BREEDING HABITAT SELECTION BY BARROW'S GOLDENEYE AND BUFFLEHEAD IN THE CARIBOO-CHILCOTIN REGION OF BRITISH COLUMBIA: NEST SITES, BROOD-REARING HABITAT, AND COMPETITION

by

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Abstract

Barrow's Goldeneye and Bufflehead are secondary cavity-nesters that rely heavily on nest sites created by primary cavity excavators. For these species, reproduction and recruitment of offspring may be highly dependent on at least these three factors: 1) the availability of nest cavities for females to lay eggs, 2) the quality and availability of brood-rearing habitat and its effect on the growth and survival of ducklings, and 3) the influence of intra- and interspecific competition on settlement patterns and breeding success. I examined these three factors, and provided recommendations aimed at sustaining Barrow's Goldeneye and Bufflehead populations in areas of intensive land management.

Barrow's Goldeneye used primarily abandoned Pileated Woodpecker cavities located in aspen trees with a diameter at breast height greater than 35 cm. Active nest sites were typically higher above ground, had relatively larger entrance diameters and floor areas, and the bottom of the canopy was higher than unused cavities. Bufflehead used abandoned Northern Flicker cavities in aspen trees with diameters larger than 25 cm. Bufflehead cavities had larger entrance diameters than unused cavities, and smaller floor areas. More than 90% of all cavities used by both species were located within 200 m of a body of water. The nesting ecology of Bufflehead was similar in natural cavities and nest boxes, but Barrow's Goldeneye had greater nest success in natural cavities than in boxes.

Wetland selection by Barrow's Goldeneye and Bufflehead was influenced by a complex of factors including the lake's physical characteristics, water chemistry, food supply, and to a lesser degree, aquatic vegetation. I found positive correlations between invertebrate abundance within a wetland and Barrow's Goldeneye duckling masses at day 40, prefledging survival, and first year return rates, but not recruitment as breeders.

Experimental removal of goldeneye nest sites did not result in a decrease in the number of goldeneye breeding pairs in the treatment area, suggesting habitat saturation prevented dispersal to new sites. The number of goldeneye broods declined, but this did not result in increased brood survival for other species. These results suggest that either, 1) goldeneye do not have a direct effect on other species' brood survival rates, or 2) the ecological interactions between these species are complex and changes in response variables, such as reproductive success of subordinate species, may not be detected in such a short term study, or 3) there are other costs of coexistence that were not measured in this study.

Forest management should protect primary cavity-nesting species, by leaving mature and old aspen. Conserving aspen stands close to rich brood-rearing wetlands, will help maintain nest sites for cavity-nesting waterfowl in central British Columbia, and aid in the production and survival of their young.

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Chapter 1

INTRODUCTION

1.1 INTRODUCTION

Determining the external (environmental) and intrinsic (demographic) factors that limit the growth of bird populations is a central issue in the field of avian ecology and conservation. Several ecological factors essentially set upper limits to bird populations, including 1) habitat availability, 2) food abundance, 3) climate, 4) disease, and 5) the density of competitors and predators. All of these factors can have an immediate influence on the survival and reproductive success of individual birds and, therefore, population numbers (Gauthier 1988, Gill 1990). Of particular importance is the availability of breeding habitats; areas in which birds occupy, either continuously or periodically, during the reproductive period and contain resources necessary for individual reproductive success and survival (Kaminski and Weller 1992).

Nest site and brood-rearing habitat quality are two major factors influencing the selection of breeding habitat by waterfowl. Both have fitness consequences through their direct influence on adult survival and production of offspring. Nest sites are a particularly essential resource for cavity-nesting waterfowl because previous studies have suggested that natural cavity availability limits population growth for several species (van Balen et al. 1982, Savard 1988, Newton 1994). Wetland selection by breeding pairs and females with broods also influences reproductive success and recruitment through the availability of food, cover from predators, and other essential resources.

In general, an evolutionary 'ideal' individual should maximize reproductive success by assessing interrelated cost and benefit trade-offs among available habitat choices (Morris 1987). If female waterfowl are able to sample and assess the quality of required breeding resources then they should select sites that offer the highest probability of reproductive success during the nesting and post-hatching periods, while at the same time maximizing their own survival probability. Examining individual preference for habitats that influence reproduction and survival allows us to identify important habitat characteristics, and use this information when formulating management guidelines aimed at supporting waterfowl populations.

Habitat selection is a hierarchical process involving decisions being made at several spatial scales by a prospecting individual (Owen 1972, Wiens 1973, Johnson 1980, Martin and Eadie 1999). For breeding waterfowl, habitat selection can occur at the landscape, wetland, and nest site (or foraging site) scales (Johnson 1980). A bird may first select a general area in which to breed, then within this area select among the available patches, and then within this, a nest site (or other habitat component; Pribil and Picman 1997). For a full understanding of habitat selection, it is essential to consider more than one spatial scale.

Traditionally, habitat selection has been inferred from 1) correlations between reproductive success and various habitat characteristics, or 2) comparing characteristics between habitats used and habitats available but not used (Pribil and Picman 1997). For this latter method, the most common measure of habitat use for a species is simply occurrence, but other studies have used density as a measure of the intensity of habitat use (Jones 2001).

1.2 Thesis Focus

This thesis will focus on the role of nest site selection, brood-rearing habitat selection, and competition, on the demographics of Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*). For these species, reproduction and the subsequent survival and recruitment of offspring may be highly dependent on at least these three factors: 1) the availability of nest cavities for females to lay eggs; 2) the quality and availability of brood-rearing habitat and its effect on the growth and survival of ducklings; and 3) the influence of intra- and interspecific competition on settlement patterns and breeding success. In this thesis, I examine all three of these factors, and provide recommendations aimed at sustaining Barrow's Goldeneye and Bufflehead populations in areas of intensive land management.

1.3 Nest Site Habitat Selection – Chapters 2 and 3

Riparian areas have been widely recognized as important areas of biodiversity (e.g. Doyle 1990, Eckert et al. 1991, Stocek 1994) offering unique ecological assemblages that are characterized by the interface between terrestrial and aquatic habitats. These areas support disproportionately more species than most other habitat types (Thomas et al. 1979, Morgan and Wetmore 1986, Bunnell and Dupuis 1993, Morgan 1993, Stocek 1994). The wetlands and associated riparian areas of the Cariboo-Chilcotin area of central British Columbia are rich breeding grounds for several species of waterfowl (McKelvey et al. 1989) and have previously received considerable attention (Erskine 1972, Gauthier 1985, Savard 1986, Boyd and Savard 1987, Boyd et al. 1989, Eadie 1989, Savard 1991, Thompson 1996).

Of special interest in this region, illustrating a key link between forests and wetlands, are the riparian habitat requirements of cavity nesting waterfowl, such as Barrow's Goldeneye and Bufflehead. These species thrive in the Cariboo-Chilcotin area, and it has been reported that 60% of the world's population of Barrow's Goldeneye breed in B.C. (McKelvey et al. 1989). Uncertainty in local Barrow's Goldeneye and Bufflehead population stability illustrates a need to examine habitat requirements and factors affecting the populations in this area.

1.3.1 Cavity Nesters and Riparian Habitat

For most birds, the quality of the nest site directly affects reproductive success (Dow and Fredga 1985, Gauthier 1988). Barrow's Goldeneye and Bufflehead are secondary cavity-nesters (SCN) that rely heavily on cavities created by primary cavity excavators (PCE) such as Pileated Woodpeckers (*Dryocopus pileatus*) and Northern Flickers (*Colaptes auratus*), respectively (Bellrose 1976, Kaminski and Weller 1992, Bonar 2000). All of these birds are part of a community heavily dependent on trees for survival and/or reproduction and are therefore potentially sensitive to forest removal. Habitat alteration, such as logging, could have important demographic consequences on these species. By determining the nest site requirements of these species, and incorporating them into forest management guidelines, it should be possible to minimize the impact of forest harvesting on nest sites.

Several previous studies have described the biology and habitat requirements of many PCE and SCN species throughout North America, and the effects of forestry management on these birds (see Thomas 1979, Fischer and McClelland 1983 for bibliographies). These studies have shown an overwhelming preference for deciduous trees such as trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Harestad and Keisker (1989) found all of their 243 PCE nests in deciduous trees, of which 88% were in trembling aspen. Coniferous trees such as Douglas-fir (*Pseudotsuga menziesii*) and spruce (*Picea engelmannii* and *P. glauca*) appear to be rarely used by PCE species. Overall, PCEs appear to have predictable preferences that may aid in locating and protecting nest sites for SCNs like Barrow's Goldeneye and Bufflehead.

1.3.2 Secondary Cavity Nesting Waterfowl

Studies quantifying the characteristics of nest trees selected by Barrow's Goldeneye and Bufflehead are scarce. Considering their dependence on PCE species, one might expect similar habitat requirements. Indeed, the few studies that exist have shown that *Bucephala* nest mainly in deciduous trees (Prince 1968, Erskine 1972, Peterson and Gauthier 1985). However, dead conifers also offer natural cavity sites originating from weathered holes created by fallen tree limbs and hollowed out areas in the tops of broken trees (Prince 1968, Kaminski and Weller 1992, Thompson 1996). SCN waterfowl may have no preference for particular species of trees, they may instead simply rely on the availability of cavities near wetlands.

Numerous studies have quantified the characteristics of Wood Duck (*Aix sponsa*) cavities and nest trees (see Table 17-3 in Kaminski and Weller 1992). Several authors cite forest and canopy openness as a major proximate factor that attracts nesting Wood Ducks (Prince 1968, Gilmer et al. 1978, Robb 1986). Additionally, Robb (1986) reported that Wood Duck nest success tended to increase with increasing distance from water, which he suggested was related to a reduction in the density of predators, especially raccoons (*Procyon lotor*).

1.3.3 Nest Site Limitations to SCN Species and Nest Box Programs

For cavity-nesting birds, the availability of suitable nest sites likely limits abundance (Jones and Leopold 1967, Thomas et al. 1979, Dennis and Dow 1984, Newton 1994). Nest box programs often increase populations, particularly in areas of intensive forest management (McComb and Noble 1981, Brush 1983, Savard 1986). Barrow's Goldeneye, Common Goldeneye (*B. clangula*), and Wood Duck populations increased with the addition of nest boxes (Siren 1951, Johnson 1967, Eriksson 1982, Savard 1986), although Bufflehead did not (Gauthier and Smith 1987). For Bufflehead, it was concluded that territorial behaviour may instead be limiting their breeding populations (Gauthier and Smith 1987).

1.3.4 Primary Objectives of Chapters 2 and 3

In Chapter 2, I describe the physical characteristics of natural cavity nest sites suitable for Barrow's Goldeneye and Bufflehead, at four scales (forest stand, forest patch, nest tree, and nest site) and quantify factors influencing the use of cavities. I also estimate the density and availability of Barrow's Goldeneye and Bufflehead natural cavities within the study site. I assess nest site selection with three commonly used techniques: 1) by inferring habitat selection when habitats are used disproportionately to their estimated availability, 2) by comparing areas used to those unused (Pribil and Picman 1997), and 3) by examining correlations between habitat characteristics and reproductive success.

Nest site selection should optimize tradeoffs among several factors: 1) accessibility, 2) protection from weather, predators, and competitors, and 3) proximity to suitable breeding pair and brood-rearing habitat. If Barrow's Goldeneye are limited by the availability of suitable nest cavities, and Bufflehead are not, then I expect to find active goldeneye nest sites at greater distances from water, and further into forested areas. I also hypothesize that there is a cost for nesting far from water, in terms of duckling mortality during overland movements. Hence, birds nesting closer to water should have higher reproductive success. An alternative prediction is that there is an edge effect cost to nesting close to water, in terms of increased predation and nest parasitism.

Much of what is known about cavity nesting waterfowl is based primarily on nest box studies (e.g., Froke 1983, Dow and Fredga 1985, Gauthier 1985, Savard 1986, 1988, Eadie 1989, Zicus 1990, Thompson 1996), but this information may not represent natural cavities (Moller 1989, 1992, Robertson and Rendell 1990, Purcell et al. 1997). Therefore, a more detailed analysis of *Bucephala* members nesting in natural cavities is necessary. In Chapter 3, I compare reproductive parameters (e.g., nest initiation dates, clutch size, nesting success rates) for birds nesting in natural cavities versus those in artificial nest boxes.

1.4. Brood-rearing Habitat Selection – Chapters 4 and 5

The breeding grounds of *Bucephala* members have previously been described as Nearctic areas abundant with boreal and temperate shallow (< 3 m deep) wetlands, rich in aquatic invertebrate prey with nearby nesting cavities (Kaminski and Weller 1992). It has been hypothesized that reproduction in birds is timed so that the breeding cycle coincides with maximum availability of food for nesting adults or developing young (Immelmann 1971). Recruitment among waterfowl may be particularly sensitive to the quantity and quality of food resources available, both in terms of the energy and nutritional requirements of egg-laying females as well as the growth and developmental requirements of ducklings. Prey abundance directly affects protein acquisition and influences reproductive parameters such as 1) timing of reproduction, 2) propensity to breed, 3) clutch size, 4) egg mass and composition, 5) egg fertility and hatchability, 6) offspring size, and 7) overall reproductive success of the birds (Drobney 1982, Sedinger 1992). Therefore, nutrition during the duckling growth period influences future survival and reproduction by its effect on body size and nutrient reserves.

1.4.1. Primary Objectives of Chapters 4 and 5

In Chapter 4, I assess the role of biotic and abiotic characteristics in lake selection by breeding Barrow's Goldeneye and Bufflehead in central British Columbia. The continued loss of waterfowl breeding habitat in North America has given rise to increased efforts to conserve wetland areas by preserving threatened lakes, and restoring damaged ones. To achieve these objectives, habitat characteristics that influence lake selection by breeding waterfowl need to be identified. Understanding the relationships between aquatic habitat characteristics, lake selection, and reproductive success is important for successful conservation and management of waterfowl populations.

In Chapter 5, I examine relationships between food density and the following reproductive parameters of Barrow's Goldeneye: egg sizes, clutch sizes, hatching dates, duckling growth rates, prefledging survival, and recruitment. Although it is commonly reported that prey abundance influences juvenile growth and survival, few studies have actually examined this relationship due to the difficulty in 1) associating nutrition and survival, and 2) estimating survival and future fecundity. I examine this relationship by relating food abundance in brood-rearing habitats to duckling growth, survival, and recruitment.

If duckling growth rates are significantly limited by food availability, then I hypothesize that broods occupying low quality foraging sites will have lower survival and recruitment rates compared to those raised on high quality sites. I also hypothesize that ducklings on low quality sites will spend more time feeding and less time resting or being vigilant.

1.5. Interspecific Competition – Chapter 6

Members of the genus *Bucephala* exhibit intensive intraspecific and interspecific aggression, maintaining well defended territories from which they exclude other individuals (Savard and Smith 1987, Gauthier 1985). A high degree of diet overlap exists between these birds (Eadie et al. 1995) and, therefore, food, and/or mates, are considered the most likely defended resources (Savard and Smith 1987, Gauthier 1985). However, we still lack a clear understanding of the effects interspecific interactions have on Barrow's Goldeneye and Bufflehead populations.

In Chapter 6, I attempt to reduce Barrow's Goldeneye abundance to examine whether co-existence results in negative fitness consequences for Bufflehead in terms of suppressed reproductive output (number of broods seen), and decreased reproductive success (duckling survival rates). I predict that there are fitness costs of coexistence incurred by the subordinate Bufflehead. If Barrow's Goldeneye competitively exclude Bufflehead, then Bufflehead abundance should be negatively correlated with goldeneye density, and goldeneye should occupy higher quality foraging sites. If this hypothesis is true, then the experimental removal of goldeneye nest sites will cause goldeneye breeding pairs to leave the treatment area, and will result in replacement by Bufflehead. As a result, I predict that the number of Bufflehead breeding pairs, broods, and duckling survival rates, will increase. Furthermore, I hypothesized that Barrow's Goldeneye influence the abundance of other local waterfowl species, and thus, local community diversity. If this hypothesis is true, then I expect to see higher species diversity on ponds of similar habitat characteristics that do not contain goldeneye. This study may enable us to predict the effects of artificially increasing or decreasing goldeneye abundance through nest box programs on the waterfowl community, including Bufflehead.

Finally, in Chapter 7, I summarize my findings and management recommendations discussed throughout this thesis, aimed at conserving the breeding habitat of these birds, other cavity nesting birds, and waterfowl in general.

1.6. Study Area

I conducted this study from May to August, 1997-2001, on approximately 600 km^2 in the Cariboo Parklands near Riske Creek, located in central British Columbia (51° 52' N, 122° 21' W). The area is characterized by a rich mixture of naturally fragmented deciduous and coniferous forest amongst grasslands and prairie pothole wetlands. Deciduous species include trembling aspen, balsam poplar and black cottonwood (*Populus balsamifera spp.*), interspersed within coniferous Douglas fir, hybrid spruce (*Picea glauca* x *engelmannii*) and lodgepole pine (*Pinus contorta*). The study site consists of mature forest (both continuous and naturally fragmented) not previously cut (Martin and Eadie 1999).

The 130+ waterbodies located in this study site vary greatly in size (e.g., range = 0.1 to 54.0 ha, n = 117) and chemical properties. Detailed descriptions of the physical, chemical, and biological characteristics of the Riske Creek wetlands (for 1984 and 1985) are in Boyd and Savard (1987) and Boyd and Smith (1989). In general, the wetlands are relatively shallow and small, with various amounts of submergent, emergent, and shoreline vegetation. The wetlands have been characterized as being chemically heterogeneous (Topping and Scudder 1977, Boyd and Savard 1987) with salts accumulating to various degrees between neighbouring lakes. Previous studies reported that salinity ranged from 0 (fresh) to 10.1 (mesosaline), pH from 7.1 (neutral) to 10.1 (alkaline), alkalinity from 108 to 6230 ppm $CaCO_3$, and conductivity from 42 to 17050 μhos/cm (Topping and Scudder 1977, Boyd and Savard 1987). Almost all lakes are devoid of fish (Boyd and Smith 1989).

Common emergent vegetation includes bulrush (*Scirpus acutus*), cattail (*Typha latifolia*), and foxtail barley (*Hordeum jubatum*). Precipitation averages 35 cm annually and mean daily temperatures range from 21.9 °C in July (Environment Canada 2002) to -11.6 °C in January (Savard 1986).

Both the Barrow's Goldeneye and Bufflehead populations have been well studied in the Cariboo-Chilcotin region (e.g., Erskine 1972, Gauthier 1985, Savard 1986, Eadie 1989, Thompson 1996). Approximately 200 goldeneye and 100 Bufflehead nest boxes were present in my study site from previous research programs (Savard 1986, Thompson 1996).

1.7. Terminology Used Throughout the Thesis

Authors of habitat selection studies have been inconsistent in their use of habitat-related terminology, and there is a need for standardized operational definitions (Hall et al. 1997, Jones 2001). Throughout this thesis, I use the following definitions put forth by Johnson (1980) and Jones (2001): *Habitat* is the distinctive bio-physical environment that animals use for survival and reproduction (Jones 2001); *abundance* refers to the actual quantity of a resource that is in the environment (Johnson 1980); *availability* refers to the quantity of that habitat that is accessible to the animal, and may have a density-dependent function; *used* habitat is defined as habitat that is occupied by the species being studied and *unused* habitat is unoccupied; *habitat selection* refers to the hierarchical process of decision making that results in the disproportionate use of habitats, and influences the survival and fitness of individuals. While selection is the process in which an animal chooses a habitat, *preference* is the likelihood that a habitat will be selected if offered on an equal basis with others. The *usage* of a resource is the quantity of that resource that is utilized by a consumer, and therefore, usage is said to be *selective* when factors are used disproportionately to their availability.

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Chapter 2

SELECTION OF NATURAL CAVITIES AS NEST SITES BY BARROW'S GOLDENEYE AND BUFFLEHEAD

2.1. Abstract: Barrow's Goldeneye and Bufflehead are secondary cavity-nesting waterfowl that rely primarily on cavities excavated by Pileated Woodpeckers and Northern Flickers, respectively. Relatively little research has been conducted on the availability and use of natural cavities by these birds. The purpose of this chapter is to describe the physical characteristics of natural cavity nest sites used by Barrow's Goldeneye and Bufflehead, at four spatial scales (forest stand, forest patch, nest tree, and nest site) and to identify factors influencing the use of cavities. I found 3.4 goldeneye cavities per hectare in aspen forests, and 0.2 cavities/ha in coniferous forest stands. Bufflehead cavity density was 6.7 cavities/ha in aspen forests, and 1.6 cavities/ha in coniferous forests. Cavities used by Barrow's Goldeneye were higher above ground, had relatively larger entrance diameters and floor areas, were predominately in aspen trees with a diameter at breast height (DBH) greater than 35 cm, and the bottom of the canopy was higher. Bufflehead used cavities with larger entrance diameters, smaller floor areas, and were in aspen trees with a DBH greater than 25 cm, compared to unused cavities. For both species, there were no differences in distances to the nearest body of water for used and unused cavities. Because cavity-nesters depend on trees for reproduction, they are potentially sensitive to forest removal. Habitat alteration, such as logging, could have important population consequences on these, and other cavity-nesting species. Knowledge of the biophysical characteristics of these nest sites, and preferences exhibited by nesting females, should help managers avoid suitable nest trees during forest harvesting.

2.2. INTRODUCTION

Determining the environmental factors that limit species' abundance is a central problem in the field of avian ecology and conservation. Five ecological factors essentially set upper limits to bird populations: habitat availability, food supply, predation, disease, and climate. All of these can influence the reproductive success and survival of individual birds and, therefore, population size (Gauthier 1985, Gill 1990).

Of particular importance is the availability of breeding habitats, areas which contain resources necessary for reproductive success and survival (Kaminski and Weller 1992). Nest site availability is one such resource, particularly for cavity nesting birds. Previous studies have shown that natural cavity availability can limit population growth of several species (van Balen et al. 1982, Savard 1988, Newton 1994). Cavity nesting is advantageous to a brooding female and her clutch by offering protection from predators and adverse weather conditions (von Haartman 1957, Zeleny 1977). Potential influences on cavity abundance include the rate of excavation by primary cavity excavators (PCEs), forest harvesting, and natural cavity loss from tree blow-down (Aitken et al. 2002). As well, cavity availability is affected by intra- and interspecific competition for nest sites, and behavioral limitations of species to locate existing cavities.

Barrow's Goldeneye and Bufflehead are secondary cavity-nesting (SCN) waterfowl that rely heavily on cavities created by Pileated Woodpeckers and Northern Flickers, respectively (Kaminski and Weller 1992). Relatively little research has been conducted on the availability and use of natural cavities by goldeneye (both Barrow's and Common) and Bufflehead. For goldeneye, previous nest box programs have resulted in population increases, suggesting that nest sites are limiting (Siren 1951, Johnson 1967, Savard 1988). Bufflehead nest box provision has failed to change population numbers, and authors have reported an excess of empty boxes (Gauthier and Smith 1987). Due to the unusually large cavity size required by goldeneyes, it is believed that they are more limited than other SCNs (Savard 1986, Eadie 1989).

Considering their direct dependence on abandoned cavities, one might expect goldeneye and Bufflehead to occupy nesting habitat that is similar to those of PCEs, albeit in areas proximal to suitable wetlands. From the perspective of cavity-nesting waterfowl, important nest site characteristics such as distance to the nearest pond, and distance from forest edge, may be constrained not only by cavity abundance, but also by the selection process made by the primary excavators. Therefore, behavioral trade-offs likely exist for cavity nesting waterfowl searching for a suitable nest site while remaining close to productive wetlands for foraging and brood rearing.

Although few studies exist, *Bucephala* cavities have thus far been reported to occur mainly in deciduous trees (Prince 1968, Erskine 1972, Peterson and Gauthier 1985). Several studies that have described the biology and habitat requirements of PCE species throughout North America have reported a widespread preference for deciduous trees, particularly trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*; see Thomas 1979, Fischer and McClelland 1983 for bibliographies). In one study, all 243 PCE nests found were in deciduous trees with 88% in trembling aspen (Harestad and Keisker 1989). Coniferous trees such as Douglas-fir (*Pseudotsuga menziesii*) and spruce (*Picea engelmannii* and *P. glauca*) are rarely used by PCEs when aspen and birch are available (McClelland and Frissell 1975, Madsen 1985). It has even been reported that Pileated Woodpeckers avoid Douglas-fir for nesting (Bull and Meslow 1977). Regardless, dead conifers can offer natural cavities to secondary cavity nesters, originating from weathered holes created by fallen tree limbs and hollowed out areas in the tops of broken trees (Prince 1968, Kaminski and Weller 1992, Thompson 1996). The degree to which these unexcavated holes are used by tree nesting waterfowl is likely influenced by their availability and proximity to water.

Along with tree species, the presence of heartwood decay (indicated by fungal conks such as *Fomes igniarius* and *F. fomentarius*) is often cited as an important characteristic influencing selection of nest trees by PCE species (Conner et al. 1976, Keisker 1986, Martin and Eadie 1999, Bunnell et. al 2002). Minimum DBH of trees that can feasibly house a PCE cavity is also consistently reported as an important factor (Bull and Meslow 1977, Keisker 1986, Martin and Eadie 1999). Overall, PCEs appear to have predictable preferences that may aid in locating and protecting nest sites for secondary cavity nesters like Barrow's Goldeneye and Bufflehead.

Because cavity-nesters depend on trees for reproduction, they are potentially sensitive to forest removal. Habitat alteration, such as logging, could have important population consequences on these, and other cavity-nesting species. To prevent this from happening, the habitat requirements of these birds must be determined and incorporated into forest management guidelines. Knowledge of the biophysical characteristics of these nest sites, and any preferences exhibited by nesting females, should help managers avoid potential nest trees during forest harvesting. To obtain a full understanding of nest site selection, it is essential to consider more than one spatial scale, because nest site selection is best viewed as a hierarchical process from a macro- to micro-habitat scale (Johnson 1980). For example, a bird may select a general geographic area in which to breed, then within this area, select among the available patches, and then within a patch, select a nest site (Johnson 1980, Pribil and Picman 1997).

The purpose of this study is to describe the physical characteristics of natural cavity nest sites suitable for Barrow's Goldeneye and Bufflehead, at four spatial scales (forest stand, forest patch, nest tree, and nest site) and to quantify factors influencing the use of cavities. I also estimate the density of Barrow's Goldeneye and Bufflehead natural cavities within the study site. I assessed nest site selection with three commonly used techniques: 1) inferring habitat selection when habitats are used disproportionately to their estimated availability, 2) by comparing used habitat to unused (Pribil and Picman 1997), and 3) examining correlations between habitat characteristics and reproductive success.

2.3. METHODS

2.3.1. Study Area

This study took place at Riske Creek, B.C., from April-August 1997-2000. General details of the study area are provided in Chapter 1.

2.3.2. Locating Natural Cavities

Two techniques were used to locate natural cavity nest sites in April and May of each year. First, thorough searches were conducted through forest stands surrounding lakes that contained paired birds. Searches were performed along ad hoc transects with 2-4 persons spread out at ca. 10-m distances, walking perpendicular from the water's edge for ca. 500 m. For each lake, these transects were performed around the entire lake so that all forest cover with a 500-m radius from shore had been searched. Second, natural cavity nests were located by following females returning to nest sites to incubate after feeding. This method proved to be more effective in locating cavity nests ($n = 31$ of 41 goldeneye, and 65 of 100 Bufflehead cavity nests) and had the advantage of being unbiased with respect to my choice of habitat types in which to conduct transect searches. However, it must be acknowledged that this search technique can be biased toward successfully nesting females. Because most box-nesting females carried individual nasal tags, I directed my efforts at females known to not be incubating in boxes. Although some deserted and early-failing nests may have gone undetected, I am confident that I located the nest sites (boxes or cavities) of over 90% of the breeding pairs for both species each year, because few broods of unknown origin appeared on ponds at hatching.

Cavities were accessed using ladders, tree spikes, and climbing ropes, and were inspected using mirrors and flashlights. Two of the 41 goldeneye cavity nests had "open-top" entrances located in trees with broken tops. None of the 100 Bufflehead nests were in open-top cavities.

2.3.3. Cavity Characteristics

2.3.3.1. *Forest Stand Scale*

Initial results of this study, as well as previous literature, indicated that aspen stands typically contained much higher densities of suitable cavities (for various species of cavity-nesters) than conifer stands. To quantitatively compare goldeneye and Bufflehead cavity densities in aspen and coniferous stands, I established 28 transects around 14 randomly selected ponds (one transect per stand type, per pond). All transects were located within 500 m of the shoreline of their respective lake.

Transects through coniferous stands were randomly located at each lake, and ran 200 m into the forest (perpendicular to the shoreline) and were 100 m wide (total area covered = 2 ha). In each conifer transect, two line transects, each 1 m wide and 200 m long, were used to assess tree density (stems/ha), species composition, and average diameter at breast height (DBH, measured at 1.3 m above ground). Aspen stands were typically small clumps, and therefore these transects were much smaller (75 x 50 m, 0.38 ha). Aspen clumps were randomly selected only if there was more than one clump at a chosen lake. Because aspen transects were smaller and contained fewer trees, I was able to count and measure each individual tree within these transects.

In each of the 28 transects, all trees (n = ca. 51,450 trees in 14 conifer transects, and 979 trees in 14 aspen transects) were carefully searched for suitable goldeneye and Bufflehead cavities. Cavities with entrance diameters larger than 10 cm were considered suitable for goldeneye and those larger than 5 cm, but less than 12 cm, were deemed suitable for Bufflehead. These measurements were equal to the minimum and maximum values taken from active nest sites in this study, as well as Gauthier and Smith (1987). All suitable cavities were measured (described below) and visually inspected for activity. If a cavity was occupied, the species present was recorded.

2.3.3.2. *Forest Patch Scale*

Vegetation plot surveys (as per Martin and Eadie 1999) were conducted around all active cavities (n = 141 nest plots, for both species combined) as well as two random locations within 100 m of each cavity (n = 282 random plots). Vegetation plot radii were 11.3 m (0.04 ha). Trees of DBH less than 14 cm were counted and identified to species but considered unsuitable nesting trees for the current study (based on Harestad and Keisker 1989, and Martin and Eadie 1999). All trees larger than 14 cm DBH were described as follows: tree species, DBH, and decay class. I also calculated the density of trees > 14 cm DBH (stems/ha).

