro 1942, Erskine 1972, this study), regardless of analytical approach or geographic location, have found that Odonate larvae ranked either first or second in dietary importance during reproduction.

Erskine (1972) indicated that breeding Buffleheads did not forage selectively, but fed opportunistically on invertebrate foods that were most readily available. This, however, was contrary to his data, because dragonfly larvae, water boatmen, and aquatic beetles were consumed disproportionately to their availability, but leeches, cladocerans, copepods, amphipods, caddisfly larvae, and Pelecypods were consumed in lower proportion to their availability.

Mollusks. - Compared to other *Bucephala*, Buffleheads typically consume more gastropods throughout their annual cycle, particularly Planorbid and Lymnaed snails in freshwater habitats (Cottam 1939, Erskine 1972). Erskine (1972) reported that gastropods were most important in the diet of wintering Buffleheads when they represented approximately 19 - 20% of total diet volume. During the breeding season, I found that consumption of gastropods and gastropod shell fragments exceeded 25% (Aggregate dry mass) of the diet in female Buffleheads during late laying (Table 2.2). Increased intake of gastropods during egg laying was likely essential to meet the mineral requirements of eggshell production. Additional evidence of the significance of gastropods to breeding Buffleheads was provided by Munro (1942) who reported that gizzards from several egg laying females contained over 50%(total volume) gastropods indicating that these mineral-rich foods are important to birds at other breeding locations. Notably, shell fragments comprised the majority of molluscan material consumed by Buffleheads (Table 2.2), suggesting that birds principally consumed these organisms for their mineral content.

Crustaceans. - Crustaceans were a small proportion (< 5%) of the diet in breeding Buffleheads. Cladocerans were the most frequently eaten crustaceans followed by fairy shrimp and amphipods; however, on an aggregate dry mass basis fairy shrimp represented the largest fraction of the diet of any crustacean (Table 2.2). Female buffleheads fed on fairy shrimp primarily just after arrival on breeding areas when prebreeding pairs congregated on larger athalassic wetlands before dispersing to smaller wetlands for nesting. Cladocerans, principally represented by *Daphnia*, were consumed during all reproductive periods except prelaying and incubation, but they made up < 1% of the diet.

Amphipods may comprise up to 5% (total volume) in the annual diet of Buffleheads (Cottam 1939). Despite their abundance in many wetlands used by breeding Buffleheads (Boyd and Smith 1989, pers. obs.), amphipods were found in only two birds during late laying and constituted only 1% of the diet during this period (Table 2.2). Munro (1942) partitioned his diet analyses between areas and times of the year, and found that Buffleheads ingested amphipods principally during late summer and early fall. Erskine (1972) suggested that amphipods may be equally preferred to insects by Buffleheads during summer, despite that these invertebrates were never more than 3% (total volume) of the diet in his analyses. He also indicated, however, that amphipods comprised a lower proportion of the gizzard contents than would be expected from availability in several wetlands in central British Columbia. He explained this disparity by suggesting that amphipods were digested rapidly and rendered unrecognizable by the grinding action of the gizzard. However, I think that rapid digestion of these highly keratinized invertebrates was unlikely. Low consumption of amphipods by Buffleheads, despite their availability and the birds' ability to capture these prey, suggests that Bufflehead avoid feeding on amphipods during the breeding season.

Plant foods. - Plant material generally represented ≤ 15% of the diet in breeding female Buffleheads and steadily decreased in importance from prelaying through incubation (Table 2.2). Seeds typically represented >75% of plant matter in the diet except during incubation when birds contained predominantly "unidentified" vegetation. Tubers and rootstalks of sago pondweed and chufa represented the only other recognizable plant material, but were typically a small fraction of the aggregate diet except during prelaying when they comprised approximately 7% of foods consumed. Based on combined consumption of seeds, tubers, and rootstalks, *Potamogeton* represented the most important genus of plants in the diet, followed by *Scirpus* and *Hippurus*. Seeds and tubers of other plant genera typically represented < 1% of overall diet composition. Similarly, Cottam (1939) indicated that the annual diet of Buffleheads contained < 21% (total volume) plant material and that pondweeds (Potamogeton spp.) provided the primary plant food (up to 5% total volume). Furthermore, he documented that Buffleheads ingested the seeds of *Scirpus*, *Myriophyllum*, *Ceratophyllum*, *Carex*, *Eleocharis*, *Cyperus*, and *Hippuris*, which all occurred in the diet of female Buffleheads in this study. Munro (1942) also reported *Potamogeton*, *Myriophyllum*, *Carex*, and *Scirpus* seeds from gizzard contents of Buffleheads breeding in central British Columbia; moreover, seeds were only a small component in the total volume of the diet in these birds. Erskine (1972) indicated that approximately 81% of the 36 birds he examined during spring contained plant material in their gizzard contents with 18.8% of the total volume of the ingesta represented by plant foods. This estimate most closely approximates birds in my non-RFG category of which 56% had fed on plant foods accounting for 13% of the total dry mass of the diet.

Plant foods, particularly the seeds of pondweeds and bulrushes, become increasingly important in the diet of Buffleheads during fall and winter. Erskine (1972) reported plant material in over 50% of adult Bufflehead during fall and winter with vegetation representing up to 32.4% of the total food volume of birds collected from fresh to moderately brackish wetlands. Similar to diets of breeding birds, tubers and rootstalks of pondweeds represented most of the small component of plant material in the diet of Buffleheads that was not seeds. Additionally, Gammonley and Heitmeyer (1990) reported that the diet of spring migrant Buffleheads using interior wetlands in northern California consisted primarily of seeds.

Diets during other periods in the annual cycle. - Female Buffleheads wintering on freshwater systems may continue to consume a high proportion (94%) of aquatic insects (Anderson and Ohmart 1987), whereas those wintering in marine habitats consume primarily crustaceans and mollusks. Vermeer (1982) found that gastropods, crustaceans, and vascular plants and seeds formed the majority of the diet in Buffleheads wintering in coastal habitats of southern British Columbia. Plant foods were only consumed by Buffleheads in the Fraser River Delta and were virtually absent in the diet of birds wintering in more saline areas in the Strait of Georgia. Similarly, Hirsch (1980) found that Buffleheads wintering in marine habitats along the coast of Washington fed principally on gastropods (61% total volume) and crustaceans (24% total volume). During fall migration, small flocks of Buffleheads may frequent salmonid spawning areas to feed on uncovered eggs (Munro 1923, 1942). Buffleheads also forage on the eggs of Pacific herring (*Clupea harengus pallasi*) during spring migration (March) (Munro 1942), which probably facilitates lipid storage for subsequent use during migratory movements and for clutch formation.

2.4.2 *Barrow's Goldeneye diet studies*

Aquatic insects. - Breeding female Barrow's Goldeneyes fed principally on aquatic insects during all reproductive periods (Table 2.4); zygoptera larvae, followed by the larvae and pupae of chironomids and chaoborinids, were the primary insect foods. Munro (1939) reported that Barrow's Goldeneyes breeding in southern British Columbia frequently fed on Odonate larvae and hemipterans. I suspect that the importance of hemipterans was overestimated and consumption of soft-bodied insects (e.g., chironomid and chaoborinid larvae) underestimated by Munro (1939) as his analyses were based primarily on gizzard contents (see Swanson and Bartonek 1970). Bengston (1971) reported that 24 adult females from the Icelandic population of Barrow's Goldeneyes, had fed principally on chironomid larvae (75% frequency of occurrence; 38% aggregate wet mass) and Lymnaed snails (25% frequency of occurrence; 33% aggregate wet mass) during the breeding season. He also suggested that the importance of chironomid larvae in the diet of Icelandic Barrow's Goldeneyes increased as summer progressed, whereas use of gastropods (specifically *Lymnaea* spp.) decreased. In British Columbia, the trend was just the opposite, with chironomid larvae decreasing and gastropods increasing in dietary significance as the breeding season progressed (Table 2.4).

Simuliid (Blackfly) larvae were a common food in the diet of female Barrow's Goldeneyes in Iceland, but Bengston (1971) included them with miscellaneous animal foods making a more precise evaluation of their importance impossible. Regardless, they did not exceed 18% (aggregate wet mass) of the diet, which represented the total proportion of miscellaneous animal foods. Gardarsson (1979) reported that 5 adult Barrow's Goldeneyes (sexes not specified) collected during July and August on Lake Myvatn, Iceland had fed primarily on chironomids (59% total volume) and cladocerans (26%). He speculated, however, that these results were biased in some unexplained manner and that simuliids were actually the principal food. Simuliid larvae are apparently an important food for brood hens and their ducklings, and availability of these invertebrates can be used to predict movements and distribution of female Goldeneyes and their broods in the Icelandic population (Einarsson 1988); however, current data suggest that chironomids are the primary food of Goldeneyes in this population during earlier segments of the breeding season. In Iceland, breeding Barrow's Goldeneyes foraged 39% of the time in lotic habitats where simuliid larvae are generally found (Clifford 1991). Palustrine systems, such as those used by birds in my study area, are not conducive to colonization by blackflies and hence these invertebrates were not found in any bird that I examined.

Mollusks. - Use of mollusks by breeding Barrow's Goldeneyes was markedly lower than during winter when, in coastal habitats, birds feed almost exclusively on blue mussels and various gastropods (Munro 1939, Koehl et al. 1982, Vermeer 1982). Molluscan foods, represented solely by gastropods on breeding areas, were not consumed by any birds before RFG and constituted < 1% of the diet during prelaying and early laying (Table 2.4). Ingestion of gastropod shell fragments increased during late laying and peaked during incubation when they made up approximately 16% of the diet.

Crustaceans. - Munro (1918) speculated that crustaceans were the principal food of Barrow's Goldeneyes breeding on small alkaline wetlands in British Columbia. For 5 Barrow's Goldeneyes (sexes or reproductive status not reported) using small palustrine wetlands in southern British Columbia, amphipods were > 50% of the gizzard contents (Munro 1939). This high ingestion rate of amphipods contrasts markedly with breeding birds on the Fraser Plateau, which seldom ate these crustaceans (Table 2.3). I speculate that use of amphipods in earlier studies was likely inflated by examination of gizzard contents. Interestingly, Munro (1939) also reports that 5 adults (sexes not specified) collected during the breeding season (i.e., May and June) on a wetland (Paul Lake, British Columbia) in which amphipods were common, had not consumed these organisms.

Others crustaceans are apparently avoided by breeding Goldeneyes, as fairy shrimp were abundant in several wetlands from which I collected birds, but none had consumed them. Munro (1939) also noted that several subadult Goldeneyes had not fed on fairy shrimp despite occupying a wetland where these crustaceans were readily available. Crayfish, however, are apparently a favored food for Barrow's Goldeneyes in some riverine and large lake systems in southern British Columbia (Munro 1918), but are not available in the alkaline palustrine wetlands used by breeding birds on the Fraser Plateau.

Fish eggs. - Munro (1923, 1939) reported that Barrow's Goldeneyes using freshwater habitats in late fall and early winter principally forage for salmon eggs and caddisfly larvae. Individual goldeneyes can consume up to 300 salmon eggs in one foraging bout, but Munro (1923) estimated the average daily consumption at 100 eggs per bird on Henderson Lake, British Columbia. Many of the ingested eggs were apparently drifting spawn, which suggested that loss of these eggs to waterfowl or other predators was unlikely to affect salmon production. During spring migration in British Columbia, eggs from spawning herring form the principal food (i.e., up to 49% of the aggregate wet weight of food contents) in the diet of Barrow's Goldeneyes (Vermeer 1982). Herring eggs were often the sole food ingested by Barrow's Goldeneyes in March along coastal regions of southern British Columbia.

Barrow's Goldeneyes also consume fish eggs during the breeding season when they are available. Approximately 11% (aggregate wet mass) of the diet of breeding female Barrow's Goldeneyes in the Icelandic population was comprised of fish eggs (Bengston 1971). Furthermore, the diet of breeding males in this population consisted of up to 92% fish eggs. Moreover, in a year when chironomids were less available, consumption of fish eggs by Goldeneyes increased (Bengston 1971). Most wetlands on my study area are too shallow or too alkaline to support fish populations, hence fish eggs were not found in any birds.

Plant foods. - Plant foods represented < 10% of the diet of Barrow's Goldeneyes except during incubation when they comprised 16.7% of the upper digestive tract contents (Table 2.4). Krapu and Reinecke (1992) speculated that increased consumption of plant foods during incubation was adaptive because plants are a more dependable food than aquatic invertebrates. Seeds were the majority of plant dry mass in the diet of Barrow's Goldeneyes in British Columbia. Pondweed and bulrush seeds were most frequently eaten (Table 2.3) and represented the largest vegetative fraction of the diet (Table 2.4). In the Icelandic population of Barrow's Goldeneyes, pondweed seeds also comprised the majority of plant material in the diet, but seeds represented an even smaller component (< 0.1% aggregate wet mass) of the diet (Bengston 1971) than in my study.

Similarly, Cottam (1939) reported that annual diets of both Barrow's and Common Goldeneyes contained up to 8% (total volume) *Potamogeton*, which chiefly represented consumption of seeds.

Diets during other periods in the annual cycle. - During winter, Barrow's Goldeneyes feed principally on blue mussels (*Mytilus edulis*) in coastal habitats of southern British Columbia (Munro 1939, Vermeer 1982). In some mainland fjords blue mussels may represent up to 95% of the aggregate wet mass of the diet (Vermeer 1982). Barrow's Goldeneyes (sexes combined) wintering in tidal fiords in southeastern Alaska fed almost exclusively on mollusks and crustaceans, with over half their diet consisting of blue mussels (Koehl et al. 1982). There were no sex-related differences in diet composition of birds wintering in coastal Alaska other than males consumed larger blue mussels than did females.

2.4.3 *Is food defence a function of territoriality in breeding Bucephala*

Species in the genus *Bucephala* defend spatially and temporally stable breeding territories (Savard 1984, 1988, Gauthier and Smith 1987). This differs from other North American ducks, which typically defend a revolving territory around their female (e.g., Mallards [*Anas platyrhynchos*], Titman 1983) or no territory at all (e.g. Northern Pintails [*Anas acuta*], Derrickson 1978). The function of fixed breeding territories in the *Bucephala* has been the subject of considerable research with remarkably diverse and sometimes elaborate conclusions. Donaghey (1975) initially hypothesized that Buffleheads established breeding territories to defend foods required by laying females (hereafter the "food defence hypothesis"). In contrast, Gauthier (1987a) suggested mate-guarding was the primary function of breeding territories in Buffleheads, which secondarily evolved into defence of a specific area rather than a revolving territory around the female to maintain vigilance over their nest site. Thus, Gauthier considered that females themselves, rather than food for females were the resource defended by males.

Savard and Smith (1987) found that Barrow's Goldeneyes were most aggressive toward species with similar diets in both spring and winter. Thus, similar to Donaghey (1975) they speculated that one of the primary functions of territorial behavior in the *Bucephala* was to protect their food supply. Subsequently, Savard (1988) suggested that breeding territories may be defended by males to reduce interference competition between their females and species with similar diets, implying that space rather than food per se was the resource defended by male Goldeneyes.

Food habits data from breeding Buffleheads in this study cast serious doubt on Gauthier's (1987a) conclusion that food defence was not a function of territoriality in the *Bucephala*. His test of the food defence hypothesis was inherently flawed because he assumed that Buffleheads fed predominantly on *nektonic* invertebrates. I found, however, that Buffleheads fed primarily on *benthic* insects and gastropods (Table 2.2). It is thus not surprising that Gauthier did not find a correlation between territory size and food density or a relationship between reproductive success and food abundance because he was measuring the wrong food. Furthermore, Gauthier's conclusion that mate guarding was the primary function of territorial behavior in *Bucephala* is interesting considering that forced copulation has never been observed in this genus (see review in Savard 1988), there is mounting evidence that many *Bucephala* exhibit long term monogamy (Savard 1985, Gauthier 1987b), and recent DNA fingerprinting studies have found no evidence of mixed paternity in unparasitized Goldeneye clutches (Eadie et al. 1995). Furthermore, protection of paternity does not explain why male *Bucephala* exclude conspecific females and subadults, congeners, and other species with similar diets from their territories. Also, protection of paternity does not provide a logical explanation why territories are not centered around the females (Donaghey 1975, Savard and Smith 1987) nor why males continue to defend breeding territories when the female is not present. Finally, it is highly unlikely that nest site protection resulted in the evolution of fixed territories, because there is very little evidence to suggest that males protect the actual nest site. In fact, several female *Bucephala* may nest in a single tree if separate nest cavities are available and breeding territories are commonly not adjacent to the nest site. Additional studies are needed to test hypotheses on the evolution of territoriality in the *Bucephala*, however, I suggest given the relatively less productive breeding habitats and ephemeral and patchy nature of foods used by Buffleheads and Goldeneyes, that the food defence hypothesis is still the most parsimonious explanation of territorial behavior in the *Bucephala*.

There was considerable overlap in the diet composition of sympatrically breeding female Buffleheads and Barrow's Goldeneyes. Diets of the two species were most similar during non-RFG when birds were settling into breeding territories. Therefore, interspecific aggression should be greatest shortly after the birds arrive on breeding areas, but this remains to be tested. The few differences in diets between the two species were likely attributable to the interacting factors of body size and nutritional requirements during egg production rather than adaptations to reduce interspecific competition for food (see below). The overall similarity in diets of Buffleheads and Goldeneyes and corresponding high degree of interspecific aggression between these species provide additional support for the food defense hypothesis in explaining the evolution of territoriality in breeding *Bucephala*.

Similar to its congeners, the diet of Common Goldeneyes typically contains > 75% animal material (Munro 1939). Cottam (1939) suggested that Barrow's Goldeneyes consumed proportionately more insects but less crustaceans than did Common Goldeneyes. However, Common Goldeneyes also commonly feed on Trichopteran, Odonate, and Ephemeropteran larvae, and both the larval and adult forms of corixids and coleopterans (see review in Eadie et al. 1995). Odonate and Trichopteran larvae are particularly important in the diet of Common Goldeneyes. Thus, high levels of interference competition to defend better foraging sites for odonate larvae may provide one explanation for why Common and Barrow's Goldeneyes seldom breed sympatrically.

2.4.4 *Adaptive significance of modifications in digestive tract morphology*

Rapid changes in the digestive tract morphology of birds can occur in response to changes in food volume (Ankney 1977) and quality (Moss 1974, Miller 1975, Paulus 1982, Drobney 1984, Kehoe et al. 1988) or to meet protein demands during periods of elevated requirements (e.g., reproduction, migration, molt) either through direct provisioning of protein via tissue catabolism (Ankney 1977, Korschgen 1977, Raveling 1979) or through entrained modifications to enhance exogenous nutrient assimilation (Moss 1972, Thompson and Drobney 1996). Gut morphology of female Buffleheads and Barrow's Goldeneyes was highly dynamic during reproduction. Both species arrived on breeding areas with relatively heavy digestive tracts, especially muscular gizzards, which were probably essential to physically process and metabolize marine mollusks and crustaceans that comprise the majority of the diet for these species during winter (see above). Increased size of digestive organs may also result from increased foraging to store somatic nutrients before spring migration and subsequent egg production (Ankney 1977).

Gizzard and ceca mass of Buffleheads and Goldeneyes declined rapidly on breeding areas as diet quality improved and birds fed principally on aquatic insects (Tables 2.2 & 2.4). Reduced gizzard and ceca mass is consistent with similar patterns observed in other ducks (Miller 1975, Kehoe and Ankney 1985) and grouse (Moss 1974) with increased diet quality. The gizzard can also be an important source of somatic protein for clutch formation in waterfowl (Ankney 1977, Korschgen 1977, Raveling 1979, Krapu 1981). However, gizzard mass was stable during RFG in Buffleheads and Barrow's Goldeneyes indicating that this tissue did not provide significant amounts of protein for egg production.

Digestive tract morphology of Barrow's Goldeneyes remained relatively constant during RFG (Table 2.6), but there were several changes in digestive organs of Buffleheads consistent with greater dependency on exogenous nutrients during egg formation in this smaller species. Initially, mass of the upper digestive tract increased during prelaying. Hypertrophy of the upper digestive tract can improve protein assimilation in passerines (Dolnik and Gavrilov 1979) and may serve a similar function in breeding Buffleheads. Additionally, in birds without crops, including most ducks, enlargement of the proventriculus permits additional storage of food during foraging. Small intestine mass of Buffleheads increased during late laying, which may have improved chemical digestion and the ability of this tissue to absorb nutrients required during late RFG when Buffleheads were probably most dependent on dietary nutrients. Pancreas mass in Buffleheads increased during early laying probably to enhance production of digestive enzymes in response to intensive foraging by birds during egg synthesis.

Daily food intake (Afton and Paulus 1992) and digestive organ mass typically decline with decreased time spent foraging during incubation (Drobney 1984). During early incubation, mass and length of the small intestine and lean mass of the liver decreased in Buffleheads and Barrow's Goldeneyes (Table 2.6). In addition, mass of the upper digestive tract and pancreas also declined with onset of incubation in Buffleheads (Table 2.6). Rapid atrophy of digestive tract components during incubation supports the hypothesis that birds should maintain the smallest functional organ size because smaller organs reduce metabolic energy expenditure (Moss 1974). Atrophy in digestive tract tissues of incubating Buffleheads and Goldeneyes would reduce metabolic energy requirements and likely increase incubation constancy and corresponding nest success. Only ceca mass in Barrow's Goldeneyes increased during incubation, which likely was related to increased plant material (i.e. fiber) in the diet during this period. Elongation of the ceca enhances nutrient absorption from higher fiber plant foods through increased fermentation (Duke 1986). Buffleheads did not undergo a similar modification in their ceca because their diet consisted almost exclusively of aquatic insects during incubation (Table 2.2).