2.3.3.3. *Nest Tree Scale*

For each nest tree, I measured tree species, tree height (measured with a clinometer), DBH, percent canopy cover (measured with a spherical densiometer), average height to the bottom of the live canopy (of the most common tree species present), and distance to the nearest water and forest edge. I classified the decay stage of each nest tree according to the B.C. Wildlife Tree Classification System (Table 2.1.; Province of British Columbia 1995) that ranges from '1' indicating a live healthy tree to '8' being a dead stub with extensive internal decay.

2.3.3.4. *Nest Site Scale*

The following physical characteristics were measured for each cavity (active or inactive), and were done so only in the year the cavity was discovered, unless obvious signs of cavity modification were noticed in subsequent years: cavity height in tree, cavity type (excavated or natural), entrance hole dimensions (height and width), cavity depth (from bottom of cavity entrance to bottom of the cavity), cavity volume, and compass orientation (aspect) of the entrance.

2.3.4. Nest Success

All active nest sites were checked every 4-7 days from mid-April to July. Each year, I measured the following reproductive variables for each nest: identity of the incubating female, clutch size, hatching date, nesting success, and cause of depredation. Nests were tallied as successful if one or more eggs hatched. For detailed analysis of annual nest success rates of natural cavities and nest boxes, including sources of nest depredation, see Evans et al. (2002; Chapter 3).

2.3.5. Statistical Analyses

Two-sided *t*-tests were used to compare habitat characteristics between random and nest vegetation plots, and to compare tree and cavity densities between coniferous stands and aspen stand transects. Pearson's chi-square analysis was used to determine whether there was a significant difference between the "expected" utilization of tree-scale characteristics (tree species, DBH class, and decay class) based on their availability and the observed frequency of usage.

To establish the relative importance of particular habitat characteristics in females' nest site selection, I compared the characteristics of occupied nests to unoccupied cavities, using univariate and multivariate Generalized Linear Models (GLM) with a logit link function, using SPLUS (Statsci 2000). Occupied cavities were those used by nesting females in at least one year of the study, and unoccupied cavities were those that remained empty in all four years. Nest occupancy was treated as a dichotomous dependent variable (1 if occupied, 0 if unoccupied) and habitat characteristics as independent variables. All variables were checked for linearity, homoscedasticity and normality. Backward elimination procedures were followed when fitting logistic regression equations and Chi-squared tests were used to test for significance. Full (maximum) models were used first to avoid making Type II (false negative) errors, including all variables, possible interactions and specified quadratics. Non-significant variables were sequentially removed from the model until the model produced a significant *P* value. Criteria for selecting the best predictive model included comparing models' *P* values, R^2 values, and simplicity (parsimony). Correlations were also performed between all habitat variables (Tables 2.2 and 2.3).

Logistic regression was also used to examine the relationship between nest success and nest site characteristics for 41 goldeneye and 100 Bufflehead cavities. Because many cavities contained active nests in more than one of the four years, a random sampling process was used to select the year in which the nest fate data were used for each cavity. I then ran univariate and multivariate logistic regression models (as described above) using this randomly selected subset of nesting data. Each randomization and regression analysis was repeated 1000 times and mean values and variances of the resulting Wald Statistics and *P* values were calculated. For cavities that were used only once, the same nest fate was used in each iteration.

The level of significance was 95% ($\alpha = 0.05$) for all tests.

2.4. RESULTS

2.4.1. Aspen and Coniferous Transects (Forest Stand Scale):

Despite having significantly lower tree densities, aspen transects contained far more suitable cavities per hectare than did the coniferous transects (Table 2.4). Suitable cavity densities for goldeneye averaged 3.4 ± 0.8 cavities/ha in aspen and 0.2 ± 0.6 per ha in coniferous transects. For Bufflehead, densities were 6.7 ± 1.3 cavities per ha in aspen and 1.6 ±. 0.9 per ha in coniferous stands.

Figures 2.1 and 2.2 present the tree species composition for both transect types, as well as the proportion of suitable cavities found in each tree species. In both transect types, aspen trees contained the largest proportion of suitable cavities for both bird species (99% in aspen transects; 82% in coniferous transects). Aspens accounted for only 16% of the trees present in the coniferous transects and the proportion of suitable cavities found in aspen was consistently higher than the proportion of aspen trees available, for both transect types (aspen transects: $\chi^2_3 = 19.4$, *P*

< 0.001, $n = 979$ trees; coniferous transects: $\chi^2_3 = 225.4$, $P < 0.0001$, $n =$ ca. 51,450 trees). Lodgepole pine was the dominant species in the coniferous stands (average = 43%), but contained only 5% of the suitable cavities in these stands (Figure 2.2.). Douglas-fir were less common than pine, but contained more cavities than pine in both transect types. No suitable cavities were found in spruce trees.

2.4.2. Vegetation Plots (Forest Patch Scale):

For both Barrow's Goldeneye and Bufflehead, vegetation plots containing active cavities had significantly higher aspen densities, and lower conifer and total tree densities (Tables 5 and 6). Trees in nest plots for both bird species were larger in mean diameter than trees in the random vegetation plots. Multivariate logistic analysis produced a model containing aspen density, total tree density, and DBH, as the best predictors of the presence of an active Barrow's Goldeneye cavity in a 0.04 ha vegetation plot ($WS_{121} = 109.7$, $P < 0.001$, $R^2 = 0.7$). For Bufflehead, a model containing density of aspen, Douglas-fir, Lodgepole pine, and spruce best predicted the likelihood of finding an active cavity in a plot ($WS_{298} = 419.5$, $P < 0.001$, $R^2 = 0.9$). Nest plots also had more suitable cavities per plot (mean number of cavities per nest plot = 0.6 ± 0.07, random plots = 0.1 ± 0.05, $P < 0.001$, $F_{422} = 74$), indicating that tree cavities are clumped, not distributed randomly. Overall, nest plots were more open than random plots and consisted predominately of aspen trees.

2.4.3. Comparing Available Cavities to Used Cavities (Nest Tree Scale):

2.4.3.1. *Tree Species*

For both goldeneye and Bufflehead, greater than 70% of available and active cavities were in aspen trees (Figure 2.3.), but tree species used by nesting females were distributed proportionately to the occurrence of cavities (goldeneye: $\chi^2_3 = 2.3$, $P = 0.3$, $n = 75$; Figure 2.3a; Bufflehead: $\chi^2_3 = 1.2$, $P = 0.6$, $n = 176$; Figure 2.3b). Douglas-fir trees accounted for 19% of available cavities and 24% of active goldeneye nest sites. Lodgepole pine cavity-trees were scarce ($n = 3$) and cavities were not found in spruce trees. Similar patterns were found for Bufflehead (Figure 2.3b).

2.4.3.2. *DBH*

Barrow's Goldeneye selected cavity-trees that had a DBH greater than 35 cm (average DBH used = 38.6 ± 1.9 cm, $n = 41$; $\chi^2_5 = 44.5$, $P < 0.001$, $n = 75$; Figure 2.4a) using them disproportionately more relative to availability (size classes 1-4 pooled and compared to classes 5 and 6 combined: $\chi^2_5 = 15.6, P < 0.001, n = 75$). Only 4 of 41 active goldeneye cavities were found in trees with a DBH of less than 35 cm, although many apparently suitable cavities existed in these trees. Bufflehead also selected larger diameter trees ($\chi^2_5 = 37.9, P < 0.001, n = 176$) with all active cavities being in trees of 25 cm DBH or larger (average DBH used = 32.0 ± 0.7 cm, n = 89; Figure 2.4b). Bufflehead made disproportionate use of trees larger than 30 cm DBH (size classes 1-3 pooled and compared to classes 4-6: $\chi^2_5 = 6.6, P < 0.01, n = 75$).

2.4.3.3. *Decay Class*

Suitable goldeneye cavities were found in trees of all decay classes, but the majority of those available and used were found in decay classes 1-2 (live and healthy - live with some internal decay; average decay class used = 2.4 ± 0.2, n = 41; Figure 2.5a). Active nest sites were distributed throughout the decay classes proportionately to their occurrence (goldeneye: $\chi^2_6 = 37.4, P = 0.3, n = 75$). Bufflehead had more suitable cavities in decay classes 1 and 3-6, and used these at nearly equal rates (average decay class used = 3.8 ± 0.1, n = 89; Figure 2.5b). As with goldeneye nests, Bufflehead cavities in each decay class were used proportionately to their availability ($\chi^2_6 = 42.8, P = 0.2, n = 176$). For both bird species, conifer trees containing active nest sites showed advanced stages of decay (average conifer decay class was 4.8 ± 0.5 for goldeneye and 4.4 ± 0.3 for Bufflehead).

2.4.4. Comparing Used to Unused Cavities (Nest Site and Nest Tree Scales):

Barrow's Goldeneye used cavities that, on average, 1) were higher above ground, 2) had a larger entrance diameter, 3) larger floor area, 4) were in larger diameter trees, and 5) had a greater than average canopy height, compared to unused cavities (univariate logistic regression, Table 2.7.). Distance of cavity from water, distance of cavity from forest edge, cavity volume, and aspect, had no significant effects on the models predicting active goldeneye nest sites (Table 2.7.). The only significant multivariate model contained cavity height above ground and DBH (Wald Statistic (WS_{73}) = 4.6 and 13.95, and $P = 0.03$ and 0.002, respectively), but these two variables were positively correlated to each other ($r = 0.4, P < 0.001$).

Bufflehead nested in cavities that typically had 1) a larger entrance diameter, 2) a smaller floor area, and 3) were located in larger diameter trees than those of unoccupied cavities (Table 2.8.). The height of the cavity above ground was not a significant factor in predicting cavity use by Bufflehead, nor were variables such as distance of cavity from water, distance of cavity from forest edge, cavity volume, and aspect. A multivariate logistic model containing 1) entrance diameter ($WS_{174} = 7.75$, $P = 0.005$), 2) DBH ($WS_{174} = 26.2$, $P = 0.001$), and 3) floor area ($WS_{174} = 8.7$, $P = 0.003$) was best for predicting cavity use. Correlations between the three variables in the multivariate model were nonsignificant (highest r value was 0.2 for entrance diameter and floor area, Table 2.3.). No significant interactions, nor higher order polynomials, were found.

2.4.5. Cavity Characteristics and Nest Success Rates:

Forty-one goldeneye cavities were found, and during the four years of this study these cavities supported 92 goldeneye nests. Sixty (65%) were successful, 18 (20%) were depredated, and 14 (15%) were abandoned. During this same period, 100 Bufflehead cavities were found, which supported 231 nests. One hundred and sixty-four of the 231 nests were successful (71%), 50 (22%) were depredated, and 17 (7%) were abandoned. Habitat measurements did not differ significantly between successful and depredated nests (Tables 9 and 10). Therefore, variables such as cavity height above ground, entrance diameter, and distance from forest edge did not covary with nest success, within the range of values for used nest sites.

2.5. DISCUSSION

Nesting resources may not be evenly distributed, and the quality of nesting structures likely differs across the landscape. Hence, cavity-nesting waterfowl should exhibit habitat selectivity at different spatial scales as they try to secure nesting opportunities. These scales likely reflect ecological processes that provide suitable cavities in areas near feeding habitat. For cavity nesting waterfowl, the basic requisite of a suitable nest cavity should include accessibility, protection from predators and adverse climatic conditions, and proximity to suitable breeding-pair and brood habitat (Kaminski and Weller 1992). Nest site selection likely involves trade-offs between any or all of these factors. My study showed that Barrow's Goldeneye are selecting cavities that are high above ground, and have relatively large entrance diameters and floor areas. Although goldeneye did not demonstrate active selection for any particular tree species, most cavities were found in aspen trees, with diameters greater than 35 cm, and with relatively high heights to the bottom of the canopy. Bufflehead selected cavities with a larger entrance diameter, and smaller floor area compared to cavities available but left unused. And like goldeneye, Bufflehead showed no selection for tree species, but nests were more commonly found in aspen trees, and in trees with diameters greater than 25 cm. For both species, there were no differences in distances to the nearest body of water for used and unused cavities.

2.5.1. Cavity Densities (Forest Stand and Forest Patch Scales)

Aspen transects (stand scale) had fewer trees per hectare, higher cavity densities, and higher heights to the bottom of the canopy, compared to the coniferous transects. Goldeneye and Bufflehead nest plots (patch scale) also had fewer trees, higher cavity densities, and because they were predominately in aspen stands, had higher average heights to the bottom of the canopy, than random vegetation plots within 100 m of nest sites. These results are similar to what have been reported by other studies. The density of Bufflehead cavities in aspen parklands approximately 100 km south of my study site were five times higher in aspen than in coniferous forests (Gauthier 1985, Peterson and Gauthier 1985), similar to my findings. The mean tree density around occupied Common Goldeneye and Wood Duck cavities in New Brunswick, was 24% less than the mean values of random plots, and trees had larger DBH values in stands with nests (Prince 1968). And, similar to Barrow's Goldeneye and Bufflehead in my study, plots with Wood Duck nest cavities contained significantly more cavities than did random plots (Gilmer et al. 1978).

Although the selection of trees by woodpeckers for nest hole construction most likely influences the location and availability of cavities used by ducks, it seems that these cavities are often clustered in comparatively open, aspen stands, which coincidentally allow for easier detection and use by waterfowl. Perhaps visibility and suitable cavity availability are, in fact, primary factors affecting nest site selection by waterfowl, and other factors such as inner cavity dimensions (discussed below) are secondary. It may even be that specific cavity characteristics are secondary because they actually aid in making the cavities more visible to prospecting ducks (such as large entrance diameters and high canopies). If such were true, I should expect cavities close to, and facing forest edge to be occupied more often than other, less conspicuous sites because waterfowl prospect by flying from wetlands towards the forest edge and into the forest interior. Although I did not find used cavities significantly closer to forest edge nor water, than unused cavities (Table 2.2.), other researchers have (Wood Ducks; McComb and Noble 1981).

2.5.2. Nest Tree Species, Decay Class, and DBH (Nest Tree Scale)

Aspen was clearly the most important cavity-producing tree used by goldeneye and Bufflehead, accounting for 77% of all available nests and 78% of all used nests. Previous studies on cavity-nesting waterfowl suggest that the use of aspen for nest sites is widespread. Gilmer et al. (1978) found two thirds of active Wood Duck nests (*n* = 31) in aspen stands (reported as mature aspen, >60 years old) with densities as high as 4.0-5.5/ha. For other species of secondary cavity nesters, studies in British Columbia have also identified trembling aspen as the most commonly used cavity-tree, and consistently report aspen to be used disproportionately more than would be expected from their availability (Peterson and Gauthier 1985, Harestad and Keisker 1989, Steeger and Machmeer 1996, Walters 1996, Martin and Eadie 1999). Furthermore, studies have also reported an avoidance of Douglas-fir, citing its slow pattern of decay as an explanation (Harestad and Keisker 1989).

The patterns of usage of tree species and decay-classes exhibited by Barrow's Goldeneye and Bufflehead are presumably closely tied to the preferences of the primary cavity excavators, Pileated Woodpeckers and Northern Flickers, respectively. PCEs prefer trees that are relatively easy to excavate, such as those with decayed heartwood but relatively hard sapwood (Harestad and Keisker 1989, Lundquist and Mariani 1991). Such conditions are most often provided by tree species such as trembling aspen, western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western white pine (*Pinus monticola*; Zarnowitz and Manuwal 1985, Harestad and Keisker 1989, Lundquist and Mariani 1991). Northern Flickers prefer dead or partly dead aspens (Raphael and White 1984, Harestad and Keisker 1989), while Pileated Woodpeckers nested exclusively in trembling aspen (Harestad and Keisker 1989), and avoided Douglas-fir (Bull and Meslow 1977). However, in a Douglas-fir forest in Oregon, Pileated Woodpeckers nested in Douglas-fir in proportion to their availability (Mannan et al. 1980), results that are similar to mine. It therefore appears that although aspens are a preferred species, primary cavity-nesting birds are flexible in their selection and able to adjust to local forest compositions (Harestad and Keisker 1989). For primary excavators, selection of cavity trees likely depends on their strength as excavators, and thus, it may be that the state of decay of a tree is more important than the tree species.

Unexcavated cavities may form in trees that have been infected through limb detachment, lightning strikes, top breakage, or other trunk wounds (Newton 1994). However, in this study, these cavities were more often than not, unoccupied. Therefore, goldeneye and Bufflehead may be more heavily dependent on abandoned cavities of PCEs than natural-formed cavities, and thus, their range of choices is constrained to a large extent by the preferences of PCEs and the availability of these cavities near wetlands.

A preference for tall trees has been observed in a variety of woodpeckers and several other secondary cavity nesting birds (Nilsson 1984, Raphael and White 1984, Rendell and Robertson 1989) and several possible explanations exist. First, trees must be large enough for a cavity volume that can support an incubating female, and tall trees generally have large DBH's suitable for large cavities. As well, predation risks may be lower for nests in higher cavities because they are less conspicuous to ground predators and presumably more difficult and energetically expensive to access (Nilsson 1984, Rendell and Robertson 1989).

Larger trees are also likely to have thicker walls and offer greater thermal stability (insulation). Thicker walls would also make cavities less vulnerable to large predators such as black bears which have been observed depredating cavities in this study as well as others (Steeger and Machmer 1996, Walters 1996, Evans et al. 2002). Furthermore, tall trees often provide a more open canopy which allows for easier access to and from the cavity and may also be easier to find when prospecting. An open canopy may be of particular importance to waterfowl, considering their limited ability to fly through forested areas. Although an open canopy may make cavities more conspicuous to predators, this may be a necessary trade-off with accessibility.

2.5.3. Cavity Entrance Size and Floor Area (Nest Site Scale)

Internal cavity dimensions such as entrance diameter, depth, volume, and floor area are important characteristics for several species of cavity nesters, including Bufflehead (Peterson and Gauthier 1985), Common Goldeneye (Prince 1968), and Wood Ducks (Robb and Bookhout 1995). A minimum entrance diameter is necessary for birds to access a cavity and thus it is not surprising that large-bodied Barrow's Goldeneye use larger than average entrance diameters (range for used cavities: 10-20 cm). Bufflehead are also a relatively large cavity nester and they too are selecting entrances that are, on average, larger than what is available. However, Bufflehead avoid cavities with entrance diameters larger than 12 cm (range for used cavities: 5-12 cm). In a study of six cavity nesting passerines, nest entrance widths were closely correlated with the size of the species occupying a cavity and it was suggested that birds are selecting cavity openings just large enough to allow entrance, perhaps to lessen the number of predators able to gain access to the nest (Nilsson 1984). It may also be that by selecting smaller cavities, Bufflehead are avoiding competition with larger cavity nesters such as goldeneye, Hooded Mergansers (*Lophodytes cucullatus*), and Wood Ducks (*Aix sponsa*). If this is true for all cavity nesters, then it is also reasonable to assume that larger cavities selected by goldeneye and Bufflehead may be in less demand from smaller competitors such as Tree Swallows (*Tachycineta bicolor*), chickadees (*Poecile* spp.), nuthatches (*Sitta* spp.), and Bluebirds (*Sialia* spp.). Thus it appears that there is a species-specific optimal entrance size that balances the need to gain access while lessening predation risks and interspecific competition.

Cavity nesters should also select floor areas that allow females to incubate effectively. Although goldeneye use cavities with floor areas larger than what are available, Bufflehead select floor areas smaller than those found in unused cavities. Although this study failed to find any significant relationship between nest success and floor area, cavity volume, or depth, it has been previously reported that increased cavity volume and depth lowers predation risks (Zeleny 1977, Moed and Dawson 1979, Peterson and Gauthier 1985, Gauthier and Smith 1987). Nest success rates for Wood Ducks increase with cavity volume and depth (Robb 1986), and clutch sizes in some passerines increase with cavity floor area (Zeleny 1977, Moed and Dawson 1979).

It should be noted that the Riske Creek study site has artificial nest boxes present that many goldeneye, and to a lesser extent, Bufflehead use annually. It is assumed that without the presence of these boxes, birds would be forced to nest in natural cavities that remained empty through the duration of this study, or else forego breeding altogether. In this case, the results of my study might be different, and this must be considered when comparing my study to areas where boxes are not present.

Regardless, my results show that certain cavity and habitat characteristics appear to be selected by these birds, and that simply counting the number of cavities in an area without determining selected physical characteristics could be misleading and may not provide an accurate index of potential nesting habitat. It should also be noted that some cavities with 'suitable' dimensions may be unsatisfactory to goldeneye and Bufflehead due to factors not considered in this study.

And finally, many potential nest sites (cavities and boxes) in my study area remained unused, particularly for Bufflehead. If cavities are not limiting at my study site, then perhaps other factors such as local predation levels, or intra- and interspecific competition on ponds, limits the density of breeders and cavity use (and therefore recruitment rates and population growth). Territorial behavior that limits access to local breeding pair and brood rearing habitat is already thought to affect Bufflehead (Gauthier and Smith 1987) and Common Goldeneye (Fredga and Dow 1984) nest densities and probably influences Barrow's Goldeneye densities also (Savard 1986).

2.6. MANAGEMENT RECOMMENDATIONS

Forest harvesting can have important demographic effects on cavity-nesting birds. However, by determining patterns of nest site selection by these birds it may be possible to minimize the loss of nest trees during forest removal. Because 60% of the world's population of Barrow's Goldeneye breed in British Columbia (McKelvey et al. 1989), a province where forestry is one of the main industries, it becomes particularly important to understand their nesting habitat requirements. My results indicate that aspen stands, particularly those within 200 m of a wetland, should be managed to assure the protection of nest sites for these birds. Figure

2.6 shows that retaining aspen stands within 200 m of a wetland would protect over 90% of the natural cavities used by both goldeneye and Bufflehead. Retaining aspen stands within 100 m of a wetland would protect over 70% of the these cavities.

Forest management should also encourage primary cavity-nesting species' abundance, particularly Pileated Woodpeckers and Northern Flickers. Managers should act in ways to conserve existing and potential cavity-trees, particularly large aspen in early and middle stages of decay (decay classes 1-4), and Douglas-firs in late stages of decay (decay classes 4-6). It is further recommended that aspen trees be protected as patches to guard against wind and blow-down, which will thus affect the longevity of the trees. Patches may also aid in keeping cavities less conspicuous to predators. Protecting entire aspen stands will also allow young trees to replace older, fallen trees and ensure a continuous supply of cavities over time.

2.7. LITERATURE CITED

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Table 2.1. Tree decay-stage classification system applied to cavity trees at Riske Creek, British Columbia, 1997-2000 (taken from Province of British Columbia 1995).

Stage	Description of Tree
1	Live, healthy; no visible signs of decay.
2	Live, unhealthy; visible signs of decay or growth deformities including insect damage, broken limbs, and cracks.
3	Recently dead; needles still present, hard heartwood, roots stable.
4	Dead; no needles, hard heartwood, spongy sapwood, 50% of branches lost, loose bark, top usually broken, roots stable.
5	Dead, spongy heartwood, soft sapwood, internal decay, most branches and bark absent, roots beginning to soften.
6	Dead; no branches or bark, tops broken off, heartwood and sapwood sloughing from upper bole.
7	Dead; stubs > 3 m in height, extensive internal decay, outer shell may be hard, lateral roots completely decomposed
8	Dead; stubs < 3 m in height, extensive internal decay, outer shell may be hard, lateral roots completely decomposed

Table 2.2. Pairwise correlation coefficients between Barrow's Goldeneye cavity characteristics at Riske Creek, British Columbia (1997-2000). Numbers (1-8) along the top of the table correspond to the numbered characteristics down the side.

	Habitat Variable	2	3	4	5	6	7	8	9
1	Cavity Height Above Ground (m)	0.10	0.60	0.38***	0.07	-0.03	0.01	0.04	0.03
2	Entrance Diameter (cm)	1	-0.05	0.10	0.09	-0.10	0.04	0.07	0.04
3	Floor Area (cm2)		1	0.02	0.10	0.80***	0.05	0.10	0.10
4	DBH (cm)			1	0.06	0.04	0.02	0.07	0.08
5	Bottom of Canopy (m)				1	0.02	0.04	0.40***	0.2
6	Cavity Volume (L)					1	0.02	0.03	0.33*
7	Aspect (degrees)						1	0.02	0.02
8	Distance to Nearest Water (m)							1	0.50***
9	Distance to Forest Edge (m)								1

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

Table 2.3. Pairwise correlation coefficients between Bufflehead cavity characteristics at Riske Creek, British Columbia (1997-2000). Numbers (1-8) along the top of the table correspond to the numbered characteristics down the side.

	Habitat Variable	2	3	4	5	6	7	8	9
1	Cavity Height Above Ground (m)	0.10	-0.10	0.10	0.01	0.02	0.01	0.10	0.10
2	Entrance Diameter (cm)	1	0.20	0.01	-0.04	0.30	0.03	0.10	0.20
3	Floor Area (cm^2)		1	0.10	0.10	0.80***	0.01	0.20	0.03
4	DBH (cm)			1	0.02	0.22*	0.02	-0.01	0.06
5	Bottom of Canopy (m)				1	0.10	0.04	0.20	0.1
6	Cavity Volume (L)					1	0.10	0.2	0.2
7	Aspect (degrees)						1	0.04	0.04
8	Distance to Nearest Water (m)							1	0.50***
9	Distance to Forest Edge (m)								1

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

Table 2.4. Results of paired *t*-tests between aspen (75 x 50 m, $n = 14$) and conifer stand transects (200 x 100 m, $n = 14$) at Riske Creek, British Columbia (1997-2000). See meth for definition of suitable.

	Aspen Transects		**Conifer Transects**		
	Mean	SE	Mean	SE	*P*
Average Tree Density (stems/ha)	253.6	31.8	919	124.3	0.005
Average DBH (cm)	27.1	0.4	18	0.3	0.001
Suitable Goldeneye Cavities (/ha)	3.4	0.8	0.2	0.6	0.005
Suitable Bufflehead Cavities (/ha)	6.7	1.3	1.6	0.9	0.01
Total Suitable Cavities (/ha)	10.1	2	1.8	0.8	0.005

Table 2.5. Results of *t*-tests between habitat features from Barrow's Goldeneye nest vegetation plots ($n = 41$) and adjacent random plots ($n = 82$) at Riske Creek, British Columbia (1997-2000).

Habitat Feature	**Nest Plots**		**Random Plots**		
	Mean	SE	Mean	SE	*P*
Density (trees/ha):					
Trees	20	1.7	43	1.9	0.001
Aspen	10.2	1	6.1	0.7	0.001
Douglas-fir	1.5	0.7	13.6	0.5	0.001
Lodgepole Pine	1.2	0.7	19.1	0.5	0.001
Spruce	6.2	1.1	4.2	0.8	0.1
DBH (cm)	29.3	0.5	27.2	0.3	0.01

Table 2.6. Results of *t*-tests between habitat features from Bufflehead nest vegetation plots ($n = 100$) and adjacent random plots ($n = 200$) at Riske Creek, British Columbia (1997-2000).

Habitat Feature	**Nest Plots**		**Random Plots**		
	Mean	SE	Mean	SE	*P*
Density (trees/ha):					
Trees	13	0.9	39.8	1.6	0.001
Aspen	9.1	0.6	5.6	0.4	0.001
Douglas-fir	1.1	0.4	13.2	0.3	0.001
Lodgepole Pine	0.6	0.4	17.8	0.3	0.001
Spruce	1.2	0.3	3.1	0.2	0.01
DBH (cm)	29.2	0.3	27.3	0.2	0.01

Table 2.7. Univariate analysis between characteristics of used ($n = 41$) and unused ($n = 34$) Barrow's Goldeneye cavities at Riske Creek, British Columbia (1997-2000). See text for multivariate logistic regression results.

Characteristic	**Used**		**Unused**		***t*-test**	
	Mean	SE	Mean	SE	*t*	*P*
Cavity Height Above Ground (m)	12.6	0.6	8.7	0.7	-4.3	0.001
Entrance Diameter (cm)	13.2	0.3	11.8	0.4	-2.6	0.01
Floor Area (cm2)	299.1	15.7	252.3	22.3	-2.1	0.02
DBH (cm)	47.2	2	26.4	2.2	-6.9	0.001
Bottom of Canopy (m)	13.7	0.9	10	1	-2.8	0.01
Cavity Volume (L)	16.7	1	16.2	1.1	-0.3	0.8
Aspect (degrees)	173.2	17.8	179.4	18.7	0.3	0.8
Distance to Nearest Water (m)	90.4	13.5	91.3	14.7	0.05	0.9
Distance to Forest Edge (m)	10.2	1.6	9	1.7	-0.5	0.6

Table 2.8. Univariate analysis between characteristics of used ($n = 89$) and unused ($n = 87$) Bufflehead cavities at Riske Creek, British Columbia (1997-2000). See text for multivariate logistic regression results.

Characteristic	**Used**		**Unused**		***t*-Test**	
	Mean	SE	Mean	SE	*t*	*P*
Cavity Height Above Ground (m)	7.3	0.5	8	0.5	0.9	0.4
Entrance Diameter (cm)	8.5	0.2	6.5	0.2	-9.2	0.001
Floor Area (cm^2)	187.4	8.4	222.1	7.2	3.1	0.001
DBH (cm)	36.3	0.9	27.9	0.9	-6.5	0.001
Bottom of Canopy (m)	9.8	0.7	9.8	0.7	-0.02	0.9
Cavity Volume (L)	5.4	0.2	5.5	0.2	0.4	0.7
Aspect (degrees)	158.8	9.6	145.4	7.9	1.5	0.5
Distance to Nearest Water (m)	43.8	7	55.2	6.1	1.4	0.2
Distance to Forest Edge (m)	2.5	0.5	2	0.4	-0.3	0.8

Table 2.9. Univariate analysis between habitat characteristics of successful and unsuccessful Barrow's Goldeneye cavities at Riske Creek, British Columbia (1997-2000). Results are from 1000 randomizations using 92 nest fates for 41 cavities. See text for multivariate logistic regression results.

Characteristics	**Successful**		**Unsuccessful**		***t*-test**			
	Mean	SE	Mean	SE	Mean t	SE	Mean P	SE
Cavity Height Above Ground (m)	12.9	1	11.8	1	1	0.02	0.4	0.01
Entrance Diameter (cm)	13.2	0.5	12.9	0.7	0.4	0.01	0.7	0.01
Floor Area (cm^2)	309.9	25.9	303.4	38.9	0.4	0.01	0.7	0.01
DBH (cm)	46.7	3.7	48	2.7	0.4	0.01	0.7	0.01
Bottom of Canopy (m)	14	1.4	13.1	1.2	0.6	0.01	0.6	0.01
Cavity Volume (L)	16.4	1.3	17.1	2	0.4	0.01	0.7	0.01
Distance to Nearest Water (m)	96.2	17.5	79.5	18.9	0.6	0.01	0.6	0.01
Distance to Forest Edge (m)	8.7	1.9	13.1	2.7	1.4	0.02	0.2	0.01

Table 2.10. Univariate analysis between habitat characteristics of successful and unsuccessful Bufflehead cavities at Riske Creek, British Columbia (1997-2000) Results are from 1000 randomizations using 231 nest fates for 100 cavities. See text for multivariate logistic regression results.