2.4.5 *The role of exogenous nutrients in meeting the nutritional requirements for clutch formation*

Omnivorous and herbivorous ducks often accumulate prebreeding fat reserves by increasing consumption of high carbohydrate plant foods during late winter and spring migration (Drobney and Fredrickson 1979, Miller 1987). Buffleheads and Barrow's Goldeneyes apparently obtain a large fraction of their prebreeding lipid reserves during spring migration by feeding on fish eggs (Vermeer 1982). Female Buffleheads and Barrow's Goldeneyes in 1994 acquired protein required for clutch formation by consuming aquatic invertebrates on breeding areas (Chapter 4). Even in 1993 when Goldeneyes catabolized somatic protein to produce egg protein, most of the protein required still originated from their diet. Insect foods provide an excellent substrate for producing eggs due to the high metabolic efficiency of converting animal protein and lipids to albumen and yolk (Krapu and Reinecke 1992). Some calcium for eggshell production originated from catabolism of somatic minerals in both species during the 1993 breeding season (Chapter 4), but most mineral requirements were met by consumption of gastropods, gastropod shell fragments, and possibly other invertebrates. Furthermore, Buffleheads occasionally consumed avian egg shell fragments and small bones as alternative sources of calcium (Table 2.1). Similarly, nesting King Eiders have been found to ingest bones from lemmings and fish (Upenski 1972 cited in Krapu and Reinecke 1992) and female Common Goldeneyes have been observed eating egg shell fragments from nest boxes (Eadie et al 1995).

Buffleheads showed more variation in their diet during the breeding season than did Barrow's Goldeneyes, which is consistent with my hypothesis that smaller species of waterfowl will show greater modification in their diet composition than will larger species to meet the nutritional demands of reproduction. An apparent example of the interaction between body size and nutritional demands for egg production is the higher proportional consumption of gastropods by Buffleheads when mineral requirements for eggshell production were elevated during RFG. Smaller body size apparently limits the potential contribution of somatic mineral to eggshell synthesis in Buffleheads (Chapter 4), requiring females to increase ingestion of foods that provide a rich source of calcium.

Female Barrow's Goldeneyes are over twice the size of female Buffleheads (Chapter 1). Therefore, nutrient storage is less constrained by body size in Goldeneyes than in Buffleheads. This allows them to maintain and utilize absolutely greater nutrient reserves and consequently reduces their reliance on exogenous nutrients during clutch formation. This prediction was supported by my food habits data, which indicated that diets of Goldeneyes changed little during reproduction, despite marked differences in nutritional requirements between reproductive periods.

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CHAPTER 3. EGG LAYING INTERVALS AND ENERGETIC COSTS OF EGG FORMATION IN BUFFLEHEADS AND BARROW'S GOLDENEYES

3.1 INTRODUCTION

Daily energy costs of egg production in waterfowl (Anseriformes), relative to their daily basal metabolic energy requirements, show that reproductive costs for this order are among the highest recorded for birds (King 1973, Ricklefs 1974, Walsberg 1983). However, this relationship assumes that waterfowl lay an egg per day, which is not the case with many species that rely principally on endogenous reserves for egg production (e.g., Lesser Snow Geese [*Anser caerulescens caerulescens*] Ryder 1971, Schubert and Cooke 1993; Canada Goose [*Branta canadensis*] Kossack 1950, Vermeer 1970; Common Eider [*Somateria mollissima*] Watson et al. 1993) or for those species that nest in relatively unproductive habitats (e.g., Common Goldeneyes [*Bucephala clangula*] Eadie et al. 1995).

Time between successive eggs in the clutch (hereafter laying intervals), can directly effect reproductive success (Watson et al. 1993) and the energetic cost of egg formation in birds, yet they have seldom been investigated. Most information on laying intervals of waterfowl (Anseriformes) is anecdotal or was derived from single or multiple daily nest visits that require elaborate assumptions to estimate actual laying time (see Watson et al. 1993, Schubert and Cooke 1993). This study , however, used improved electronic technology to monitor laying intervals of cavity nesting Buffleheads (*Bucephala albeola*) and Barrow's Goldeneyes (*Bucephala islandica*) breeding in central British Columbia.

Egg laying intervals have received little attention in energetic studies of ducks, in part, because most species that have been studied presumably lay an egg per day (Drobney 1980, Alisauskas and Ankney 1994). However, ducks in the genus *Bucephala* have extended laying intervals that have been estimated from observational studies to range, on average, from 1.5 days between eggs in Barrow's Goldeneye (M. Jackson, pers. comm. in Bellrose 1980) to 2 days in Bufflehead (Erskine 1972, Gauthier 1993) and Common Goldeneye (Eadie et al. 1995; but see Johnson 1967). Extended ovulation periods, which occur in nearly all species of Mergini, may be the consequence of birds using less productive breeding habitats. Given that egg size is apparently highly repeatable in birds (Lessells et al. 1989), extending laying intervals is the only option birds have to substantially reduce their daily energy requirements for reproduction without decreasing fecundity. This study was conducted to investigate factors affecting laying intervals in female Buffleheads and Barrow's Goldeneyes and model the energetic consequences of extended laying periods on the costs of reproduction in these species.

3.2 METHODS

3.2.1 *Determining egg laying intervals and laying times*

Frequency of egg laying was monitored using Hobo-temp© miniature temperature loggers (hereafter temperature loggers) rather than by using single or multiple daily nest checks. Nest monitoring systems consisted of an external data logger and 2 m cable equipped with a terminal thermistor. In general, this system was similar to the device for monitoring nest attendance developed by Flint and MacCluskie (1995), but modified for use with cavity nesting birds. Thermistors were implanted in artificial wooden eggs (hereafter thermistor eggs) painted to resemble those of Buffleheads and Barrow's Goldeneyes. A hole just large enough to insert the thermistor probe was drilled through the center of the egg, and the probe secured using silicone adhesive . The thermistor tip protruded slightly above the dorsal surface of the egg to ensure contact with laying females. A second hole was drilled in the ventral surface of the egg (only halfway through) to insert a wooden dowel rod that served to position and stabilize the egg within the nest box.

Bufflehead and Barrow's Goldeneye nests monitored in this study were located in nest boxes designed to closely approximate dimensions of natural nest cavities. Thermistor eggs were typically placed in nests containing < 3 eggs to monitor egg laying intervals throughout clutch formation. When a suitable nest was located, I used a cordless drill to make two holes in the box floorboard just large enough to insert the dowel mounted thermistor egg and thermistor cable. The height and position of the thermistor egg was regulated using two small hose clamps, of which one was positioned adjacent to the floorboard in the interior of the box and the second against the exterior face of the box floorboard. The thermistor egg was centrally located in the nest box to ensure that a female in the box would be in contact with the temperature probe. The temperature logger was connected to the thermistor cable, placed in a small plastic bag for waterproofing, and mounted directly below the box with generally < 20 cm of thermistor cable exposed to the external environment. Temperature loggers were programmed to record the temperature in the nest every 4.8 minutes for 6 days, after which they were replaced with another reset logger. Data from the removed temperature logger were subsequently downloaded to a personal computer for analysis.

A total of 30 Barrow's Goldeneye nests and 14 Bufflehead nests were equipped with thermistor eggs throughout the breeding season in 1995. Of these nests, 23 Goldeneye nests and 9 Bufflehead nests provided data on one or more egg laying intervals. Egg laying times were recorded as the time of entry into nest boxes, which was supported by multiple observations of freshly laid eggs within 20 minutes of a female arriving at her nest including several observations late in their clutch.. Birds were considered to have left their nest when the temperature dropped by ≥ 0.5C followed by a steady descent in nest temperature. Similarity in egg coloration and maximum egg breadth (width), which both show high repeatability within the clutches of individual females (Watson et al. 1993, Eadie et al. 1995), were used to exclude parasitically laid eggs when determining egg laying intervals and times for the host female. The time that female *Bucephala* spent in their nest cavities increased with successive eggs in nonparasitized nests (J. Thompson, unpubl. data). Therefore, laying events that corresponded to parasitically laid eggs were usually obvious because they did not conform to this pattern. Furthermore, parasitic eggs were typically laid rapidly and were represented by sharp narrow peaks in the temperature data. Nests were generally not visited by female Goldeneyes between successive eggs, but intermediate visits were more common in Buffleheads. If nonlaying visits were extensive and/or prolonged, data from these nests were excluded from analyses due to lack of certainty on visits when eggs were laid.

3.2.2 *Egg composition*

During the 1993 and 1994 field seasons, Bufflehead and Barrow's Goldeneye clutches were collected in association with laying females (Canadian Wildlife Service Permits PC BK 93/15 & 94/12) for studies of nutrient reserve use during egg production (Chapter 4). Eggs were boiled over low heat and then frozen for subsequent proximate analyses. Later, boiled eggs were thawed, individually separated into yolk, albumen (including egg membranes; see Alisauskas 1986), and shell, and dried to constant mass at 80° C. Because egg lipid is confined to the yolk (Romanoff and Romanoff 1949), dried yolks were washed with petroleum ether in a modified Soxhlet apparatus (Dobush et al. 1985) to determine lipid and lean dry mass (i.e., protein) mass of this egg component. Dried albumen and lean yolk mass were summed to calculate egg protein content. Egg mineral content was the mass of the dried egg shell.

3.2.3 *Statistical analysis*

Analysis of variance (ANOVA) (PROC GLM; SAS Institute 1985) was used to determine if laying intervals differed relative to egg sequence and clutch size. If the overall model was significant ($P \leq 0.05$), differing intervals or clutch sizes were determined using a Tukey - Kramer multiple comparisons test. Additionally, analysis of covariance (ANCOVA) (PROC GLM; SAS Institute 1985) was used to investigate whether laying intervals differed relative to date, mean egg size (volume), egg sequence, and clutch size when controlling for the effects of each variable. If interactions were not significant ($P > 0.05$) in the comprehensive model, they were deleted and the data reanalyzed. Similarly, if main effect variables were not significant ($P > 0.05$), the least significant variable was deleted and the data reanalyzed in a stepwise procedure until only significant variables remained. Only significant predictive variables are presented in the results and discussion unless otherwise stated.

3.3 RESULTS AND DISCUSSION

3.3.1 *Laying intervals*

Mean laying interval (± SE) for Buffleheads ($n = 23$ intervals, 9 clutches) was 48.36 ± 2.35 hr, which was similar ($F = 1.94$, $P = 0.1668$) to that of Barrow's Goldeneyes ($n = 87$ intervals, 23 clutches), which laid on average, every 45.32 ± 1.40 hr. Variability in laying intervals was also similar between these species ranging from 24.5 - 71.4 hr in Buffleheads ($CV = 19.56$) to 23.1 - 75.1 hr between eggs in Barrow's Goldeneyes ($CV = 20.71$).

Laying intervals were longer ($F = 7.59$, $P = 0.0016$ Bufflehead; $F = 2.79$, $P = 0.0164$) Barrow's Goldeneye) between earlier laid eggs than between later laid eggs in the clutch for both species (Table 3.1). The interval between eggs 3 and 4 in Buffleheads was 18.6 - 20.6 hr greater ($P \leq 0.05$) than intervals between subsequent eggs, but the sample size for laying intervals between eggs 3 and 4 was small ($n = 3$). However, longer laying intervals earlier in the clutch are corroborated by a previous observational study that indicated a similar laying pattern in Buffleheads (Erskine 1972). Likewise, more substantial data for early laying intervals in Barrow's Goldeneyes (Table 3.1),

Table 3.1. Mean egg laying intervals (hr) for Buffleheads and Barrow's Goldeneyes relative to egg sequence.

Laying intervals	Species[a]	N[b]	Mean ± SE[c]	Range
Egg 2 - 3	BUFF	-	-	-
	BAGO	10	47.60 ± 0.95	42.33 - 51.55
Egg 3 - 4	BUFF	3	65.36 ± 3.89	58.09 - 71.41
	BAGO	17	48.21 ± 2.91	23.13 - 75.14
Egg 4 - 5	BUFF	5	46.71 ± 0.81	44.28 - 48.33
	BAGO	21	45.75 ± 1.61	24.08 - 65.42
Egg 5 - 6	BUFF	8	44.78 ± 3.22	24.48 - 54.47
	BAGO	19	46.87 ± 1.90	34.43 - 73.09
Egg 6 - 7	BUFF	7	45.05 ± 2.17	32.34 - 49.25
	BAGO	12	38.54 ± 2.92	23.58 - 56.38
Egg 7 - 8	BUFF	-	-	-
	BAGO	7	37.29 ± 2.75	25.32 - 47.44
Egg 8 - 9	BUFF	-	-	-
	BAGO	1	38.00	-

[a] Species codes are BUFF = Bufflehead and BAGO = Barrow's Goldeneye.
[b] Sample size.
[c] Mean ± standard error.

indicated that birds had longer ($P \leq 0.05$) laying intervals between eggs 2 through 5 than between subsequent eggs in their clutch. This decrease in length of laying interval with egg sequence in female *Bucephala* was similar to the pattern reported for Giant Canada Geese (*B. c. maxima*), which had longer laying intervals between eggs earlier in their clutch (Cooper 1978).

Additionally, I used ANCOVA to determine whether variation in laying intervals was attributable to laying date, egg sequence, egg size, and clutch size after controlling for effects of each these variables. There were no significant ($P < 0.05$) interactions in the initial models for either Buffleheads or Goldeneyes, so interaction terms were dropped and data analyzed relative only to main effects. Laying intervals were not related to clutch size ($P > 0.05$) or mean egg size ($P > 0.05$) in either species, so these variables were subsequently deleted from models. For Buffleheads, laying intervals declined ($F = 4.43$, $P = 0.0482$) by 0.35 hr/day independent of egg sequence, but laying interval also declined ($F = 6.5$[illegible], $P = 0.0184$) relative to egg sequence, when the date effect was controlled. Laying intervals in Barrow's Goldeneyes differed ($F = 11.57$, $P = 0.0010$) only relative to laying sequence, and declined, on average, by 2.15 hr with each egg laid. There was also a trend ($F = 2.45$, $P = 0.1215$) for Barrow's Goldeneyes with larger clutch sizes to have shorter laying intervals.

To some degree, extension of laying intervals in breeding *Bucephala* is ultimately facilitated by cavity nesting, which exposes eggs to lower daily predation rates than those experienced by ground nesting ducks. Average nest success of Barrow's Goldeneyes using nest boxes in central British Columbia was 46% (Savard 1988). Buffleheads nesting in artificial cavities have higher nest success (32 - 89%; Gauthier 1988) probably as a result of lower intraspecific brood parasitism. Furthermore, nest success estimates derived from nest box studies are probably conservative because birds nesting in better concealed natural cavities are likely more successful (Gauthier 1988; but see Lundberg and Alatalo 1992, Nilsson 1984). In any event, these nest success rates are considerably higher than the 5 - 15% average success rates for many ground nesting ducks in the Northern Great Plains (Sargeant et al. 1984).

Only species that have high nest predation, low egg viability, or short optimal breeding seasons should be under strong directional selection to reduce egg laying intervals (Watson et al. 1993). Notably, Common Eiders, which experience high rates of nest depredation (Milne 1976), have the shortest laying intervals (27.7 ± 3.4 hr) of species in the Mergini investigated thus far (Watson et al. 1993) (see alternative explanation below). Given that in many regions of the Northern Great Plains over 80% of duck nests are depredated, it is likely that there has also been strong, but perhaps more recent, selective pressure on species breeding in prairie environments to reduce their laying intervals (hence egg exposure period). In their review of laying intervals, Alisauskas and Ankney (1992) indicate that nearly all species of prairie nesting ducks lay on a daily interval despite a wide range in final clutch size for these species. Thus, laying intervals rather than overall fecundity (i.e., clutch size) may be the reproductive trait most heavily influenced by predation in nesting waterfowl.

A laying interval that minimizes risk of predation may not be optimal if it simultaneously increases nutritional constraints on laying rate. Lack (1968) suggested that laying rates in birds were ultimately related to the ability of females to acquire sufficient energy for egg production. Conversely, Astheimer (1985) indicated that because laying intervals were generally constant within a species, this reproductive trait was under strong genetic control and subject to selection. However, laying intervals were not fixed in female *Bucephala* and differed relative to egg sequence. More importantly from a nutritional perspective, laying interval declined with date in female Buffleheads after controlling for the effect of egg sequence. Because availability of invertebrate foods consumed by female Buffleheads likely increases over the period of egg synthesis (Murkin and Kadlec 1986a, 1986b), reduced laying intervals between later laid eggs are consistent with the hypothesis that improved nutrient availability can proximately influence laying intervals in at least some species of birds. Possibly, in waterfowl, nutrition generally has a positive influence on laying rate rather than decreasing it from some optimal (i.e. selected) level, particularly given the ability of most waterfowl to meet short term nutritional deficits by catabolizing somatic tissue.

Alternatively, ducks may ideally lay at 24 hr intervals if they can acquire sufficient nutrients. Thus, reduce l genetic regulation of laying intervals may have permitted ancestral anatids to colonize less productive boreal and montane habitats by distributing energetic costs of reproduction over a longer period of time (see below). Because of low predation rates on the arboreal nests of female *Bucephala*, there has been little selection to reduce laying intervals as indicated by considerable individual variation in laying rates of Buffleheads (Table 3.2) and Barrow's Goldeneyes (Table 3.3). Furthermore, highly variable intraspecific laying rates in female *Bucephala* generally support proximate rather than genetic regulation of the time interval between eggs. Thus, environmental factors, such as food availability, may constrain both the rate and extent of reproductive effort in nidifugous birds.

It is unclear, however, why laying intervals decreased with egg sequence in female *Bucephala*, irrespective of date. Daily energy costs for clutch formation in female Buffleheads and Goldeneyes are highest concurrent with eggs 1 through 5 assuming birds lay an 8 egg clutch (Chapter 4). Thus, shorter laying intervals coincide with declining daily costs of egg production in both species. Similarly, the short laying interval of female Common Eiders is likely related to the fact that they experience peak reproductive costs for only day (see Alisauskas and Ankney 1992) during production of their small clutches (4 - 5 eggs).

Longer laying intervals between earlier eggs in female *Bucephala* may also represent temporal limitation on mobilization of somatic nutrients during the early portion of clutch formation. Williams (1981) suggested that the 3 - 4 day laying intervals in *Eudyptes* penguins, which rely exclusively on endogenous nutrients during

Table 3.2. Individual variation in laying intervals (hr) in female Buffleheads nesting in central British Columbia. This table includes only those data from females in which ≥ 3 laying intervals were recorded. Females were arranged ascending order of mean laying interval.

	Laying interval[a]				
Female	3 - 4	4 - 5	5 - 6	6 - 7	Mean
1	.	47.46	48.50	46.10	47.35
2	58.09	48.14	49.54	46.05	50.46
3	66.58	45.35	40.15	.	50.69
4	71.41	48.33	47.22	48.05	53.75

[a] Time period between laying of successive eggs in the clutch, e.g., laying interval 3 - 4 refers to the time (hr) between the third and fourth eggs.

Table 3.3. Individual variation in laying intervals (hr) in female Barrow's Goldeneyes nesting in central British Columbia. This table includes only those data from females in which ≥ 3 laying intervals were recorded. Birds were arranged ascending order of mean laying interval.

Female	Laying interval[a]							
	2 - 3	3 - 4	4 - 5	5 - 6	6 - 7	7 - 8	8 - 9	Mean
1	-	40.11	40.15	40.19	36.10	-	-	39.14
2	-	-	48.50	45.54	24.37	-	-	39.47
3	-	43.45	39.12	46.52	38.29	34.43	38.00	39.97
4	-	38.19	45.41	47.13	36.09	36.53	-	40.67
5	47.17	46.50	37.41	34.43	-	-	-	41.38
6	-	50.48	44.19	43.51	28.20	-	-	41.60
7	49.03	38.24	24.08	47.36	48.00	47.44	-	42.36
8	-	23.13	48.32	73.09	23.58	44.51	-	42.53
9	-	-	47.50	48.00	38.33	38.57	-	43.10
10	47.46	48.10	48.01	47.21	37.46	-	-	45.65
11	42.33	52.39	65.42	47.46	47.50	25.32	-	46.74
12	51.55	44.47	47.22	47.55	-	-	-	47.70
13	-	50.07	44.04	50.00	-	-	-	48.04
14	47.31	49.37	47.25	50.39	-	-	-	48.58
15	-	45.41	52.03	47.41	56.38	-	-	50.31
16	49.05	75.14	47.05	42.22	48.20	-	-	52.33
17	43.41	71.12	48.00	57.11	-	-	-	54.91

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[a] Time period between laying of successive eggs in the clutch, e.g., laying interval 2 - 3 refers to the time (hr) between the second and third eggs.

clutch formation, may be related to the time required for somatic mineral catabolism to form the relatively heavy eggshells in these species. It is also interesting to note that calcium requirements figure prominently in the dietary requirements for egg production in female Buffleheads (Chapter 2) and in clutch size determination of Barrow's Goldeneyes (Chapter 4). However, because of lower environmental lipid availability in many habitats used by breeding waterfowl (Ankney et al. 1991), time required for mobilizing endogenous fat plus the additional cost of protein deposition in yolks and albumen may be more likely to limit rates of yolk formation in early laid eggs of female anatids.

3.3.2 *Egg composition and costs of egg and clutch formation in Buffleheads and Barrow's Goldeneyes*

Fresh egg mass of Buffleheads averaged 36.61 g (n = 127), which was 24.6% mineral (% dry mass) and contained equal proportions of lipids (37.7%) and protein (37.7%) (Table 3.4). Unincubated Barrow's Goldeneye eggs averaged 66.38 g (N = 230) and were comprised of 25.5% mineral, 36.5% lipids, and 38.0% protein (Table 3.4). Based on the mean energy content of fat (39.77 kJ/g) and protein (23.86 kJ/g) (Kleiber 1961), total energy content of an average Bufflehead egg was 327.06 kJ, while that of a Barrow's Goldeneye egg was 578.32 kJ. Using the measured conversion efficiency (77%) of dietary nutrients to egg nutrients in domestic chickens (Brody 1945), a Bufflehead egg has a direct metabolic cost of 402.3 kJ and that of a Goldeneye would require 711.3 kJ. Based on the modal clutch size of 8 eggs for Buffleheads and 8.5 eggs for Barrow's Goldeneyes (Chapter 4), total energy required for clutch formation would be 3218 kJ in Buffleheads and 6046 kJ in Goldeneyes. However, this estimate is conservative because it does not account for additional energy required for growth of the oviduct and activity costs of behavioral changes associated with reproduction.

Table 3.4. Mean fresh mass and composition of Bufflehead and Barrow's Goldeneye eggs.[a]

Variable	Bufflehead			Barrow's Goldeneye		
	N[b]	Mean ± SE[c]	CV[d]	*N*	Mean ± SE	CV
Fresh egg mass[e]	127	36.61 ± 0.20	6.19	230	66.38 ± 0.22	5.02
Yolk mass[f]	128	7.70 ± 0.07	10.87	228	13.31 ± 0.06	6.94
Yolk lean mass[f]	127	2.56 ± 0.05	21.57	228	4.36 ± 0.02	7.27
Yolk fat	127	5.14 ± 0.04	8.65	228	8.95 ± 0.04	7.18
Albumen mass[f]	128	2.58 ± 0.02	9.89	228	4.96 ± 0.02	7.02
Egg protein mass[f]	128	5.14 ± 0.03	6.93	228	9.32 ± 0.04	5.75
Egg lipid mass	128	5.14 ± 0.04	8.75	228	8.95 ± 0.04	7.33
Egg mineral mass[f, g]	128	3.36 ± 0.03	9.79	230	6.24 ± 0.02	6.02

[a] Measurements are in g.
[b] Sample size.
[c] Mean ± standard error.
[d] Coefficient of variation.
[e] Mass of unincubated eggs.
[f] Dry mass.
[g] Equivalent to dry shell mass.

To compare energy requirements for egg formation in Buffleheads and Goldeneyes, I calculated energetic costs of egg production as a proportion of daily basal metabolic rate (BMR) (see King 1973). Using Aschoff and Pohl's (1970) allometric equation for estimation of BMR in nonpasserines and mean body mass of non-RFG birds (Chapter 4), I estimated that daily BMR was 136.34 kJ/day and 261.15 kJ/day for nonbreeding Buffleheads and Goldeneyes respectively. As a proportion of daily metabolic costs, energy content of a Bufflehead egg was equivalent to 240% of BMR while that of a Goldeneye egg was equivalent to 221% of BMR. However, because laying intervals were extended in Buffleheads and Barrow's Goldeneyes, daily energy costs for egg production were reduced to 118% of daily BMR in Buffleheads and 117% of daily BMR in Goldeneyes. Notably, Buffleheads reduced their proportionately greater energetic costs of egg production to nearly equal the daily costs in Goldeneyes by having slightly longer laying intervals.

Additional to extending laying intervals, breeding Buffleheads and Goldeneyes also reduce peak daily energy requirements for clutch formation by initiating lipid and protein deposition in developing ovarian follicles 8-9 days before the start of laying (Chapter 4). For the modal clutch size, this extends the costs of clutch formation over approximately 23 days in Buffleheads and 25 days in Goldeneyes.

3.3.3 *Conclusions*

As a proportion of daily BMR, daily energetic costs of egg production in the *Bucephala* are among the lowest documented for ducks (see Alisauskas and Ankney 1992 for comparative values). Only swans, geese, and eiders have comparatively low daily reproductive costs, which results from smaller egg mass relative to body mass in larger species and extended laying intervals. In contrast, reduced daily energetic costs of egg production in Goldeneyes and Buffleheads originate exclusively from extended laying intervals. This begs the question as to whether Buffleheads and Goldeneyes extend their laying intervals because of energetic constraints or because they are cavity nesters, which experience considerably lower nest predation rates than ground nesting ducks (Erskine 1972, Gauthier 1988, Savard 1988). The only light that I can shed on this question comes from comparison with another cavity nesting anatid. Wood Ducks (*Aix sponsa*), which also commonly breed in relatively unproductive wetlands, lay 1 egg/day despite producing an even larger clutch than do either Buffleheads or Goldeneyes (Bellrose 1980). Female Wood Ducks apparently maintain daily laying rates by storing and using proportionately greater lipid reserves (Drobney 1982) than do Buffleheads or Goldeneyes (Chapter 4). This suggests that the rate of egg production in *Bucephala* is not necessarily extended because they nest in a relatively safe location, but because they must do so to meet their nutritional requirements for egg production.

3.3.4 *Research recommendations*

Experimental studies with captive ducks should be designed to further investigate whether laying intervals have a genetic basis. Laying females could be assigned to several treatments including unlimited food (control) and series of restricted diets. Subsequently, laying intervals would be closely monitored to determine if they were affected by diet manipulations. If laying intervals were extended with declining nutrient availability, this would provide considerable support that this reproductive trait is under little genetic control. Additional variables could be manipulated in this design to investigate other factors (e.g., age, pair density) that potentially influence laying rates in waterfowl.

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CHAPTER 4. COMPARATIVE NUTRITIONAL ECOLOGY OF BREEDING FEMALE BUFFLEHEADS AND BARROW'S GOLDENEYES: USE OF NUTRIENT RESERVES DURING CLUTCH FORMATION

4.1 INTRODUCTION

Annual variation in the number of eggs laid by individual female waterfowl (Anseriformes) and generally low heritability of clutch size (Findlay and Cooke 1987, Lessells et al. 1989) provide little support for genetic regulation of clutch size in this group of birds. Furthermore, long term studies of precocial birds suggest that mean clutch size is either not increasing, or increasing at a very slow rate (Rockwell et al. 1987), despite strong directional selection for higher fecundity in birds (Perrins 1965; Bryant 1979; DeSteven 1980; Smith 1981; Alerstam and Högstedt 1984; Roskaft 1985). Clutch size in waterfowl, and probably most nidifugous birds, is therefore determined primarily by environmental and behavioral factors (e.g., nutrition, habitat use, population density, and age/experience). Thus, investigation of proximate influences on clutch size will ultimately provide greater insight into evolution of avian breeding strategies and life history tactics.

Ducks (Anatinae) generally breed in highly productive wetland systems that provide a readily available source of nutrients during clutch formation, incubation and brood rearing. For example, many species of dabbling ducks (*Anas* spp.) and pochards (*Aythya* spp.) breed in association with highly productive ponds and marshes in the Northern Great Plains, whereas nesting eiders (*Somateria* spp. and *Polysticta stelleri*) often congregate around fertile Arctic river deltas and intertidal zones (Alisauskas and Ankney 1992). However, some species of sea ducks (Mergini), particularly those in the genus *Bucephala*, breed in unproductive wetlands generally associated with montane or boreal regions. Ecological and physiological adaptations that these species have evolved to cope with nutritional demands of reproduction on mesotrophic and oligotrophic wetlands have not been studied and warrant investigation (Ankney and Alisauskas 1991a).

This study investigated nutritional strategies for egg production in two congeneric species of cavity nesting waterfowl, Buffleheads (*Bucephala albeola*) and Barrow's Goldeneye (*Bucephala islandica*). These species are the smallest and largest members, respectively, of their genus and breed sympatrically in the northwestern portion of their distribution, specifically in the interior regions of British Columbia, the Yukon, and Alaska (Bellrose 1976, Palmer 1976). Both species are primarily carnivorous, feeding principally on aquatic insects throughout the breeding season (Chapter 1). Perhaps most significantly. Barrow's Goldeneyes and Buffleheads have extended egg laying intervals (> 24 hrs) (Chapter 2), which may be a critical adaptation to meet specific nutritional demands of egg production in waterfowl breeding in wetland habitats with lower productivity than those used by most anatids.

This research was conducted to (1) investigate somatic nutrient dynamics of female Barrow's Goldeneyes and Buffleheads in relation to investment of nutrients into reproduction, breeding wetland limnology, date of rapid follicular growth initiation, and year, (2) ascertain if there is a specific macronutrient that may limit clutch size and egg laying rate in breeding *Bucephala*, and (3) evaluate energetic consequences of body size on nutritional tactics of sympatrically breeding congeneric ducks. My hypotheses were (1) that clutch size in these carnivorous species was constrained primarily by lipid demand and (2) that the smaller body size of Buffleheads limits their nutrient storage capacity, making them more dependent on exogenous nutrients than larger Barrow's Goldeneyes.

4.2 METHODS

4.2.1 *Reproductive periods*

Prebreeding and laying female Barrow's Goldeneyes (N = 71) and Buffleheads (N = 70) were shot or captured at their nest site (Canadian Wildlife Service Permits PC BK 93/15 & 94/12) from arrival on breeding areas through laying in 1993 and 1994. All specimens were categorized into reproductive stages to report mean mass of specific muscle groups and carcass composition components. Rapid Follicular Growth (RFG) was indicated by ≥ 1 developing follicle weighing ≥ 0.14 g (dry mass) in Buffleheads and ≥ 0.17 g (dry mass) in Goldeneyes. Females that had initiated RFG were categorized as follows: Prelayers (≥ 1 rapidly developing ovarian follicle, but lacking post-ovulatory follicles), Early Layers (>number of rapidly developing ovarian follicles than post-ovulatory follicles), and Late Layers (> number of post-ovulatory follicles than rapidly developing ovarian follicles). Adult birds with no RFG were classified as Non-RFG birds and consisted primarily of prebreeders (i.e., birds collected before more than 10% of females had initiated RFG) and several nonbreeders (i.e., birds collected after > 90% of females had initiated RFG).

4.2.2 *Necropsies and carcass composition*

All specimens were weighed (0.1 g) in the field lab and external structural measurements made. All measurements (0.01 mm) were made with digital calipers and included *bill width* - at widest dimension of premaxilla, *central culmen* - from mid intersection of skin and premaxilla to tip of bill nail, *diagonal culmen* - from proximal tip of posterior lateral lobe of premaxilla to bill nail, *skull length* - from external occipital protuberance to tip of bill nail, *skull width* - lateral dimension of head immediately posterior to eyes, *tarsus length* - from proximal to lateral condyles of the metatarsus, and *middle toe length* - from base of nail to junction of toe with metatarsus. *Keel length* (0.01 mm), from tip of cranial process to end of medial caudal process, was measured following removal of one half of pectoralis muscle during the final necropsy. Subsequently, esophageal and proventricular contents of each specimen were removed and stored in individually labeled vials of 70% ethanol for diet composition analyses (Chapter 2). Finally, carcasses were opened by cutting with surgical scissors along the right side of the body, dorsal to the breast muscles, and the ovaries, oviduct, and oviducal egg (if present) were removed and stored in individually labeled vials containing 10% formalin. If oviducal eggs were hard-shelled, they were boiled and processed using the same procedure as for previously laid eggs (see below). Carcasses were then labeled using leg tags, sealed in individually labeled plastic bags, and frozen for final necropsies and carcass composition analyses.

Carcasses of female Goldeneyes and Buffleheads were thawed and necropsied to evaluate organ and specific muscle mass dynamics during the breeding period (See Chapter 1 for digestive tract morphometrics). To examine major proteinaceous tissue dynamics, the left breast muscles (pectoralis and supra-coracoideus), left leg muscles (muscles attached to the femur and tibiotarsus), gizzard, and heart were excised, stripped of adhering fat, washed, and blotted dry with a paper towel before weighing (0.01 g) on a Mettler balance. Breast and leg tissues were subsequently dried to constant mass at 80° C and saved for later lipid extractions.

When necropsies were completed, each specimen was plucked and excised organs, excluding one half of the breast and leg muscles, and the liver, were returned to the body cavity. The remaining carcass was cut into small pieces, placed in an aluminum drying pan, oven-dried to constant mass at 80° C, and then ground into a fine homogenate using a Moulinex coffee grinder. Dried cellulose thimbles were filled with approximately 10 g of dried homogenate and subsequently washed with petroleum ether in a modified Soxhlet apparatus to extract lipids (Dobush et al. 1985). Lean thimble contents were placed into Coors porcelain crucibles and burned at 550° C in a muffle furnace for approximately 10 h to derive ash and ash-free lean or protein content of samples. Lipid and protein content of the left breast and leg muscles and liver were determined independently using the same procedures outlined for the entire carcass.

For each bird, I estimated total somatic lipid, protein, and mineral content using procedures described in Ankney and Afton (1988) and Ankney and Alisauskas (1991b). Somatic ash was determined directly from ash content of the homogenate sample, adjusted for total ingesta-free body mass. Subcutaneous, visceral, and abdominal fat samples were taken from some birds, individually weighed, and refrozen for stable isotope analyses. The cumulative mass of these fat samples was later added to the total somatic lipid mass of each specimen from which these samples were derived. In general, somatic lipid content was calculated as the sum of carcass, breast, leg, and liver fat deposits. Somatic protein was the sum of the lean dry mass of the carcass minus somatic ash plus lean dry masses of the left breast and leg muscles and liver.

4.2.3 *Reproductive tissue composition*

Reproductive tracts of each bird were subdivided into rapidly developing ovarian follicles (RDFs), ovary, and oviduct. Subsequently, the ovary of each specimen was examined using a Leitz dissecting microscope to locate and remove all post-ovulatory follicles (POFs). Each POF was severed from the ovary at its base and weighed (0.0001 g). The number of POFs (N_{pof}) was considered the best estimate of the number of eggs laid by each female. Validity of this technique to determine laying histories of female American Coots (*Fulica americana*) was recently evaluated with satisfactory results (Arnold et. al, in press). Furthermore, POFs are even more evident on the ovaries of ducks than coots during RFG (J. Thompson, pers. observ.).

Each rapidly developing follicle and the oviduct was weighed (0.01 g), dried to constant mass at 80° C, and then reweighed. The dry oviduct was placed in a Coors porcelain thimble and ashed at 550°C. The remaining mineral mass (M_{ovid}) was subtracted from the dry oviduct mass to estimate proteinaceous mass of the oviduct

(P_{ovid}). Lipid content of each developing follicle (L_{fol}) and the remaining ovary tissue (L_{ovary}) was determined by petroleum ether extraction in a modified Soxhlet apparatus. The remaining follicle (P_{fol}) and ovary (P_{ovary}) mass were recorded as protein.

Clutches of laying females were collected for all birds whose nest sites were located and accessible (*n* = 13 Buffleheads, *n* = 34 Barrow's Goldeneyes). Additional clutches were collected from incubating birds (*n* = 26 Buffleheads, *n* = 23 Barrow's Goldeneyes), but incubated eggs were not analyzed to determine egg macronutrient composition.

All eggs in clutches of laying females were analyzed for lipid, protein, and mineral content to account for individual variation in commitment of these macronutrients to egg synthesis (see Chapter 3 for procedures). Lipid, protein, and mineral content of eggs from each clutch were summed to determine total clutch nutrient commitment by the corresponding female. For laying females whose clutches were not located, reproductive nutrient commitment was estimated as indicated below. Total reproductive lipid (R_{lipid}) investment of each bird was determined as

$$R_{lipid} = (\Sigma L_{fol}) + L_{ovary} + \overline{L}_{egg} (N_{pof})$$

where $\overline{L}_{egg}$ was mean lipid content of Bufflehead or Barrow's Goldeneye eggs. Reproductive protein ($R_{protein}$) was estimated as

$$R_{protein} = (\Sigma P_{fol}) + P_{ovary} + P_{ovid} + N_{pof} (\overline{P}_{yolk} + \overline{P}_{albumen})$$

where $\overline{P}_{yolk}$ and $\overline{P}_{albumen}$ were mean protein content of yolk and albumen in Bufflehead or Barrow's Goldeneye eggs. Reproductive mineral (R_{min}) was estimated using

$$R_{min} = M_{ovid} + N_{pof} (\overline{M}_{egg})$$

where $\overline{M}_{egg}$ was mean mass of the eggshell for Buffleheads or Barrow's Goldeneye.

4.2.4 *Clutch size determination*

Mean clutch size of Buffleheads and Goldeneyes was determined using several techniques that should have reduced or eliminated bias in counts associated with parasitically laid eggs (i.e., eggs laid in the nest of a host by one or more additional females). Initially, I conducted microscopic post-ovulatory follicle (POF) counts on the ovaries of all females to determine the number of eggs they had laid (see Arnold et al. [in press] for validity of this technique). For females that had not finished laying and had less than the maximum number of developing follicles, I added the number of POFs and RDFs to estimate final clutch size. For late laying (*n* = 10 Buffleheads, *n* = 21 Barrow's Goldeneyes) and incubating females (*n* = 26 Buffleheads, *n* = 23 Barrow's Goldeneyes) whose clutches I located, I determined eggs laid by the host female in parasitized nests by grouping morphologically similar eggs. Generally, egg width, which is highly repeatable among eggs laid by the same female (Erskine 1972, Eadie et al. 1995), could be used to identify morphologically similar eggs that corresponded closely with counts of POFs in late laying females. POFs regressed rapidly as females began incubation, thus clutch size in these birds was estimated exclusively from counts of morphologically similar eggs.

4.2.5 *Assessment of breeding habitat*

Water chemistry (i.e. pH, alkalinity, conductivity, and total phosphorous) and primary productivity (i.e. chlorophyll a) was determined for all wetlands where female Buffleheads and Barrow's Goldeneyes were collected. A single water sample (using a 50 ml sterile centrifuge tube) was taken from each wetland within 1-3 days after it became ice-free to determine total phosphorous concentration. Each sample was collected from the deepest wetland zone during early spring to reduce variation associated with biological uptake of phosphorous (LaBaugh 1989). Most samples were acquired using a canoe to avoid disruption and suspension of sediments near the collection site. Water samples were stored in a chilled cooler until they were filtered through a Whatman GF/C glass microfibre filter to remove suspended particles. Subsequently, 40 ml of the filtrate from each wetland was placed into another sterile centrifuge tube, and the filtered samples frozen for transport to the university laboratory. Total phosphorous concentration of each sample was determined using a HACH phosphorous test kit (PhosVer 3 Phosphate Reagent Powder Pillows).

Portable meters were used to measure conductivity (Hanna Instruments Model 8033) and pH (Canlab Model 607) from 2 - 4 June 1993. Readings were taken at an approximate depth of 30 cm in 1-1.25 m of water if wetland depth permitted; otherwise readings were taken in the deepest water located. Three measurements of pH and conductivity were made in each wetland and averaged to determine the mean values for that basin.

To estimate total alkalinity, one water sample was taken from each wetland (3-18 June 1993) using a clean 250 ml plastic bottle that was submerged upside-down, uprighted, and allowed to fill in 0.75 m of water if depth permitted. In shallow wetlands, samples were taken in the deepest water located as during pH and conductivity measurements. Total alkalinity was subsequently determined in the field using an Orion Total Alkalinity Test Kit (Orion Research Inc., Boston, MA).

Another water sample was collected from each wetland (19 June - 3 July 1993) using the same procedure described for total alkalinity to determine chlorophyll a content. Samples were filtered through a Whatman GF/C glass microfibre filter using a Nalgene hand pump. Filters were subsequently treated with a magnesium carbonate slurry to preserve pigments, folded in half, and wrapped in aluminum foil before storing in a chilled cooler until samples could be frozen at the end of the day. Samples were later processed in the laboratory using the protocol described in Strickland and Parsons (1968) to estimate the concentration of chlorophyll a pigment.

Water chemistry (i.e., pH, alkalinity, conductivity, and total phosphorous) and primary productivity (i.e., chlorophyll a) data on each wetland were condensed into two multivariate measures of wetland type using principal components analysis (PROC PRINCOMP, SAS Institute Inc. 1985). The first principal component score (PC_1) of the correlation matrix indicated positive correlation among pH, alkalinity, conductivity, and total phosphorous for wetlands used by breeding female Buffleheads and Barrow's Goldeneyes, but loaded primarily on pH, alkalinity, and conductivity (Table 4.1). The second principal component score (PC_2) indicated positive correlation between total phosphorous and chlorophyll a in wetlands where both species were collected, and also loaded principally on these same variables. Thus, higher PC_1 scores (i.e., positive scores) indicated wetlands with relatively higher pH, conductivity and alkalinity whereas higher PC_2 scores indicated wetlands with relatively higher total phosphorous and chlorophyll a. To facilitate interpretation of analyses involving these multivariate measures of habitat type, I converted them to categorical variables. Wetlands with principal components scores < 0 were converted to 0, whereas wetlands with scores > 0 were designated as 1.