Characteristics	**Successful**		**Unsuccessful**		***t*-test**			
	Mean	SE	Mean	SE	Mean *t*	SE	Mean *P*	SE
Cavity Height Above Ground (m)	7.4	0.6	6.8	0.9	0.9	0.02	0.5	0.01
Entrance Diameter (cm)	8.8	0.2	8.8	0.3	0.5	0.01	0.6	0.01
Floor Area (cm^2)	186.4	6.7	190.1	10.4	0.5	0.01	0.6	0.01
DBH (cm)	36.4	1.1	35.9	1.5	0.7	0.01	0.6	0.01
Bottom of Canopy (m)	9.5	0.8	10.7	1.2	0.8	0.02	0.5	0.01
Cavity Volume (L)	5.3	0.3	5.7	0.4	0.9	0.01	0.4	0.01
Distance to Nearest Water (m)	45.4	6.6	39.5	13.3	0.6	0.01	0.6	0.01
Distance to Forest Edge (m)	2.6	0.6	2.1	0.7	0.6	0.01	0.6	0.01

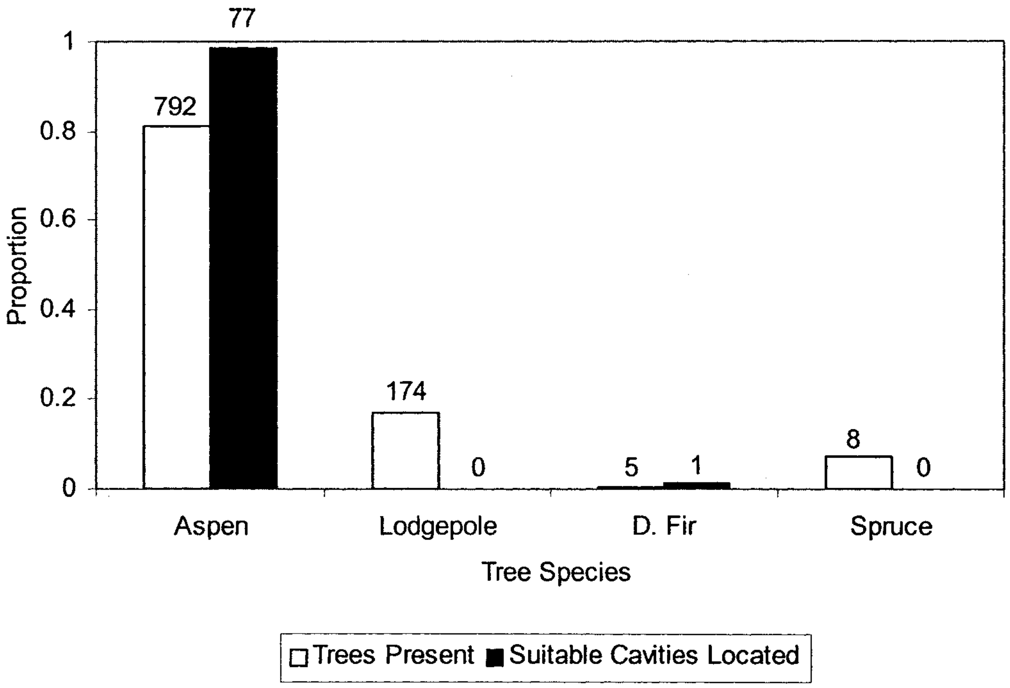

Figure 2.1. Proportion of trees present in aspen transects, and proportion of suitable cavities found in each species at Riske Creek, British Columbia (1997-2000). Data are for Barrow's Goldeneye and Bufflehead suitable cavities combined (*n* = 979 trees and *n* = 78 cavities).

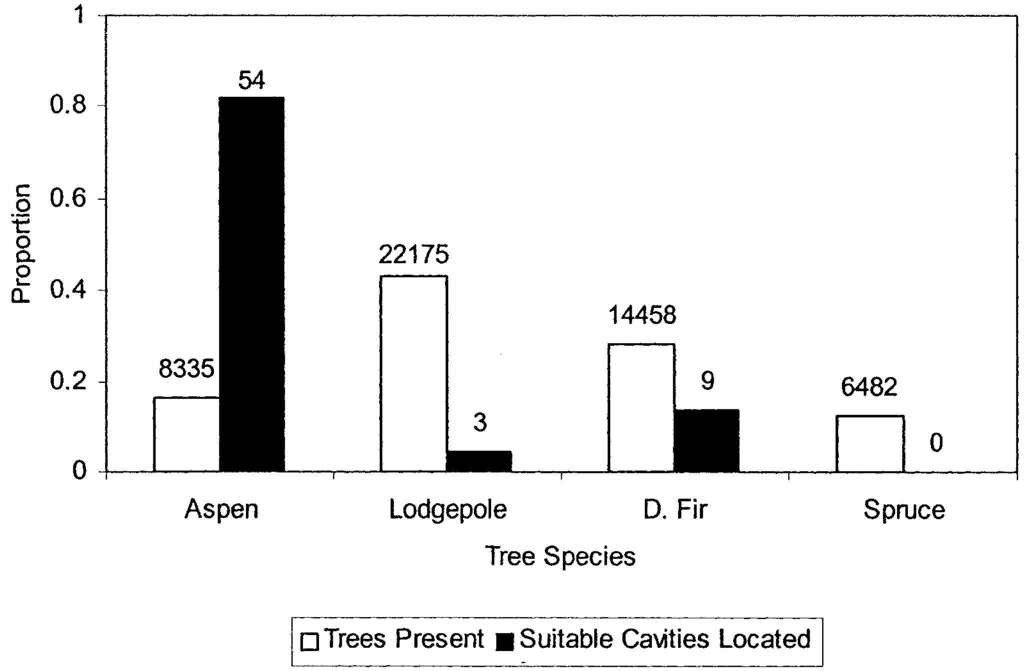

Figure 2.2. Proportion of trees present in conifer transects, and proportion of suitable cavities found in each species at Riske Creek, British Columbia (1997-2000). Data are for Barrow's Goldeneye and Bufflehead suitable cavities combined (*n* = 51,450 trees and *n* = 66 cavities).

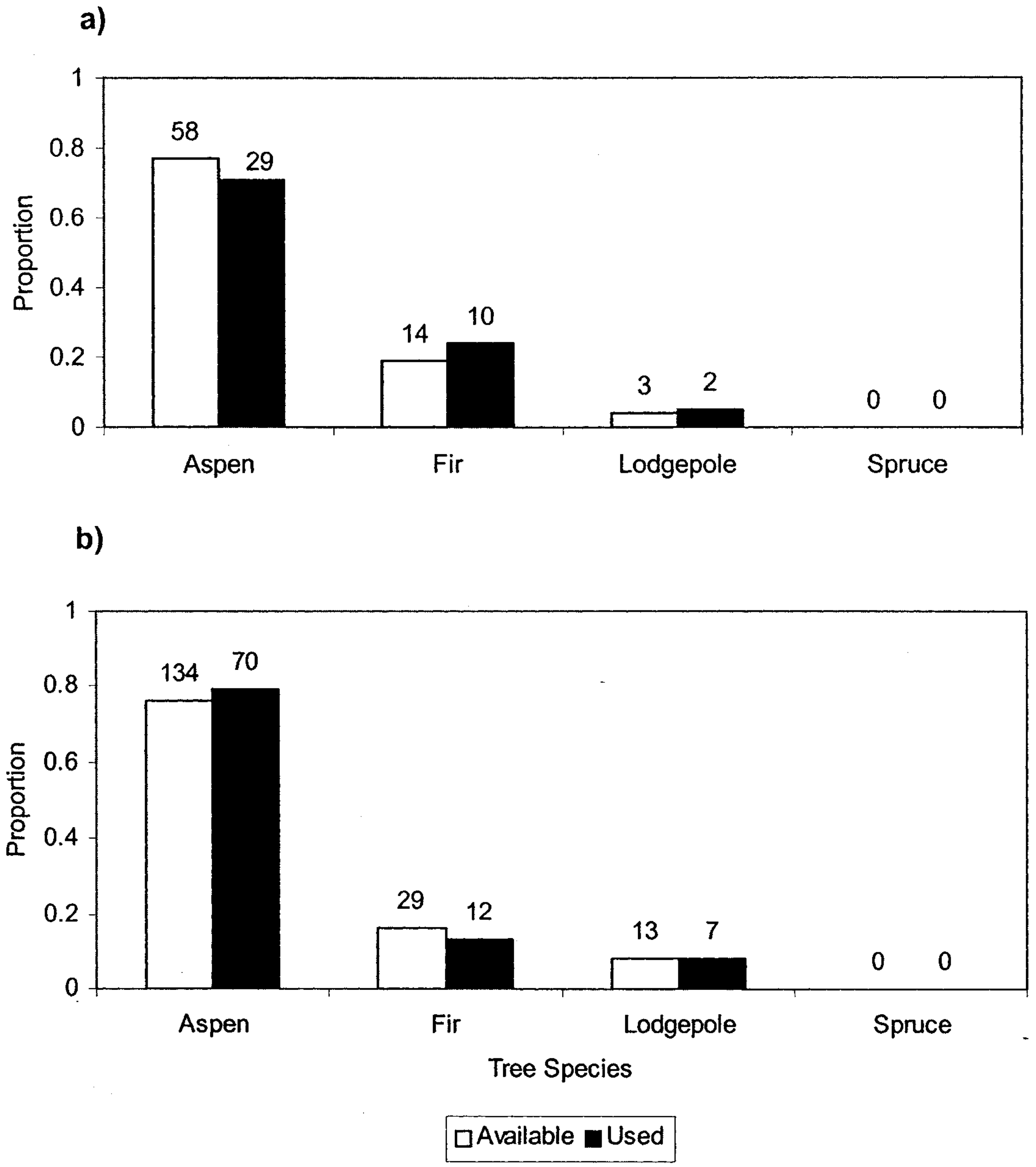

Figure 2.3. Proportion of a) Barrow's Goldeneye and b) Bufflehead cavities available versus used for four tree species at Riske Creek, British Columbia (1997-2000). Numbers above columns are sample sizes for each group. Number of Goldeneye cavities available = 75, number used = 41. Number of Bufflehead cavities available = 176, number used = 89.

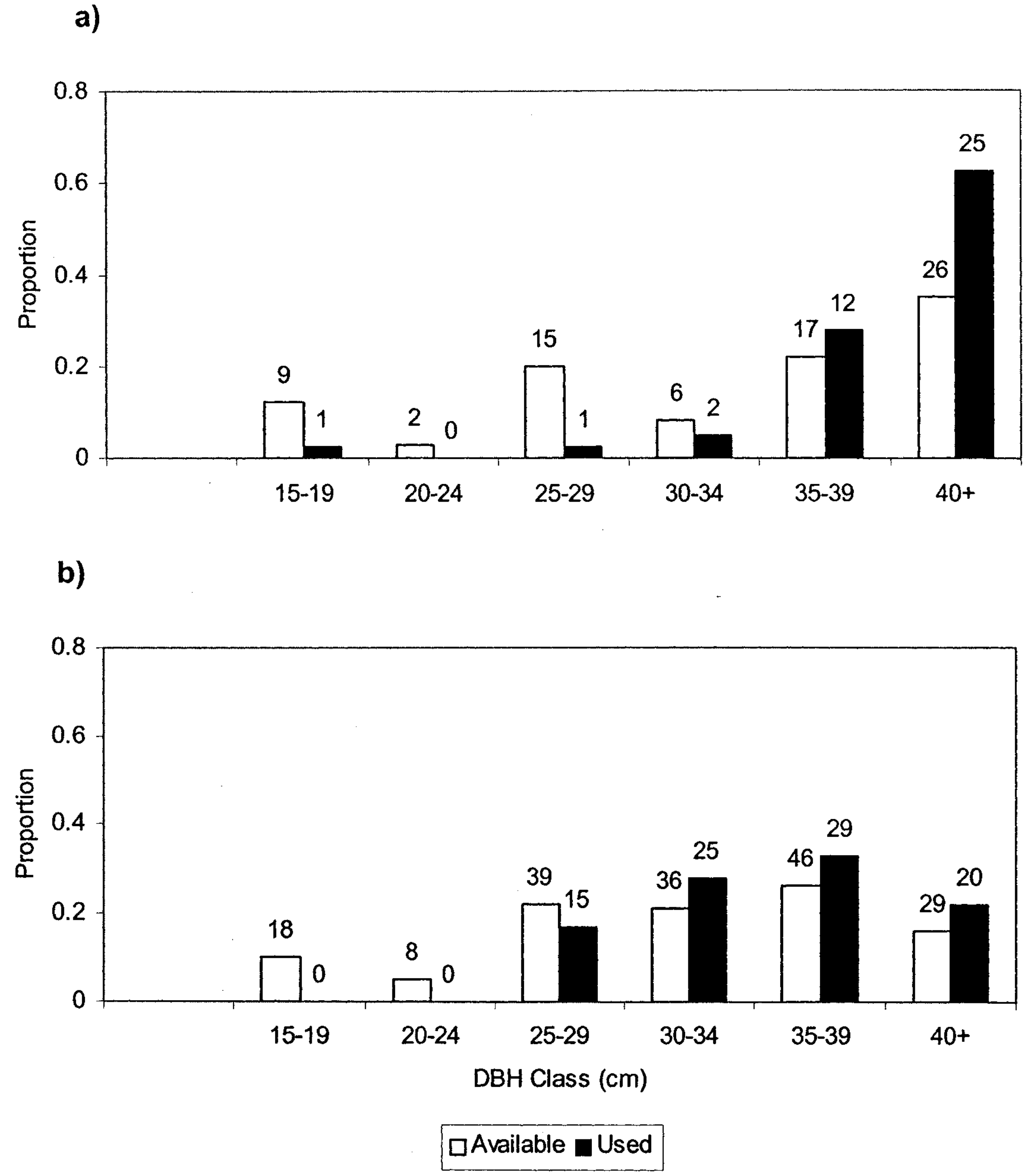

Figure 2.4. Proportion of available and used a) Barrow's Goldeneye and b) Bufflehead cavities found in DBH classes at Riske Creek, British Columbia (1997-2000). Numbers above columns are sample sizes for each group. Number of Goldeneye cavities available = 75, number used = 41. Number of Bufflehead cavities available = 176, number used = 89.

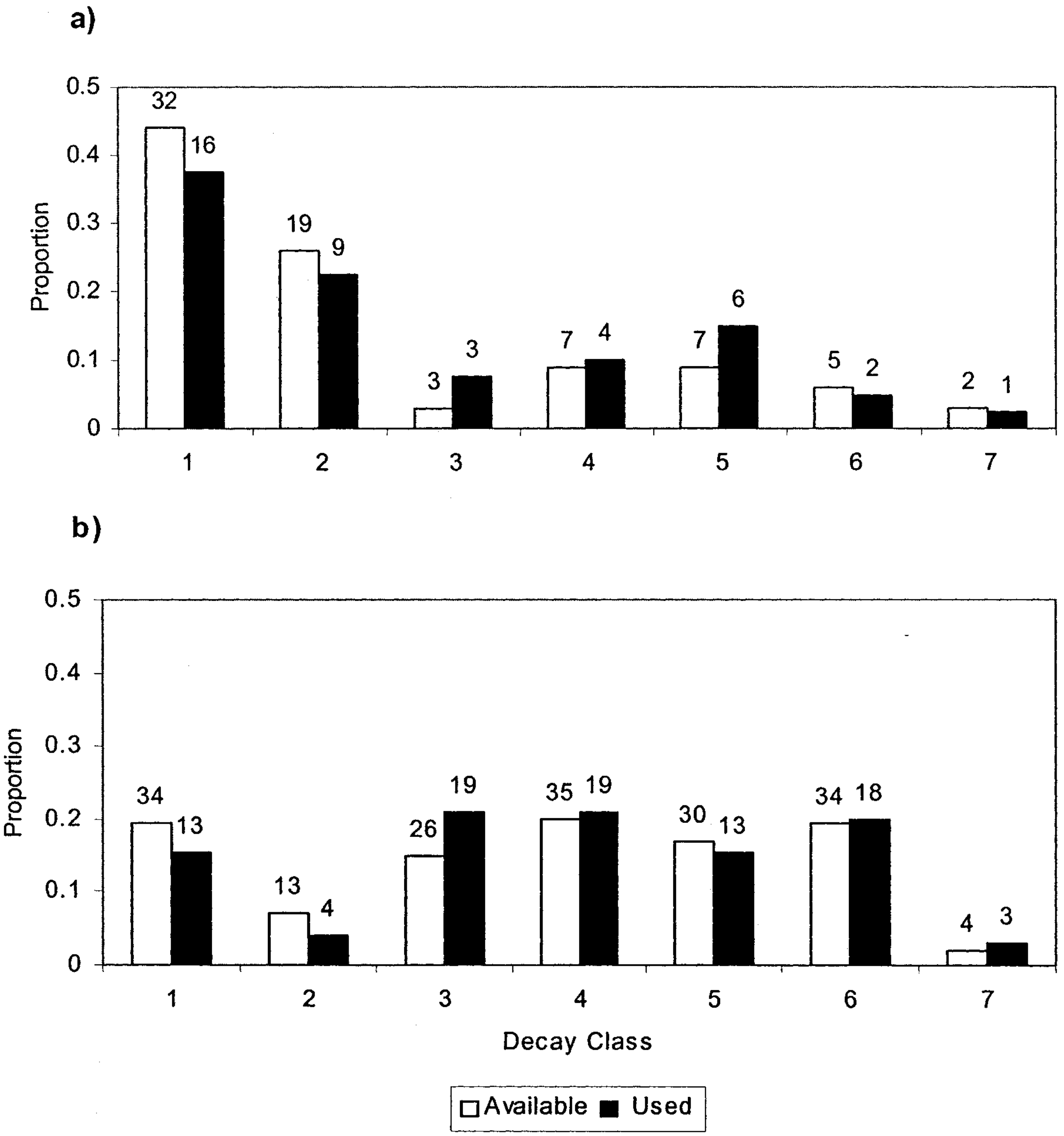

Figure 2.5. Proportion of available and used a) Barrow's Goldeneye and b) Bufflehead cavities found in seven decay classes at Riske Creek, British Columbia (1997-2000). Numbers above columns are sample sizes for each group. Number of Goldeneye cavities available = 75, number used = 41. Number of Bufflehead cavities available = 176, number used = 89.

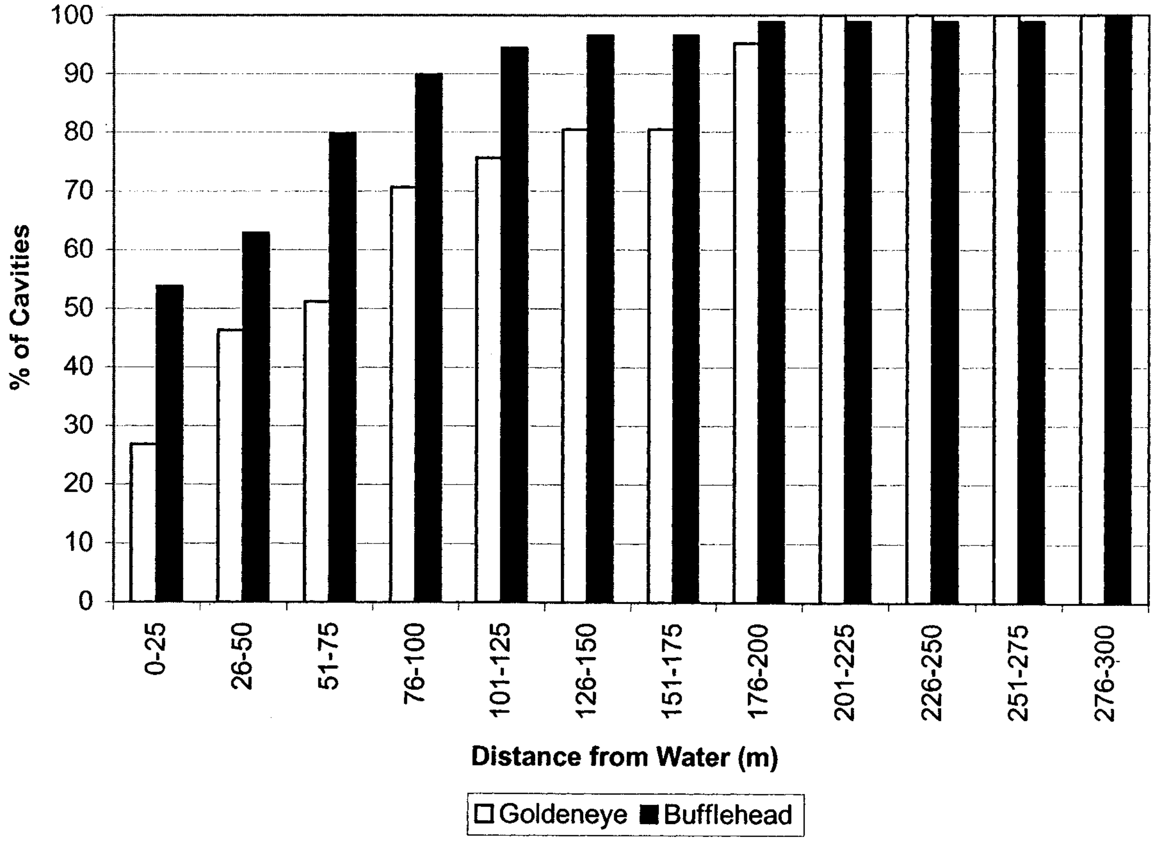

Figure 2.6. Cumulative frequency distribution of Barrow's Goldeneye and Bufflehead cavities with respect to distance from water.

Chapter 3

A COMPARISON OF CHARACTERISTICS AND FATE OF BARROW'S GOLDENEYE AND BUFFLEHEAD NESTS IN NEST BOXES AND NATURAL CAVITIES

3.1. Abstract. Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) are cavity-nesting waterfowl that have received considerable attention in studies using nest boxes, but little is known about their nesting ecology in natural cavities. I found larger clutch size, lower nesting success, and different major predators for Barrow's Goldeneyes nesting in boxes versus those nesting in natural cavities, but few differences for Bufflehead. I suggest that these differences are attributed to the location and physical differences between Barrow's Goldeneye nest boxes and natural cavities that affect their conspicuousness to predators and conspecific nest parasitising females. Goldeneye boxes were concentrated in highly visible locations such as trees at water or forest edge. Natural cavity nests, on the other hand, were often abandoned Pileated Woodpecker (*Dryocopus pileatus*) cavities, which were more dispersed throughout the forest interior and concealed under dense canopy cover. Bufflehead natural cavity nests were typically closer to edges, which may account for their similarity with boxes. I conclude that in some respects, studies of Barrow's Goldeneye that use nest boxes may not be representative of birds nesting in natural cavities, whereas those of Bufflehead are more likely to be so.

3.2. INTRODUCTION

Many ornithological studies have used nest boxes to examine the breeding biology and life histories of cavity-nesting species. Research using nest boxes includes perhaps the oldest ongoing field studies on any animal species, beginning in the Netherlands in the 1920s and in Britain in the 1940s (Moller 1989) and has influenced theories in avian biology, including population regulation (Lack 1954, Krebs 1971), life history evolution (Lack 1954, Boyce and Perrins 1987), quantitative genetics (van Balen 1984), and sexual selection (Alatalo et al. 1986). At least 65 species of cavity-nesting birds in North America and Europe use boxes (Eadie et al. 1998).

Nest boxes are also valuable for conservation programs aimed at augmenting target species' abundance, having increased populations for 22 of 23 studied species (Eadie et al. 1998). Highly successful programs have included Eastern Bluebirds (*Sialia sialis*, Gowaty and Bridges 1991), Wood Ducks (*Aix sponsa*, Nichols and Johnson 1990), and American Kestrels (*Falco sparverius*; Hamerstrom et al. 1973).

Despite the utility of nest boxes for birds, researchers, and managers, the behavior and demographics of birds nesting in boxes are likely to differ from those of birds nesting in natural sites (Nilsson 1986). Nest box studies may be biased in two important ways: they often reduce nest predation levels to a fraction of their natural levels, and they reduce ectoparasite loads when researchers consistently remove old nests at the end of each breeding season (Moller 1989). In fact, it has long been believed that cavity nesters have higher nesting success rates than do ground-nesting birds (Lack 1954), a belief that has arisen primarily from the results of nest box studies. Some now argue that this belief may be inaccurate, as studies of populations using natural cavities have begun to show (Purcell et al. 1997). Nilsson (1984a) found nest predation to be 62% lower in nest boxes than cavities for five passerine species, and nesting success in natural holes was nearly identical to that of open-nesting species (Nilsson 1986). Other studies have reported that nest box populations experience lower rates of predation, lay larger clutches (Robertson and Rendell 1990), and fledge more young (Nilsson 1986, Kuitunen and Aleknonis 1992) than populations in natural sites.

Nest boxes may alter other key ecological processes such as population dynamics and intraspecific social interactions like conspecific brood parasitism (Moller 1989, Eadie et al. 1998). The addition of artificial nesting structures may also produce artificially high densities of breeding birds, which may have negative influences on other species' breeding ecology, such as increasing competition for nest sites or food resources. In some species, these changes may even lead to precipitous declines in productivity and result in population instability and decline (Eadie et al. 1998). More information on birds nesting in cavities will allow further understanding of the factors that regulate populations of secondary cavity nesters and influence community structure (Purcell et al. 1997).

Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) are cavity-nesting waterfowl that have received considerable attention in studies using boxes (Gauthier 1985, Savard 1986, Eadie 1989, Thompson 1996). However, little is known about the nesting ecology of these birds in natural cavities. This is also true for Common Goldeneyes (*B. clangula*), which now nest predominately in nest boxes across their range in north-western Europe (Eriksson 1982, Fredga and Dow 1984). The purpose of this study was to compare nest characteristics, fate, and sources of predation of Barrow's Goldeneyes and Bufflehead breeding in nest boxes and natural cavities.

3.3. METHODS

3.3.1. Study Area

This study took place at Riske Creek, B.C., from April-August 1997-1999. General details of the study area are provided in Chapter 1.

3.3.2. Nest Boxes

Barrow's Goldeneye and Bufflehead nest boxes have existed in the study area since 1981 (Savard 1986). In 1998 and 1999, I repaired or replaced boxes worn by weather or destroyed by predators (ca. 15%, annually) and added boxes to some areas. These boxes varied in their dimensions for both species as a result of the differing needs of previous studies (Table 3.1.) and were located 3-6 m above ground in various species of trees. No predator-exclusion devices were used and old nests were not removed between breeding seasons. Nest boxes were accessed using ladders.

Females were captured on the nest or wetland, banded, and marked with plastic nasal tags of different shapes and colors for individual identification (Savard 1986). Known multiple observations for the same female in successive years were excluded from the analysis, although some birds remained unmarked (fewer than 30 % each year) and may have been included more than once.

3.3.3. Natural Cavities

Two techniques were used to locate natural cavity nest sites in April and May of each year. First, thorough searches were conducted through forest stands surrounding lakes that contained paired birds. Searches were performed along ad hoc transects with 2-4 persons spread out at ca. 10 m distances, walking perpendicular from the water's edge for ca. 500 m. Second, natural cavity nests were located by following females returning to nest sites to incubate after feeding. This method proved to be more effective in locating cavity nests (*n* = 31 of 41 goldeneyes, and 65 of 100 Bufflehead cavity nests) and had the advantage of being unbiased with respect to my choice of habitat types in which to conduct transect searches. However, it must be acknowledged that this search technique can be biased toward successful females. Since most box-nesting females carried individual nasal tags, I directed my efforts at females known to not be incubating in boxes. Although some deserted and early-failing nests may have gone undetected, I feel confident that I located the nest sites (boxes or cavities) of over 90% of the breeding pairs for both species each year because few broods of unknown origin appeared on ponds at hatching.

Cavities were accessed using ladders, tree spikes, and climbing ropes, and were inspected using mirrors and flashlights. Two of the 41 goldeneye cavity nests had "open-top" entrances located in trees with broken tops, and were included in the analysis. No Bufflehead nests were found in open-top cavities.

3.3.4. Physical Characteristics of Nest Sites

I measured the following characteristics of each nest box and natural cavity: tree species, tree height, box or cavity height in tree, entrance hole dimensions (height and width), and distance of nest to the nearest water. I also measured the distances of nest sites from forest edge. Internal cavity measurements (depth, length, and width of floor) were measured to the nearest cm with measuring tapes, and cavity volume and floor area were then calculated using these values.

3.3.5. Reproductive Variables

All active nest sites (boxes and cavities) were checked every 4-7 days from mid-April to July. I measured the following reproductive variables for each nest: clutch size, hatching date, nesting success, source of predation, and identity of the incubating female. Clutch size refers to the number of eggs in the nest, which may have been laid by more than one female. Nests were tallied as successful if one or more eggs hatched.

3.3.6. Conspecific Nest Parasitism

Conspecific nest parasitism occurs frequently in populations of goldeneyes and Bufflehead (Gauthier 1985, Eadie 1989). Detailed information on daily egg-laying rates in each nest site was not collected in this study, and therefore, I was unable to calculate accurate nest parasitism rates. However, since females of both species typically lay 8-10 eggs (Gauthier 1985, Thompson 1996), I considered nests containing more than 10 eggs to have been parasitised. Although this technique likely produced conservative estimates of nest parasitism, it allowed us to compare minimum estimates between nest types.

3.3.7. Statistical Analyses

Average values of physical characteristics of nest sites did not differ significantly between years, so data were pooled. Two-tailed independent *t*-tests were used to compare the physical characteristics of box nests to cavity nests. Within a species, and nest type, there was no annual variation in clutch sizes, so data were pooled across years for analysis of each nest type. Hatching dates did not differ between box nests and cavity nests among the three years, and these data were also pooled across years for subsequent analysis. Multiway contingency data analysis (PROC CATMOD, SAS 2000) was used to examine associations among nest fate, nest type, and year. Backward elimination techniques were used to select the best log-linear model during this analysis. Within-year comparisons of nest fates between nest types were made using chi-square tests with Bonferroni adjustments ($\alpha = 0.05/n$ comparisons). Values reported are means ± SE. A significance level of $P < 0.05$ was used throughout the analyses.

3.4. RESULTS

3.4.1. Physical Characteristics of Nest Site

Physical characteristics of box nests and cavity nests are presented in Table 3.2. Natural nest cavities used by goldeneyes were twice as far from water ($t_{213} = -5.1$, $P < 0.001$), farther from forest edge ($t_{213} = -7.9$, $P < 0.001$), and located higher in trees ($t_{213} = -18.1$, $P < 0.001$) than box nests. The mean nest volume of goldeneye cavities was only about half the size of box nests ($t_{213} = 10.6$, $P < 0.001$), as was the floor area ($t_{213} = 20.5$, $P < 0.001$).

Nest cavities used by Bufflehead were also higher in trees ($t_{146} = -11.7$, $P < 0.001$) than box nests (Table 3.2.). Although Bufflehead cavity nests were located farther from water than box nests ($t_{146} = -2.8$, $P < 0.01$), distances from the forest edge were similar ($t_{146} = -1.6$, $P < 0.1$). Bufflehead cavity nests had a smaller nest site volume ($t_{146} = 16.3$, $P < 0.001$) and floor area ($t_{146} = 16.9$, $P < 0.001$) than box nests.

For both species, active natural cavities were most commonly found in aspen and Douglas-fir trees. Both species most commonly used nest boxes on aspen trees.

3.4.2. Clutch Sizes

Mean clutch sizes of goldeneye were significantly larger in box nests than in cavity nests (box nests: 10.5 ± 0.2 eggs; cavity nests: 7.5 ± 0.4; $t_{273} = 6.3$, $P < 0.001$), but for Bufflehead, mean clutch sizes were similar in both nest types (box nests: 8.4 ± 0.3 eggs; cavity nests: 8.5 ± 0.2; $t_{216} = -0.6$, $P < 0.5$).

Twenty-five percent of goldeneye box nests contained more than 10 eggs, compared to only 5% of cavity nests, indicating that nest parasitism was higher in box nests ($\chi^2_1 = 8.9$, $P < 0.01$, $n = 275$). For Bufflehead, only 8% of nests in boxes had more than 10 eggs, compared to 17% of nests in cavities ($\chi^2_1 = 4.5$, $P < 0.03$, $n = 218$).

3.4.3. Hatching Dates

There were no differences between mean Julian hatching dates of nests in boxes compared to nests in cavities, for either species. The mean Julian hatching date for goldeneye eggs in box nests was 165.9 ± 1.4 (14 June) and 166.4 ± 2.4 (15 June) in cavity nests ($t_{191} = -0.3$, $P = 0.6$). Bufflehead had mean Julian hatching dates of 169.3 ± 0.6 (18 June) for eggs in box nests, and 169.5 ± 1.6 (18 June) for eggs in cavity nests ($t_{109} = -0.2$, $P = 0.7$).

3.4.4. Nest Fates

The log-linear model examining associations between Barrow's Goldeneye nest fate, nest type, and year showed interactions between nest fate and nest type ($\chi^2_2 = 7.3$, $P < 0.05$, $n = 305$), and nest fate and year ($\chi^2_2 = 12.4$, $P < 0.01$, $n = 305$). Further analysis indicated that nest fates did not differ significantly among box nests throughout the study, nor did they differ among cavity nests between 1997 and 1998 (Figure 3.1a). However, nesting success in cavities dropped from 86% in 1997 and 78% in 1998 to 54% in 1999, as a result of higher levels of nest predation. Goldeneye nests in natural cavities had significantly higher nesting success rates than those in boxes in 1997 and 1998 (1997: $\chi^2_2 = 7.7$, $P < 0.02$, $n = 91$; 1998: $\chi^2_2 = 8.6$, $P < 0.01$, $n = 106$). However, no differences in nest fates were detected in 1999 ($\chi^2_2 = 1.2$, $P = 0.5$, $n = 107$; Figure 3.1a).

For Bufflehead, the log-linear model showed an interaction between nest fates and year ($\chi^2_2 = 14.8$, $P < 0.001$, $n = 225$). This was a result of increased predation rates experienced by all

Bufflehead nests (boxes and cavities) in 1999 (compared to 1997: $\chi^2_2 = 8.0$, $P < 0.05$, $n = 150$; compared to 1998: $\chi^2_2 = 9.9$, $P < 0.01$, $n = 182$; Fig 2a). Within each of the three years, nest fates of Bufflehead nests in boxes and cavities did not differ (1997: $\chi^2_2 = 0.2$, $P = 0.9$, $n = 43$; 1998: $\chi^2_2 = 1.1$, $P = 0.6$, $n = 75$; 1999: $\chi^2_2 = 5.1$, $P = 0.07$, $n = 107$).

Goldeneye nests in boxes were less successful than Bufflehead nests in boxes through all three years of the study, (1997: $\chi^2_2 = 6.5$, $P < 0.05$, $n = 100$; 1998: $\chi^2_2 = 10.9$, $P < 0.01$, $n = 103$; 1999: $\chi^2_2 = 7.6$, $P < 0.05$, $n = 99$). There were no differences in cavity-nest fates between the two species over the three years (1997: $\chi^2_2 = 1.8$, $P = 0.4$, $n = 32$; 1998: $\chi^2_2 = 0.4$, $P = 0.8$, $n = 78$; 1999: $\chi^2_2 = 1.3$, $P = 0.5$, $n = 115$) and both species experienced markedly higher levels of cavity predation in 1999 (Figures 1a and 2a).

3.4.5. Sources of Predation

The types of predators that preyed on goldeneye nests in boxes differed from those responsible for cavity predation, in all three years (1997: $\chi^2_2 = 37.0$, $P < 0.001$, $n = 38$; 1998: $\chi^2_2 = 9.4$, $P < 0.05$, $n = 42$; 1999: $\chi^2_2 = 7.8$, $P < 0.05$, $n = 43$). The major predator on box nests was Black Bears (*Ursus americanus*; Figure 3.1b). Hair samples found at the entrances of depredated box nests showed that the main small mammal predators were Red Squirrels (*Tamiasciurus hudsonicus*), Pine Marten (*Martes americana*), and Fisher (*Martes pennanti*). European Starlings (*Sturnus vulgaris*) also destroyed goldeneye eggs, apparently in attempts to usurp the nest site. Bears did not prey on cavity nests, but small mammals and starlings were important (Figure 3.1b). Small mammal predation increased in cavities in 1999. Aside from Black Bear predation on box nests, all other predators had similar effects on both nest types in 1998 and 1999.

Predation on Bufflehead nests (boxes and cavities) was low in 1997 ($n = 4$ of 43 nests) and 1998 ($n = 8$ of 75 nests) with the main predators being bears, squirrels, and starlings (Figure 3.2b). There were no significant differences in the types or levels of predation between Bufflehead box nests and cavity nests for these two years. In 1999, predation levels increased in both box nests and cavity nests ($n = 32$ of 107 nests, with 26 depredated cavity nests), and small mammals were responsible for nearly all depredations (Figure 3.2b).

3.5. DISCUSSION

There were marked differences in the clutch size, nesting success, and patterns of predation of Barrow's Goldeneye nesting in boxes versus those in natural cavities, but few differences for Bufflehead. In these respects, studies of Barrow's Goldeneye that use nest boxes are not representative of birds nesting in natural cavities, whereas those of Bufflehead are more likely to be so.

3.5.1. Nest Site Location and Predation

The most obvious physical difference between Barrow's Goldeneye box nests and natural cavity nests is their degree of conspicuousness to predators and parasitising conspecifics. Goldeneye boxes were concentrated in highly visible locations such as on trees at water or forest edge. Cavity nests, on the other hand, were often abandoned Pileated Woodpecker (*Dryocopus pileatus*) cavities, which were more dispersed throughout the forest interior and concealed under dense canopy cover. For goldeneye, the higher conspicuousness of nest boxes to predators may have been responsible for the higher rates of predation and nest parasitism (see below). The most common nest-box predators were bears and small mammals (Red Squirrels, Fishers, and Pine Martens) and the placement of nest boxes on forest and water edge allowed for easy detection by these animals. Furthermore, cavity nests were significantly higher in the nest tree than box nests, which may have deterred some of the small mammal predators. The height of the nest site within a tree influences the nesting success of many cavity-nesting species. Female Common Goldeneye and Wood Ducks prefer higher boxes and experience lower predation rates (Prince 1968, Dow and Fredga 1985). Studies of Tree Swallows (*Tachycineta bicolor*; Rendell and Robertson 1989), European Starlings, Blue Tits (*Parus caeruleus*), and Marsh Tits (*P. palustris*; Nilsson 1984b) also show that predation rates decrease with increasing nest height.

The fates of Bufflehead nests in cavities were similar to those of box nests, perhaps because the physical characteristics of the two nest types were not significantly different. For example, Bufflehead cavity nests and box nests were located at equal heights in trees and equal distances from the forest edge, and therefore were equally exposed to predators.

Bufflehead nest sites (boxes and cavities) may experience lower rates of predation than Barrow's Goldeneye sites because their smaller entrance area may exclude medium-size mammal species. Cavity size is an important variable affecting species occupancy, and individuals that select smaller holes may experience reduced predation risk and competition with larger species (Moed and Dawson 1979, Peterson and Gauthier 1985).

Most comparative studies of box versus cavity nesters have found lower rates of predation and higher fledging success in box nests than in natural sites; examples include the European Starling, Great Tit, Blue Tit, Nuthatch (*Sitta europea*; Nilsson 1975), and Tree Swallow (Robertson and Rendell 1993). These results are opposite to ours, which I suspect is due primarily to the presence of bears at my site, a major box predator in my study that has not been reported by others. Bears may be unusual nest box predators and thus limit the generality of this result. An earlier study of Common and Barrow's Goldeneye, located only 70 km south-east of my study, found little to no bear depredation of box nests (J. Eadie, pers. comm.).

3.5.2. Clutch Size

Clutches in Barrow's Goldeneye box nests were significantly larger than in cavity nests. Two plausible explanations exist for this result. First, my results suggest that increased levels of conspecific nest parasitism may occur in boxes (also see Eadie 1989), and this may be attributed to their increased degree of conspicuousness. Second, all natural cavities were smaller than boxes and thus the larger basal area of boxes may allow for larger clutches (Nilsson 1984a).

The more likely explanation is that larger clutch sizes in box nests resulted from increased levels of conspecific nest parasitism (Eadie 1989). Like predators, parasitic females can more easily detect artificial nest sites, and my conservative estimates indicated parasitism to be 20% higher in box nests. Previous studies of goldeneye estimated nest parasitism to be 8% higher in box nests than in cavity nests, and 15-61% higher in Wood Duck box nests (Eadie et al. 1998). Other species that have been reported to experience higher conspecific brood parasitism in box nests than in cavity nests include Black-bellied Whistling Ducks (*Dendrocygna autumnalis*; Delnicki 1973), Eastern Bluebirds (Gowaty and Bridges 1991), Barn Swallows (Moller 1987), and European Starlings (Evans 1988).

This is a concern for managers because high levels of parasitic egg-laying in Wood Duck box nests has frequently led to lower overall reproductive success at the population level (Haramis and Thompson 1985, Semel et al. 1988). In an extreme case, Semel et al. (1990) found a negative exponential relationship between the number of eggs laid and overall nesting success across six separate Wood Duck populations.

Correlations between floor area and clutch size have been shown in several passerine species, with authors suggesting that basal area may limit the clutch size that can be incubated efficiently (van Balen 1984, Gustafsson and Nilsson 1985). However, nest site volume had no effect on the clutch sizes of Bufflehead (Gauthier 1988), Common Goldeneye (Eriksson 1979), Bluebirds (Moller 1982), Plain Titmouse (*Parus inornatus*), House Wren (*Troglodytes aedon*), and Ash-throated Flycatcher (*Myiarchus cinerascens*; Purcell et al. 1997). Cavity volume may also influence crowding factors and induce females to lay smaller clutches (Karlsson and Nilsson 1977, van Balen 1984, Robertson and Renell 1990). However, since goldeneye and Bufflehead are determinant egg layers and their precocial young remain in the nest site for only two days, crowding is less likely to affect their clutch sizes.

Several other hypotheses also appear unlikely. There is often a negative correlation between laying date and clutch size, but I found no significant differences in initiation dates between boxes and cavities. Female age differences in the different nest types could also affect clutch size (Gauthier and Smith 1987) but I have little information on this as only a few females were of known age in my study. However, I would expect to see timing differences (e.g., nest initiation dates) if females nesting in boxes and cavities differed dramatically in their ages. No differences were seen in this study. Clutch sizes did not vary significantly among ponds, and therefore it is unlikely that variation in local food productivity levels are a factor.

It therefore would seem that nest site characteristics such as nest type and location (e.g., conspicuous boxes), and perhaps basal area and volume influence clutch sizes for Barrow's Goldeneye but not for Bufflehead. Factors such as laying date, female age, food availability, and predation risk are likely to be less important.

For Barrow's Goldeneye, my general findings are similar to those of van Balen et al. (1982), Nilsson (1984a), and Moller (1989) for other species, in that the breeding ecology in artificial nest structures differs considerably from that in natural cavities. In contrast, I recorded few physical or biological differences for Bufflehead. Unnaturally low nest predation in nest boxes of other studies appears to be an artifact of nest box designs (Moller 1989). In my study the design and placement of goldeneye nest boxes contributed to artificially high predation rates.

3.6. MANAGEMENT RECOMMENDATIONS

Nest boxes are an important management tool for species experiencing drastic population declines, particularly in areas under intensive forest harvesting, where the availability of natural cavities is limited (Eadie et al. 1998). Nest-box programs are normally considered an effective conservation tool, particularly for cavity-nesting waterfowl (Eriksson 1982, Fredga and Dow 1984, Savard 1986). However, there may be hidden costs to these programs. Extrapolating from my results, I speculate that nest-box programs may in fact create population sinks for Barrow's Goldeneye, attracting large numbers of breeding birds that experience unnaturally high levels of predation and parasitism. As such, recommendations for future nest-box programs under similar circumstances include installing predator guards (specifically, bear deterrents) and placing boxes in less conspicuous locations, farther from ponds or forest edges, in locations similar to those of natural cavities. In my case, preventing bear predation of Barrow's Goldeneye nest boxes would have returned success rates to levels similar to those of natural cavities. Nest parasitism would still continue in conspicuous boxes along edges, but this is less of a concern as abandonment rates, presumably caused in part by egg dumping (as suggested by Eadie 1989), were low. Therefore, I do not consider nest parasitism itself to have had a large effect on the nesting success of Barrow's Goldeneye nests in this study.

On a different note, increasing goldeneye abundance may have a considerable effect on the rest of the waterfowl community considering their extremely aggressive territorial behavior, particularly towards congeners such as Bufflehead (Savard 1986), as well as predicted increases in competition for nest sites with other cavity-nesting species (see Nilsson 1984a, Robertson and Rendell 1990). Although well intentioned, nest-box programs have often taken place without consideration for the entire bird community. Few studies have examined the effects of increasing the abundance of selected species on the breeding ecology of other species (Hogstad 1975, Bock et al. 1992). Clearly, more comparative studies involving nest box programs are warranted.

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Table 3.1. Nest box dimensions and number of boxes made available each year to Barrow's Goldeneye and Bufflehead at Riske Creek, British Columbia, Canada, 1997-1999.

Species	Number of boxes Available	Length x Width x Height	Volume (L)	Floor Area	Entrance Size (cm)
Barrow's	139	39 x 25 x 26	25.4	650	11 x 13
Goldeneye	71	50 x 25 x 28	35	700	11 x 10
	24	41 x 25 x 26	26.7	650	12 x 12
Bufflehead	43	28 x 15 x 15	6.3	225	7 x 7
	54	32 x 18 x 20	11.5	360	8 x 8
	21	28 x 18 x 18	9.1	324	8 x 8

Table 3.2. Physical characteristics of active Barrow's Goldeneye and Bufflehead nest sites in nest boxes and cavities, 1997-1999. Available but unused nest sites were not included in the analysis. Nest sites used more than once were included only once.

Characteristic	**Goldeneye**				**Bufflehead**			
	Cavity		**Nest Box**		**Cavity**		**Nest Box**	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
n	41		174		100		46	
Tree species used (%)								
Aspen	72	--	66	--	81	--	91	--
Douglas-fir	23	--	9	--	12	--	2	--
Lodgepole pine	5	--	22	--	7	--	7	--
White spruce	0	--	3	--	0	--	0	--
Tree height (m)	26.2	1.2	13.3	0.3	14.6	0.8	13.6	0.7
Nest height (m)	12	0.8	3.8	0.9	6.6	0.4	3.9	0.2
Distance from water (m)	89.7	13	41.3	3.4	37.1	5.5	24.5	4.5
Distance from edge (m)	13.7	3.1	3.4	0.5	3.5	1	2.6	0.7
Entrance size (cm)	14 x 12	0.3 x 0.2	11 x 12	0.2 x 0.2	9 x 9	0.1 x 0.1	8 x 8	0.1 x 0.1
Nest site volume (L)	16	0.1	28.6	0.4	5.5	0.1	8.7	0.1
Nest floor area (cm^2)	299	16	641	6	189	4	293	4

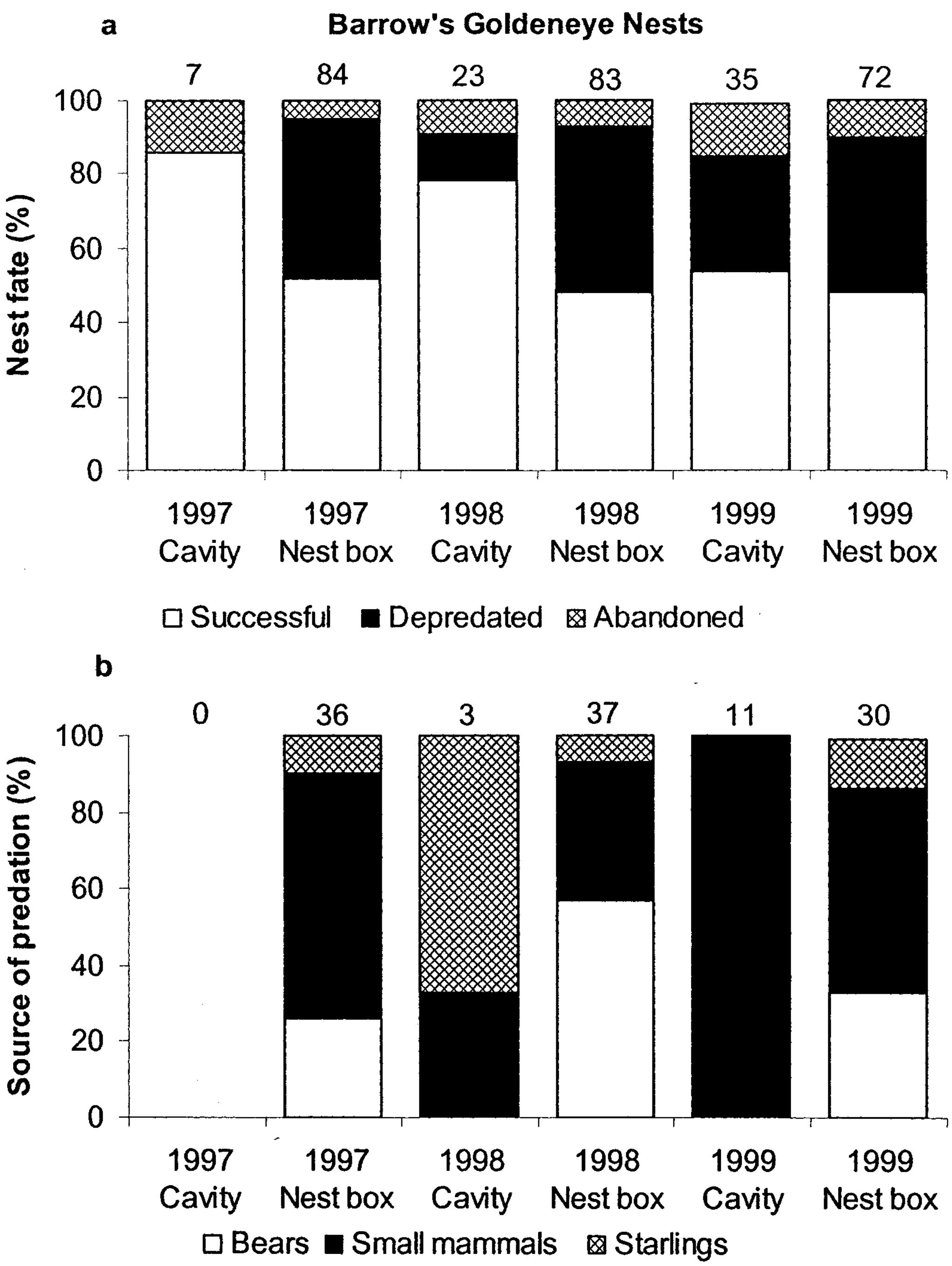

Figure 3.1. (a) Fates of Barrow's Goldeneye nests (successful, depredated, or abandoned) in boxes and natural cavities and (b) sources of nest predation from 1997-1999, at Riske Creek, British Columbia, Canada. Numbers above columns represent sample sizes.

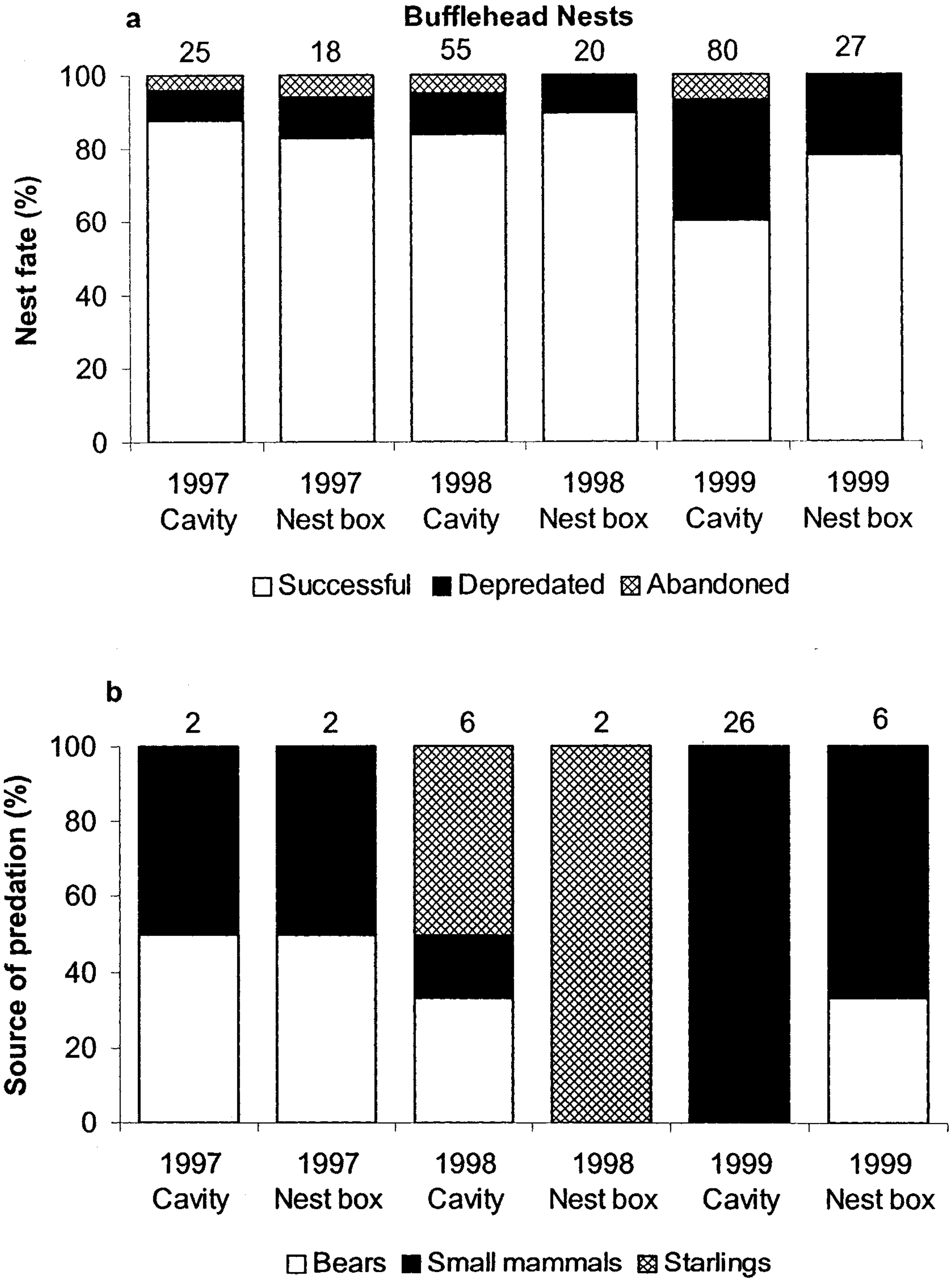

Figure 3.2. (a) Fates of Bufflehead nests (successful, depredated, or abandoned) in boxes and natural cavities and (b) sources of nest predation from 1997-1999, at Riske Creek, British Columbia, Canada. Numbers above columns represent sample sizes.

Chapter 4

LAKE SELECTION BY BARROW'S GOLDENEYE AND BUFFLEHEAD BREEDING PAIRS AND FEMALES WITH BROODS

4.1. Abstract: Factors influencing initial lake selection by waterfowl breeding pairs and brood-rearing females are poorly understood but are likely influenced by a complex of factors including the lake's physical characteristics, water chemistry, aquatic vegetation, food supply, and density of competitors and predators. The quality of a lake selected by breeding females and broods likely affects fitness. The purpose of this study was to assess the role of biotic and abiotic characteristics in lake selection by breeding Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) in central British Columbia, Canada. Lake size was the most important factor influencing lake occupancy by both species' breeding pairs and broods. Lake depth was also an important feature for breeding pairs, but not for broods, and the abundance of invertebrate prey influenced lake usage by goldeneye pairs and broods, but not Bufflehead. Water chemistry properties such as dissolved oxygen and specific conductivity were highly correlated to these factors and may serve as more easily measured variables for managers. The continued loss of waterfowl breeding habitat in North America has given rise to increased efforts to conserve wetland areas by preserving threatened lakes, and restoring damaged ones. To achieve these objectives, we must identify the various abiotic and biotic habitat characteristics of the lake ecosystem that influence lake selection by breeding waterfowl. Understanding the relationships between aquatic habitat characteristics, lake selection, and reproductive success is important for successful conservation and management of waterfowl populations.

4.2. INTRODUCTION

Breeding waterfowl require access to two essential habitat characteristics for successful reproduction: suitable nest sites and productive foraging locations. Nest site habitat selection, occurs upland from the bodies of water used by waterfowl for breeding and brood-rearing. But waterfowl also depend heavily on lakes, and thus lake selection by breeding females and broods likely affects fitness. Therefore, understanding the relationships between aquatic habitat characteristics, lake selection, and reproductive success is also important for successful conservation and management of waterfowl populations.

Factors influencing initial lake selection by breeding pairs and brood-rearing females are poorly understood but are likely influenced by a complex of factors including the lake's physical (morphometric) characteristics, water chemistry, aquatic vegetation, food supply (McNicol et al. 1987), and density of competitors and predators (Fretwell and Lucas 1970, Wiens 1989). Of the above, invertebrate prey abundance is commonly suggested to be an important factor, due largely to the high energy and protein requirements of breeding females and developing young (Eriksson 1978, Hellquist 1980, Talent et al. 1983, Paquette 1995). Because of such high nutritional demands, reproduction in birds is generally timed to match the maximum availability of food for nesting adults or developing young (Immelmann 1971). Food resources on the breeding grounds affect the timing of reproduction, as well as clutch size, egg mass and composition, and a female's ability to renest (Sedinger et al. 1995).

Therefore, lake selection by ducks should depend on an individual's ability to assess the availability of aquatic invertebrates, and females should actively sample potential brood-rearing areas prior to hatch, becoming familiar with the lakes' food supply (and other factors that may enhance brood survival; Bellrose 1976). Previous studies have documented such reconnaissance behaviors (Erikson 1978) and others have reported females moving their broods long distances (>5 km) to brood-rearing areas with higher food levels (e.g., Common Goldeneye [*B. clangula*]; Eriksson 1979, Eadie and Keast 1982, Wayland and McNicol 1994). These overland movements have an associated mortality risk, because young are particularly susceptible to predation (Ball et al. 1975, Savard 1988). Taking such risks in search of higher quality foraging areas has potentially higher fitness payoffs than remaining in areas with lower food quality and abundance.

Many previous waterfowl studies of lake selection suffer from three important drawbacks that I attempt to address in this study. Firstly, although studies consistently report correlations between lake selection and food supply, few have measured invertebrate abundance directly. Chemical and physical variables such as pH, conductivity, alkalinity, total phosphorus, lake area and depth, have frequently been used to indirectly evaluate lake food production levels (e.g., Sparling and Nalewajko 1970, Hellquist 1980, Paquette 1995, Thompson 1996); albeit, in many cases these variables have positive associations with waterfowl abundance (Patterson 1976, Murphy et al. 1984, Desgranges and Darveau 1985, Boyd and Savard 1987, Alvo et al. 1988, McAuley and Longcore 1988, Diefenbach and Owen 1989). Secondly, few studies have examined the relationship between habitat quality and reproductive success. And finally, most of these studies have dealt with only a few species of dabbling ducks, and occurred mostly in the prairie pothole regions of central Canada and the United States (Mack and Flake 1980, Godin and Joyner 1981, Talent et al. 1982, Mulhern et al. 1985).

The Cariboo Parklands of central British Columbia are one of the most productive lake systems in the province (McKelvey and Munro 1983), containing an unusually high density and diversity of water bodies (Boyd and Savard 1987). Detailed information regarding lake selection by waterfowl in this region is limited (Boyd and Savard 1987, Savard et al. 1994). Identifying and understanding the factors related to waterfowl selection and usage of lakes in this area will assist managers in recognizing and maintaining productive breeding sites. Barrow's Goldeneye and Bufflehead are particularly plentiful in central British Columbia, and although both species exploit a variety of lake habitats, they are most commonly associated with forested lakes that provide an adequate supply of nearby cavity nest sites (Kaminski and Weller 1992). Clearly, it is not only necessary to identify the habitat characteristics selected by goldeneye and Bufflehead for their nesting biology, but it is also important to determine the relationship between habitat characteristics and reproductive success.