4.2.6 *Statistical analysis*

Carcass components can show significant intraspecific variation in response to structural size (Alisauskas and Ankney 1987, Ankney and Afton 1988, Ankney and Alisauskas 1991b). To develop an index of overall structural body size, I conducted principal components analysis (PROC PRINCOMP, SAS Institute Inc. 1985) using the eight morphological measurements I made on all birds (See section on necropsies and carcass composition). The first principal component score (PC_{1BS}) of the correlation matrix was based on positive correlation among the eight variables with loadings ranging from 0.47 (skull length) to 0.10 (bill width) in Buffleheads and 0.44 (skull length) to 0.25 (skull width) in Barrow's Goldeneyes. Corresponding eigenvalues were 2.67 and 3.01 and PC_{1BS} explained 33% and 38% of total variance in structural variables for Buffleheads and Barrow's Goldeneyes, respectively. I subsequently used least squares regression to determine if a significant relationship existed between the PC_{1BS} scores

Table 4.1. Results from principal components analysis on limnological variables of wetlands on which breeding female Buffleheads and Barrow's Goldeneyes were collected.

Species	N[a]	Eigenvalues	Variables	Eigenvectors	
				PC_1	PC_2
Bufflehead	64	$PC_1 = 2.26$	pH	0.5150	-0.1152
		$PC_2 = 1.23$	Conductivity	0.5846	-0.0819
			Alkalinity	0.5957	-0.0160
			Total phosphorous	0.1947	0.6613
			Chlorophyll a	-0.0162	0.7365
Barrow's Goldeneye	54	$PC_1 = 2.13$	pH	0.5116	-0.1094
		$PC_2 = 1.57$	Conductivity	0.5785	-0.0890
			Alkalinity	0.6008	-0.0214
			Total phosphorous	0.2047	0.6796
			Chlorophyll a	-0.0260	0.7196

[a] Number of different wetlands that birds were collected on. More than one bird was collected on several wetlands.

for each bird (i.e., an index of body size) and somatic fat protein and mineral reserves. Lipid reserves were unrelated to body size in either species ($P = 0.12$ Buffleheads, $P = 0.40$ Barrow's Goldeneyes). However, somatic protein and mineral were related to body size in both species as indicated by the following relationships:

Buffleheads

Protein = $56.93 + 0.549\mathrm{PC}_{1\mathrm{BS}}$

$F = 7.261, P = .00083$

Mineral = $11.17 + 0.096\mathrm{PC}_{1\mathrm{BS}}$

$F = 3.601, P = 0.0507$

Barrow's Goldeneyes

Protein = $145.87 + 2.202\mathrm{PC}_{1\mathrm{BS}}$

$F = 23.751, P = 0.0001$

Mineral = $27.82 + 0.398\mathrm{PC}_{1\mathrm{BS}}$

$F = 5.555, P = 0.0204$

Residuals from these regression equations were used to derive a new size-corrected value (y_i) for carcass protein and mineral for each female using the equation in Ankney and Alisauskas (1991b):

$$y_i = y_{obs} - [a + b(PC_1)] + \overline{Y}_{obs}$$

where y_{obs} equals the unadjusted carcass variable from an individual bird and $\overline{Y}_{obs}$ equals the mean of the unadjusted carcass variable for all specimens. Only somatic protein and mineral values corrected for body size were used in data analyses.

Effects of year and reproductive status on body mass, somatic nutrient reserves, and selected proteinaceous tissues were investigated using two-way analysis of variance (ANOVA) (PROC GLM; SAS Institute Inc. 1985). In this analysis, if there was no significant ($P < 0.05$) year - reproductive status interaction, the interaction term was deleted from the model and the data reanalyzed. Means were presented by year only for variables with a significant ($P < 0.05$) annual effect. Unless denoted otherwise, all reported differences were significant at $P < 0.05$.

To evaluate effects on somatic nutrient reserves of birds during RFG, I used a general linear model with type III sums of squares (PROC GLM; SAS Institute Inc., 1985). The initial analysis of covariance (ANCOVA) model was Somatic nutrient (S-NUTRIENT) = Reproductive nutrient (R-NUTRIENT), YEAR, wetland PC_1, wetland PC_2, Date (RFGDATE), plus all two-way interactions, where for year, 1993 = 1 and 1994 =2, for wetland PC_1 and PC_2, scores < 0 = 0 and scores >0 = 1, and RFGDATE = the day that RFG was initiated in each year relative to the date when the first bird for that species initiated RFG (e.g., Bufflehead - RFGDATE = 1 for 12 April 1993 and 10 April 1994; Barrow's Goldeneye - RFGDATE = 1 for 9 April 1993 and 5 April 1994). The period of RFG (up to ovulation of the first ovum) was estimated by multiplying the maximum number of growing follicles by the interval (days) that eggs are laid (Alisauskas and Ankney 1992). If interactions were not significant ($P > 0.05$) in the comprehensive model, they were removed from the model and the data reanalyzed. Similarly, if main effect variables were not significant ($P > 0.05$), the least significant variable was deleted and data reanalyzed in a stepwise procedure until only significant variables remained. Only significant predictive variables are presented in the results unless otherwise stated.

A second ANCOVA model was used to determine if final clutch size was related to size of nutrient reserves in each species following the procedure recommended by Sedinger et. al (unpubl. ms.). Only Goldeneyes and Buffleheads with < the maximum number of RDFs were used in this analysis because their final clutch size (i.e. total number of eggs laid) cou'd be predicted (Bufflehead - N = 35; Barrow's Goldeneye N = 26). The general model in this analysis was S-NUTRIENT = R-NUTRIENT, final clutch size (CLUTCH SIZE), RFGDATE, YEAR, wetland PC_1, and wetland PC_2. The same protocol for deletion of nonsignificant interactions and main effects described for the previous model was used in this analysis. Additional statistics are described in the results.

4.3 RESULTS

My sample of breeding female Buffleheads ($n = 70$) was distributed among reproductive categories as follows: Non-RFG ($n = 18$), Prelaying ($n = 9$), Early laying ($n = 16$), and Late laying ($n = 27$). Barrow's Goldeneye females ($n = 71$) were distributed among those categories as follows: Non-RFG ($n = 16$), Prelaying ($n = 12$), Early laying ($n = 18$), and Late laying ($n = 25$).

4.3.1 *General breeding biology*

Mean clutch size of Buffleheads was similar between years ($P = 0.1178$) and averaged 6.89 ± 0.18 (SE) eggs ($n = 63$). Clutch size of Barrow's Goldeneyes differed between years ($P = 0.0222$) and averaged 7.33 ± 0.30 eggs ($n = 24$) in 1993 and 8.21 ± 0.23 eggs ($n = 28$) in 1994. Mean clutch size of Buffleheads laying in nest boxes (7.20 ± 0.24 eggs; $n = 20$) was not different ($F = 1.43$, $P = 0.2372$) from those laying in natural cavities (6.74 ± 0.24 eggs; $n = 43$). Most laying Goldeneyes I collected were using nest boxes (n = 43). rather than natural nest sites (n = 9). However, this limited data indicated that nonparasitized clutches of Goldeneyes using nest boxes (8.02 ± 0.21 eggs) were, on average, larger ($F = 6.52$, $P = 0.0138$) than nonparasitized clutches of females laying in natural cavities (6.78 ± 0.32 eggs).

The period of RFG for an individual follicle ovum was estimated by multiplying the maximum number of growing follicles by the mean egg laying interval (days) (see Alisauskas and Ankney 1992). The validity of this procedure is supported by the close correlation between laying intervals and ovulation intervals in birds (Astheimer 1985). Maximum number of growing follicles in female Buffleheads was four and their mean laying interval was 2.02 days (Chapter 2); thus, the period of RFG for an individual follicle averaged 8.1 days. Maximum number of developing follicles in Barrow's Goldeneyes was 5 and their mean laying interval was 1.89 days (Chapter 2), so RFG for an individual follicle was estimated at 9.4 days.

4.3.2 *Categorical analysis of nutrient reserves and major proteinaceous tissues by reproductive status and year*

Dynamics of body mass, somatic nutrients, and mass of major proteinaceous tissues relative to reproductive status and year in breeding female Buffleheads and Barrow's Goldeneyes are compared in Table 4.2. Fresh body mass (i.e, live or recently collected body mass) is only an index of true body mass because it includes mass of ingesta and mass of enlarged reproductive tissues in breeding birds. However, because live body mass is the measure of body mass reported in most field studies conducted on Buffleheads and Barrow's Goldeneyes, I have included it in Table 4.2 for comparative purposes. Additionally, I report a better measure of true body mass based on the plucked, ingesta and reproductive tissue-free carcass mass. Carcass mass varied among reproductive statuses ($P = 0.0001$) and between years ($P = 0.0014$) in female Buffleheads, but among statuses ($P = 0.0019$) in female Barrow's Goldeneyes. In 1993, carcass mass was highest in Non-RFG Buffleheads, which consisted principally of birds that had recently arrived on breeding wetlands. Carcass mass subsequently declined ($P \leq 0.05$) and was lowest in birds during Late laying. In 1994, carcass mass of Buffleheads at arrival on breeding areas was nearly identical to 1993, but birds reached peak mass during early laying and declined ($P \leq 0.05$) to minimum carcass mass by Late laying. Female Barrow's Goldeneyes attained their highest average carcass mass during Prelaying and subsequently lost mass ($P \leq 0.05$) through Late laying during both years of study.

Table 4.2. Results from two-way ANOVA investigating the effects of reproductive status and year on body mass, somatic nutrients, and major proteinaceous tissues of breeding Buffleheads and Barrow' Goldeneyes. Data from 1993 and 1994 were pooled for variables when there was no significant annual effect.

			Reproductive Status[a]				Effects[b]	
Variable	Species[c]	Year[d]	Non-RFG	Prelayers	Early laying	Late Laying	Status	Year
Fresh body mass	BUFF	Pooled[e]	327.88 ± 6.62[f]	329.94 ± 7.13	346.79 ± 6.50	335.77 ± 5.89	NS	NS
	BAGO	Pooled[g]	798.98 ± 16.21	841.30 ± 12.97	866.41 ± 11.18	846.30 ± 14.39	0.0209	NS
Carcass mass[h]	BUFF	1993[i]	271.51 ± 6.73	262.55 ± 3.39	249.35 ± 3.96	236.49 ± 3.08	0.0001	0.0014
		1994[j]	272.69 ± 13.07	264.36 ± 8.07	281.71 ± 12.37	257.91 ± 4.82		
	BAGO	Pooled	670.94 ± 10.53	692.10 ± 11.57	652.99 ± 11.33	638.53 ± 7.17	0.0019	NS
Body lipid	BUFF	Pooled	26.40 ± 2.55	17.89 ± 1.59	11.09 ± 0.69	8.55 ± 0.52	0.0001	NS
	BAGO	Pooled	50.83 ± 4.07	74.07 ± 6.07	49.44 ± 4.38	30.38 ± 1.56	0.0001	NS
Body protein[k]	BUFF	1993	55.13 ± 2.21	59.43 ± 1.25	56.68 ± 0.79	55.13 ± 0.68	0.0072	0.0372
		1994	59.46 ± 1.02	58.56 ± 1.52	60.57 ± 1.88	57.53 ± 0.73		
	BAGO	Pooled	150.91 ± 1.99	151.06 ± 1.79	147.40 ± 1.57	146.82 ± 1.01	NS	NS
Body mineral[k]	BUFF	Pooled	11.49 ± 0.16	11.62 ± 0.25	11.69 ± 0.20	10.98 ± 0.15	0.0143	NS
	BAGO	Pooled	27.16 ± 0.27	28.59 ± 0.63	28.44 ± 0.55	27.74 ± 0.33	NS	NS
Left breast muscles[k]	BUFF	Pooled	7.64 ± 0.10	7.26 ± 0.34	7.40 ± 0.13	7.06 ± 0.08	0.0067	NS
	BAGO	Pooled	19.03 ± 0.25	19.51 ± 0.35	19.27 ± 0.25	19.06 ± 0.17	NS	NS
Left leg muscles[k]	BUFF	Pooled	2.91 ± 0.06	2.90 ± 0.05	2.82 ± 0.05	2.69 ± 0.04	0.0057	NS
	BAGO	Pooled	7.55 ± 0.13	7.40 ± 0.14	7.65 ± 0.14	7.54 ± 0.10	NS	NS

Table 4.2. Continued.

Variable	Species[c]	Year[d]	Reproductive Status[a]				Effects[b]	
			Non-RFG	Prelayers	Early laying	Late Laying	Status	Year
Liver[k]	BUFF	1993	3.34 ± 0.22	3.29 ± 0.16	3.38 ± 0.13	3.26 ± 0.15	NS	0.0056
		1994	3.91 ± 0.52	3.55 ± 0.20	3.90 ± 0.45	3.69 ± 0.11		
	BAGO	Pooled	7.97 ± 0.37	8.82 ± 0.32	8.15 ± 0.24	8.30 ± 0.19	NS	NS
Gizzard[h]	BUFF	Pooled	5.70 ± 0.26	4.72 ± 0.26	4.17 ± 0.15	4.39 ± 0.14	0.0001	NS
	BAGO	Pooled	22.09 ± 1.86	18.08 ± 0.95	15.72 ± 0.61	15.04 ± 0.62	0.0001	NS
Heart[h]	BUFF	Pooled	4.07 ± 0.11	4.01 ± 0.16	3.65 ± 0.06	3.50 ± 0.06	0.0001	NS
	BAGO	Pooled	8.35 ± 0.21	8.69 ± 0.28	8.43 ± 0.24	7.81 ± 0.13	0.0136	NS

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[a] See definitions in methods.

[b] No significant ($P < 0.05$) interactions, therefore data were reanalyzed using only main effects in the model. Probability values are presented for significant main effects. NS = Not significant ($P > 0.0.5$).

[c] BUFF = Bufflehead, BAGO = Barrow's Goldeneye.

[d] Separate means were presented for each year only when there were significant ($P < 0.05$) annual effects in the model.

[e] Mean ± SE

[f] Pooled sample sizes for Bufflehead - Non-RFG = 18, Prelayers = 9, Early Layers = 16, Late Layers = 27.

[g] Pooled sample sizes for Barrow's Goldeneye - Non-RFG = 16, Prelayers = 12, Early Layers = 18, Late Layers = 25.

[h] Wet mass (Carcass mass excludes mass of ingesta and reproductive tissue).

[i] 1993 sample sizes for Bufflehead - Non-RFG = 13, Prelayers = 4, Early Layers = 12, Late Layers = 16.

[j] 1994 sample sizes for Bufflehead - Non-RFG = 5, Prelayers = 5, Early Layers = 4, Late Layers = 11.

[k] Lipid-free dry mass. Body protein and mineral have been corrected for variation in body size.

Patterns of lipogenesis differed between female Buffleheads and Barrow's Goldeneyes, but both species catabolized fat during egg laying. Female Buffleheads arrived on breeding areas with their highest average levels of body fat, which was gradually catabolized until less than one-third of the original mass remained during late laying. Lipid mass was lower ($P \leq 0.05$) in prelaying Buffleheads than in non-RFG birds indicating that fat reserves were not stored on breeding areas. Lipid mass was highest in prelaying Barrow's Goldeneyes indicating that approximately 31% of their fat reserves were acquired after arrival on breeding wetlands. Body fat was used during laying and was at its lowest mass during late laying.

Body protein mass varied among reproductive statuses ($P = 0.0072$) and between years ($P = 0.0372$) in female Buffleheads, accounting for the annual difference in carcass mass described above; however, protein mass was consistent between years ($P > 0.05$) and among reproductive periods ($P > 0.05$) in female Barrow's Goldeneyes. In 1994, protein mass of female Buffleheads was generally 2 -4 g (dry mass) higher than in 1993. Additionally, data from 1993 indicate that female Buffleheads lost ($P \leq 0.05$) body protein from prelaying to late laying, whereas in 1994, protein mass was relatively constant.

Somatic mineral differed by reproductive status ($P = 0.0143$) in female Buffleheads, and declined ($P \leq 0.05$) from early to late laying. Somatic mineral of Barrow's Goldeneye females was similar among reproductive periods ($P > 0.05$) and years ($P > 0.05$).

To assess potential sources of catabolized somatic protein and monitor mobility in the distribution of body protein, changes in specific proteinaceous tissues were investigated in both species relative to reproductive status and year. There were no annual differences ($P > 0.05$) in mass of any specific proteinaceous tissue except for lean liver mass ($P = 0.0056$) in female Buffleheads. Lean liver mass in female Buffleheads did not differ by reproductive status ($P > 0.05$), but was consistently higher during the breeding season in 1994. Lean dry mass of left breast and leg muscles gradually declined ($P = 0.0067$) from arrival through late laying in female Buffleheads. Female Goldeneyes did not show significant variation ($P > 0.05$) in breast, leg, or liver protein mass between years or reproductive periods. Gizzard mass (wet) of both species was highest during Non-RFG, i.e., upon arrival from wintering areas and declined rapidly ($P \leq 0.05$) thereafter. Heart mass (wet) declined in Buffleheads ($P = 0.0001$) and Barrow's Goldeneyes ($P = 0.0136$) from early reproductive periods (i.e. Non-RFG and prelaying) to late laying.

4.3.3 *Nutrient reserve dynamics during egg production*

Lipid reserves of female Buffleheads and Barrow's Goldeneyes declined with investment in reproductive lipid and were lower with later dates of RFG initiation (Table 4.3). For every gram of reproductive fat produced by female Buffleheads, somatic lipid content declined by 0.26 g. Concurrently, lipid reserves were lower by 0.27 g/day as the breeding season progressed, i.e., Buffleheads that initiated RFG later, did so with less body fat than did birds that bred earlier. Barrow's Goldeneyes had a higher rate of somatic lipid investment in their clutch; body lipid mass declined by 0.65 g for every gram of reproductive fat synthesized. Body fat also declined by 0.80 g/day independent of investment in reproductive tissue, indicating that later laying Goldeneyes started RFG with lower lipid reserves.

Variation in somatic protein of female Buffleheads and Barrow's Goldeneyes was attributable to different variables between species, and between years in Goldeneyes (Table 4.3). Carcass protein of Buffleheads differed only between years, and was 2.08 g lower in 1993 than in 1994. Somatic protein was analyzed by year in Goldeneyes because of an interaction ($P = 0.0250$) between year and wetland PC_2.

Table 4.3. Results from ANCOVA based on type III sums of squares relating somatic nutrients (g) of female Buffleheads and Barrow's Goldeneyes to reproductive nutrient investment (g; R-NUTRIENT), year, date of RFG initiation, and wetland type.

		Model							
Dependent variable[a]	Species[b]	*F*	*P*	R^2	Intercept	Source[c]	Estimate	F	P[d]
LIPID	BH	35.73	0.0001	0.59	20.35	R-LIPID	-0.26	53.30	0.0001
						RFGDATE[e]	-0.27	26.12	0.0001
	BG	37.13	0.0001	0.59	82.37	R-LIPID	-0.65	68.89	0.0001
						RFGDATE[f]	-0.80	9.26	0.0037
PROTEIN	BH	6.06	0.0172	0.11	58.40	YEAR	93 = -2.08 94 = 0.00	6.06	0.0172
	BG(93)[g]	6.40	0.0053	0.32	155.64	R-PROTEIN	-0.11	9.06	0.0056
						RFGDATE	-0.24	5.31	0.0292
	BG(94)	3.73	0.0657	0.14	154.06	RFGDATE	-0.41	3.73	0.0657

Table 4.3. (continued)

Dependent variable[a]	Species[b]	Model			Intercept	Source[c]	Estimate	F	P[d]
		F	*P*	R^2					
MINERAL	BH(93)[h]	18.55	0.0002	0.37	12.13	R-MINERAL	-0.08	18.55	0.0002
	BH(94)	6.26	0.0222	0.26	10.85	$PC_{1\text{wtld}}$	0 = 0.87[i] 1 = 0.00	6.26	0.0222
	BG(93)[j]	4.93	0.0347	0.15	28.52	R-MINERAL	-0.03	4.93	0.0347
	BG(94)	10.71	0.0033	0.32	31.63	RFGDATE	-0.25	10.71	0.0033

---

[a] Somatic protein and mineral reserves were corrected for variation in body size (see Methods).

[b] Sample sizes for Bufflehead (1993 - *n* = 33; 1994 - *n* = 20) and Barrow's Goldeneye (1993 - *n* = 33; 1994 - *n* = 24).

[c] Nonsignificant ($P < 0.05$) main effects deleted from model (see Methods).

[d] Probability that slope = 0.

[e] RFGDATE = 1 for 12 April 1993 and 10 April 1994.

[f] RFGDATE = 1 for 9 April 1993 and 5 April 1994.

[g] Years analyzed separately due to a year*$PC_{2\text{wtld}}$ interaction ($P = 0.0250$) in the overall model.

[h] Years analyzed separately due to a year*$PC_{1\text{wtld}}$ interaction ($P = 0.0200$) in the overall model.

[i] 0 = Wetlands with relatively lower pH, conductivity, and alkalinity (see Methods).

[j] Years analyzed separately due to a year*RFGDATE interaction ($P = 0.0005$) in the overall model.

In 1993, somatic protein declined by 0.11 g for every gram of reproductive protein produced and was lower by 0.24 g/day, independent of reproductive tissue growth, as the breeding season progressed. In 1994, variation in somatic protein was explained solely by RFGDATE indicating that birds that delayed initiation of RFG started ovarian development with 0.41 g less protein for every day of the delay. In both years, Goldeneyes that started RFG later did so with lower somatic protein mass.

Data on somatic mineral were analyzed by year for both species because of an interaction between year and wetland PC_1 ($P = 0.0200$) in Buffleheads and an interaction ($P = 0.0005$) between year and RFGDATE in Goldeneyes. In 1993, Bufflehead mineral reserves declined by 0.08 g for every gram of reproductive mineral produced (Figure 4.1). However, in 1994, body mineral varied only in response to wetland limnology (i.e. wetland PC_1), indicating that mineral reserves were higher in wetlands with above average pH, alkalinity, and conductivity. As observed in Buffleheads, somatic mineral content of Goldeneyes declined by 0.03 g for every gram of reproductive mineral produced in 1993 (Figure 4.2). In 1994, somatic mineral differed only by RFGDATE denoting that goldeneyes breeding early in the season had more body mineral than did late nesters.

4.3.4 *Clutch size and nutrient reserves*

If clutch size is limited by nutrient reserves, then clutch size should be positively related to size of nutrient reserves after controlling for other factors. Lipid and mineral reserves in female Buffleheads were related to final clutch size (Table 4.4), but the relationship was negative. These results indicate that Buffleheads with smaller clutches stopped laying with greater lipid and mineral reserves than did birds with larger clutches. Factors such as RFGDATE and Year were generally better predictors of nutrient reserves during late laying than was clutch size or reproductive nutrient investment in this small anatid.

Fig. 4.1. Relation between somatic mineral mass of female Buffleheads and their corresponding commitment to reproductive mineral (i.e., eggshell) in 1993. See Table 4.3 for equation describing this relationship.

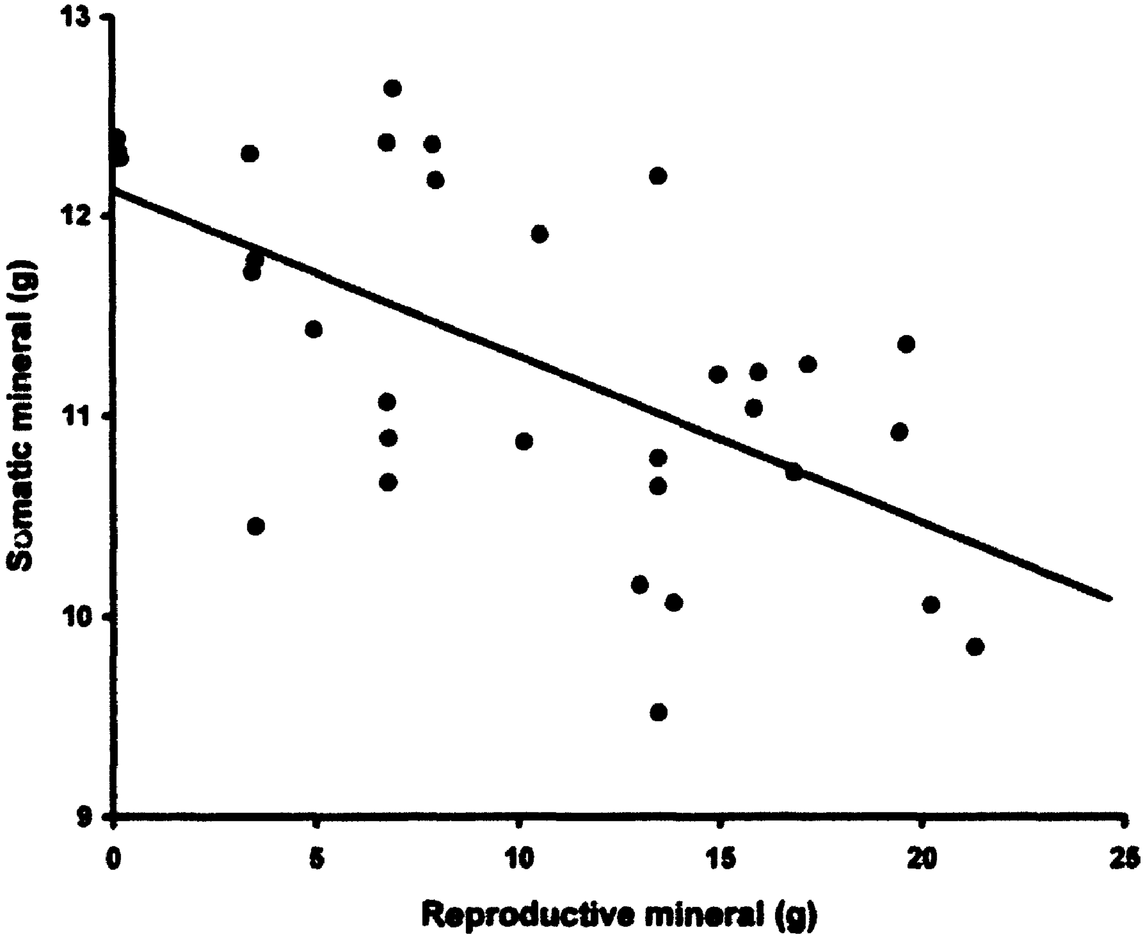

13
12
11
10
9
0
5
10
15
20
25
Somatic mineral (g)
Reproductive mineral (g)

Fig. 4.2. Relation between somatic mineral mass of female Barrow's Goldeneyes and their corresponding commitment to reproductive mineral (i.e., eggshell) in 1993. See Table 4.3 for equation describing this relationship. Some data points represent multiple observations.

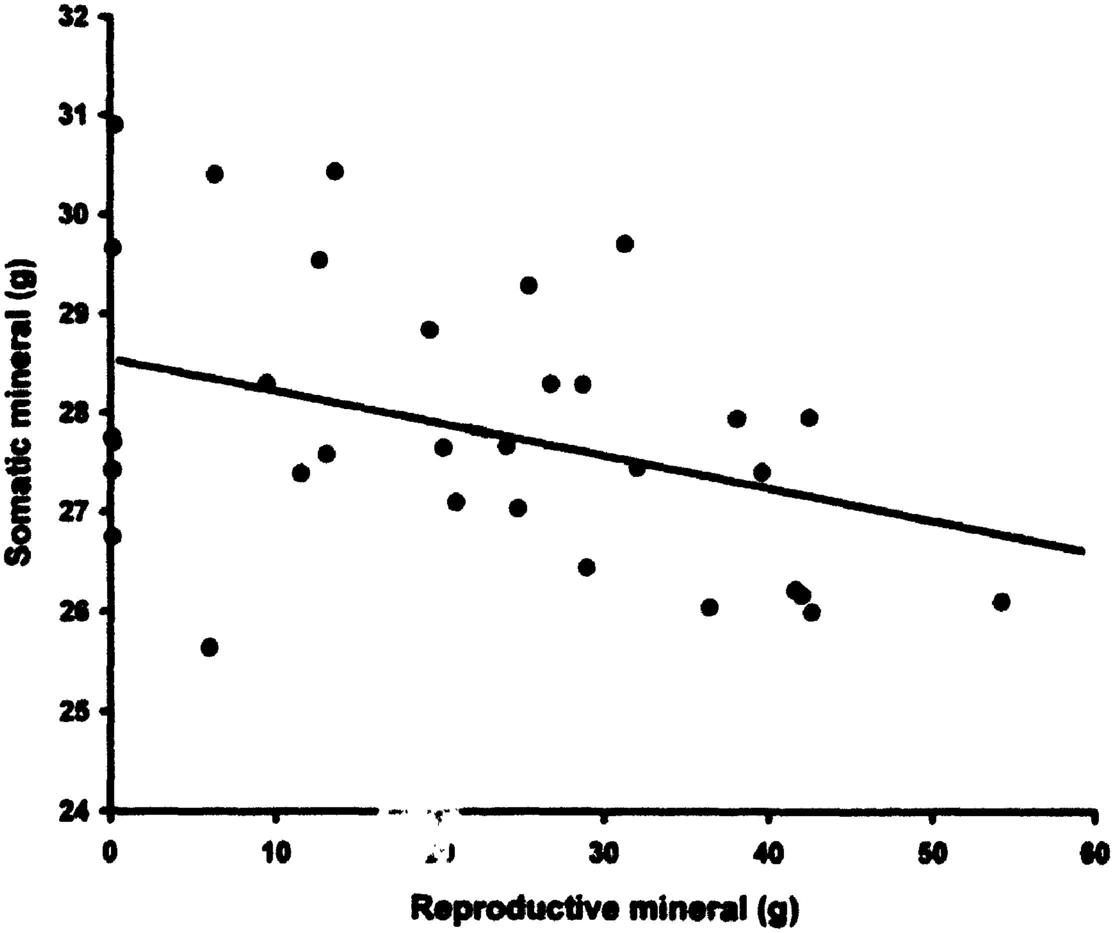

32
31
30
29
28
27
26
25
24
Somatic mineral (g)
0
10
20
30
40
50
60
Reproductive mineral (g)

Table 4.4. Results from ANCOVA based on type III sums of squares relating somatic nutrients of female Buffleheads and Barrow's Goldeneyes to final clutch size.The general form of the model was S-NUTRIENT = clutch size, RFGDATE, year, R-NUTRIENT, PC_{1wtld} and PC_{2wtld}. Clutch size was treated as a continuous variable rather than a categorical variable in this analysis.

		Model							
Dependent variable[a]	Species[b]	F	P	R^2	Intercept	Source[c]	Estimate	F	P[d]
LIPID	BUFF	10.02	0.0004	0.39	16.53	CLUTCH SIZE	-0.61	6.52	0.0157
						RFGDATE[e]	-0.20	17.04	0.0002
	BAGO	3.55	0.0311	0.33	53.19	CLUTCH SIZE	-2.44	2.49	0.1289
						YEAR	93 =-10.01 94 = 0.00	5.72	0.0258
						PC_{1wtld}[f]	0 = 9.02 1 = 0.00	4.88	0.0380
PROTEIN	BUFF	3.85	0.0319	0.19	59.96	CLUTCH SIZE	-0.26	0.74	0.3975
						YEAR	93 = -2.73 94 = 0.00	7.66	0.0093
	BAGO	2.95	0.0724	0.20	160.75	CLUTCH SIZE	-1.30	3.06	0.0935
						YEAR	93 = -4.94 94 = 0.00	4.82	0.0386

Table 4.4. (continued).

Dependent variable[a]	Species[b]	Model F	Model P	Model R^2	Intercept	Source[c]	Estimate	F	P[d]
MINERAL	BUFF	4.82	0.0148	0.23	13.02	CLUTCH SIZE	-0.23	7.04	0.0123
						YEAR	93 = -0.62 94 = 0.00	4.95	0.0332
	BAGO	4.23	0.0273	0.27	25.02	CLUTCH SIZE	0.78	6.60	0.0172
						R-MINERAL	-0.10	7.64	0.0110

---

[a] Somatic protein and mineral reserves were corrected for variation in body size (see Methods).

[b] Sample sizes for Bufflehead (BUFF; N = 35) and Barrow's Goldeneye (BAGO; N = 26).

[c] Nonsignificant ($P < 0.05$) main effects deleted from model with exception of CLUTCH SIZE (see Methods).

[d] Probability that slope = 0.

[e] RFGDATE = 1 for 12 April 1993 and 10 April 1994.

[f] Wetlands with $PC_{1wtld} = 0$ have relatively high pH, alkalinity, and conductivity.

Similarly, the relationship between somatic protein and final clutch size in Barrow's Goldeneyes was negative and nearly significant ($P = 0.0935$), suggesting that Goldeneyes with smaller clutches stopped laying with greater protein reserves than did birds with larger clutches. In addition, somatic protein mass of late laying goldeneyes also differed between years indicating that during late laying, females had 4.94 g less protein in 1993 than 1994. Variation in lipid mass of late laying Goldeneyes was explained by year and wetland type rather than by clutch size. Late laying females had 10.01 g less fat in 1993 than in 1994, and birds on wetlands with higher pH, alkalinity, and conductivity typically had 9.02 g more fat than did birds breeding on wetlands where these chemical variables were lower.

The only evidence that nutrient reserves may constrain clutch size in either species was a significant positive relationship of body mineral content to final clutch size ($P = 0.0172$) and a corresponding negative relationship of body mineral content to reproductive mineral investment ($P = 0.0110$) in female Barrow's Goldeneyes. Females that laid larger clutches had, on average, 0.78 g more mineral for each additional egg in the clutch. Furthermore, rate of decline in somatic mineral mass during late laying was 0.10 g for every gram of egg mineral produced, which is greater than the average rate of loss over the entire period of RFG (Table 4.1).

4.3.5 *Significance of RFG initiation date on clutch size, egg size, and clutch volume*

Date of RFG initiation had a negative affect ($P = 0.0103$) on clutch size of Buffleheads during both years (Figure 4.3), but only affected number of eggs laid by Barrow's Goldeneyes during 1994 ($P = 0.0545$; Figure 4.4). RFGDATE did not effect mean egg size (i.e., egg volume) in either Buffleheads ($P = 0.6098$) or Barrow's Goldeneyes ($P = 0.9893$). Similar to clutch size, clutch volume was negatively related to date of RFG initiation in Buffleheads ($P = 0.0242$; Figure 4.5) and in Goldeneyes during 1994 ($P = 0.0461$; Figure 4.6).

Fig. 4.3. Relationship between clutch size and Julian date that rapid follicular growth was initiated in female Buffleheads (years pooled). Regression line is Clutch size = 7.81 - 0.05 (RFGDATE), n = 63, F = 7.00, P = 0.0103., r^2 = 0.10. Some data points represent multiple observations.

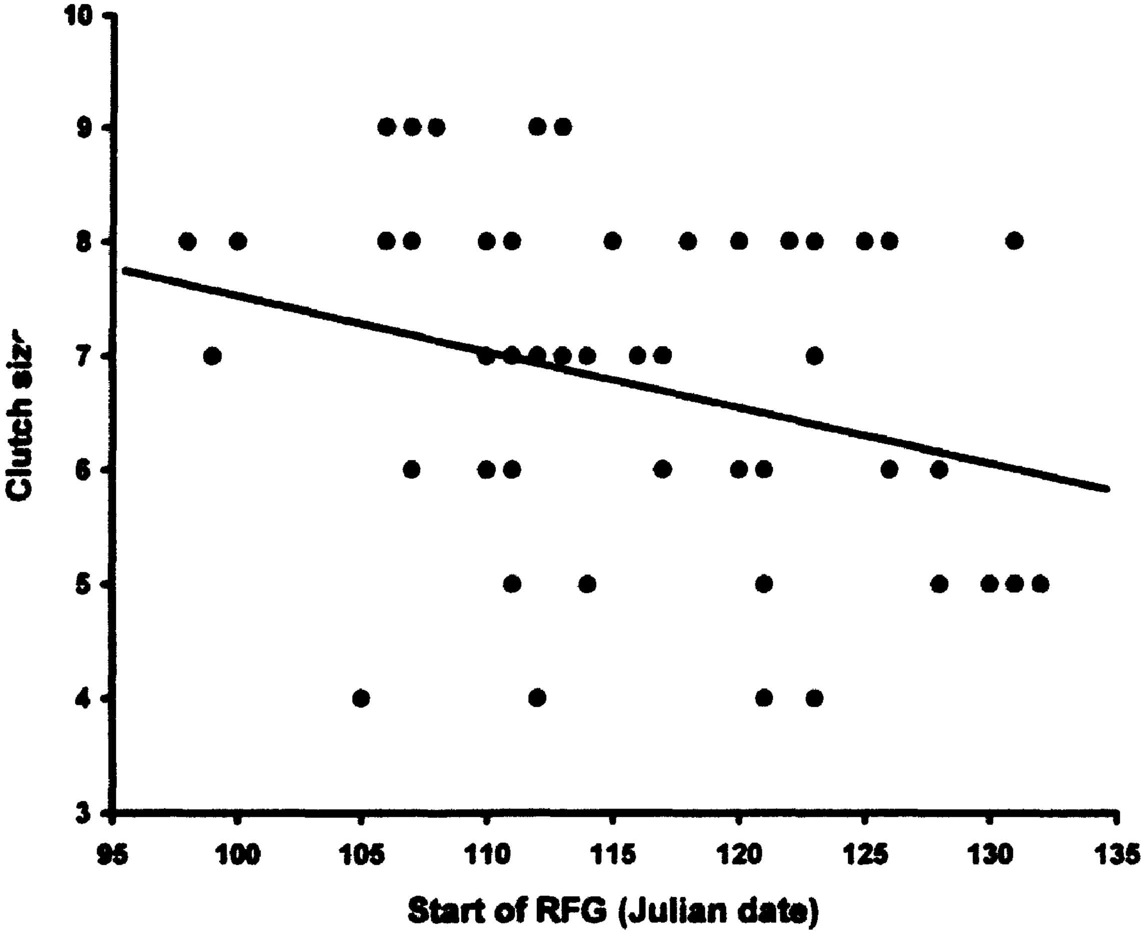

Clutch siz
10
9
8
7
6
5
4
3
95
100
105
110
115
120
125
130
135
Start of RFG (Julian date)

Fig. 4.4. Relationship between clutch size and Julian date that rapid follicular growth was initiated in female Barrow's Goldeneyes in 1993. Regression line is Clutch size = 9.20 - 0.06 (RFGDATE), n = 28, F = 4.05, $P = 0.0545$., $r^2 = 0.13$. Some data points represent multiple observations.

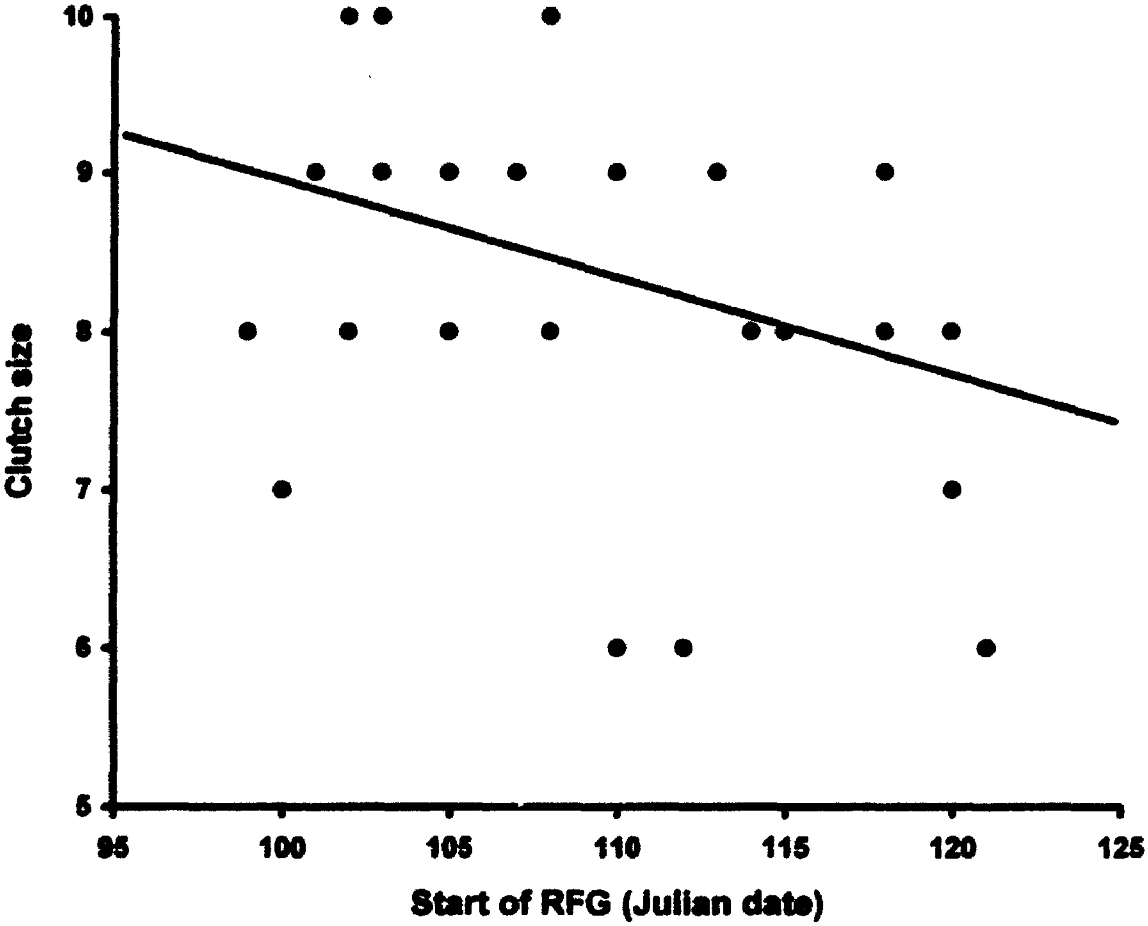

10
9
8
7
6
5
95
100
105
110
115
120
125
Clutch size
Start of RFG (Julian date)

Fig. 4.5. Relationship between clutch volume (cm^3) and Julian date that rapid follicular growth was initiated in female Buffleheads (years pooled). Regression line is Clutch volume = 262.75 - 1.71 (RFGDATE), $n = 63$, $F = 5.34$, $P = 0.0242$., $r^2 = 0.08$. Some data points represent multiple observations.