The purpose of this study was to assess the role of biotic and abiotic characteristics, including invertebrate prey productivity, vegetation cover, water chemistry, lake morphology, and proximity of suitable nest sites, in lake selection by breeding Barrow's Goldeneye and Bufflehead in central British Columbia. In doing so I use two of the most frequently used indicators of lake selection by waterfowl: 1) presence/absence comparisons, indicating lake use, or selection, and 2) measures of the relative density of birds present, indicating intensity of use. If spatial variation in lake quality is an important determinant of egg size, offspring body size, survival, and future reproductive output (Cooch et al. 1991, Larsson and Forslund 1991), then females should not only be assessing the quality of a potential nest site, but also the quality of brood-rearing areas in attempts to increase the likelihood of duckling survival and future fitness. I, therefore, predict that lake usage by goldeneye and Bufflehead breeding pairs and broods is influenced by a combination of three main factors: aquatic invertebrate prey abundance, the density of other breeding pairs, and the proximity of suitable nesting cavities.

4.3. METHODS

4.3.1. Study Area

This study took place at Riske Creek, B.C., from April-August 1997-2000. General details of the study area are provided in Chapter 1.

4.3.2. Population Surveys

Weekly ground-based surveys of Barrow's Goldeneye and Bufflehead were conducted on the lakes from mid-April to mid-August, encompassing the egg-laying, incubation, and brood-rearing periods, and were used to categorize lakes as used or unused by breeding pairs (before hatch) and by females with broods (after hatch). All lakes were also opportunistically surveyed at least once more per week on an ad hoc basis. All birds observed were counted and classified based on age (adult, juvenile, or duckling size class), gender, and whether they were alone, paired, or in a group. Approximately 70% of adult female goldeneye, and 30% of adult female Buffleheads were individually marked with nasal tags. I used two measures of waterfowl use of lakes: 1) presence/absence on surveys, and 2) densities of breeding pairs and broods. Lakes were classified as 'unoccupied' if no pairs, or broods, were seen on that pond throughout the surveys. Conversely, a lake was deemed to be 'occupied' if at least one established breeding pair or brood was seen on that lake in more than one survey.

Breeding pair densities and brood densities were calculated two ways for each lake: by dividing its annual mean number of breeding pairs, or broods, by 1) the total surface water area of the wetland, and 2) the area of water 0-2 m deep. Savard et al. (1994) highlight conflicting results and interpretation problems related to the area unit used to calculate bird density (e.g., using total area, area of water less than 2 m in depth, and less than 1 m in depth). Although the majority of previous studies have used total area of water to calculate density, Savard et al. (1994) clearly show that using area of water 0-2 m deep may be more appropriate when trying to relate waterfowl densities to wetland characteristics, at least with respect to foraging locations or food requirements.

4.3.3. Lake Habitat Characteristics

Lake habitat characteristics were measured for comparisons between 1) lakes occupied and unoccupied by goldeneye and Bufflehead, and 2) densities of these birds on occupied lakes. Over the 4 years of this study, a total of 60 occupied, and 15 unoccupied lakes were examined (15 occupied lakes per year, 1997-2000, and 5 unoccupied lakes per year, 1998-2000). The unequal number of occupied and unoccupied lakes sampled, and in some cases, unequal sampling efforts (e.g., aquatic invertebrate sampling; see below), were a result of other study objectives and methodologies not outlined here (see Chapter 5).

4.3.3.1. *Aquatic Invertebrate Sampling*

I indexed the benthic chironomid larvae and nektonic invertebrate biomass in lakes occupied and unoccupied by breeding pairs and broods each year, to compare their respective levels of food abundance within, and between, years. The lakes ranged from low to high invertebrate biomass as previously determined by Boyd and Smith (1989). Occupied lakes were sampled four times a year (in June and July), and unoccupied lakes were sampled twice (15 June and 15 July).

.The invertebrate species analyzed were those reported in previous studies to be components of goldeneye (Barrow's and Common) and Bufflehead duckling diets (see Eriksson 1976, Sedinger 1992, Gauthier 1993, Poysa and Virtanen 1994, Eadie et al. 1995). These included chironomid larvae, amphipods (*Gammarellus*), dragonfly larvae (Anisoptera), damselfly larvae (Zygoptera), caddisfly larvae (Trichoptera), mayfly larvae (Ephemeroptera), water boatmen (Corixidae), aquatic beetles (Coleoptera), and others (see Eriksson 1976, Eadie et al. 1995) . Benthic dwelling chironomid larvae were sampled using a benthic coring device (Swanson 1978), whereas nektonic invertebrates were sampled with water column activity traps (Murkin et al. 1983).

Four sampling stations were randomly established within each lake. At each station, water column activity traps were placed 45 cm below the water surface on poles located at 0.5 m and 1.0 m water depths. Four traps were set at each station (2 per pole, 16 per lake, per sampling period) for 24 hours and then samples were bagged and analyzed in the lab. Macroinvertebrates were identified to order, family, or genus, and separated into 5 mm size classes according to body length, and counted. For each taxon, and each size class, a subsample of >100 randomly chosen individuals was oven-dried at 105 °C for 24 hours and then weighed to the nearest 0.01 g to calculate mean dry-weight biomass. These dry weights were then used to calculate mean biomass values across taxa, per sample, and then summed for total biomass.

Chironomids were sampled at each station, at a water depth of 1.0 m to correlate with the generalized feeding zone of goldeneye. Twenty benthic core samples were taken at each station during each sampling period (80 per lake). Care was taken to not sample previously disturbed sites. Mud cores were bagged and analyzed in the lab by placing each sample into sucrose solutions (specific gravity 1.12 units), which floated the invertebrates to the surface for ease of counting. Randomly selected samples were periodically double-checked by sifting through them in dissecting trays, to ensure accurate counts. Body lengths were measured and individuals were tallied in 5 mm size classes. One hundred randomly chosen individuals from each size class were oven-dried (as per above) to calculate mean dry-weight biomass values. Benthic core samples were not taken in 2000 because results from 1997-1999 were highly correlated to the activity trap results ($r = 0.7$, $P < 0.001$, for all three years combined).

Mean invertebrate biomass values were calculated for each sampling session, for each lake. For most lakes, activity trap results showed little variation between sampling sessions within a year and, therefore, data were pooled for each lake, within a year, and an annual average biomass value was calculated. Chironomid samples showed much more variation between sampling times, within each lake, but Spearman's rank correlations were highly significant each year (1997: $r_s = 0.9$, $P < 0.0001$; 1998: $r_s = 0.8$, $P < 0.0001$; 1999: $r_s = 0.6$, $P < 0.01$;), indicating that the relative rankings of each lake varied little between sampling sessions, within a year. This suggests that there was more variation among lakes than within. Therefore, chironomid samples were also pooled within a lake each year, and an annual average biomass value was calculated and used for subsequent analyses.

4.3.3.2. *Vegetation Sampling*

Submergent vegetation sampling took place during one week in late July of 1999 and 2000. Percent cover of submergent vegetation was estimated for each lake using 1 m x 1 m quadrates placed at 1 m water depths. Twenty randomly located plots were measured for each lake. Quadrats were divided into 10 equal subplots and the percent cover of each plant species present was estimated to the nearest 5%. An estimate of total percent plant cover was obtained for each quadrate by adding the individual values of all plants present. The mean value of the 20 quadrats was calculated for each lake and used in subsequent analyses. Estimates of percent forest cover within 100 m of the shoreline were obtained for each lake from Boyd and Savard (1987), and checked for any major changes that may have occurred since 1987.

4.3.3.3. *Water Chemistry Sampling and Physical Characteristics*

I measured pH, dissolved oxygen, and conductivity (TDS) levels in all study lakes in July, 1999-2000, using a Corning Checkmate II water chemistry meter (Corning Inc. 1999). Twenty measurements were taken for each variable, at random locations, twice a year, and mean values for each lake were calculated within years. Measurements were taken at the water surface, from kayaks, and were read directly from the chemistry meter. Lake area (both total lake area, and 0-2 m deep area) and mean lake depth measurements were taken from Boyd and Savard (1987).

4.3.3.4. *Counting Nest Sites*

Thorough searches were conducted through forest stands surrounding all lakes to determine the number of natural cavities located within 100 m of each lake. Searches were performed along ad hoc transects with 2-4 persons spread out at ca. 10 m distances. Further details of nest searches are provided in Chapters 2 and 3. Nest boxes located at each lake were also counted.

4.3.4. Statistical Analysis

Lake habitat characteristics were analyzed in relation to two response variables: 1) the occurrence of ducks on a lake (presence or absence) and 2) the density of breeding pairs and broods present. Habitat characteristics of occupied and unoccupied lakes were pooled by lake, over the 2-4 years, and compared using two-sided *t*-tests. Correlations were also performed between all habitat variables. Analysis of variance (ANOVA) and Spearman's rank correlations were used to examine aquatic invertebrate data within and among lakes, within and among years. Kendall's concordance correlation was used to compare annual rankings of activity trap means to chironomid means.

Univariate and multivariate analysis was performed using a Generalized Linear Model (GLM) with a logit link function, in SPLUS (Statsci 2000). Lake occupancy was treated as a dichotomous dependent variable (1 if occupied, 0 if unoccupied) and habitat characteristics as independent explanatory variables. Backward elimination procedures were followed when fitting logistic regression equations and chi-squared tests were used to test for significance of the variables added to the model. Full (maximum) models were used first to avoid making Type II (false negative) errors, including all variables, possible interactions and specified quadratics. Criteria for selecting the best predictive model by comparing the models' P values, R^2 values, and simplicity (parsimony).

Linear regressions (univariate and multivariate) were used to examine relationships between breeding pair and brood densities and the various lake characteristics. Simple correlations were also used to examine relationships between habitat characteristics and waterfowl densities.

All levels of significance were 95% ($\alpha = 0.05$) unless Bonferroni adjustments were necessary, in which case the significance level was determined by dividing $\alpha = 0.05$ by the number of comparisons made.

4.4. RESULTS

4.4.1. Lake Habitat Characteristics

Mean values and ranges for the various physical, chemical, and biological habitat measurements are shown in Table 4.1., and pairwise correlations between these are presented in Table 4.2. Lake size, mean lake depth, and percent forest cover within 100 m of the shoreline were all positively correlated. Mean activity trap biomass was positively correlated to mean benthic core biomass (chironomid larvae biomass), and dissolved oxygen, but negatively associated with conductivity values. Both activity trap biomass and chironomid biomass were negatively related to percent forest cover. There were no significant relationships between percent cover of submergent vegetation and aquatic invertebrate biomass, nor between submergent vegetation and any of the water chemistry measurements.

Representatives of 14 species of aquatic invertebrates were found in the activity traps, but samples were typically dominated by amphipods, tricoptera, zygoptera, and dytiscidae adults and larvae (Table 4.3.). Mean invertebrate biomass values varied widely among lakes, and Spearman's rank correlation analysis showed consistent annual rankings of lakes for both activity trap ($r_s = 0.9$, $P < 0.001$), and benthic core samples ($r_s = 0.8$, $P < 0.001$). Therefore a lake's relative productivity level was predictable between years. Concordance correlation showed a lake's relative ranking for activity trap biomass was very similar to its ranking for benthic core samples within years (1997: $W = 0.7$, $P < 0.001$; 1998: $W = 0.7$, $P < 0.001$; 1999: $W = 0.6$, $P < 0.001$), and across years ($W = 0.6$, $P < 0.001$).

4.4.2. Lake Use by Breeding Pairs

Of the 132 lakes surveyed annually, 70% were occupied, on average, each year by Barrow's Goldeneye (74%, 69%, 68%, and 70% in 1997-2000). Lakes used by Barrow's Goldeneye breeding pairs had more aquatic invertebrates, were larger in size, deeper, and had a greater number of nest sites available within 100 m of shoreline (Table 4.4.). The multivariate model that best predicted lake occupancy by goldeneye pairs contained three of these parameters: mean activity trap biomass (Wald Statistic (WS_{78}) = 4.2, $P = 0.04$), lake size ($WS_{78} = 5.3$, $P = 0.02$), and mean lake depth ($WS_{69} = 3.7$, $P = 0.05$). However, lake size and mean lake depth were significantly correlated ($r = 0.6$, $P < 0.01$). No significant interactions, nor higher order polynomials were found. Logistic regression found no relationships between lake occupancy by goldeneye pairs and mean chironomid biomass, percent submergent vegetation, nor any of the water chemistry measurements.

Similar results were found for Bufflehead. Of the 132 lakes, an average of 85% were occupied by Bufflehead over the 4 years (81%, 81%, 82%, and 89% in 1997-2000). Lake occupancy by Bufflehead was positively related to lake size, mean lake depth, and the number of nest sites available within 100 m of shoreline (Table 4.5.). However, in contrast to goldeneye, occupancy by Bufflehead was not related to mean activity trap biomass. There was also no relationship between the presence of Bufflehead and mean chironomid biomass, percent submergent vegetation, or any of the water chemistry measurements. The only significant multivariate model included lake size ($WS_{78} = 1.5, P = 0.2$) and mean lake depth ($WS_{69} = 1.1, P = 0.3$), and accounted for 16% of the variation ($WS_{78} = 6.6, P = 0.05$).

4.4.3. Lake Use by Females with Broods

Lake use by goldeneye females with broods was positively associated with mean activity trap biomass, and lake size, but negatively related to submergent vegetation cover (Table 4.4.). A logistic regression model containing mean activity trap biomass ($WS_{78} = 0.4, P = 0.5$), lake size ($WS_{78} = 0.03, P = 0.8$), mean lake depth ($WS_{69} = 1.1, P = 0.3$), and number of nest sites within 100 m ($WS_{78} = 5.5, P = 0.01$) explained 47% of the variation in lake occupancy by goldeneye broods ($WS_{78} = 24.5, P = 0.001$).

Bufflehead females with broods were positively associated with lake size only (Table 4.5.). Although significant differences were not detected, Bufflehead broods were more commonly found on lakes that had less chironomid biomass, less submergent vegetation, lower levels of dissolved oxygen, and higher conductivity (Table 4.5.). A multivariate model containing mean activity trap biomass ($WS_{78} = 3.1, P = 0.07$), lake size ($WS_{78} = 11.1, P = 0.001$), and mean lake depth ($WS_{69} = 0.2, P = 0.7$), explained 48% of the variation ($WS_{78} = 40.8, P = 0.001$).

4.4.4. Breeding Pair Densities and Habitat Characteristics

The density of breeding goldeneye pairs, using total water area, was positively correlated with mean activity trap biomass ($t_{58} = 3.3, P < 0.01$; Figure 4.1a), and dissolved oxygen levels ($t_{28} = 2.5, P < 0.02$), and negatively related to lake size ($t_{58} = -4.1, P < 0.001$), and conductivity ($t_{28} = -2.6, P < 0.01$; Table 4.6.). No linear relationship was found with chironomid biomass (Figure 4.2a). A multivariate model containing mean activity trap biomass ($t_{58} = 4.1, P < 0.001$), lake size

($t_{58} = -2.7$, $P < 0.01$), and mean lake depth ($t_{49} = 2.5$, $P < 0.01$), explained 33% of the variation ($F_{3,56} = 9.3$, $P < 0.001$).

The density of breeding goldeneye pairs, using area of water 0-2 m deep, was positively correlated to mean lake depth only ($t_{49} = 4.5$, $P < 0.001$; Table 4.7.). No linear relationships were found with activity trap (Figure 4.1b), nor chironomid (Figure 4.2b) biomass. However, a multivariate model containing mean activity trap biomass ($t_{58} = 1.1$, $P = 0.3$), mean chironomid biomass ($t_{43} = 0.9$, $P = 0.4$), lake size ($t_{58} = -4.7$, $P < 0.001$), mean lake depth ($t_{49} = 5.9$, $P < 0.0001$), and percent submergent vegetation ($t_{28} = -1.2$, $P = 0.2$), explained 67% of the variation ($F_{5,55} = 9.7$, $P < 0.001$).

Bufflehead pair densities were positively related to percent cover of submergent vegetation ($t_{28} = 2.1$, $P < 0.05$), and goldeneye pair densities ($t_{58} = 6.1$, $P < 0.001$; Figure 4.3a), and negatively related to lake size ($t_{58} = -2.0$, $P < 0.05$), pH ($t_{28} = -2.1$, $P < 0.05$), and conductivity ($t_{28} = -2.0$, $P < 0.05$; Table 4.6.). There were no relationships between Bufflehead pair densities and mean activity trap biomass ($t_{58} = 0.2$, $P = 0.9$; Figure 4.4a), mean chironomid biomass ($t_{43} = 0.2$, $P = 0.8$; Figure 4.5a), nor mean lake depth ($t_{49} = 0.9$, $P = 0.3$). A multivariate model containing lake size ($t_{58} = -2.8$, $P < 0.01$), mean activity trap biomass ($t_{58} = 0.9$, $P = 0.3$), mean chironomid biomass ($t_{43} = 1.9$, $P = 0.06$), and percent cover of submergent vegetation ($t_{28} = 2.5$, $P < 0.05$), explained 37% of the variation ($F_{4,56} = 5.4$, $P < 0.001$).

There were no univariate relationships between Bufflehead pair densities and wetland habitat characteristics, when densities were expressed as 0-2 m area (Table 4.7.). However, a multivariate model containing lake size ($t_{58} = -3.3$, $P < 0.01$), mean lake depth ($t_{49} = 2.5$, $P < 0.05$), mean activity trap biomass ($t_{58} = 0.4$, $P = 0.7$), mean chironomid biomass ($t_{43} = 0.64$, $P = 0.5$), and percent cover of submergent vegetation ($t_{28} = 0.01$, $P = 0.9$), explained 37% of the variation ($F_{5,55} = 2.8$, $P < 0.05$). The results of this model were nearly identical to the model for Bufflehead pair densities expressed as total water area.

4.4.5. Brood Densities and Habitat Characteristics

Univariate linear regression indicated positive associations between goldeneye brood densities (using total water area) and mean activity trap biomass ($t_{58} = 4.5$, $P < 0.001$; Figure 4.6a), mean chironomid biomass ($t_{45} = 2.9$, $P < 0.01$; Figure 4.7a), goldeneye breeding pair densities ($t_{58} = 6.8$, $P < 0.001$), and dissolved oxygen levels ($t_{28} = 2.6$, $P < 0.01$). Negative univariate associations were found with lake size ($t_{58} = -3.9$, $P < 0.001$), pH ($t_{28} = -1.6$, $P = 0.05$), and conductivity ($t_{28} = -2.6$, $P < 0.05$). Goldeneye brood densities did not vary with mean lake depth nor submergent vegetation cover (Table 4.6.). The best multivariate model included lake size ($t_{58} = -2.4, P < 0.05$), mean activity trap biomass ($t_{58} = 1.3, P = 0.2$), mean chironomid biomass ($t_{43} = 1.1, P = 0.3$), and percent cover of submergent vegetation ($t_{28} = 0.8, P = 0.4$), and explained 45% of the variation ($F_{4,56} = 7.4, P < 0.001$).

When densities were expressed in terms of area of water that was 0-2 m deep, univariate linear regression indicated a positive association between goldeneye brood densities and mean activity trap biomass ($t_{58} = 2.4, P < 0.01$; Figure 4.6b), and a negative relationship with submergent vegetation cover ($t_{28} = -3.4, P < 0.001$; Table 4.7.). A multivariate model that included lake size ($t_{58} = -3.8, P < 0.001$), mean lake depth ($t_{49} = 5.1, P < 0.001$), mean activity trap biomass ($t_{58} = 0.3, P = 0.7$), mean chironomid biomass ($t_{43} = 1.4, P = 0.2$), and percent cover of submergent vegetation ($t_{28} = -3.7, P < 0.001$), explained 74% of the variation ($F_{5,55} = 14.1, P <$ 0.001).

For Bufflehead brood densities, significant positive relationships were found with dissolved oxygen ($t_{28} = 2.6, P < 0.05$; Table 4.6.), Bufflehead breeding pair densities ($t_{58} = 3.5, P < 0.001$), and goldeneye brood densities ($t_{58} = 3.4, P < 0.001$; Figure 4.8a). Bufflehead brood densities did not vary with activity trap biomass ($t_{58} = 0.7, P = 0.5$; Figure 4.9a) nor chironomid biomass ($t_{43} = 0.1, P = 0.9$; Figure 4.10a), and there were no significant multivariate models.

For Bufflehead brood densities expressed in terms of area of water that was 0-2 m deep, a significant positive relationship was found with mean lake depth ($t_{49} = 3.0, P < 0.01$), and a negative correlation was found with dissolved oxygen ($t_{28} = -2.4, P < 0.01$; Table 4.7.). A multivariate model containing lake size ($t_{58} = -0.6, P < 0.5$), mean lake depth ($t_{49} = 2.2, P < 0.05$), mean activity trap biomass ($t_{58} = 1.2, P = 0.3$), mean chironomid biomass ($t_{43} = 0.6, P = 0.6$), and percent cover of submergent vegetation ($t_{28} = -2.2, P < 0.05$), explained 44% of the variation ($F_{5,55} = 3.8, P < 0.05$).

4.5. DISCUSSION

A variety of factors can affect lake selection by waterfowl, including food availability, predation risks, natal philopatry by breeding females, and space for territorial birds (Eriksson 1978). Factors associated with increased prey densities such as aquatic vegetation and water chemistry are also cited as selection factors (Kaminski and Prince 1981, Murkin et al. 1983, Talent et al. 1982). For Barrow's Goldeneye and Bufflehead, lake use was also expected to be influenced by the proximity of suitable nesting cavities, and the presence of other territorial pairs. The results of this study support my predictions and indeed suggest that the quality of breeding habitat for goldeneye and Bufflehead pairs and broods is distinguished by a combination of these factors, particularly lake size, aquatic invertebrate prey biomass, and the presence of proximal nesting sites (within 100 m of the shoreline).

Lake size appears to be the most important factor influencing lake occupancy by breeding pairs and broods of both species'. Lake depth was also an important feature for breeding pairs, but not for broods, and the abundance of invertebrate prey was associated with lake usage by goldeneye pairs and broods, but not Bufflehead. However, we must question the validity of using lake size and lake depth as predictors of lake occupancy, for two reasons: 1) if birds are selecting lakes by chance, than we would predict that larger lakes are more likely to be occupied, and 2) lake depth was highly correlated to lake size. Despite these potential problems, several studies continue to report positive associations between lake size and lake use by aquatic birds, citing increased prey species richness, and more space for territorial birds (Nilsson and Nilsson 1978, Heglund et al. 1994, Savard et al. 1994, Paquette 1995, Dodson et al. 2000; see section 4.5.2.). If we remove lake size and lake depth as potential predictors of lake occupancy we are left with invertebrate prey abundance, which was associated with lake usage by goldeneye only.

For density of pairs and broods, lake size and depth consistently accounted for most of the variation in multivariate models, for both species. But here again, we run into problems with using lake size and depth as predictors of goldeneye and Bufflehead densities. Lake size had a negative association with densities of both species and this is likely a result of the fact that, by nature, smaller lakes have higher densities than larger lakes because we are calculating density based on a smaller denominator (# of birds/lake size). For example, a 1 ha lake with 10 pairs on it would have a density of 10 pairs per hectare, whereas a 10 ha lake with 10 pairs on it would have a density of only 1 pair per hectare.

I found several differences for densities calculated by total water surface area, versus surface area of water 0-2 m deep, and these are discussed below. However, I think that the latter calculation of density remains more biologically meaningful because both species are rarely seen in water deeper than 2 m, especially when foraging (Savard et al. 1994).

4.5.1. Invertebrate Abundance

Chemical and structural heterogeneity among lakes results in different aquatic invertebrate compositions and abundances (Topping and Scudder 1977, Reynolds 1979). In my study, not only did the presence of goldeneye pairs and broods vary with a lake's prey biomass, there was also a direct relationship between food supply and pair densities (when expressed as total lake area), and brood densities (for both calculations of density, but univariate analysis only). Similar results have been found for Common Goldeneye (Eriksson 1978, Eadie and Keast 1982), Mallards (Pehrsson 1984, Ball and Nudds 1989), American Green-winged Teal (*Anas crecca carolinensis;* Paquette 1995), and Black Ducks (*Anas rubripes*; Parker et al. 1992, Staicer et al. 1994). Common Goldeneye females are known to move their broods from hatching lakes to brood-rearing lakes that have higher invertebrate abundance (Eriksson 1978, Poysa and Virtanen 1994) or that lack fish, which compete with goldeneye for invertebrates (Eriksson 1979, Eadie and Keast 1982). In my study, overland movement occurred to a limited extent (4 year mean = 9% of goldeneye broods and 14% of Bufflehead broods switched lakes after hatching) and the majority of movements were to lakes where I did not measure habitat characteristics. Therefore, my study can not provide evidence for movements to higher quality lakes, but my results do show that goldeneye occupy higher quality lakes, and that lakes unoccupied by both species support the lowest abundance of food. Therefore, this study supports others that found food abundance to be an important factor in lake usage by goldeneye breeding pairs and broods (Eriksson 1979, Eadie and Keast 1982, Poysa and Virtanen 1994).

These results were expected, because aquatic macro-invertebrates are an important source of energy and protein for breeding waterfowl, particularly for developing ducklings (Sugden 1973, Swanson and Meyer 1973). Experiments have revealed a positive relationship between invertebrate abundance and growth rates of Black Duck ducklings (DesGranges and Rodrigue 1986, Hunter et al. 1986), and in Iceland, annual production rates of waterfowl were positively correlated with annual invertebrate abundance (Gardarsson and Einarsson 1994). Clearly, individual duckling growth and survival, and thus eventual recruitment, may be directly linked to macroinvertebrate prey abundance. It is therefore not surprising to see goldeneye pairs and broods occupying lakes with higher food abundance.

However, it is surprising that similar results were not found for Bufflehead pairs and broods. Lake use by Bufflehead was not related to food supply, but instead was associated with the physical characteristics of lakes such as lake size, mean lake depth, and the presence of nest sites within 100 m of the shoreline. Lakes used by Bufflehead pairs and broods had lower food abundance than those used by goldeneye (compare Table 4.4. and 4.5.), and although not statistically significant, also had less prey biomass than those lakes not used by Bufflehead (Table 4.5.). This suggests that Bufflehead are using less than optimal foraging locations in areas with high densities of goldeneye. It may be that Bufflehead pairs are prevented from accessing the higher quality foraging areas due to competitive exclusion by the larger, more aggressive goldeneyes. During aggressive territorial interactions between these species, goldeneye are predominately the aggressor and Bufflehead the target (Savard 1986). Figures 4.3 and 4.8 have less than 1:1 relationships between Bufflehead and goldeneye densities (most apparent for brood densities, Figure 4.8), further supporting the idea that Bufflehead densities decrease in areas of high goldeneye numbers. In other words, increases in goldeneye density may make these lakes less suitable for Bufflehead, in which case Bufflehead chose to occupy lakes where lower food abundance and less interference balance out. It would therefore appear that Bufflehead have a higher tolerance to lower prey abundance than do Goldeneye. In other words, occupying these seemingly suboptimal lakes may have higher fitness payoffs for Bufflehead, compared to remaining on lakes with high goldeneye densities. This would be an example of Ideal Despotic Distribution (Fretwell and Lucas 1970, Parker and Stuart 1976), highlighting a potential resource-assessment strategy in which resource cues correlating with expected gain in fitness are monitored and result in adaptive strategy shifts in the individual's behaviour (Parker and Stuart 1976).

Therefore, it is plausible that Bufflehead are forced to satisfy basic reproductive requirements on suboptimal lakes (or lakes that seem to be of lower quality when densities of competitors are not considered; Fretwell and Lucas 1970). Parents can enhance brood survival by providing several types of care: 1) brooding young to assist them in maintaining optimal body temperatures, 2) locating suitable brood-rearing habitats, 3) warning and protecting young from predators, and 4) aiding young in competitive interactions with other waterfowl (Afton and Paulus 1992). It may be that because of direct competitive interference, Bufflehead have evolved different strategies from those of goldeneye, in order to best balance these factors and optimize their reproductive success.

Lake selection should depend on an individual's ability to assess the availability of aquatic invertebrates, and thus, breeding females should actively sample potential brood-rearing areas prior to hatch, becoming familiar with the local food supply (and other factors that may enhance egg production and brood survival; Bellrose 1976). My data show that invertebrate abundance in lakes is consistent across years, indicating that lakes vary predictably in their annual productivity.

4.5.2. Lake Size, Water Chemistry, Plants, and Invertebrates

A positive relationship between lake use by aquatic birds and lake size has been well documented (Nilsson and Nilsson 1978, Heglund et al. 1994, Savard et al. 1994). Larger lakes commonly have higher species richness in phytoplankton, zooplankton, and aquatic macrophytes (Dodson et al. 2000), and offer more space for territorial birds such as goldeneye and Bufflehead. Lakes occupied by teal were also larger in size, had higher total phosphorus, alkalinity, conductivity, and presumably, higher invertebrate abundance (Paquette 1995). Limnological characteristics such as these also appear to be useful indices of lake suitability for aquatic birds, as several studies have shown strong associations between ion and nutrient levels and aquatic bird abundance, prey abundance, foraging efficiency, and breeding success (Hutchinson 1957, Nilsson and Nilsson 1978, Wiens 1985, Heglund et al. 1994). In my study, densities of goldeneye pairs and broods, and Bufflehead broods, were positively correlated to dissolved oxygen levels, when densities were calculated as total area. And, goldeneye pair and brood densities, as well as Bufflehead pair densities were negatively correlated to conductivity levels. However, when densities were expressed as area of water 0-2 m deep, only Bufflehead brood densities and dissolved oxygen levels remained significantly related.

Invertebrate abundance was positively related to dissolved oxygen levels, but negatively correlated to conductivity, and did not vary with pH, perhaps due to the low variability of pH values found between my study lakes (range = 8.4-9.9).

Lake use by both goldeneye and Bufflehead broods was negatively associated with submergent vegetation, and broods most commonly used lakes with less than 30% submergent cover. This may be a result of the inability of ducklings to forage efficiently in areas of dense vegetation. Dense stands of submergent vegetation also limit invertebrate abundance because of a lack of dissolved oxygen (Staicer et al. 1994). On the other hand, water bodies completely devoid of aquatic vegetation also have few invertebrates because of a lack of structure, wave stability, and low algae production (Kadlec and Smith 1992). Subsequently, insectivorous ducklings avoid lakes either lacking submergent vegetation or containing too much (Keith 1961). Therefore, a balance between submergent vegetation and invertebrate abundance exists for sufficient foraging habitat for diving ducks.