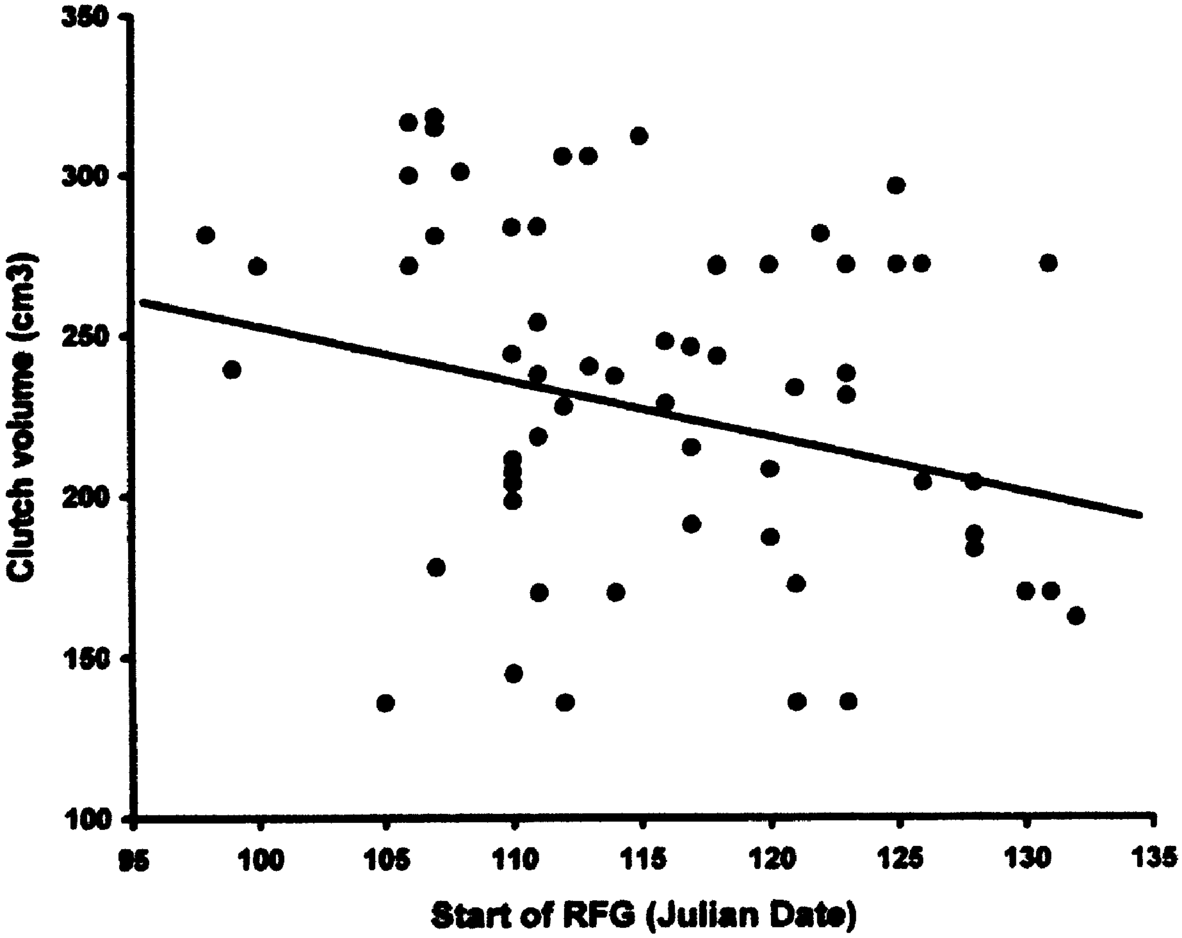
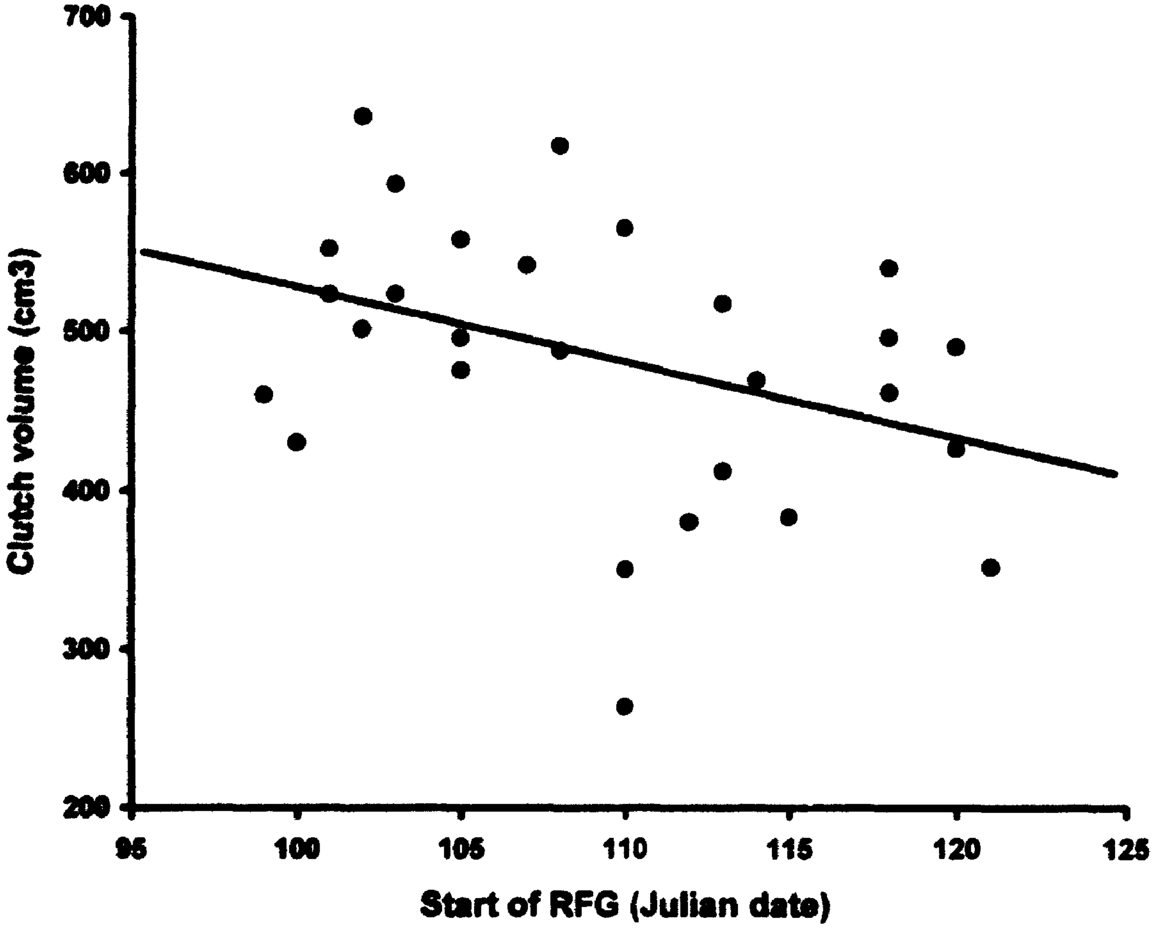

350
300
250
200
150
100
95
100
105
110
115
120
125
130
135
Clutch volume (cm3)
Start of RFG (Julian Date)

Fig. 4.6. Relationship between clutch volume (cm^3) and Julian date that rapid follicular growth was initiated in female Barrow's Goldeneyes in 1994. Regression line is Clutch volume = 555.59 - 4.79 (RFGDATE), $n = 28$, $F = 4.39$, $P = 0.0461$., $r^2 = 0.14$. Some data points represent multiple observations.


700
600
500
400
300
200
Clutch volume (cm3)
95
100
105
110
115
120
125
Start of RFG (Julian date)

4.3.6 *The relation between body size and clutch size, egg size, and clutch volume*

Clutch size was not related to body size (PC_{1BS}) of Buffleheads when considered independently ($P = 0.8004$) or when controlling for the effects of RFGDATE on clutch size ($P = 0.8745$). Likewise, clutch size in Barrow's Goldeneyes was not related to body size when evaluated alone ($P = 0.9129$) or when accounting for RFGDATE ($P = 0.7235$). However, when years were analyzed separately, there was a trend ($P = 0.0751$) for structurally larger Goldeneyes to lay larger clutches in 1994 (Figure 4.7). Interestingly, accounting for RFGDATE actually weakened the relationship ($P = 0.1340$) between body size and clutch size of Goldeneyes in 1994. Egg size was not related to body size in Buffleheads ($P = 0.1166$) and Barrow's Goldeneyes ($P = 0.8693$). Probability that egg size was influenced by body size was similar after controlling for RFGDATE. Clutch volume was also unrelated to body size in Buffleheads ($P = 0.7247$) and Barrow's Goldeneyes in 1993 (0.0644), but in 1994, Goldeneye clutch volume was positively related to body size ($P = 0.0416$; Figure 4.8). Remarkably, the trend (in Goldeneye clutch volume in 1993 was for larger birds to lay smaller clutches explaining the annual effects in the overall model. Correcting clutch volume for RFGDATE made body size a marginally nonsignificant ($P = 0.0777$) predictor of Goldeneye clutch volume in 1994.

4.4 DISCUSSION

4.4.1 *Variation in clutch size of Buffleheads and Barrow's Goldeneyes*

Erskine (1972) reported that mean clutch size of Buffleheads ($n = 201$) nesting in natural cavities in British Columbia was 8.8 ± 0.16 (SE) eggs. Likewise, Gauthier (1989) indicated that the mean number of eggs laid by Buffleheads in the Cariboo Parklands of south -central British Columbia ranged from 7.2 to 8.8 eggs ($n = 157$; clutches from natural cavities and nest boxes pooled). These clutch size estimates ranged from 0.3 - 1.9 eggs larger than mean clutch size that I determined using egg morphology and ovary

Fig. 4.7. Trend between clutch size and body size (PC_{1BS}) of female Barrow's Goldeneyes in 1994. Trend line is Clutch size = 8.16 + 0.23 (PC_{1BS}), $n = 28$, $F = 3.44$, $P = 0.0751$, $r^2 = 0.12$. Some data points represent multiple observations.

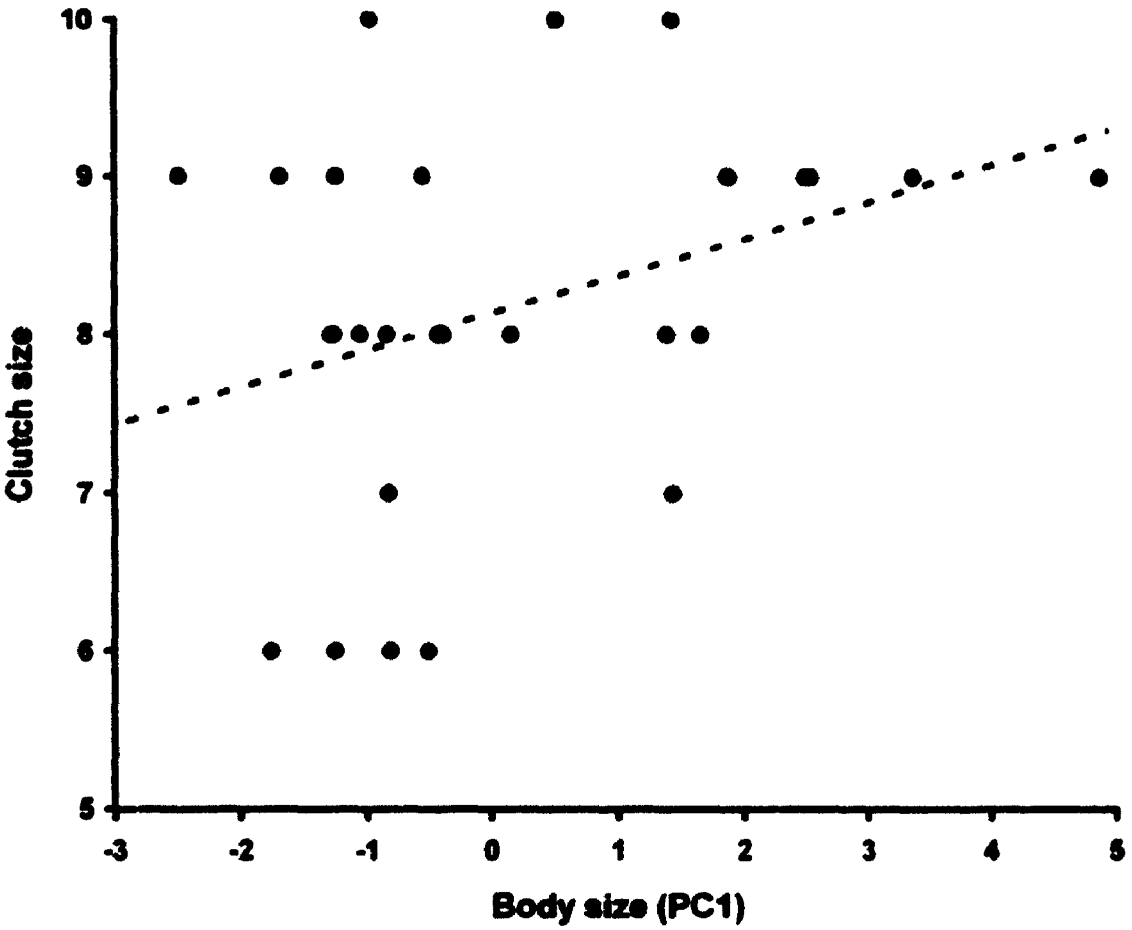
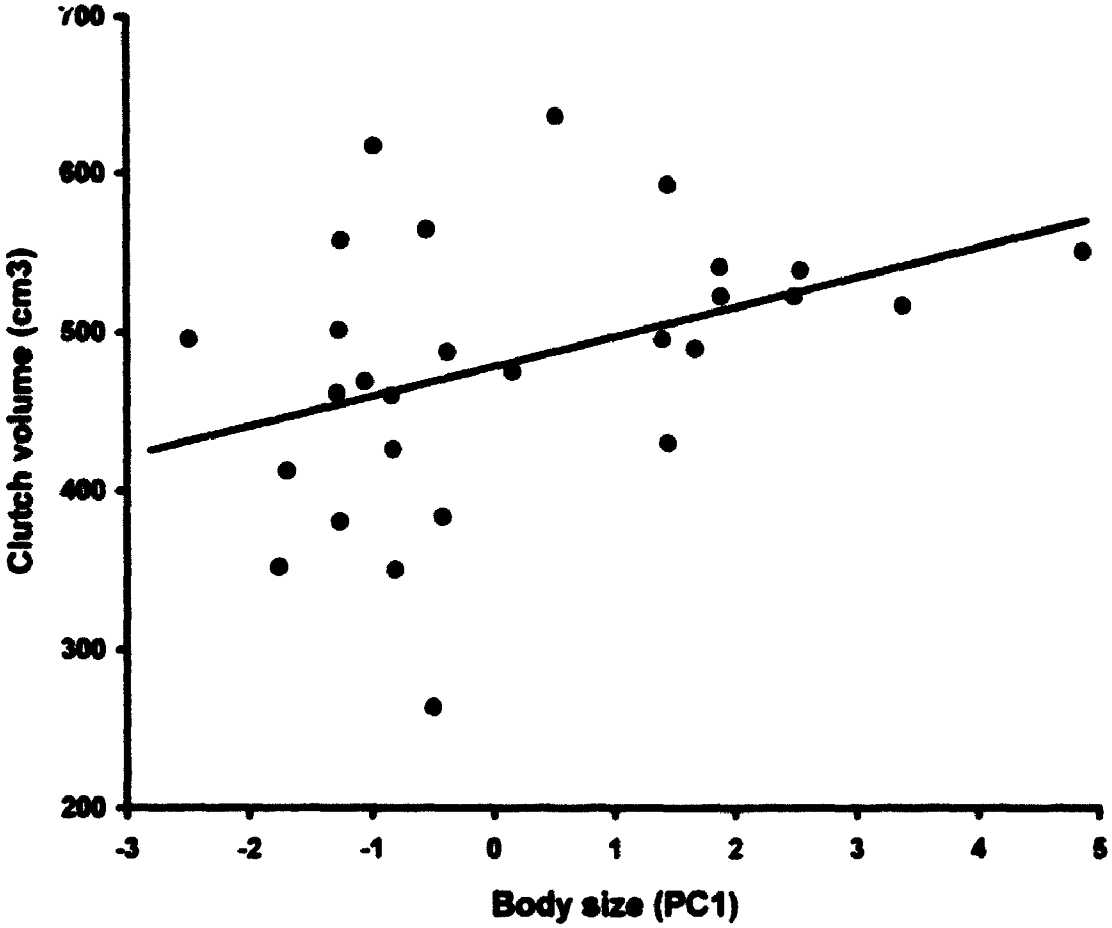

10
9
8
7
6
5
-3
-2
-1
0
1
2
3
4
5
Clutch size
Body size (PC1)

Fig. 4.8. Relationship between clutch volume (cm^3) and body size (PC_{1BS}) of female Barrow's Goldeneyes in 1994. Regression line is Clutch volume = 478.14 + 18.56 (PC_{1BS}), $n = 28$, $F = 4.59$, $P = 0.0416$, $r^2 = 0.15$. Some data points represent multiple observations.


700
600
500
400
300
200
-3
-2
-1
0
1
2
3
4
5
Clutch volume (cm3)
Body size (PC1)

examinations. However, modal clutch size of 8 eggs recorded during both years of my study (Figure 4.9), was only 0.8 eggs less than the average or highest annual mean clutch size in these previous studies. Higher mean clutch size for Buffleheads in previous studies may be partially related to undetected parasitically laid eggs. However, rates of brood parasitism are generally low in Buffleheads (5.3% of nests [Gauthier 1987a]; 7.5% of nests [Erskine 1990]), thus other factors may have contributed to slightly lower clutches in this study (see below).

Similarly, mean clutch size of Barrow's Goldeneyes was 1.5 - 2.4 eggs lower in this study than previously reported estimates, primarily because I used techniques for determination clutch size that excluded most parasitically laid eggs. Savard (1988a) reported that mean clutch size of Barrow's Goldeneyes, from the same central British Columbia population I studied, ranged from 6.6 ± 0.6 (± SE) eggs in 1981 to 9.8 ± 0.4 eggs in 1984, but these estimates were based exclusively on egg counts from nest boxes. Rates of brood parasitism, are high in this population, with 40% or more of nests containing parasitically laid eggs (Savard 1988a). Furthermore, the previous definition of parasitized clutches (> 13 eggs; J. M. Eadie *in* Savard 1988a) was very conservative, resulting in many parasitized nests being included with normal clutches, thus underestimating the extent of brood parasitism. Data from my study suggest that few female Barrow's Goldeneyes lay > 10 eggs (Figure 4.10), thus most clutches containing ≥ 11 eggs likely result from parasitic laying.

Mean clutch size for female *Bucephala* nesting in recently erected nest boxes (< 2 years old) is generally lower than that for females laying in natural cavities and older nest boxes (M. Jackson in Erskine 1972, Savard 1988a). However, I found no difference in mean clutch size of Buffleheads nesting in boxes and natural cavities and mean clutch size of Goldeneyes using nest boxes was actually higher than that of females nesting in natural cavities In these other studies, smaller clutches in relatively new nest boxes may have originated from disproportionate use of artificial cavities by first time breeders

Fig. 4.9. Clutch size frequency of Buffleheads nesting in central British Columbia during 1993 and 1994. Post-ovulatory follicle counts from host females and egg morphology were used to correct clutch size in nests that were parasitized. Modal clutch size in both years was 8 eggs.