Likewise, extremely acidic and basic lakes generally have sparser and less complex vegetation, fewer invertebrates, and fewer ducks (Swanson 1985, Elmberg et al. 1994, Poysa and Virtanen 1994). The reduced diversity and quality of prey in acidified lakes has markedly affected the growth, feeding behaviour, and survival of ducklings of several species (Blancher and McAuley 1987, Haramis and Chu 1987, McAuley and Longcore 1988). For example, foraging costs increased and survival decreased for Ring-necked Duck ducklings on lakes of lower pH (<6.1; McAuley and Longcore 1988). However, lake use by the Pacific Loons (*Gavia pacifica*) and Horned Grebes (*Podiceps aurtus*) in Alaska were positively correlated to pH (Heglund et al. 1994), as were Black Duck brood densities in Nova Scotia. These latter results contrast with my finding of a negative relationship between pH and goldeneye brood densities (when calculated using total area), and are likely due to the different pH ranges between those studies and mine (my study: pH range = 8.4-9.9 and mean = 9.3; Alaska: range = 5.5-10, mean =

7.9; and Nova Scotia: range = 5.0-7.1, mean = 5.9). In an earlier study at Riske Creek, Barrow's Goldeneye pair densities increased with pH, while Bufflehead pair densities decreased (Savard et al. 1994). A preference for more acidic lakes has also been reported for Common Goldeneye, with authors concluding that acidic lakes tend to be devoid of fish that are effective competitors for invertebrate prey (Eriksson 1979, Eadie and Keast 1982, DesGranges and Darveau 1985, Nummi and Poysa 1991). All lakes in my study lacked fish and therefore this would not have been a factor, but Barrow's Goldeneye broods still had higher densities on more acidic lakes (however, lowest pH recorded was 8.4). And finally, Elmberg et al. (1994) found no relationship between Common Goldeneye abundance and pH.

Once again, correlations between lake use and pH are likely a result of the association between pH and food abundance (Poysa and Virtanen 1994). Although, it must be pointed out that my study found no relationship between these two variables (see Table 4.2.).

4.6. CONCLUSIONS

Use of lakes by goldeneye and Bufflehead breeding pairs and broods appears to be dependent on lake size and depth (although potential problems with using these variables as predictors of lake use are discussed above), aquatic prey biomass, availability of proximal nest sites, and to a lesser degree, the amount of submergent vegetation cover. Water chemistry properties such as dissolved oxygen and specific conductivity seem to be highly correlated to these factors and may serve as more easily measured variables for lake managers. Other studies have found direct relationships between aquatic bird abundance and pH, but in my study, pH was only related to goldeneye brood density, and only when brood density was calculated using total lake area. Overall, pH appeared to be unimportant in predicting lake use by pairs and broods in my study. These contrasting results are probably due to the lack of variation in pH levels among lakes in my study.

While goldeneye and Bufflehead densities seem to be reflected by parameters that are crucial for nutrient requirements of breeding females and developing young, there likely exists a trade-off between selecting lakes with hydrochemical levels that provide maximum invertebrate abundance, remaining within close proximity to forests and suitable cavity availability, and avoiding competition and predation. In fact, it seems most likely that waterfowl abundance has a parabolic relationship to water chemistry and submergent vegetation levels, with birds avoiding lakes at either extreme.

One must be careful in interpreting these associations as causal. Experimental studies are necessary to further examine the correlations described in this study. Also important to note is that reporting associations with invertebrate abundance does not address differences in prey availability due to differences in behaviour, size, colour, or edibility (Armstrong and Nudds 1985). Therefore, my study does not actually address resource selection by these birds, but instead merely presents correlations between selected habitat characteristics, including food abundance, and lake use by goldeneye and Bufflehead.

This study also supports the findings of Savard et al. (1994), which highlight how relationships between bird densities and habitat characteristics can vary depending on the area unit used to calculate densities.

4.7. MANAGEMENT RECOMMENDATIONS

The continued loss of lake habitat in North America has given rise to increased efforts to preserve threatened lakes, restore damaged ones, and maximize waterfowl production levels. In order to efficiently achieve these objectives, we must identify the various abiotic and biotic habitat characteristics of the lake ecosystem that influence lake selection by breeding waterfowl. For any habitat to support breeding waterfowl it must offer a complex of ecological parameters, including nest site availability, protection from predators and adverse weather conditions, and adequate food supplies. Identifying the various components of lake ecosystems that influence lake selection will assist in achieving the goals of managing waterfowl populations.

Variations between species' morphological and behavioral traits has likely resulted in different habitat requirements, probably related to dietary requirements (Sedinger 1992). This study focused only on Barrow's Goldeneye and Bufflehead; other species likely have other preferences and therefore have different management needs. However, a large number of waterfowl species rely heavily on invertebrate prey items, and the protection of productive lakes would benefit them as well. The results of this and other studies suggest that changes in limnological conditions will affect waterfowl selection of lakes due to changes in invertebrate abundance (see also McNicol et al. 1987, DesGranges and Houde 1989). Levels of primary production within a lake, including trophic structure and total biomass throughout the aquatic food web, are mediated by a host of interacting physical and chemical factors (Wetzel 1975). Subtle changes in the aquatic environment will result in associated changes in trophic relationships with waterfowl, affecting prey availability, foraging efficiency, nutrient intake rates, and thereby potentially affecting waterfowl populations. Finally, since several researchers have demonstrated strong correlations between limnological variables, lake nutrient status, and aquatic bird abundance, I suggest these options as a more efficient and less expensive way for managers to assess lake habitat quality, rather than the labour intensive methods of sampling invertebrates.

4.8. LITERATURE CITED

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Table 4.1. Descriptive statistics for wetland habitat variables measured in lakes sampled at Riske Creek, British Columbia (1997-2000). *N* = 60 occupied and 15 unoccupied lakes.

Habitat Variable	**Mean**	**SE**	**Minimum**	**Maximum**
Lake size (ha)	8.9	1.1	0.3	41.7
Mean lake depth (m)	1.5	0.08	0.6	3.1
% Forest cover within 100 m	20.5	3.3	0	92.7
% Submergent vegetation	32	4.6	0	100
Activity trap biomass (g/sample)	108.7	9.5	19	394
Benthic core biomass (g/sample)	2.01	0.4	0.3	10.2
pH	9.3	0.1	8.4	9.9
Conductivity (mg/L)	5785	1000	1567	15041
Dissolved O2 (mg/L)	12.3	0.8	7.4	17.8

Table 4.2. Pairwise correlation coefficients between biotic and abiotic habitat variables for lakes sampled at Riske Creek, British Columbia (1997-2000). Numbers (1-9) along the top of the table correspond to the habitat variables numbered down the side.

	Habitat Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	Lake size (ha)	1	0.41***	0.46***	-0.03	-0.22	-0.25	0.26	0.73***	-0.26
2	Mean lake depth (m)		1	0.53***	0.01	-0.25	-0.27	0.01	0.09	-0.11
3	% Forest cover within 100 m			1	-0.13	-0.43***	-0.4**	-0.03	0.42	-0.34
4	% Submergent vegetation				1	-0.12	-0.14	-0.11	-0.04	-0.12
5	Activity trap biomass					1	0.79***	-0.08	-0.5*	0.66**
6	Benthic core biomass						1	-0.09	-0.7***	0.7***
7	pH							1	0.40	0.39
8	Conductivity (mg/L)								1	-0.27
9	Dissolved O2 (mg/L)									1

* = $P < 0.01$

** = $P < 0.001$

*** = $P < 0.001$

Table 4.3. Descriptive statistics for invertebrate species' biomass (g/sample) in all activity trap samples (*n* = 4600) at Riske Creek, British Columbia (1997-2000).

Species	**Mean**	**SE**	**Minimum Mean**	**Maximum Mean**	**% of Total Biomass**
Total Biomass	108.7	9.5	19	394	--
Amphipod	35.9	6.7	0.03	278.39	33.1
Tricoptera	18.9	0.1	0	8.7	17.4
Zygoptera	16.1	1	0	46.8	14.8
Dytiscidae adult	10.2	2.2	1.2	80.6	9.4
Dytiscidae larvae	9.7	1.3	0	74.8	8.9
Corixidae	8.4	2.1	0	115.3	7.7
Hirudinea	6.2	2.3	0	122.3	5.7
Notonectidae	3.7	0.7	0	23.5	3.4
Hydracarina	1.7	0.3	0	18.4	1.5
Chironomid	0.6	0.12	0	4.3	0.55
Haliplidae adult	0.6	0.16	0	7.4	0.55
Cladocera	0.5	2.3	0	97.1	0.5
Ephemeroptera	0.03	0.01	0	0.7	0.03
Haliplidae larvae	0.03	0.03	0	2.1	0.03
Culicidae	0.001	0.001	0	0.04	0.001
Heleidae	0.004	0.002	0	0.08	0.001

Table 4.4. Descriptive statistics and results of univariate logistic regression for habitat variables of occupied ($n = 60$) and unoccupied ($n = 15$) wetlands by Barrow's Goldeneye breeding pairs and broods, at Riske Creek, British Columbia (1997-2000).

Habitat Variable	**Goldeneye Pairs**						**Goldeneye Broods**					
	Occupied		**Unoccupied**				**Occupied**		**Unoccupied**			
	Mean	SE	Mean	SE	WS	*P*	Mean	SE	Mean	SE	WS	*P*
Lake size (ha)	10.2	1.2	2.9	2.8	5.9	0.01	10.4	1.2	4.4	2.1	4.8	0.02
Mean lake depth (m)	1.6	0.1	1.2	0.2	3.8	0.05	1.6	0.1	1.4	0.2	1.3	0.3
% Forest cover within 100 m	21.1	3.8	23.8	8.3	0.1	0.8	24.1	4.1	13.2	5.7	2.7	0.1
% Submergent vegetation	26.4	4.9	52.1	11.7	3.2	0.07	25.1	4.8	61.2	9.7	8.4	0.003
Activity trap biomass	121.1	10.3	65.1	23.4	6.3	0.01	125.3	10.4	61.3	17.6	7.1	0.01
Benthic core biomass (chironomids)	2.1	0.3	1.4	1.1	0.4	0.5	2.1	0.3	0.7	1.1	1.3	0.2
pH	9.3	0.1	9.2	0.2	0.2	0.7	9.2	0.1	9.6	0.2	3.2	0.07
Conductivity (mg/L)	5762	1087	5986	3171	0.04	0.9	5939	1044	3014	4431	0.6	0.4
Dissolved O2 (mg/L)	12.5	0.8	10.6	2.4	0.6	0.4	12.2	0.8	13.9	3.4	0.3	0.6
Number of nest sites within 100 m	3.6	0.3	2	0.8	4.1	0.04	3.9	0.3	1.1	0.6	10.4	0.001

Table 4.5. Descriptive statistics and results of univariate logistic regression for habitat variables of occupied (n = 60) and unoccupied (n = 15) wetlands by Bufflehead breeding pairs and broods, at Riske Creek, British Columbia (1997-2000).

Habitat Variable	**Bufflehead Pairs**						**Bufflehead Broods**					
	Occupied		**Unoccupied**				**Occupied**		**Unoccupied**			
	Mean	SE	Mean	SE	WS	*P*	Mean	SE	Mean	SE	WS	*P*
Lake size (ha)	9.9	1.2	2.9	3.2	4.4	0.03	13.4	1.2	3.3	1.4	15.5	0.001
Mean lake depth (m)	1.5	0.08	1.14	0.2	4.1	0.04	1.6	0.1	1.3	0.1	3.5	0.06
% Forest cover within 100 m	22.4	3.7	15.3	9.8	0.5	0.5	25.5	4.6	15.4	4.6	2.4	0.1
% Submergent vegetation	29.3	4.7	54.4	13.9	2.7	0.1	25.9	5.8	41.7	7.3	2.8	0.09
Activity trap biomass	112.2	10.4	109.9	27.8	0.01	0.9	104.7	12.8	113.4	14.1	0.2	0.6
Benthic core biomass (chironomids)	2.1	0.3	0.6	1.2	3.3	0.07	1.6	0.4	2.9	0.5	3.4	0.06
pH	9.23	0.07	9.5	0.1	2.6	0.1	9.3	0.08	9.3	0.1	0.01	0.9
Conductivity (mg/L)	6171	1048	2509	3057	2.1	0.2	7140	1175	3463	1539	2.6	0.1
Dissolved O2 (mg/L)	11.9	0.8	15.6	2.3	2.6	0.1	11.2	0.8	14.2	1.2	3.2	0.06
Number of nest sites within 100 m	1.8	0.2	1	0.7	3.9	0.05	1.1	0.3	0.4	0.3	2.7	0.1

Table 4.6. Pairwise correlation coefficients and P values for Barrow's Goldeneye and Bufflehead breed pair and brood densities (expressed as # of birds per hectare of total lake area), and wetland habitat features, at Riske Creek, British Columbia (1997-2000). $N = 60$ occupied and 15 unoccupied lakes.

Habitat Variable	**Goldeneye**				**Bufflehead**			
	Pair Density		Brood Density		Pair Density		Brood Density	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Density								
Goldeneye pairs	--	--	0.61	0.001	0.77	0.001	-0.03	0.77
Goldeneye broods	0.61	0.001	--	--	0.55	0.001	0.37	0.001
Bufflehead pairs	0.77	0.001	0.55	0.001	--	--	0.36	0.001
Bufflehead broods	-0.03	0.77	0.37	0.001	0.36	0.001	--	--
Habitat								
Lake size (ha)	-0.31	0.001	-0.35	0.001	-0.25	0.03	-0.1	0.55
Mean lake depth (m)	0.06	0.67	-0.11	0.38	-0.14	0.28	-0.03	0.82
% Forest cover within 100 m	-0.12	0.35	-0.11	0.4	-0.1	0.48	-0.11	0.4
% Submergent vegetation	0.03	0.83	-0.1	0.53	0.25	0.04	0.21	0.08
Mean activity trap biomass	0.35	0.001	0.46	0.001	0.02	0.85	0.08	0.49
Mean chironomid biomass	0.22	0.15	0.41	0.01	0.03	0.83	0.01	0.94
pH	-0.19	0.31	-0.31	0.05	-0.36	0.04	-0.12	0.51
Conductivity (mg/L)	-0.53	0.01	-0.53	0.02	-0.4	0.04	0.02	0.94
Dissolved O2 (mg/L)	0.52	0.02	0.53	0.01	0.14	0.56	0.51	0.01

Table 4.7. Pairwise correlation coefficients and P values for Barrow's Goldeneye and Bufflehead breedi pair and brood densities (expressed as # of birds per hectare of 0-2 m deep water), and wetland habitat features, at Riske Creek, British Columbia. N = 60 occupied and 15 unoccupied lakes.

Habitat Variable	**Goldeneye**				**Bufflehead**			
	Pair Density		Brood Density		Pair Density		Brood Density	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Density								
Goldeneye pairs	--	--	0.55	0.0001	0.25	0.03	0.27	0.02
Goldeneye broods	0.55	0.0001	--	--	0.1	0.37	0.32	0.01
Bufflehead pairs	0.25	0.03	0.1	0.37	--	--	0.15	0.18
Bufflehead broods	0.27	0.02	0.32	0.01	0.15	0.18	--	--
Habitat								
Lake size (ha)	-0.11	0.35	-0.21	0.06	-0.21	0.08	0.11	0.31
Mean lake depth (m)	0.51	0.001	0.24	0.06	0.08	0.53	0.37	0.01
% Forest cover within 100 m	0.08	0.52	0.11	0.44	-0.04	0.78	0.07	0.61
% Submergent vegetation	-0.21	0.1	-0.39	0.001	0.02	0.84	-0.1	0.43
Mean activity trap biomass	0.01	0.9	0.27	0.02	0.11	0.36	-0.13	0.28
Mean chironomid biomass	0.04	0.8	0.27	0.07	0.06	0.7	0.22	0.13
pH	-0.2	0.3	-0.19	0.3	-0.01	0.95	-0.03	0.9
Conductivity (mg/L)	-0.3	0.2	-0.43	0.07	-0.25	0.31	0.16	0.52
Dissolved O2 (mg/L)	0.19	0.42	0.25	0.3	0.01	0.95	0.5	0.03

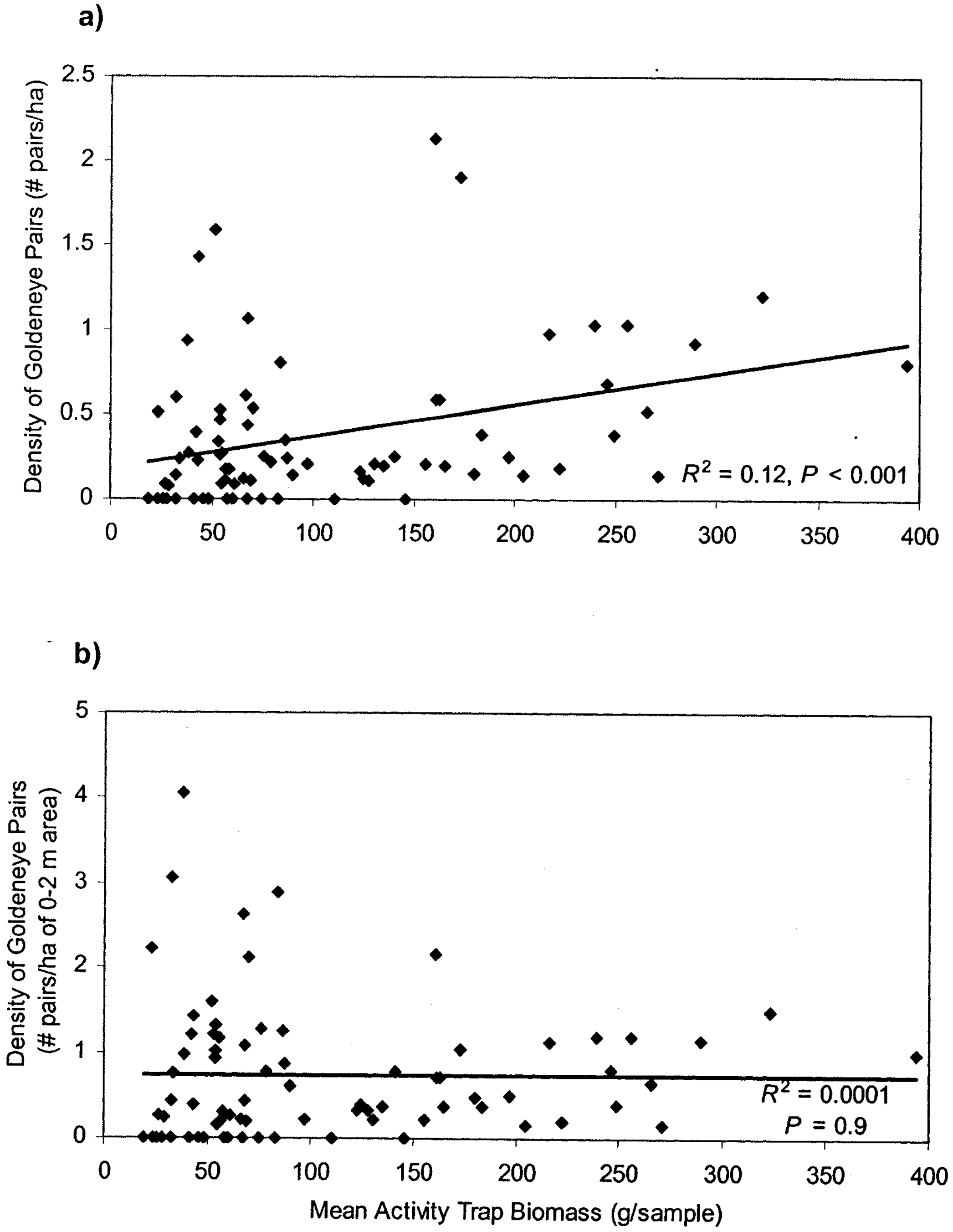

Figure 4.1. Density of Barrow's Goldeneye breeding pairs compared to mean activity trap biomass for each lake, Riske Creek, BC, 1997-2000. Pair densities are expressed as the number of pairs a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

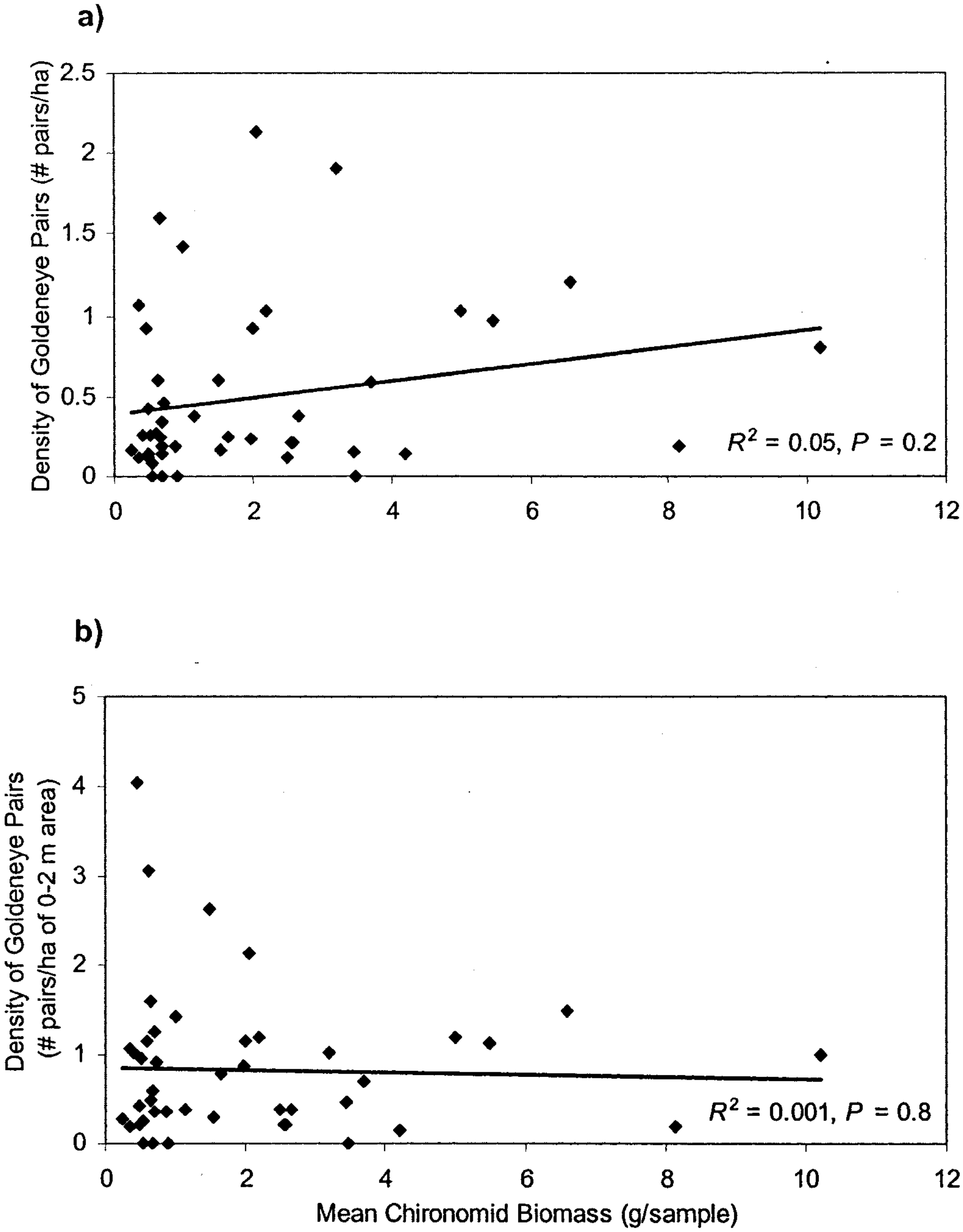

Figure 4.2. Density of Barrow's Goldeneye breeding pairs compared to mean chironomid biomass (from benthic core samples) for each lake, Riske Creek, BC, 1997-1999. Pair densities are expressed as the number of pairs a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

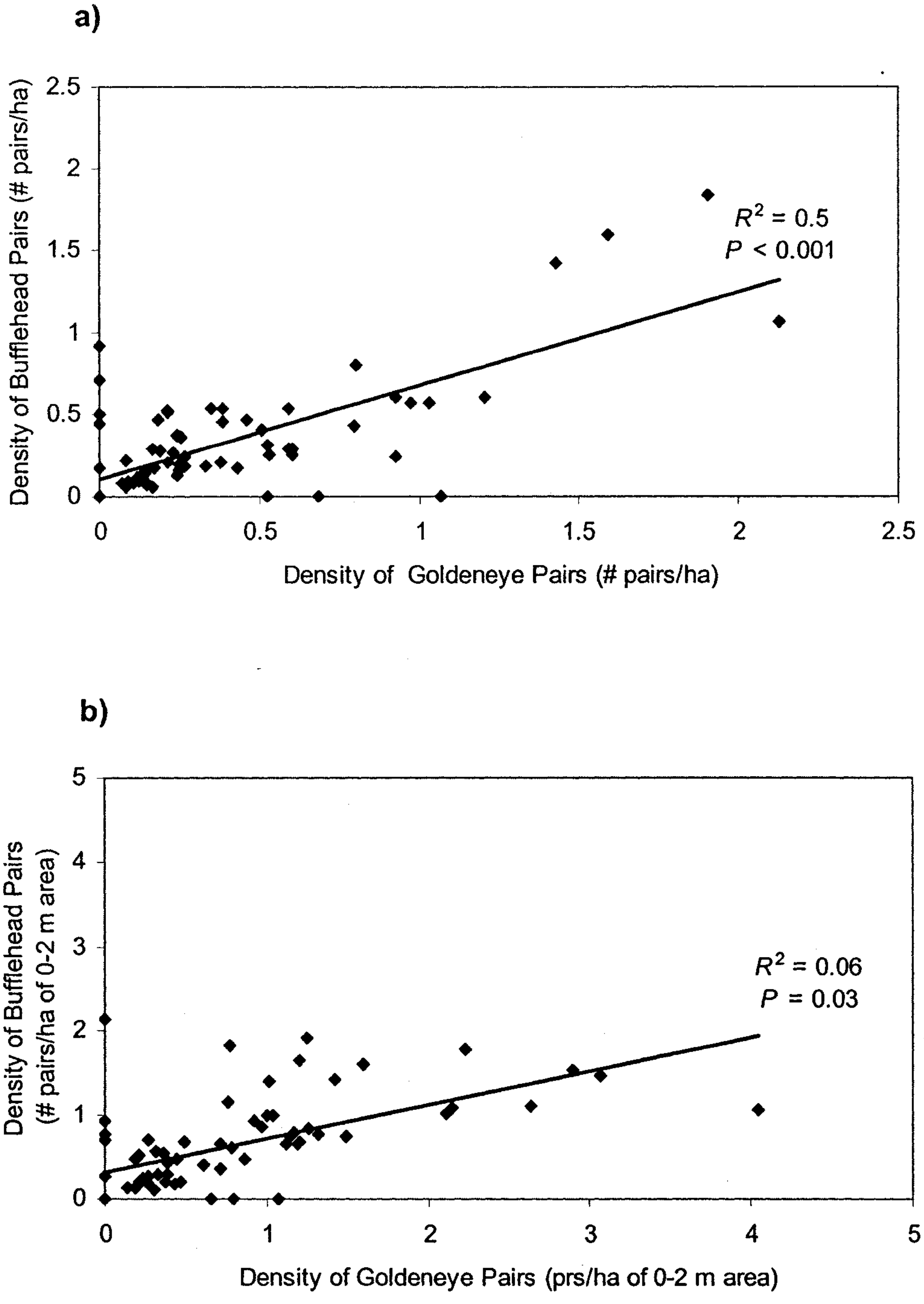

Figure 4.3. Density of Barrow's Goldeneye breeding pairs compared to Bufflehead pair densities on the same lakes, Riske Creek, BC, 1997-2000. Pair densities are expressed as the number of pairs a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

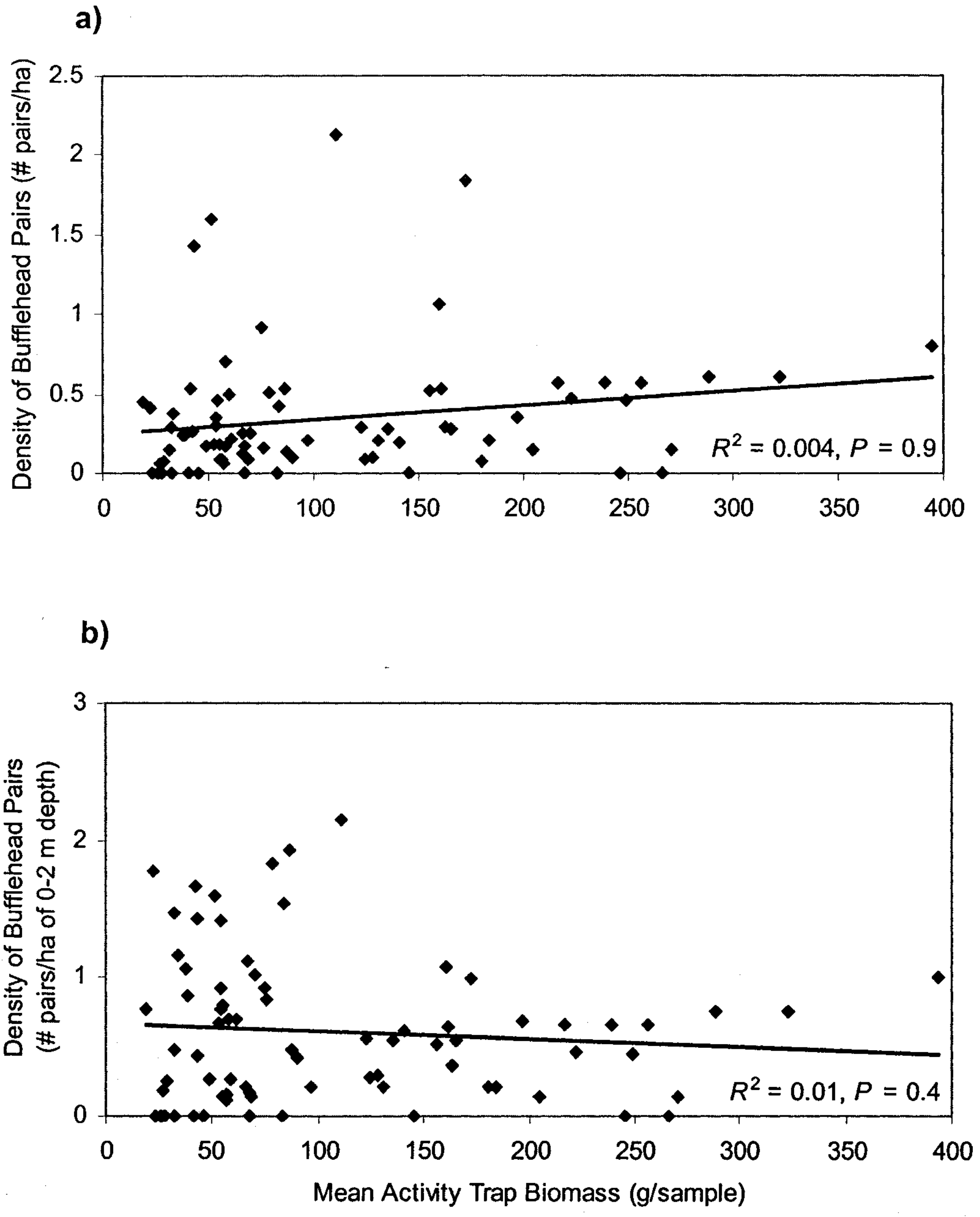

Figure 4.4. Density of Bufflehead breeding pairs compared to mean activity trap biomass for each lake, Riske Creek, BC, 1997-2000. Pair densities are expressed as the number of pairs a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

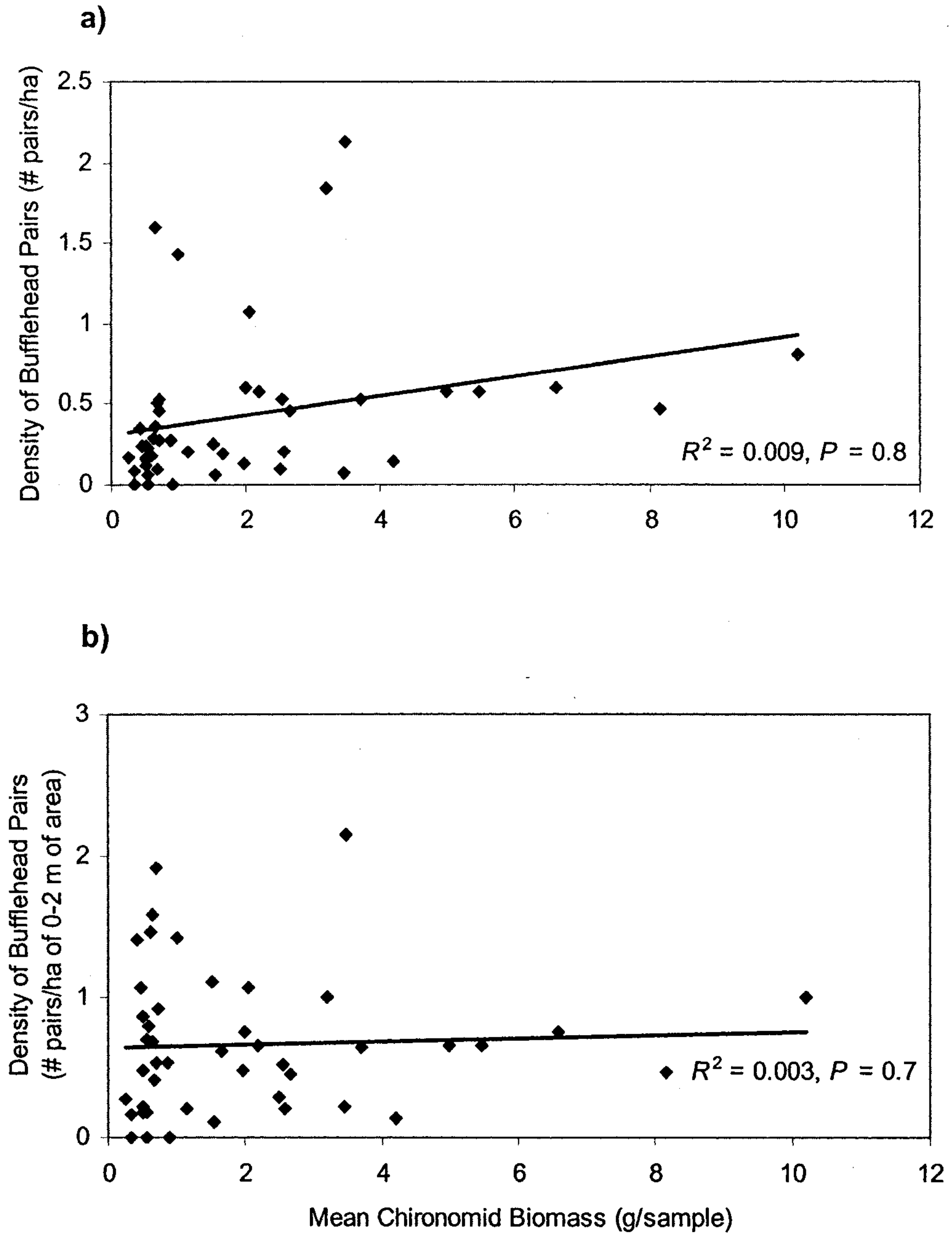

Figure 4.5. Density of Bufflehead breeding pairs compared to mean chironomid biomass (from benthic core samples) for each lake, Riske Creek, BC, 1997-1999. Pair densities are expressed as the number of pairs a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

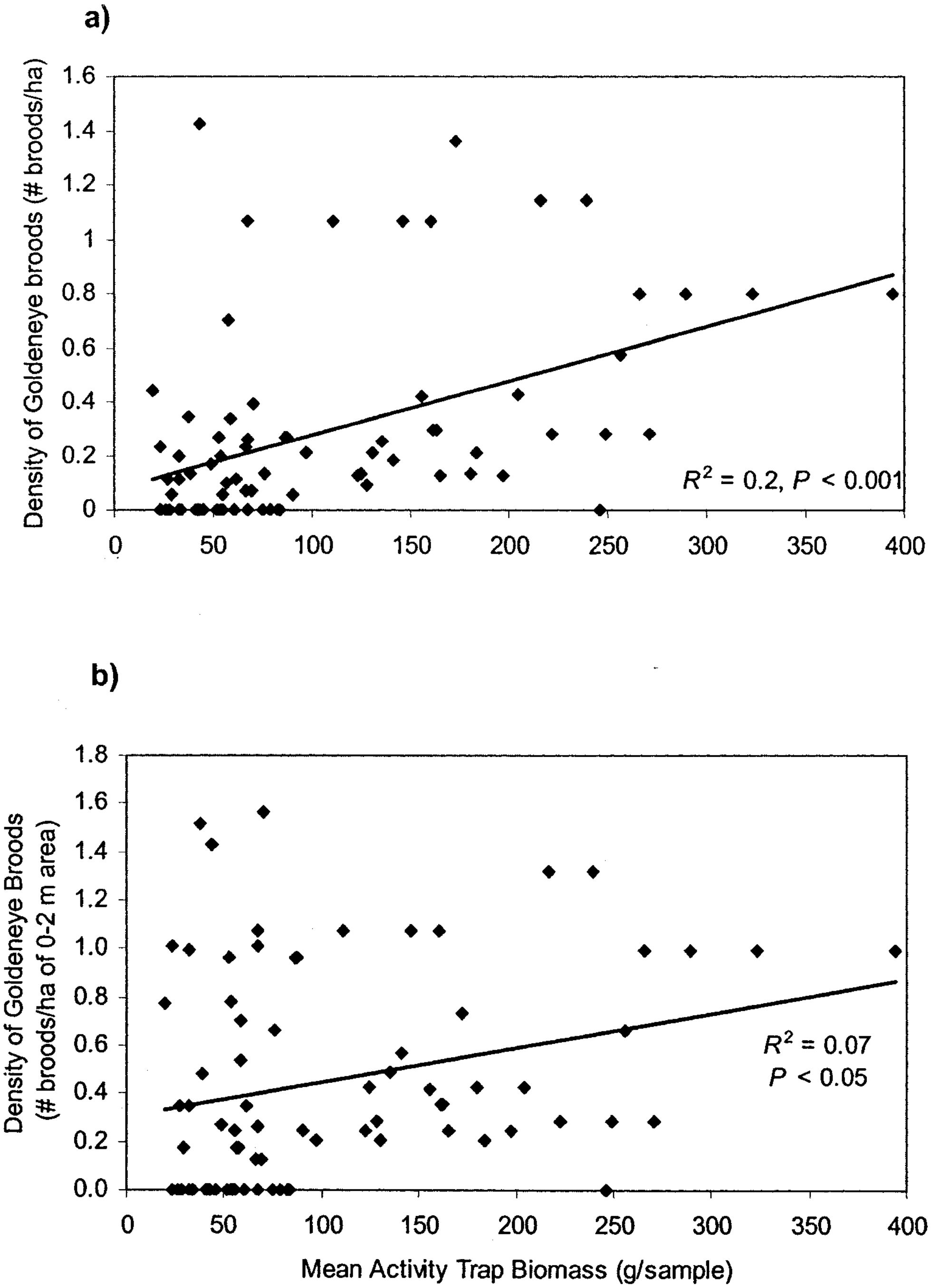

Figure 4.6. Density of Barrow's Goldeneye broods compared to mean activity trap biomass for each lake, Riske Creek, BC, 1997-2000. Brood densities are expressed as the number of broods a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

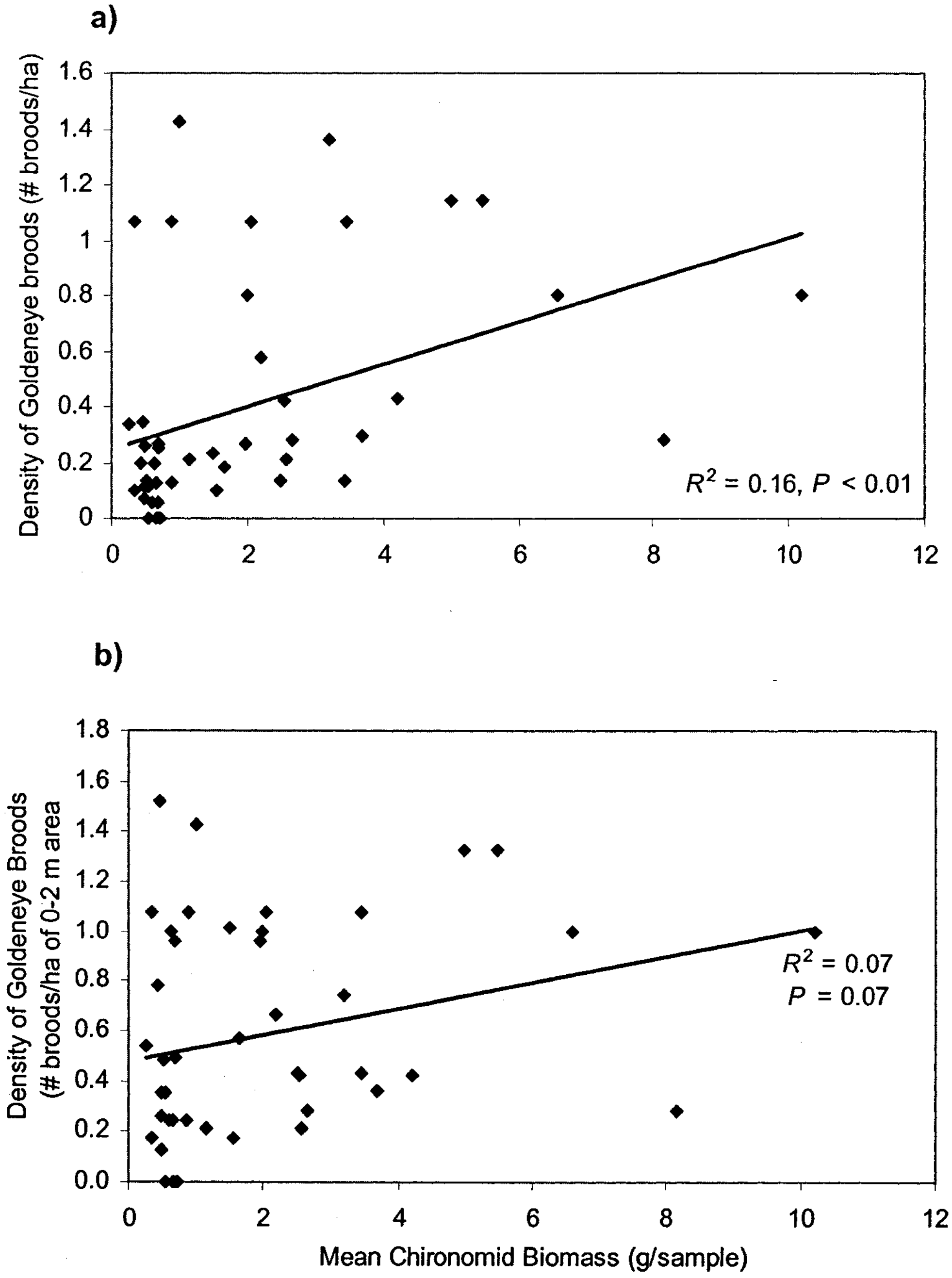

Figure 4.7. Density of Barrow's Goldeneye broods compared to mean chironomid biomass (from benthic core samples) for each lake, Riske Creek, BC, 1997-1999. Brood densities are expressed as the number of broods a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

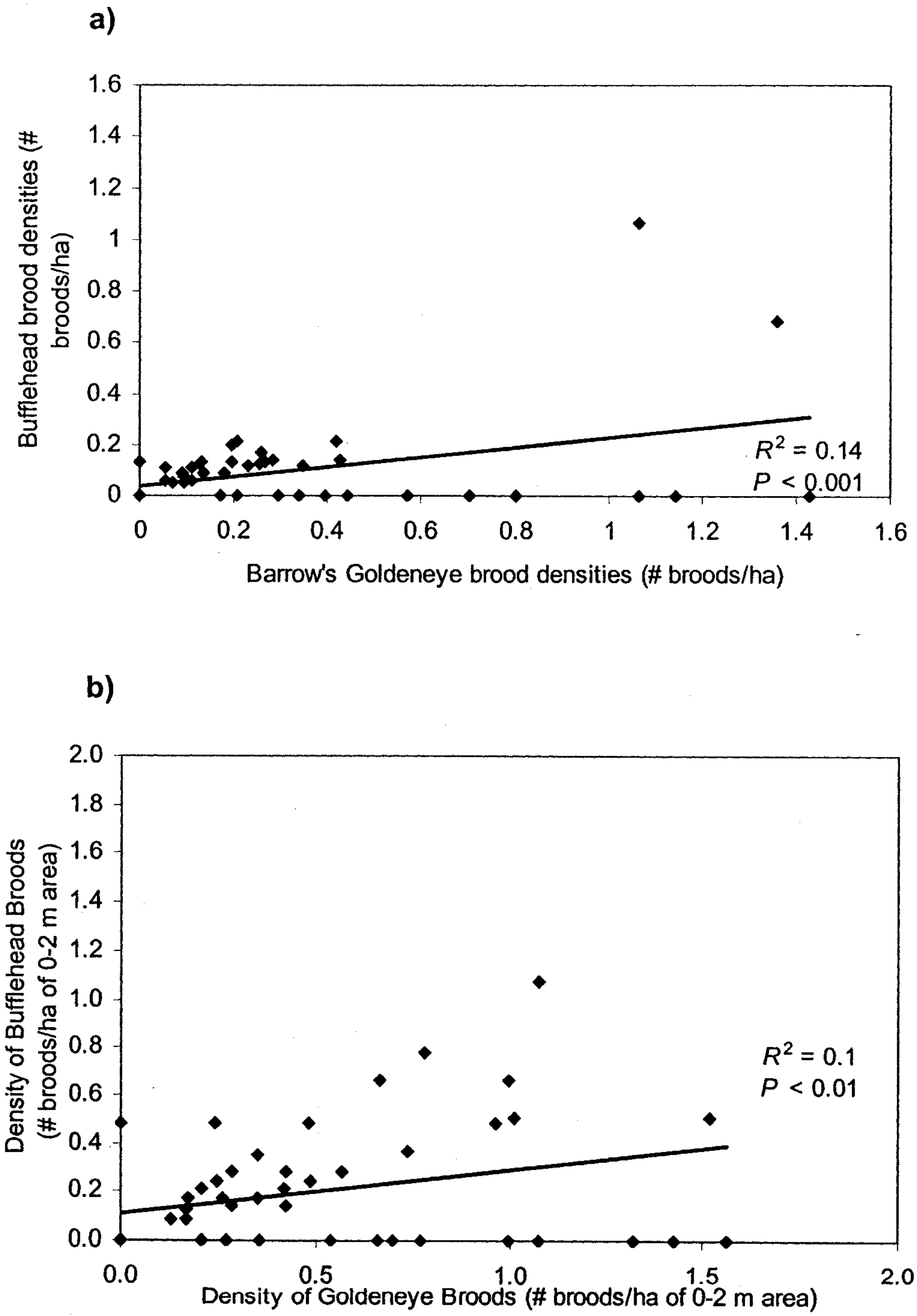

Figure 4.8. Density of Barrow's Goldeneye broods compared to Bufflehead pair densities on the same lakes, Riske Creek, BC, 1997-2000. Brood densities are expressed as the number of broods a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

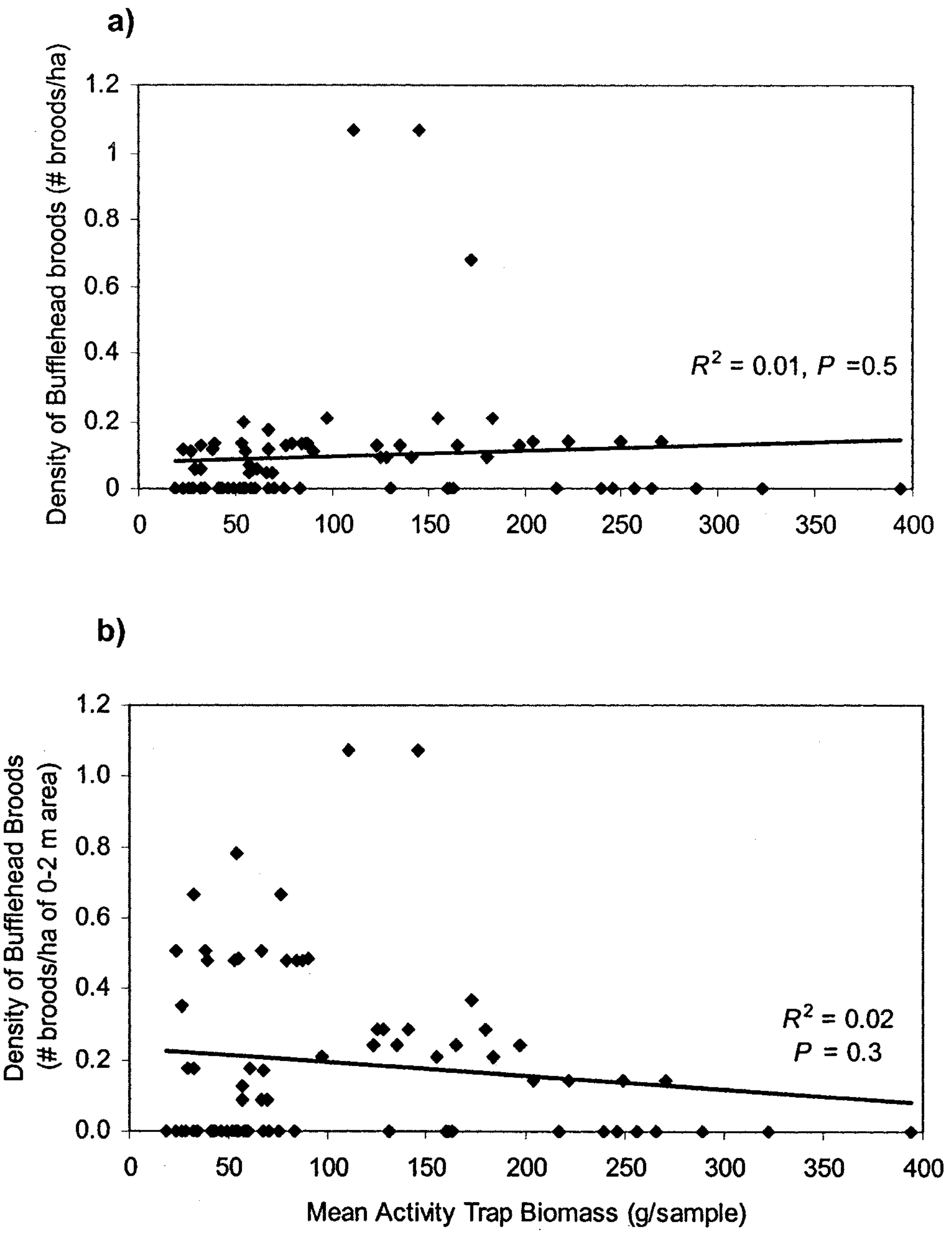

Figure 4.9. Density of Bufflehead broods compared to mean activity trap biomass for each lake, Riske Creek, BC, 1997-2000. Brood densities are expressed as the number of broods a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

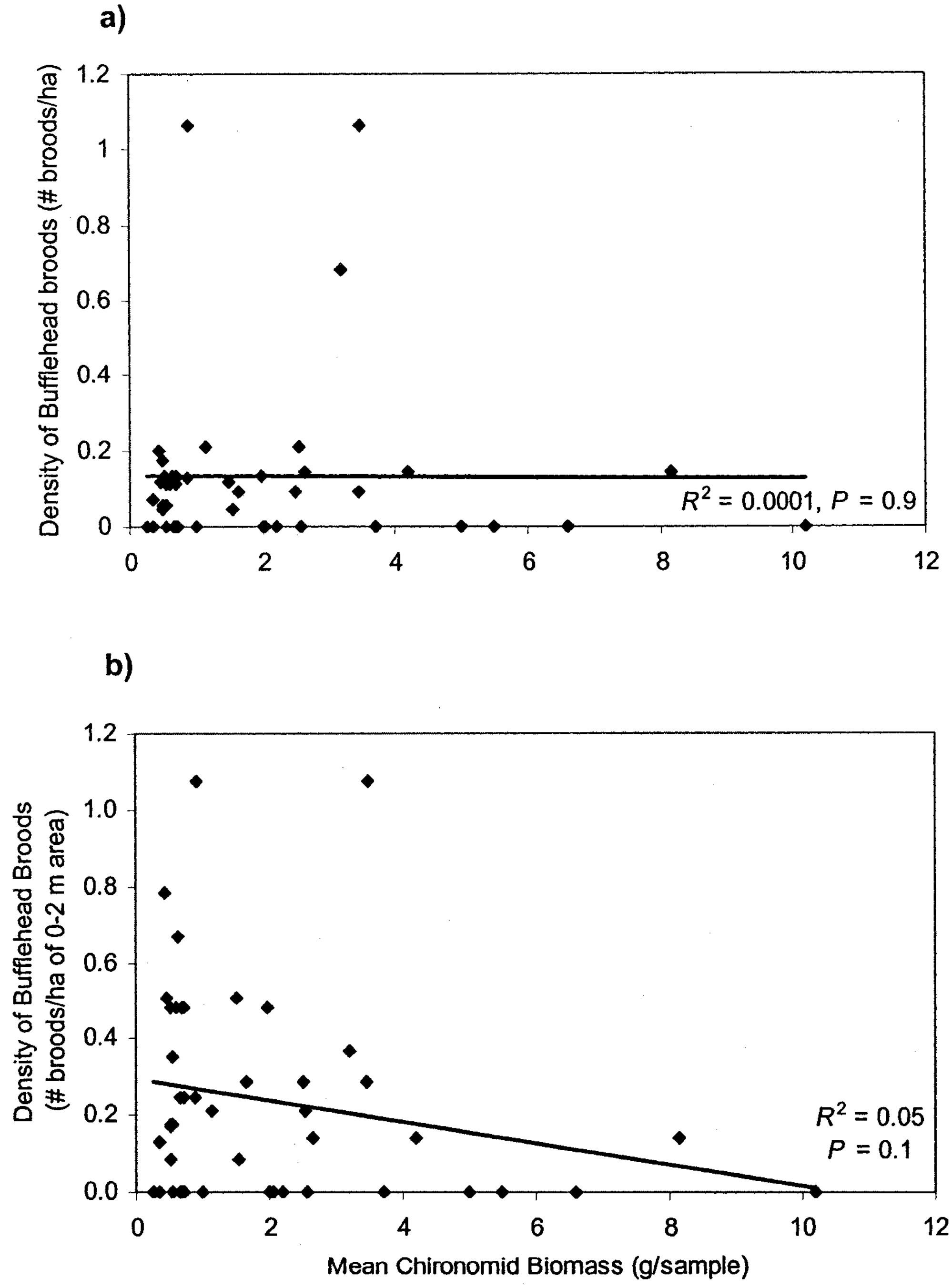

Figure 4.10. Density of Bufflehead broods compared to mean chironomid biomass (from benthic core samples) for each lake, Riske Creek, BC, 1997-1999. Brood densities are expressed as the number of broods a) per hectare of total water area, and b) per hectare of 0-2 m deep water area.

Chapter 5

FITNESS CONSEQUENCES OF BROOD-REARING HABITAT SELECTION DECISIONS BY BARROW'S GOLDENEYE

5.1. Abstract – I examined the relationship between food density and the following reproductive parameters of Barrow's Goldeneye: egg size, clutch size, hatching date, duckling growth rate, prefledging survival, and recruitment. Although it is commonly reported that prey abundance influences juvenile growth and survivorship, few studies have actually examined this relationship due to the difficulty in 1) associating nutrition and waterfowl survivorship, and 2) estimating survivorship and future fecundity. I examine this relationship by relating food abundance in brood-rearing habitats to duckling growth, survival, and recruitment.

I found positive correlations between invertebrate abundance within a wetland and Barrow's Goldeneye duckling mass at age 40 days, prefledging survival, and first year return rate. The masses of incubating females did not differ between sampled lakes, nor did nest initiation dates, clutch sizes, or mean egg masses, suggesting that older, more experienced females were not nesting disproportionately on high quality lakes.

From this study, it can be concluded that prey abundance in brood-rearing wetlands influences Barrow's Goldeneye duckling growth rates, prefledging survival, and first year return rates. However, evidence that prey abundance is directly related to recruitment patterns and therefore fitness variation among females is inconclusive. Regardless, the results of this study predict that females should be sampling local wetlands for their habitat quality and that annual philopatry and territorial defense should be higher on the more productive ponds. The use of suboptimal habitats is likely the result of intraspecific competition, where the only alternative is to forego breeding altogether. Examining birds' preferences for specific habitat characteristics that influence reproduction and survival may provide a more comprehensive understanding of ecological relationships between habitat characteristics and reproductive success.

5.2. INTRODUCTION

Breeding birds are typically associated with specific habitats that offer enough resources for successful reproduction and survival. Habitat selection decisions affect a bird's reproductive success (Osborne and Osborne 1980, Dow and Fredga 1985, Gauthier 1988). Two major factors influencing waterfowl habitat selection include nest site quality (Chapter 2) and brood-rearing habitat quality (Chapter 4); both have direct fitness consequences through their influence on the production of offspring. If breeding waterfowl are able to sample and assess the quality of essential breeding resources, then they should select sites that offer the highest probability of success during the nesting and post-hatching periods. Examining birds' preferences for specific habitat characteristics that influence reproduction and survival may provide a more comprehensive understanding of ecological relationships between habitat characteristics and reproductive success (Martin 1992). From a management perspective, understanding the relationships between habitat selection decisions and reproductive output would be valuable to wetland habitat managers and waterfowl conservation efforts.

Reproduction is an energetically demanding process and is generally timed to match the maximum availability of food to satisfy nutritional requirements by females during the egg laying period, and offspring during growth and development (Immelmann 1971). Although some migrating birds rely heavily on stored protein and lipid reserves (endogenous reserves) to produce eggs, most breeding females rely primarily on the daily intake of nutrients at the breeding site (exogenous sources; Owen and Reinecke 1979, Ankney and Afton 1988).

For juvenile birds, both environmental and maternal factors influence growth patterns, affecting survival and future reproductive output (Ricklefs and Peters 1981, Cooch et al. 1991, Sedinger and Flint 1991), although the relationship between adult body size and fecundity remains controversial, particularly in Snow Geese (*Anser caerulescens*; Alisauskas and Ankney 1990, Cooch et al. 1992). Several studies have shown that spatial and temporal variation in food abundance, quality and availability during the brood-rearing period is a major determinant of growth rates, body size, and body condition in precocial bird species (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger et al. 1995). Growth and development patterns affect first-year survival (Cooke et al. 1984), age of first breeding, clutch size, and ultimately adult fecundity, survival, and population dynamics (Sedinger 1992, Sedinger et al. 1995). Gosling size late in their first summer is strongly influenced by environmental factors (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991), which, in turn influences first year survival in Snow Geese (Cooch et al. 1993), Emperor Geese (*Anser canagicus*; Schmutz 1993), and Barnacle Geese (*Branta leucopsis*; Owen and Black 1989).

Despite its importance, brood biology remains poorly understood. For example, little is known regarding the genetic components of growth, or the selection differentials associated with birds of different size (Sedinger 1992). However, wetland selection studies consistently conclude that ducklings are dependent on aquatic macroinvertebrates as their primary source of protein and energy. If reproductive success and recruitment among waterfowl are sensitive to the quantity and quality of food resources available on breeding areas, then access to suitable foraging sites is paramount to females and their broods.

Barrow's Goldeneye (*Bucephala islandica*) exploit a variety of wetland habitats, although they are most commonly associated with forested wetlands that provide an adequate supply of nearby cavity nest sites (Kaminski and Weller 1992). Following hatch, goldeneye females lead their broods to wetlands and establish brood territories which are aggressively defended. It is believed that the function of these territories is to secure foraging sites for ducklings to feed unharrased (Savard 1988). In Chapter 4 of this thesis, I showed that food supply and wetland size explained the greatest amount of variation in wetland selection by these birds. While several other studies of habitat selection have also documented relationships between the presence or absence of waterfowl species and food abundance, many have failed to examine reproductive payoffs (Holmes 1981, Martin 1992).