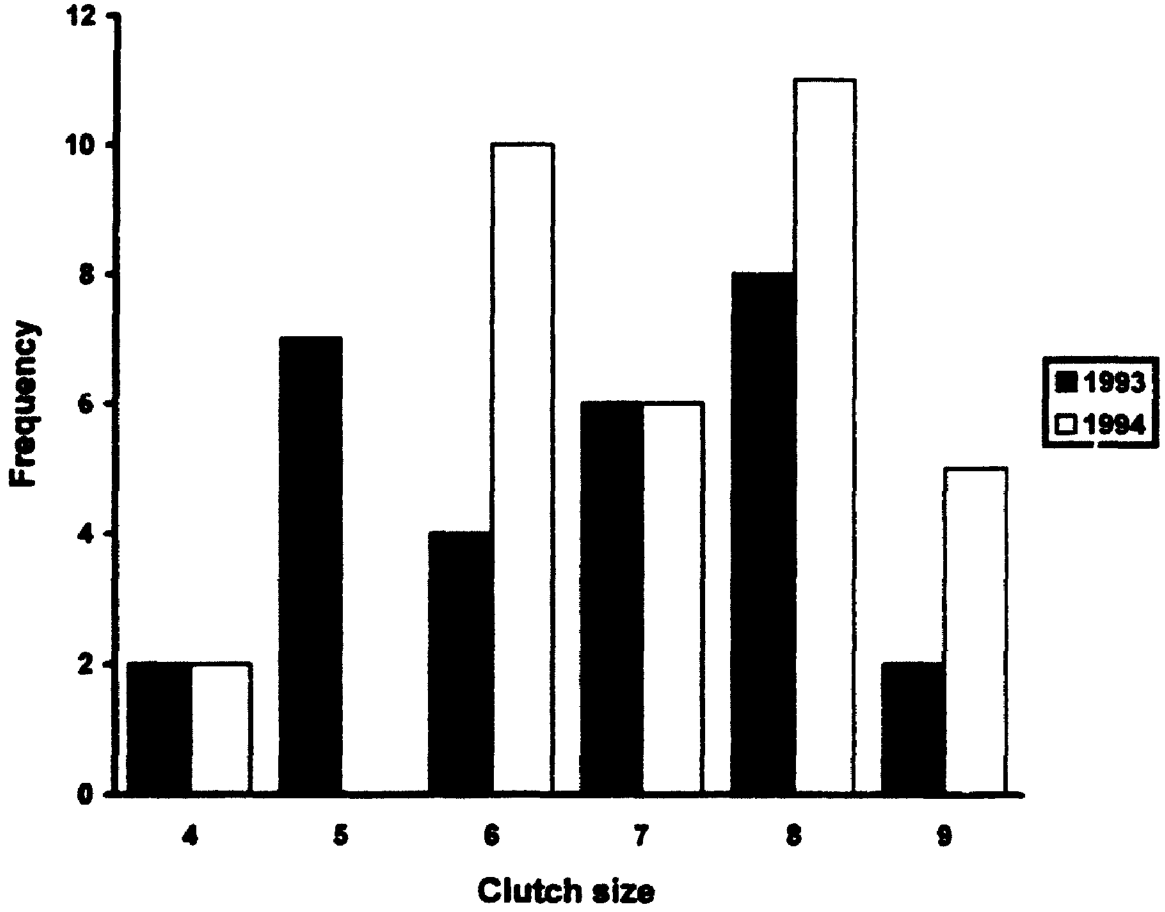
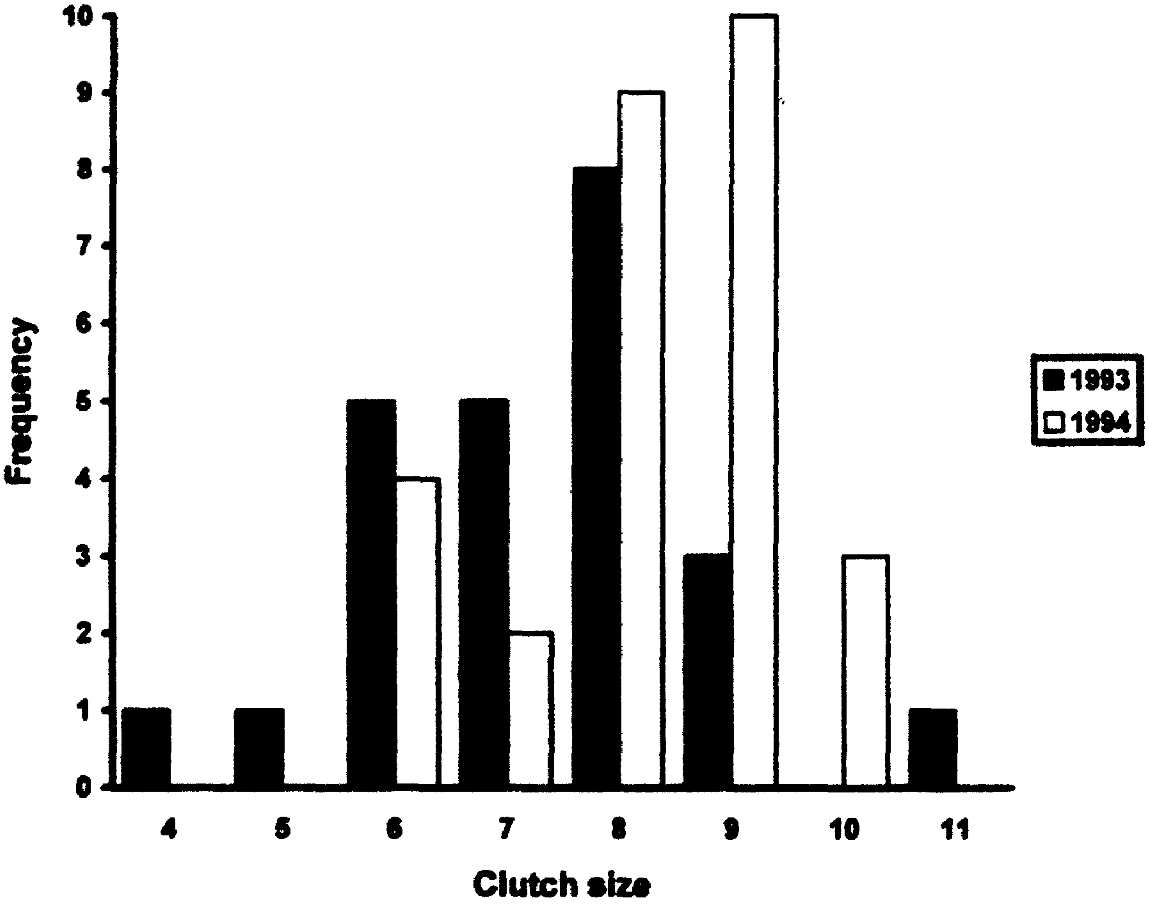

12
10
8
6
4
2
0
Frequency
4
5
6
7
8
9
Clutch size
1993
1994

Fig. 4.10. Clutch size frequency of Barrow's Goldeneyes nesting in central British Columbia during 1993 and 1994. Post-ovulatory follicle counts from host females and egg morphology were used to correct clutch size in nests that were parasitized. Modal clutch size was 8 eggs in 1993 and 9 eggs in 1994.


Frequency
0
1
2
3
4
5
6
7
8
9
10
4
5
6
7
8
9
10
11
Clutch size
■ 1993
□ 1994

or lower rates of brood parasitism in newer, less familiar nest sites. Clutch size of Buffleheads in their initial breeding attempt averages only 0.5 eggs smaller than that of older or more experienced females (Erskine 1972, Gauthier 1989). Thus, it is unlikely that smaller clutch sizes in nest boxes are entirely attributable to disproportionate use of these nest sites by younger female Buffleheads. Unfortunately, there is little evidence available to evaluate whether nest boxes are used by younger female Barrow's Goldeneyes because they can not be reliably aged after their first year (Carney 1983) and birds are not sexually mature until they are ≥ 2 years old (Savard 1987). Furthermore, natal philopatry of Barrow's Goldeneye ducklings banded in central British Columbia is apparently low (Savard and Eadie 1989), making it difficult to locate known age birds during their first reproductive attempt. Brood parasitism, however, is probably less frequent in newer nest boxes because female *Bucephala* generally locate their nest site for the upcoming breeding season from mid-June to mid-July of the previous year (Eadie and Gauthier 1985); thus, nest boxes that have been available for fewer summers are less likely to have been located by brood parasites.

Annual variation in an individual female's clutch size is common in waterfowl and provides considerable support for proximate rather than ultimate regulation of reproductive effort. Erskine (1972) monitored reproductive effort in the same female Buffleheads ($n = 14$) over 3 to 6 years and found that clutch size of an individual female could differ by as much as 4 eggs between years. However, in at least one species of sea duck, the White-winged Scoter (*Melanitta fusca*), intra-individual variation in clutch size between years is evidently low (Koskimies 1957). In a more recent study on Bufflehead reproductive ecology, Gauthier (1989) found moderate repeatability ($r = 0.565$, $n = 24$) of clutch size, but such estimates on clutch size of cavity nesting waterfowl would be much more informative and reliable if they were derived from clutches of known parentage due to the potentially confounding effects of brood parasitism.

Clutch size in birds typically declines with later nest initiation dates (Klomp 1970, Daan et al. 1988, Rohwer 1992). This general pattern was supported by a negative relationship between clutch size and date of RFG initiation in Buffleheads (Figure 4.3; also see Erskine 1972 and Gauthier 1989 for similar relationships). Because female Buffleheads that are nesting for the first time generally start laying relatively late in the breeding season (Gauthier 1989), younger birds, which also lay smaller clutches (see above), are at least partially responsible for the negative correlation between clutch size and date of nest initiation in this study. Unlike other temperate nesting ducks (Rohwer 1986, Esler and Grand 1994), it is unlikely that smaller clutches later in the breeding season result from renests in female *Bucephala*, because species in this genus rarely attempt a second nest if the first is destroyed or abandoned (Zicus 1990).

Bengston (1972) reported that mean clutch size of early nesting Barrow's Goldeneyes in Iceland was 0.9 eggs larger than in later nests. However, I found that time of RFG initiation was related to clutch size of Barrow's Goldeneyes only during the 1993 breeding season. In 1994, an earlier and warmer spring apparently improved breeding habitat conditions throughout the nesting season, diminishing the negative effect of later nest initiation dates. Additional evidence in support of improved habitat conditions in 1994 include that Goldeneyes relied exclusively on dietary protein and minerals to produce egg protein and mineral during this breeding season and mean clutch size was higher than in 1993.

4.4.2 *Use of nutrient reserves for egg production in female Bucephala*

Assuming a 100% conversion efficiency of somatic lipids to egg lipids (Ankney and Alisauskas 1991a), approximately 26% (10.69 g of 41.12 g) and 65% (49.45 g of 76.08 g) of clutch lipids were provided by lipid reserves in breeding Buffleheads and Barrow's Goldeneyes, respectively. However, individuals from both species that initiated RFG late did so with lower somatic lipid reserves. Thus, given a constant rate of contribution of fat reserves to egg formation in Buffleheads and Barrow's Goldeneyes, reduced clutch size in late nesting females (Figures 4.3 & 4.4) is probably attributable to lower somatic lipid mass at the start of RFG. In 1994, clutch size of female Goldeneyes did not decline with date, suggesting that late nesting females were able to compensate for lower fat reserves through increased dietary lipid intake.

Endogenous lipid catabolism for clutch formation has been documented in all waterfowl species studied to date (See review in Ankney and Alisauskas 1991a) with exception of White-winged Scoters (Dobush 1986, Brown and Fredrickson 1987). Nearly ubiquitous use of fat reserves by waterfowl, regardless of breeding habitat, supports the contention that anseriforms evolved this nutritional tactic to sustain relatively rapid growth of energy-rich ovarian follicles (Ankney and Alisauskas 1991a). Without use of fat reserves, ducks may lay fewer eggs, as evidenced by smaller clutches in renesting (Esler and Grand 1994) and late nesting anatids (Figures 4.3 & 4.4; see also Rohwer 1992), or extend reproduction into less optimal periods. Furthermore, extended breeding periods in female *Bucephala* would place even greater temporal constraints on other annual cycle events, such as molt and premigratory lipogenesis, possibly reducing annual survival and corresponding lifetime fitness in late nesting females.

Body protein is seldom catabolized for egg production in temperate nesting ducks, except in the most herbivorous species (Wishart 1983, Ankney and Alisauskas 1991b). Ducks that feed principally on animal matter over their annual cycle, including Northern Shovelers (*Anas clypeata*) (Ankney and Afton 1988) and Lesser Scaup (*Aythya affinis*) (Afton and Ankney 1991), actually accumulate body protein during egg laying. Buffleheads maintained stable body protein content during the breeding season (Table 4.2), and thus relied exclusively on dietary protein for clutch formation, whereas Goldeneyes catabolized somatic protein to produce egg protein in at least one year of this study (Table 4.3). Approximately 11% of clutch protein originated from catabolism of body protein in Barrow's Goldeneyes during 1993. In 1994, when warmer climatic conditions were apparently more favorable for invertebrate production, Goldeneyes did not use protein reserves for egg production. Buffleheads may have averted use of somatic protein in 1993 because of their absolutely lower protein requirements and by nesting slightly later in the spring than Goldeneyes.

Only two carnivorous ducks other than Barrow's Goldeneyes use body protein for egg production. Common eiders (*Somateria mollissima*), which feed little during RFG, rely almost exclusively on body protein to produce the protein component of their clutch (Korschgen 1977). Ruddy ducks (*Oxyura jamaicensis*), which have inordinately high protein requirements because of their disproportionately large egg mass relative to their body mass and daily laying rates, also use somatic protein to produce egg protein (Alisauskas and Ankney 1994). Barrow's Goldeneyes have relatively low daily protein requirements during egg production as a consequence of extended laying intervals, but apparently still need to catabolize body protein during some breeding seasons. Use of body protein during clutch formation in a primarily carnivorous duck with relatively low daily protein requirements suggests that protein availability (i.e. invertebrate abundance) in breeding habitats used by Goldeneyes can be periodically deficient. The breeding season (1993) that Goldeneyes utilized body protein was characterized by a cool, late spring, which likely reduced or delayed invertebrate production in wetlands used by breeding birds. I hypothesize that body protein was catabolized by Goldeneyes to maintain their normal laying rate and breeding chronology in this year. If so, catabolism of body protein is a tactic that is used by Goldeneyes only when dietary protein intake is insufficient. Facultative use of somatic protein may maintain adaptive rates of egg production protecting females from protracted clutch formation which could reduce fitness.

Use of somatic mineral to produce eggshell in temperate nesting ducks is atypical because they generally increase consumption of molluscs to meet their calcium demands (Ankney and Alisauskas 1991a). Somatic mineral supplied approximately 8% of clutch minerals in Buffleheads and 3% of clutch minerals in Goldeneyes during the 1993 breeding season. However, neither species used endogenous minerals for eggshell production in 1994. Again, climatic conditions in 1993 may have reduced gastropod availability to breeding birds necessitating catabolism of somatic minerals to maintain typical egg laying rates. Clutch size in Goldeneyes, which was limited by mineral availability (Table 4.4), was lower in 1993 than in 1994, further suggesting that gastropods or other dietary sources of calcium were less available to birds in the initial year of this study.

Coefficients of determination for regression of somatic fat on clutch fat were relatively high in Buffleheads ($r^2 = 0.59$) and Goldeneyes ($r^2 = 0.59$) compared to values for other temperate nesting ducks (see review in Ankney and Alisauskas 1991a), suggesting improved fit by using most females' individual lipid commitment to their clutch rather than using average egg fat content to derive an estimate of clutch lipid investment (see methods). Coefficients of determination for regressions of somatic protein and mineral on their respective clutch nutrients were low (Table 4.3) and similar in magnitude to those reported for other species (Ankney and Alisauskas 1991a). These results suggest that using estimates derived from mean protein and mineral content of each species' eggs may be just as precise and much less labor intensive than determining the amount of these nutrients in the clutch of each female. Regardless, the question remains of why is there so much unexplained variation in somatic protein and mineral reserves of Buffleheads and Goldeneyes in years when these nutrients were related to clutch nutrient investment? Alisauskas and Ankney (1994) suggested that much of this variation may be attributed to differences between individuals in these carcass components at the start of laying and variation among individuals in the ability to acquire and metabolize nutrients from their diet. Additionally, much of the variation in nutrient reserves of Buffleheads and Goldeneyes may ultimately be related to differences in food availability between breeding territories (see Högstedt 1980). This hypothesis is supported by variation in somatic minerals of Buffleheads in relation to nesting wetland limnology (Table 4.3), which in turn probably affected the availability of aquatic invertebrates consumed by breeding birds.

4.4.3 *Body size constraints on somatic nutrient use*

Body size influences nutrient reserve use by breeding waterfowl. Larger bodied species can store absolutely greater nutrient reserves for use during clutch formation than smaller bodied species (Alisauskas and Ankney 1992), which, therefore, must rely to a greater extent on dietary nutrients for egg synthesis. Mean carcass mass of nonbreeding female Barrow's Goldeneyes was 2.5 times greater than that of nonbreeding female Buffleheads (Table 4.2). Consequently, Barrow's Goldeneyes used somatic fat at nearly three times the rate of Buffleheads for egg production. Moreover, only Goldeneyes used somatic protein to produce clutch protein. Finally, the diet of breeding Goldeneyes showed considerably less variation during egg production than did the diet of Buffleheads (Chapter 1), providing further evidence that larger body mass in Goldeneyes reduced their dependence on exogenously derived nutrients.

Use of lipid reserves is an apparent function of body mass in waterfowl, with larger species using fat reserves at a greater rate than smaller species (Alisauskas and Ankney 1992). Buffleheads, which are the smallest diving duck in North America, used fat reserves for egg production at the lowest rate of any species that incorporate somatic fat in their clutch (see review in Ankney and Alisauskas 1991a). The need for exogenous nutrient acquisition by Buffleheads becomes increasingly evident when one realizes that modal clutch mass (292.88 g) exceeds carcass mass of nonbreeding females by approximately 20 g (Table 4.2).

Somatic protein use in waterfowl that feed during RFG appears to be more related to diet during the nonbreeding season than body size. Herbivorous ducks, including the American Wigeon (*Anas americana*) (Wishart 1983) and Gadwall (*Anas strepera*)

(Ankney and Alisauskas 1991b), have the highest rates of protein use for egg production. However, protein reserve use is still greatest in larger bodied species, particularly arctic nesting geese (Ankney and MacInnes 1978, Raveling 1979, Bromley and Jarvis 1993), because they have limited foraging opportunities during egg formation. Goldeneyes use body protein to produce egg protein in some breeding seasons, but Buffleheads rely exclusively on dietary protein during reproduction. Body protein catabolism probably occurred in Goldeneyes, but not in Buffleheads in response to reduced invertebrate abundance during early spring in 1993 when most Goldeneyes, but only a few Buffleheads had initiated RFG.

Somatic mineral contribution to eggshell synthesis was slightly higher in Buffleheads than in Goldeneyes, but neither species catabolized large quantities of this reserve indicating that most calcium demand was met by their diets. Thus, Goldeneyes used all three carcass macronutrients during clutch formation in at least one year, whereas Buffleheads only used somatic lipids and mineral. Furthermore, somatic lipid, which was used to a greater extent than either protein or mineral reserves for clutch formation in both species, was catabolized at a much higher rate for egg production in Goldeneyes. This supports my hypothesis that the smaller body size of Buffleheads limits the contribution of endogenous reserves to egg production, making them more dependent than Goldeneyes on exogenous nutrients during reproduction.

Intraspecifically, there was no indication that larger body size resulted in higher clutch size, clutch volume, or greater egg size in Buffleheads. There was, however, a positive trend between body size and clutch size, and a clearly positive relationship between body size and clutch volume in Goldeneyes during one breeding season, suggesting that larger birds invested more nutrients into eggs. This relationship of body size to clutch volume resulted from larger birds laying more eggs rather than larger eggs, because body was not related to egg size in Goldeneyes. The above correlations provide additional support for nutritional limitation of clutch size in Goldeneyes and further suggest that size of nutrient reserves does not affect clutch size in Buffleheads.

4.4.4 *Clutch size limitation in Buffleheads and Goldeneyes*

Lack (1947) initially proposed that clutch size in birds was limited to the maximum number of offspring that parents could successfully nourish. However, after recognizing that many species of birds do not feed their young (e.g. waterfowl), Lack (1967, 1968) revised his earlier hypothesis to state that clutch size in species with self-feeding young was limited by food available to females at the time of laying (hereafter referred to as the "egg production hypothesis"). Bengtson (1971) provided evidence of reduced clutch size in several anatids including Gadwall, European Wigeon (*Anas penelope*), Greater Scaup (*Aythya marila*), Tufted Ducks (*Aythya fuligula*), Oldsquaw (*Clangula hyemalis*), and Black Scoters (*Melinitta nigra*) during a year with reduced food abundance. Annual variation in the number of eggs laid by individual ducks are common, and provide further support that environmental factors, e.g., food availability, rather than genetics, regulate clutch size.

Because waterfowl are capable of storing energy reserves as body tissue, Ryder (1970) extended Lack's (1967) "egg production hypothesis" to incorporate use of energy reserves for egg production. Ankney (1974) expanded Ryder's idea by noting that Arctic nesting geese stored and used specific macronutrients, i.e., lipid, protein, and mineral for egg production. He showed that size of such reserves determined clutch size in Lesser Snow Geese (hereafter referred to as the "nutrient limitation hypothesis"). At least partial reliance on endogenous nutrient reserves for egg production has been reported for all Arctic nesting geese and nearly all species of temperate nesting ducks studied thus far (Alisauskas and Ankney 1992; but see Dobush 1986, Brown and Fredrickson 1987). In species of waterfowl that utilize both dietary and somatic nutrients for clutch formation (i.e., most temperate nesting ducks), there are several hypotheses on regulation of the number of eggs laid. Three primary hypotheses explaining patterns of regulation of clutch size include the "protein limitation hypothesis" (Drobney 1980, Krapu 1981, Drobney and Fredrickson 1985), "lipid limitation hypothesis" (Ankney and Afton 1988), and "migrational-uncertainty hypothesis" (Rohwer 1992).

The "protein limitation hypothesis", initially proposed for Wood Ducks nesting in environments (e.g., southern bottomland hardwood swamps), where foods high in protein are less available than carbohydrate rich foods (Drobney 1980; see also Krapu 1981), hypothesizes that clutch size is directly regulated by lipid reserves (Drobney 1991), but proposes that protein acquisition (i.e., foraging for invertebrates) is a strong determinant of lipid deposition before laying, and the rate of lipid expenditure during laying. Wood Ducks rely primarily on stored body fat, and dietary protein and minerals for egg formation (Drobney 1980). According to Drobney and Fredrickson (1985), female Wood Ducks, and possibly other species of ducks, terminate laying when endogenous lipid depots are exhausted, but protein acquisition influences rate of lipid expenditure during laying, thereby proximately influencing clutch size.

Conversely, the "lipid limitation hypothesis" argues that because protein is far more available than lipid in most habitats used by temperate nesting waterfowl, lipid reserves are more apt to restrict clutch size than is rate of protein intake (Ankney and Afton 1988, Afton and Ankney 1991, Ankney et al. 1991, Ankney and Alisauskas 1991b). Furthermore, proponents of this hypothesis suggest that if protein availability commonly limited egg production, waterfowl would accumulate protein stores to moderate this constraint (Ankney and Afton 1988). However, waterfowl can not store protein in a concentrated labile form (Krapu and Reinecke 1992), but instead must build muscle tissue that is maintained at a higher metabolic cost than endogenous lipid reserves. Drobney and Fredrickson (1985) suggested that benefits of utilizing somatic protein may not offset the nutritional costs of storage, transportation, and maintenance of this tissue. Furthermore, because the true measure of fitness is the number of offspring produced and not the number of eggs laid, even a protein limited species may not use somatic protein during egg synthesis if it interferes with their ability to incubate or rear young (Drobney 1991) or decreases the probability of surviving for subsequent reproductive opportunities.

The "migrational uncertainty hypothesis" deemphasizes the role of endogenous nutrients in reproduction and suggests that female ducks merely incorporate fat reserves not used during spring migration into their clutch (Rohwer 1992). However, because many species of ducks store fat on breeding areas before initiation of RFG (Alisauskas et al. 1990, Barzen and Serie 1990, Ankney and Alisauskas 1991b, this study) this hypothesis has not generally been supported (Ankney et al. 1991).

Elevated mineral requirements for eggshells may also constrain clutch size and laying rate in some species of ducks (hereafter referred to as the "mineral limitation hypothesis"). Breeding waterfowl have their highest daily mineral demand during the annual cycle to meet calcium requirements for egg shell synthesis (Krapu and Reinecke 1992). Birds can store somatic minerals as cortical bone to moderate dietary calcium requirements for egg shell production (Simkiss 1967, Ankney and Scott 1980). Use of somatic mineral somatic mineral, however, does not circumvent mineral limitation of clutch size in Ruddy Ducks (Alisauskas and Ankney 1994) or Barrow's Goldeneyes (this study).

Despite rates of endogenous lipid use during egg production that were predictable based on their body mass (C. D. Ankney, unpubl data), size of lipid reserves apparently did not limit clutch size in either Buffleheads or Barrow's Goldeneyes (Table 4.4). Rather, Buffleheads with smaller clutches actually stopped laying with greater lipid reserves than birds that laid larger clutches. Because smaller clutches were probably laid by younger and/or less experienced birds (see above), retention of greater fat reserves may represent a "cautious" reproductive strategy of inexperienced birds (hereafter called the "cautious reproduction hypothesis"). Such a strategy may be adaptive because waterfowl are generally long-lived species that seldom breed successfully more than once during each breeding season. Furthermore, philopatry of female *Bucephala* to previous breeding sites is high (Erskine 1972, Gauthier 1989, Savard and Eadie 1989), and older females generally have higher reproductive success than do younger females (Dow and Fredga 1983, 1984). Therefore, decisions that increase annual survival may ultimately increase lifetime reproductive fitness in anatids. Furthermore, Buffleheads that survive to breed in subsequent years are more familiar with seasonal trends in food availability and energetic costs of incubation and brood rearing. Consequently, older or more experienced females apparently invest more body lipids into laying additional eggs. Ideally, tests of clutch size limitation should either exclude or separately analyze first time ("cautious") breeders because determining the mechanisms that regulate the number of eggs a female will lay may depend partly on her ability to anticipate future environmental conditions.

An alternative to the "cautious reproduction hypothesis" is that younger or inferior birds occupy suboptimal breeding territories, which negatively affect clutch size through reduced food availability or other factors. Thus, although these females laid fewer eggs than did those breeding in higher quality territories, they may have been laying the largest clutch possible in relation to the quality or food availability on their breeding territories. Högstedt (1980) found that Black-billed Magpies (*Pica pica*) adjusted their clutch size to the most productive number of eggs for each pairs' territory, suggesting a sliding scale of clutch size optimization ultimately regulated by variation in food availability between territories. A similar relationship may explain variation in clutch size of Buffleheads given little overall somatic contribution to their clutch, and hence much heavier dependence on dietary nutrients in their nesting territories.

As would be predicted of carnivorous waterfowl, somatic protein availability did not limit egg production in either Buffleheads or Goldeneyes (Table 4.4). However, Goldeneyes with smaller clutches stopped laying with larger protein reserves than birds with larger clutches. I surmise that this relationship may also be driven by small clutches produced by younger or less experienced birds, that on average, took a cautious approach to nutrient investment in their clutches. When necessary, experienced females may invest additional body protein into laying more eggs, which not only increases their fecundity, but concurrently reduces metabolic requirements of maintaining proteinaceous tissue during incubation when foraging constraints are greater than during any other period in the annual cycle (Afton and Paulus 1992).

Finally, clutch size was negatively related to somatic mineral mass in Buffleheads, but positively related to clutch size in Barrow's Goldeneyes (Table 4.4). As observed with the dynamics of fat reserves, Buffleheads with small clutches terminated laying with more mineral reserves supporting the "cautious reproduction hypothesis" if those birds laying smaller clutches were younger females. Conversely, mineral availability may directly limit clutch size in Barrow's Goldeneyes, which supports Alisauskas and Ankney's (1994) conclusion that calcium availability can be a proximate influence on clutch size in wild anatids. They speculated that clutch size in Ruddy Ducks was constrained by calcium availability because of this species' heavy eggshell mass relative to somatic mineral mass. However, this does not provide an adequate explanation for mineral constraints on clutch size in Goldeneyes, because eggshell mass represented a much lower fraction of body mineral mass (12.4%) than in Ruddy Ducks (33.3%). It is somewhat paradoxical that Goldeneyes do not increase consumption of gastropods during laying (Chapter 1), particularly given that mineral availability ultimately constrains clutch size. However, consumption of freshwater gastropods may reduce survival of female Goldeneyes by increasing internal parasite loads, thus birds that consume fewer snails may ultimately have greater lifetime fitness even though annual reproductive attempts are more limited. Similarly, diets of laying Lesser Scaup contain little gastropod material (5.6% aggregate dry mass; Afton and Hier 1991), which explains why this species must use mineral reserves during clutch formation (Afton and Ankney 1991, Ankney and Alisauskas 1991a).

Milonoff and Paananen (1993) concluded that nutrient availability did not influence clutch size in Common Goldeneyes (*Bucephala clangula*) and dismissed the egg production hypothesis because some precocial birds can renest if their first clutch is abandoned or depredated, and removal of Goldeneye eggs from some clutches laid in nest boxes resulted in additional eggs being laid in these nests. However, second clutches are extremely rare in female *Bucephala* (Zicus 1990), and in species of ducks that commonly renest, second clutches tend to be significantly smaller than initial clutches. Furthermore, renesting females rely almost exclusively on exogenous nutrients for producing eggs (Rohwer 1986, Esler and Grand 1994), thus providing considerable support for the egg production hypothesis. Moreover, Common Goldeneyes exhibit high rates of intraspecific brood parasitism (Eadie et al. 1995), particularly in nest boxes, which Milonoff and Paananen (1993) do not even mention as a possible explanation for large numbers of eggs being deposited in some nests. In their own egg removal experiments, these authors made no attempt to discriminate between parasitically laid eggs and those of the host despite reported morphological similarities (e.g., egg breadth) among eggs laid by the same female (Erskine 1972, Eadie 1989).

Overall, I found little evidence to support my hypothesis that clutch size was affected by the ability of Buffleheads and Goldeneyes to acquire lipids for egg production. From a nutritional perspective, only mineral availability limited clutch size in Barrow' Goldeneyes, whereas little reliance on somatic nutrients suggested that nutrient availability does not influence clutch size in Buffleheads. However, if Buffleheads, perhaps as a consequence of their small body size, have not evolved reliance on endogenous nutrients other than fat during egg laying, it is still possible that environmental availability of mineral or protein may limit clutch size. Evidence that calcium requirements may restrict clutch size in Buffleheads comes from food habits data of females during laying (Chapter 1). Gastropods and their shell fragments constituted 19.6 - 26.2% of the diet of female Buffleheads during laying compared to 0 - 4.2% in nonlaying birds, clearly indicating an increased need for exogenous calcium during eggshell formation. It is possible that Buffleheads could have laid additional eggs had calcium been more available in their nesting territories. This hypothesis could be tested through supplement provisioning of mineral (e.g. oyster shell) in the breeding territories of some females and examination of clutch size in experimental and control groups. If not, factors other than nutrition must operate to determine clutch size in Buffleheads.

Arnold et. al (1987) hypothesized that clutch size in ducks was regulated by temporal constraints imposed by egg viability and nest predation. However, the egg viability hypothesis was based on the false premise that egg viability was a genetically fixed trait within a species (Ankney et al. 1991). Furthermore. for an 8 egg clutch in female Buffleheads or Goldeneyes, the first egg sits unincubated for > 12 days, which is longer than the optimal period predicted by the egg viability hypothesis. Finally, it is doubtful that predation rates are sufficiently high in cavity nesting waterfowl to be a significant selective force shaping the number of eggs a female [illegible] lay. Perrins' (1977) model, which evaluated predation as a selective mechanism on clutch size, suggested that nest predation rates would have to approach 95% to ultimately affect reproductive effort in waterfowl. Nest success generally ranges from 64- 80% in Buffleheads (Erskine 1972, Gauthier 1989) and averages 46% in Barrow' Goldeneyes (Savard 1988a), both well above the predicted predation rates required to ultimately influence clutch size.

Energetic requirements for incubation do not apparently limit clutch size in Buffleheads or Goldeneyes. Brood parasitism is a common reproductive tactic in female *Bucephala* (Erskine 1972, Savard 1988a, Eadie 1989, Eadie et al. 1995), which provides the opportunity to monitor incubation ability of females through natural manipulations in clutch size. Consequently, reports of female *Bucephala* successfully incubating clutches 2 - 3 times the modal clutch size are common (Erskine 1972, Erikson 1979a, 1979b, J. Thompson, pers. observ.). Further evidence that female anatids can successfully incubate larger clutches than they normally lay come from other natural experiments and studies that have experimentally manipulated clutch sizes and found no detrimental effect on nest success, offspring survival, or subsequent reproductive effort of females with enlarged clutches (Hori 1969, Heusmann 1972, Clawson et al. 1979, Rohwer 1985, Lessells 1986, Milonoff and Paananen 1993). Costs of incubation are generally lower in Buffleheads and Barrow' Goldeneyes because they extend incubation periods, maintain higher daily foraging rates than similar-sized ground nesting ducks (J. Thompson, unpubl. data), and have better nest microenvironments.

An alternative to the egg production hypothesis for determination of clutch size in birds is that costs of parental care restricts the number of eggs laid (hereafter referred to as the "parental care hypothesis") (Lack 1968). Unlike most waterfowl, female *Bucephala* defend spatially and temporally stable brood rearing territories (Savard 1988b). Therefore, assumptions that parental care is not costly in these precocial nonfeeders may be premature. Generally, conspecifics, congenerics, and other potential competitors for food are most frequently excluded from brood territories (Savard and Smith 1987, Savard 1988b). Increased territorial aggression or vigilance, which is often manifested through threats, chases, attacks, and occasional killing of competitors' young by female *Bucephala*, detracts from potential foraging time. Thus, even though *Bucephala* females do not feed their young, there is considerable energetic investment in parental care of the young through maintenance of brood territories. The "parental care hypothesis" suggests that there are increased costs to raising additional young, but for species that defend and maintain brood territories and rely to some extent on endogenous reserves during egg production, increased nutrient investment in their clutch may be a tradeoff with reduced investment in defence of brood territories. Therefore, termination of laying with considerable remaining lipid reserves and maintenance of body condition during incubation (J. Thompson, unpubl. data), may represent an energy conserving tactic that allows increased vigilance/territoriality during the brood rearing period. The adaptiveness of this strategy could be measured by monitoring survival of young relative to intensity of aggression among brood rearing females. Effects on lifetime reproductive effort could be measured by survival and subsequent productivity of brood hens relative to their degree of territoriality in previous breeding seasons.

This study and others (Drobney 1980, 1991, Alisauskas and Ankney 1994) suggest that there is little support for a single macronutrient that regulates clutch size in waterfowl. Given highly variable diets, habitat use, behavioral patterns, and morphology of species in this widely distributed order of birds, it is unlikely such a powerful predictive generalization will be found. Even closely related species, such as Buffleheads and Barrow's Goldeneyes, obviously face different constraints on reproductive effort. It does appear, however, that clutch size in many species of temperate nesting waterfowl is limited by availability of one or more of the macronutrients in their clutch generally supporting the nutrient limitation hypothesis (Ankney 1974). Of egg components, fat appears to be the most directly limiting nutrient to most species (see review in Alisauskas and Ankney 1992). Other studies suggest that protein may directly (Ankney and Alisauskas 1991b, Mann and Sedinger 1993) or indirectly limit clutch size in primarily herbivorous waterfowl by influencing the rate of lipid reserve use (Drobney 1980, Drobney and Fredrickson 1985, Krapu 1981). More recent studies on nutrient reserve dynamics of Ruddy Ducks (Alisauskas and Ankney 1994) and Barrow's Goldeneyes (this study) indicate that mineral requirements can constrain clutch size in temperate nesting ducks.

4.4.5 *Conclusions and research recommendations*

Clutch size in Barrow's Goldeneyes was restricted by calcium availability during laying, providing support for the "nutrient limitation hypothesis", but evidence linking clutch size of Buffleheads to nutrient availability was more equivocal. Small body size apparently constrains somatic nutrient use by Buffleheads for clutch formation. It is possible that small species of waterfowl have not evolved the capacity to store and use larger quantities of somatic nutrients because their absolutely lower requirements can generally be met by dietary intake. However, variation in habitat quality and density of breeding birds may have negatively affected food availability in wetlands used by breeding birds in this study. Thus, until environmental availability of mineral, and possibly protein, is measured or manipulated (see above), it is impossible to reject the egg production hypothesis as an explanation for clutch size in Buffleheads

Possibly, at least for some species of waterfowl, we have been investigating nutrient limitation of clutch size on the wrong scale. Most current studies investigating nutritional constraints on clutch size in waterfowl have done so by looking for limitation at the macronutrient (e.g. lipid, protein, and mineral) level. It is possible, however, that rate and extent of egg production is limited by acquisition of a specific micronutrient (e.g. fatty acid, amino acid). In carnivorous waterfowl (e.g. Mergini), acquisition of specific fatty acids may impose a greater constraint on egg and clutch size than do specific amino acid requirements. A dietary deficiency of linoleic acid, an essential fatty acid, can restrict egg and clutch size in some species of birds (Griminger 1986). Additionally, availability or synthesis rates of arachidonic and linolenic acids can curtail rates of egg production in domestic fowl (Griminger 1986). At least some deficiencies in specific fatty acids can be circumvented by differential storage and selective catabolism by birds when daily requirements for these micronutrients are high (e.g., migration, egg production) (Heitmeyer and Fredrickson 1990, Thomas and George 1975). However, there are few data on how availability of specific fatty acids or amino acids influence the rate of laying or clutch size in wild birds.

Most research has underestimated reproductive costs in waterfowl, particularly for highly territorial species, because costs of behavioral activities associated with reproduction were not measured. Some of the decline in somatic nutrients (particularly lipid) could probably be explained by interspecific differences in activity costs during breeding. Furthermore, energetically demanding behaviors, such as aggression and foraging, are the most likely activities to increase with greater densities of breeding birds, particularly in territorial species such as Buffleheads and Goldeneyes.

Influence of breeding pair density on clutch size in waterfowl is largely unknown. Clutch size in many species of Arctic nesting geese is apparently not affected by density of breeding pairs because RFG starts before arrival on breeding grounds (Raveling 1978) and many of these species rely exclusively on somatic nutrients rather than exogenous nutrients to produce eggs (Ankney and MacInnes 1978, Raveling 1979, Bromley and Jarvis 1993). High productivity of prairie wetlands probably buffers clutch size variation resulting from increasing densities of breeding ducks to a great extent, at least within current population sizes. Furthermore, Hilden (1964) reported no density dependent influence on clutch size in Tufted Ducks and Greater Scaup nesting in mesotrophic wetlands of northern Europe. However, these species and most other waterfowl do not actively defend temporally and spatially fixed breeding territories, which would mediate much of the intra- and interspecific behavioral interactions that can negatively affect clutch size in other birds.

Clutch size stability in response to increased population density in nonterritorial birds contrasts sharply with an apparent strong influence on egg production in birds that actively defend breeding territories (e.g. most passerines). Clutch size declines with increasing population density in the Great Tit (*Parus major*) (Kluyver 1951), Blue Tit (*Parus caeruleus*) (Lack 1955), and Coal Tit (*Parus ater*) (Lack 1966). It is not clear how increasing pair density influences clutch size in birds (Klomp 1970), but it probably relates to increased competition for food or breeding territories with consequent declines in territory size and perhaps food availability, especially during the brood rearing period. Unlike most northern temperate nesting ducks, species in the genus *Bucephala* maintain spatially and temporally stable nesting territories during the breeding and brood rearing periods (Gauthier and Smith 1987, Gauthier 1987b, 1988, Savard and Smith 1987, Savard 1984, 1988b). Establishment of breeding territories by Buffleheads and Goldeneyes requires considerable energy investment for territorial defense from conspecifics, congeners, and apparently other birds with similar diets (Savard and Smith 1987). Intra- and interspecific territoriality may have evolved in the *Bucephala* to defend food in less productive habitats than those used by most other anatids and to provide undisturbed foraging opportunities for nesting females (Savard 1984, 1988b). Regardless, energy expended during territorial aggression by breeding Buffleheads and Goldeneyes may reduce foraging time and divert somatic nutrients (specifically lipid) that could have been incorporated into reproductive tissue. Allocation of energy to activity, rather than reproduction, may place additional constraints on clutch size in species that feed primarily on invertebrates by further reducing foraging time for exogenous lipid intake. Thus, density, or better yet territory size of breeding *Bucephala*, may be a significant and yet unmeasured factor affecting nutrient reserve use, foraging time, and clutch size in Buffleheads and Goldeneyes.

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Appendix 1. Use of Barrow's Goldeneye nest boxes in central British Columbia from 1993 - 1995.[a]

Species	Year			Total
	1993	1994	1995	
Barrow's Goldeneyes (*Bucephala islandica*)	62	114	95	271
Bufflehead (*Bucephala albeola*)	1	4	2	7
American Kestrel (*Falco sparverius*)	11	13	15	39
Northern Saw-whet Owl (*Aegolius acadicus*)	0	1	0	1
Northern Flicker (*Colaptes auratus*)	1	0	0	1
Tree Swallow (*Tachycineta bicolor*)	7	15	3	25
European Starling (*Sturnus vulgaris*)	19	21	5	45
Mountain Bluebird (*Sialia currucoides*)	5	10	6	21
Red Squirrel (*Tamiasciurus hudsonicus*)	1	5	0	6
Northern Flying Squirrel (*Glaucomys sabrinus*)	1	0	0	1
Unused boxes	130	74	96	301
Number of available boxes	222	221	216	659

[a] Total number of nests (all species combined) and the number of unused boxes will not be equivalent to the number of available boxes because several species or more than one individual from the same species often used the same nest box consecutively in a given year.

Appendix 2. Use of Bufflehead nest boxes in central British Columbia from 1993 - 1995.[a]

Species	Year 1993	1994	1995	Total
Bufflehead (*Bucephala albeola*)	10	21	10	41
American Kestrel (*Falco sparverius*)	4	10	8	22
Northern Flicker (*Colaptes auratus*)	0	2	3	5
Tree Swallow (*Tachycineta bicolor*)	8	9	9	26
European Starling (*Sturnus vulgaris*)	37	59	32	128
Mountain Bluebird (*Sialia currucoides*)	7	8	7	22
Red Squirrel (*Tamiasciurus hudsonicus*)	4	0	0	4
Unused boxes	40	25	39	104
Number of available boxes	98	95	94	287

[a] Total number of nests (all species combined) and the number of unused boxes will not be equivalent to the number of available boxes because several species or more than one individual from the same species often used the same nest box consecutively in a given year.

Appendix 3. Morphology of female Buffleheads and Barrow's Goldeneyes nesting in central British Columbia.[a]

	Bufflehead			Barrow's Goldeneye		
Variable	*N*[b]	Mean ± SE[c]	CV[d]	*N*	Mean ± SE	CV
Total body length	98	326.59 ± 0.80	2.42	97	433.76 ± 0.82	1.87
Skull length	98	67.51 ± 0.14	2.00	96	85.30 ± 0.13	1.55
Skull width	98	23.05 ± 0.05	2.00	97	28.68 ± 0.08	2.61
Central culmen	98	25.96 ± 0.10	3.96	97	31.60 ± 0.11	3.43
Diagonal culmen	98	30.55 ± 0.11	3.53	97	39.47 ± 0.13	3.03
Bill width	98	14.70 ± 0.04	2.70	97	18.70 ± 0.05	2.60
Bill height	98	14.20 ± 0.12	8.29	97	19.73 ± 0.20	9.91
Tarsus	98	30.04 ± 0.08	2.73	97	37.76 ± 0.09	2.45
Mid-toe length	98	49.44 ± 0.15	2.91	97	59.97 ± 0.17	2.74
Wing chord	98	157.78 ± 0.39	2.42	97	219.70 ± 0.38	1.72
Wing length	98	239.55 ± 0.80	3.30	96	327.94 ± 0.81	2.41
Plucked wing length	98	138.48 ± 0.13	0.91	96	193.44 ± 0.48	2.43

Appendix 3. (continued)

Variable	Bufflehead			Barrow's Goldeneye		
	N[b]	Mean ± SE[c]	CV[d]	*N*	Mean ± SE	CV
Keel length	98	63.15 ± 0.21	3.29	97	90.00 ± 0.21	2.34

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[a] All measurements are in mm.

[b] Sample size.

[c] Mean ± standard error.

[d] Coefficient of variation.

Appendix 4. Egg morphology of Buffleheads and Barrow's Goldeneyes nesting in central British Columbia.

Variable	Bufflehead			Barrow's Goldeneye		
	N[a]	Mean ± SE[b]	CV[c]	*N*	Mean ± SE	CV
Egg length (mm)	275	50.62 ± 0.11	3.76	463	61.68 ± 0.09	3.27
Egg width (mm)	275	36.18 ± 0.06	2.72	463	43.63 ± 0.05	2.27

[a] Sample size.
[b] Mean ± standard error.
[c] Coefficient of variation.