The purpose of this chapter is to examine the relationship between food density and the following reproductive parameters of Barrow's Goldeneye: egg sizes, clutch sizes, hatching dates, duckling growth rates, prefledging survival, and recruitment. Although it is commonly reported that prey abundance influences juvenile growth and survivorship, few studies have actually examined this relationship due to the difficulty in 1) associating nutrition and waterfowl survivorship (Sedinger 1992), and 2) estimating survivorship and future fecundity (measuring fitness; Clutton-Brock et al. 1988). I examine this relationship by relating food abundance in brood-rearing habitats to duckling growth, survival, and recruitment. I predict that duckling growth rates are limited by prey abundance and that ducklings reared on lower quality wetlands will either spend more time foraging or fledge at lower weights. I further predict that female reproductive success (measured as prefledging survival and recruitment rates) is positively associated with prey abundance in brood-rearing lakes.

5.3. METHODS

5.3.1. Study Area

This study took place at Riske Creek, B.C., from April-August 1997-2000. General details of the study area are provided in Chapter 1.

5.3.2. Aquatic Invertebrate Biomass Sampling

In 1997, 15 lakes occupied by Barrow's Goldeneye were randomly selected and sampled for their invertebrate productivity levels. Each of the 15 lakes was sampled in each of the four years when ducklings on those lakes were 10, 20, 30, and 40 days old. This allowed a comparison of productivity levels between lakes when ducklings had the same nutritional requirements. Details of the invertebrate sampling protocol are presented in Chapter 4.

Not every lake had a brood every year, although all 15 lakes had active nest sites each year. Some nests were depredated and some broods moved to other lakes after hatch. Aquatic invertebrate samples were still taken from lakes lacking broods to continue monitoring annual fluctuations in the 15 study lakes.

5.3.3. Measures of Female Quality

Female quality can affect reproductive effort (e.g., egg masses, clutch size, hatch dates; Ankney and Afton 1988) which could directly affect duckling growth and survival. Goldeneye are difficult to age reliably beyond their first year (Carney 1983), therefore, I did not know the true ages of the nesting females. However, I considered two indices of female quality 1) female mass during incubation, and 2) nest initiation dates. Older females tend to be heavier, more experienced, and competitively superior to younger females (Hepp et al. 1987). Female Barrow's Goldeneye were weighed in the last week of incubation because I was unable to weigh females before incubation (as suggested by Ankney and Afton 1988); and to prevent nest abandonment, nest sites were not disturbed during early incubation. Nest initiation dates were also examined as a function of female quality, assuming older more experienced females lay first eggs earlier. Nest initiation dates were obtained three ways: 1) directly from known first egg dates (obtained from regular nest surveys), 2) by backdating from the date the nest was discovered and the number of eggs present (goldeneye egg production rates = 1 egg every 45.3 hours; Thompson 1996), or 3) by backdating from the known hatching date (goldeneye have 30 day incubation periods; Bellrose 1976, Mallory et al. 1994; Thompson 1996).

Furthermore, maternal effects were likely suppressed by a high degree of nest parasitism (approx. 25% of all nests in this study), and brood amalgamation (approx. 28% of all broods in this study, and 22% of 91 broods located 100 km south of this site; Eadie 1989) which act as natural 'mixing' processes. Thus, mixed clutches and broods consisted of numerous unrelated ducklings produced by females of different ages and experience, who may have been feeding on wetlands of different quality during egg production.

5.3.4. Clutch Size and Mass

Active nests were checked every 4-7 days. Eggs were counted and new eggs were numbered with a waterproof marker. Egg lengths and widths were measured to the nearest 0.1 mm with calipers and masses were measured to the nearest 0.5 g with a 100 g Pesola scale. All eggs were weighed before the onset of incubation., and for each nest, a mean egg mass was calculated.

5.3.5. Duckling Growth and Survival Rates

Growth rates were obtained by marking-and-recapturing broods on the 15 sample lakes. I attempted to catch all broods at ages 1, 10, 20, 30, and 40 days. The average mass of male and female ducklings at age 40 days was compared between lakes of different invertebrate biomass. For ducklings not caught and weighed on day 40, I took the mass of the ducklings caught at the age closest to 40 days, and adjusted it to an estimated mass at age 40 days, using the mean growth rate of that brood. Duckling ages were determined by monitoring nests for hatch dates and most ducklings were weighed in the nest on the day of hatch. Each duckling was individually marked with small web piercings at first capture, and ducklings were identified and weighed at each subsequent capture. Class IIc and III ducklings (as described in Bellrose 1976) were marked with nasal tags for identification in subsequent years. For the purposes of this study, the terms 'brood survival' and 'prefledging survival' are used synonymously, and are defined as the number of ducklings within a brood that survived until the age of 40 days. This age was arbitrarily chosen because goldeneye ducklings begin flying at 40-50 days of age (Eadie et al. 1995), at which time it becomes difficult to determine if changes in brood numbers are due to mortalities, or movements to other lakes.

Like most waterfowl species, goldeneye exhibit female biased natal philopatry, and therefore calculations of inter-annual survival (annual return rates) and recruitment (defined as birds that returned paired) involved female birds only. These were calculated as the number of females that returned divided by the number of females banded in that particular brood, at age 40 days. The percentage of total ducklings banded each year that were female ranged from 40-48% (1997: 46%; 1998: 45%; 1999: 40%; and 2000: 48%).

5.3.6. Time Activity Budget Analysis

Behavioral observations were made on all broods on the 15 lakes regularly sampled for lake productivity, to see if time spent foraging differed between broods on different quality ponds. A total of 450 hours were spent observing ducklings in 1999 (15 two-hour observation bouts at each lake, with observations recorded every five minutes, for a total of 360 observations per lake) and 240 hours in 2000 (8 two-hour bouts at each lake, for a total of 192 observations per lake). Approximately 90% of adult females followed were marked with nasal tags, allowing me to individually identify most broods. I assumed that unmarked broods were the same if they were found in the same brood territory locations as the previous visit. Observation bouts were performed throughout the entire brood-rearing period and broods were observed at similar ages as they would therefore have similar nutritional requirements. Scan sampling (Altmann 1974) was used to record the 'average' behaviour of ducklings in a brood in each five minute scan sample, during two hour observations bouts. The behavioral categories recorded included feeding (skimming and diving), resting, sleeping, preening, swimming, and acting alert. An attempt was made to perform observations on days that had similar weather conditions (typically calm, overcast days). Observations were not performed on cold, windy, or rainy days because visibility was poor and ducklings' foraging activity was often markedly diminished. Each sampling day was divided into three observation periods: 1) morning (8:00-10:00), mid-day (12:00-14:00), and afternoon (16:00-18:00) and the number of observation bouts for each brood were equally distributed within these periods, and across the season. Efforts were made to minimize the disturbance of broods upon our arrival by quietly walking to the wetlands and performing observations from concealed locations. None-the-less, all observations began 30 minutes after our arrival, to allow the birds time to recover and return to 'natural' behaviours in case they were disturbed. Observations were made with binoculars and 15-60x spotting scopes.

5.3.7. Statistical Analysis

Analysis of variance (ANOVA) and Spearman's rank correlations were used to examine aquatic invertebrate data within and among lakes, within and among years. Kendall's concordance correlation was used to compare annual rankings of activity trap means to chironomid means.

Linear regression was used to compare egg size, clutch size, duckling growth, survival, and return rates to annual activity trap and chironomid mean biomass values. Backward elimination procedures were followed when fitting regression equations, and chi-squared tests were used to test for significance of the variables added to the model. Full (maximum) models were used first to avoid making Type II (false negative) errors, including all variables, possible interactions and specified quadratics. Criteria for selecting the best predictive model by comparing the models' P values, R^2 values, and simplicity (parsimony). Results for duckling growth, survival, and return rates were not significantly altered when models were weighted by brood size.

Univariate and multivariate linear regression models were also used for comparisons between response variables and the mean biomass of individual invertebrate taxa. For multiple comparisons, Bonferroni adjustments were made (fourteen taxa were examined and therefore the Bonferroni adjustment was $\alpha = 0.05/14 = 0.004$).

Comparisons were also made between sexes, within a brood and among broods, when examining relationships between duckling final weights and prefledging survival to activity trap and chironomid mean biomass values. A differential coefficient between sexes was determined within each brood by 1) subtracting the average female mass, from the average male mass, within a brood, and 2) subtracting the average female survivorship, from the average male survivorship, within a brood. These differential values did not differ between years and so were pooled and regressed against activity trap and chironomid mean biomass values.

Time activity budget observations were converted into proportions of scans spent in each behaviour, for each observation period. Averages for each behaviour were then calculated across the season for each brood. Arcsine transformations were used for data that were not normally distributed and analysis of variance (ANOVA) was used to compare averages among the 15 different lakes, using multiple broods per pond (when possible), and multiple years. Individual females with broods in both years' of observation were included in the analysis for each year. Univariate linear regression analyses were used to examine the relationship between time activity budgets and mean prey biomass per lake, for all 15 lakes.

5.4. RESULTS

5.4.1. Aquatic Invertebrate Biomass

Figure 5.1 shows the annual mean biomass of aquatic invertebrates from activity trap and benthic core samples for all 15 sampled lakes. Mean invertebrate biomass values varied widely among lakes, and Spearman's rank correlations showed consistent annual rankings of lakes for both activity trap ($r_s = 0.9$, $P < 0.001$), and benthic core samples ($r_s = 0.8$, $P < 0.001$). Therefore a lake's relative productivity levels were predictable between years. Mean activity trap biomass was strongly correlated with mean benthic core (chironomid) biomass ($r = 0.7$, $P < 0.001$ for all years combined; Figure 5.2.), and concordance correlation showed a lake's relative ranking for activity trap biomass was similar to its ranking for benthic core samples within years (1997: $W = 0.7$, $P < 0.001$; 1998: $W = 0.7$, $P < 0.001$; 1999: $W = 0.6$, $P < 0.001$), and across years ($W = 0.6$, $P < 0.001$). Over the four years of the study, there was a gradual, but non-significant, decline in mean biomass levels for both activity trap and benthic core samples (Table 5.1.).

5.4.2. Female Quality Indices, Clutch Size, Mean Egg Mass, and Nesting Success Rates

The mean nest initiation dates were similar in all four years (Chapter 3; Evans et al. 2002). Female masses during late incubation ($t_{93} = 0.9$, $P = 0.4$) and nest initiation dates ($t_{93} = 0.9$, $P = 0.4$) did not vary with mean invertebrate biomass, suggesting that higher quality females were not nesting disproportionately on higher quality lakes. Clutch size ($t_{93} = 1.5$, $P = 0.1$), mean egg mass ($t_{93} = 0.3$, $P = 0.7$), total clutch mass ($t_{93} = 1.0$, $P = 0.3$) and nesting success rates ($t_{93} = 0.7$, $P = 0.5$) were also unrelated to mean invertebrate biomass.

This study also failed to find a relationship between adult female mass and hatch date ($t_{93} = 0.4$, $P = 0.7$). Nor were any relationships found between hatch date and duckling mass at age 40 days, prefledging survival, annual return rates, and recruitment (Table 5.2.).

5.4.3. Duckling Masses

A generalized growth curve for both male and female ducklings is presented in Figure 5.3. These curves represent pooled data from mark-recapture brood-drives over the four years of the study. Males typically grew at a rate of 15.3 g/day, and females at 12.1 g/day. Because Figure 5.3 shows that duckling growth rates are effectively linear, at least until the age of 40 days, the variation in body mass and growth rates are equivalent over the range of ages that ducklings were caught in this study (1-40 days old; Cooch et al. 1997). Therefore, the subsequent comparisons of duckling growth patterns between wetlands was performed by examining duckling masses among wetlands at age 40 days.

Duckling mass at age 40 days was positively correlated to both activity trap biomass (Figure 5.4a), and chironomid biomass (Figure 5.4b), for both males and females in all years of the study. There was no significant annual variation in mean duckling mass, nor mean invertebrate biomass (Table 5.1.), so these data were pooled over the four years for subsequent analysis. Multivariate models containing both mean activity trap biomass ($t_{58} = 3.5$, $P < 0.01$) and chironomid biomass ($t_{43} = 2.9$, $P < 0.01$) explained a significant amount of the variation for both male and female mass at age 40 days (62% and 57%, respectively).

When looking at individual invertebrate taxa, and accounting for Bonferroni adjustments ($\alpha = 0.05/14$ comparisons $= 0.004$), I found male masses at age 40 days were positively related to mean amphipod biomass in 1997 (non-linear regression, $t_{13} = 3.8$, $P < 0.01$), and mean dytiscidae adult biomass in 1999 ($t_{13} = 3.6$, $P < 0.01$). Male masses were not related to zygoptera nor tricoptera levels in any year of the study. The multivariate model that accounted for the largest proportion of variation in male mass at age 40 days, included 11 of the 14 invertebrate taxa: amphipoda, Corixidae, Notonectidae, Dytiscidae larvae, cladocera, hydracarina, zygoptera, tricoptera, ephemeroptera, Chironomidae, and Hirudinea ($F_{11,49} = 3.3$, $P < 0.01$, $R^2 = 0.6$). There were no significant interactions, nor higher order predictors.

Results for female masses at day 40 were similar to those of males. Mean amphipod biomass was positively related to female mass for one of four years (non-linear regression, 1999: $t_{13} = 3.0$, $P < 0.01$). The multivariate model that best explained the variation in female mass at age 40 days was identical to the one for males (see above for taxa included; $F_{11,49} = 4.6$, $P < 0.001$, $R^2 = 0.6$). Again, there were no significant interactions, nor higher order predictors.

There were no significant differences in the mass differentials between males and females, among lakes of different invertebrate biomass (Figure 5.5.). In other words, differences in male and female masses at age 40 days remained similar between wetlands, regardless of the variation in prey production levels between ponds.

5.4.4. Time Activity Budget Analysis

The mean proportion of time that broods spent in each behaviour did not differ between years within a lake, and therefore, data were pooled for the two sample years (1999 and 2000). The overall mean time spent feeding was 44% in 1999 and 47% in 2000, for all broods combined. Mean time spent in self-maintenance behaviours (defined here as resting and preening) was 28% in 1999, and 26% in 2000. The amount of time ducklings spent feeding ($t_{28} = 0.4$, $P = 0.7$), resting and preening ($t_{28} = 1.0$, $P = 0.4$), did not vary with prey productivity (Figure 5.6.). Hence, ducklings reared on wetlands with lower food densities did not spend more time foraging, and less time resting and preening.

5.4.5. Prefledging Survival

Mean prefledging survival rates did not differ across the four years of this study (Table 5.1.). Prefledging duckling survival was positively related to mean activity trap biomass values in 1998 ($t_{15} = 2.4$, $P < 0.05$) and to mean chironomid biomass in 1999 ($t_{15} = 2.3$, $P < 0.05$). When prefledging survival was pooled across the four years, and regressed against pooled activity trap and chironomid values, positive relationships were found for both (Figure 5.7.). Removal of the extreme points in Figures 5.7a and 5.7b had no effect on these results. No univariate relationships were found between prefledging survival and the individual invertebrate taxa, although a multivariate model that included amphipoda, zygoptera, tricoptera, Chironomidae, and Dytiscidae larvae explained 22% of the variation in prefledging survival ($F_{5,55} = 2.9$, $P < 0.05$).

There were no significant differences in the prefledging survival differentials between males and females, among lakes of different invertebrate biomass (Figure 5.8.). Therefore, differences in male and female survival to the age of 40 days remained similar between wetlands, regardless of the wetland's mean invertebrate biomass.

5.4.6. Annual Return Rates

The number of female ducklings banded each year and resighted in subsequent years is presented in Table 5.3. Table 5.3 also shows the percent of banded birds that were recruited into the breeding population and the average age of first-time breeders. First year return rates were positively related to mean activity trap biomass, in the year of hatching, in two of the four years (1997: $F_{1,14} = 7.4, P < 0.05$; and 1998: $F_{1,14} = 11.9, P < 0.01$; Figure 5.9a). However, removal of extreme point in 1997 produced an non-significant result ($F_{1,13} = 3.2, P = 0.1$) for this year. First year return rates were also positively related to mean chironomid biomass in one of the three years measured (1997: $F_{1,14} = 7.0, P < 0.05$; Figure 5.9b), but again, removal of the extreme point produced a non-significant result ($F_{1,13} = 3.5, P = 0.1$). No significant relationships were found between annual return rates and any of the individual invertebrate taxa. Multivariate analysis found no significant models explaining annual return rates.

When pooled, first year return rates were associated with mean activity trap biomass and chironomid biomass values (Table 5.4.). However, second, third, and fourth year return rates, as well as recruitment rates were not significantly correlated to either invertebrate biomass index (Table 5.4.). Therefore, it appears that although ducklings reared on wetlands with higher invertebrate biomass are more likely to return to the study site after their first winter, similar patterns were not exhibited in subsequent years. However, it is important to point out that sample sizes decrease substantially in each year subsequent to banding, and the non-significant results for second, third, and fourth year return rates may be due to a lack of power

5.5. DISCUSSION

Distinct differences in food abundance levels (habitat quality) were recorded among the 15 occupied wetlands that were examined across the four years of this study. The annual rankings of lakes based on their mean invertebrate biomass values varied little, suggesting that a lake's relative productivity levels were predictable between years. I found positive correlations between invertebrate levels within a wetland and Barrow's Goldeneye duckling day 40 masses, prefledging survival, and first year return rates. The masses of incubating females did not differ between sampled lakes, nor did nest initiation dates, clutch sizes, or mean egg masses, suggesting that older, more experienced females were not nesting disproportionately on high quality lakes.

5.5.1. Incubating Female Masses, Hatching Dates, Clutch Size, and Mean Egg Mass

Female masses did not differ significantly between lakes with different prey abundance. In another study, older, experienced Common Goldeneye females were not heavier and did not lay heavier eggs, but they did initiate nests earlier (Mallory et al 1994). Goldeneye hatching dates in my study did not vary with lake quality, suggesting that there was no relationship between female experience and lake quality. As well, females on the more productive lakes did not produce significantly larger clutch sizes, nor larger eggs. These findings likely result from a combination of two factors: 1) frequent conspecific nest parasitism, and 2) females' ability to forage on several neighboring lakes during egg laying. Egg parasitism is a common phenomena in goldeneye populations (Eadie 1989) and would act to mix the eggs produced by several females, thereby reducing the likelihood of detecting any potential differences between egg masses laid by females of different age and size (quality).

Parasitic eggs may also have come from several females foraging on lakes of various productivity levels. This idea is supported by the fact that females are generally able to forage in undefended areas of nearby lakes and were often seen doing so in this study. In Ontario, virtually all nesting Common Goldeneye females foraged on higher quality lakes (defined by their absence of fish which are effective competitors for invertebrates) irrespective of the location of their nest site (Mallory 1991). Thus, it is possible that in my study, females on low quality lakes may have periodically foraged on higher quality sites during the egg laying process, and thus nutrient intake for these females would increase, resulting in similar mean egg masses between lakes (holding female quality/body size constant). In this study, clutch size was not related to egg mass, a result that is consistent with other waterfowl studies (Rohwer and Andersson 1988).

My finding of similar clutch sizes among lakes contrast with the findings of three previous studies of Common Goldeneye, which found clutch size to vary with an index of habitat quality (Eadie and Keast 1982, Eriksson 1983, Mallory et al. 1993). However, these previous studies did not measure invertebrate levels directly, instead indexing relative abundance of macroinvertebrates by the presence or absence of fish competitors. In those studies, the amount of resources female Common Goldeneye invested in a clutch was higher on lakes devoid of fish. Similar results were found for Tree Swallows (*Tachycineta bicolor*) foraging on emerging aquatic invertebrates from fishless lakes (Blancher and McNicol 1991). Furthermore, Bengtson (1971) showed that several other species of waterfowl lay larger clutches when food was more abundant. Reasons for my different results may be that these previous studies did not measure food abundance directly, nest parasitism rates may be higher in my study which would mix clutches more and negate differences between females, and females in my study may be experiencing sufficient prey abundance, or else are foraging on other lakes that do. As well, all of the lakes in my study lacked fish.

5.5.2. Duckling Growth and Survival

Barrow's Goldeneye ducklings are precocial, and thus, adult females lead their young to foraging areas. The growth and survival of these ducklings is therefore influenced by the female's ability to locate productive areas. Some hens are believed to sample potential brood-rearing areas prior to hatch, becoming familiar with the wetland's food supply, predation risks, and other factors that may enhance brood survival (Bellrose 1976). Factors influencing initial wetland selection for brood-rearing are poorly understood, although food availability seems important (Talent et al. 1983, Pehrsson 1984, and see Chapter 4 this thesis). Furthermore, studies examining the relationship between habitat selection (specifically, food availability) and duckling survival are scarce, and the few that do exist offer conflicting results. Bufflehead, for example, have larger brood densities and higher duckling survival rates on wetlands with higher food density, but growth rates were unaffected by food levels (Gauthier 1987). A study of Barrow's Goldeneye broods on rivers and streams found territory site selection was linked to black fly larvae abundance, but duckling growth and survival were not examined (Einarrson 1988). For other species, Black Duck and Mallard duckling growth rates increased with invertebrate densities (Hunter et al. 1984) and Mallards had higher than average mortality rates when reared on gravel quarries believed to have low invertebrate densities (Street 1977). In another study, Mallard duckling mortality was higher on ponds containing fish which competed for invertebrate food (Hill et al. 1987). Increased competition for food was also thought to be responsible for lower survival rates in larger Long-tailed Duck broods (Pehrsson 1984).

Other evidence suggests food availability as a major determinant of growth rates and survival. Experiments have revealed a positive relationship between invertebrate abundance and growth rates of Black Duck ducklings (DesGranges and Rodrigue 1986, Hunter et al. 1986). Annual production rates for several species were positively correlated to invertebrate abundance in Icelandic wetlands (Gardarsson and Einarsson 1994). Lower growth rates of ducklings on acidified wetlands were attributed to a decrease in invertebrate biomass (Haramis and Chu 1987, Rattner et al. 1987), although lower pH levels may have had a more direct physiological affect on ducklings (Eriksson 1984).

Conversely, several studies have failed to find a link between food availability and duckling survivorship, although these studies suffered from small sample sizes or failed to follow marked birds beyond brood-rearing. Poysa and Virtanen (1994) for example, found no relationship between duckling survival and food abundance, but admittedly did not follow broods even as far as fledging. The effects of prey availability may be a subtle one that affects population-level processes such as recruitment, and adult life-history traits such as egg size and clutch size, and differences in these variables are difficult to detect, especially in short-term studies.

Further evidence of the importance of suitable foraging sites to goldeneye broods is provided by the unusually aggressive territorial defense of brood-rearing areas by females, which is believed to be in defense of food supplies (Savard 1988). Therefore, wetland selection in these birds likely involves striking a balance between two counteracting forces: searching for rich foraging areas while minimizing agonistic territorial interactions with other females. As a result, some females are prevented from settling on preferred high quality lakes, and are instead forced to utilize less optimal feeding areas. We should expect that those birds establishing territories on higher quality wetlands would be older, competitively superior females and those birds forced onto lesser quality sites are younger, less experienced birds. Unfortunately, my study did not index the age and quality of territorial females, and movements from hatching lakes to different brood-rearing lakes were rare and typically involved lakes not measured in this study. However, my pre-hatch index of female quality, obtained by comparing the masses of incubating females, as well as hatch dates, indicated that there were no differences in female quality between lakes prior to hatch.

Other studies have reported overland movements to richer feeding areas by Barrow's Goldeneye (Einarsson 1988), Common Goldeneye (Eriksson 1978, Poysa and Virtanen 1994, Wayland and McNicol 1994), and Bufflehead (Gauthier 1987). Common Goldeneye broods have been recorded making moves of up to 2 km between ponds (Siren 1952). Movements of 8 km have been reported for Mallard broods (Dzubin and Gollop 1972) and 3 to 14 km for Eiders (*Somateria mollissima*; Minot 1980). Overland movements are believed to involve inherent risks of predation and exhaustion, and thus I expect such moves are made to increase potential benefits related to duckling growth and survival. These risky movements likely result from attempts to locate better quality foraging areas, lessen competitive interference, and/or lower predation risks. Several studies have concluded that they are initiated by a female when hatching lakes do not fulfill the food requirements of a brood, reporting that females consistently move to wetlands with higher prey densities (Eriksson 1978, Talent et al. 1982, Hunter et al. 1984, Gauthier 1987). Females may be in search of a minimal threshold level of food abundance, at which time duckling mortality may become independent of prey levels. The results of my study suggest short-term payoffs, in terms of prefledging survival, for birds that successfully move to higher quality brood-rearing areas. Females remaining on lower quality sites are likely doing so because of competitive exclusion.

If the food resources within a lake are predictable from year to year, as suggested in this study, then one should expect older females to select higher quality lakes in subsequent years, having learned through experience where to take their young in order to maximize her brood's survival, and therefore her own reproductive fitness. Also, ideal free distribution theory would suggest that early arrivers (breeding pairs arriving from migration, or broods arriving after hatch) should in all likelihood, select the best feeding patches (wetlands) and subsequent arrivals should continue to select these areas as well, until a threshold is reached in which it becomes more advantageous to choose areas of lesser quality (e.g., food supply) that have a lower density of competitors (Fretwell and Lucas 1970). Sampling of other, nearby foraging sites by goldeneye seems common. Females were often observed leaving broods for short periods to forage in other areas, either on the same wetland or neighboring sites. I suggest these recesses have three possible functions 1) allowing females to sample and compare the suitability of other locations, 2) providing females with other food items not available in the current brood location, or 3) avoiding competition for food with their own offspring. A combination of all three factors may drive females to periodically abandon broods, leaving them vulnerable to predators or aggressive attacks from other territorial females.

My study shows that goldeneye duckling prefledging survival, day 40 masses, and first year return rates are positively associated with food abundance of the brood-rearing lake. However, due to small sample sizes and a lack of power, my results do not suggest a relationship between second and third year return rates, recruitment, and food. Therefore, it appears that ducklings raised on higher quality wetlands have, at least, a short-term, but perhaps non-permanent advantage, although larger sample sizes may have shown patterns supporting long-term advantages.

It may be that the short-term benefits to ducklings on higher quality ponds are particularly advantageous during years when post-hatch environmental conditions are poor. Ducklings growing faster and gaining larger body sizes are more resistant to weather related stresses like chilling and starvation (Sedinger 1992). It is apparent that this advantage disappears as the ducklings mature over their next two years.

Other possible explanations exist for the apparent lack of a long-term advantage. There may be a minimum threshold body mass that must be obtained by ducklings before fall migration.

Ducklings reared on lower quality wetlands may simply need to remain on the breeding grounds longer to gain appropriate premigration mass, and/or they may chose not to return to the breeding grounds in their first year. Once juvenile birds become flight capable they are able to move to other wetlands and access other foraging areas. At this time in the season brood territories are no longer defended and birds are free to forage in higher quality areas. It is possible that lighter birds remain on the breeding grounds longer and continue to gain mass until they finally migrate at weights similar to other birds. Admittedly, I have no information regarding this possibility. Finally, conditions on the wintering grounds may allow lighter ducklings to compensate by gaining relatively more mass, to a point where mortality and recruitment rates become independent of body mass, particularly after they reach the age of two.

5.5.3. Maternal Effects on Duckling Size and Survival

Factors other than habitat quality have been found to influence growth and survival patterns of juvenile birds. Numerous studies have found heritabilities for life history traits including egg size, clutch size, and body size (reviewed in Boag and Van Noordwijk 1987). Hatch date is also influenced by female quality and is considered an important determinant of juvenile body size as late hatching birds often have lower growth rates due to deteriorating foraging conditions as the season progresses (Sedinger and Flint 1991, Cooch et al. 1991). A small variation in nesting dates attributes substantial variation in fitness in Snow Geese (Findlay and Cooke 1987). Female quality may also affect extrinsic factors such as territory quality (e.g., prey abundance; Williams 1994), something that I suspect is a very important determinant of foraging opportunities for goldeneye ducklings.

Despite my inability to directly account for maternal effects in this study, it can be argued that many of these factors have also been positively linked to available food supplies (Sedinger and Flint 1991). Clutch size, egg mass, and offspring body size may be a result of female age, size, and quality, but they are also influenced by nutrient intake rates (food availability) by both the female and the offspring. Regardless, many of the broods in this study were mixed by either nest parasitism, or brood amalgamation, and thus consisted of numerous unrelated ducklings. Furthermore, adult female masses and mean hatch dates did not differ significantly between lakes, and late hatching broods were not considered in this analysis.

5.5.4. Activity Time Budget Analysis

Examining time allocation strategies of animals can be useful in assessing behavioral strategies that have evolved to optimize fitness (King 1974). Foraging time budget analysis can be interpreted as an animal's ability/strategy to obtain essential nutrients, and can also indicate the level of resources available to an animal in its environment, with animals theoretically spending more time foraging when prey items are scarce. Mallard and Black Duck ducklings, for example, spent more time feeding when food availability was low (Hunter et al. 1984). Black Duck ducklings also reportedly reduced their time spent resting and foraged more widely in lakes experimentally acidified (DesGranges and Rodrigue 1986). For Ring-necked Duck ducklings, foraging costs increased, and survival decreased, on wetlands with reduced prey diversity and quality (McAuley and Longcore 1988).

In habitats with predictable food resource levels, such as the wetlands in my study, optimal foraging theory predicts that animals should allocate all foraging time to patches that consistently yield the highest energetic and/or nutritional return (Charnov 1976, Houston and McNamara 1985). This strategy would only be adaptive on wetlands that exhibit small temporal and spatial fluctuations in aquatic invertebrate abundance. For Barrow's Goldeneye and other insectivorous ducks, it is doubtful that processing times are a major limiting factor as invertebrates are highly digestible and pass into the intestine quickly (Swanson and Bartonek 1970). It is more likely that search time for these prey items is limiting, and therefore intake rates would be more dependent on prey abundance, rather than saturation of the digestive tract.

However, the fact that my study found no relationship between time spent foraging and prey abundance suggests an alternative limiting factor that is independent of food supply and search time, such as the physiological constraints involved in diving. A minimal recovery time must be spent on the surface after each dive, and the length of these pauses between dives correlates to the length of the previous dive (for goldeneye and Surf Scoters *Melanitta perspicillata*, see Ydenberg 1988, and Beauchamp 1992). Therefore, it may be that this mandatory recovery time prevents birds on poorer quality wetlands from spending more time foraging. If all broods spend equal amounts of timing foraging, and birds on higher quality ponds have higher prey encounter rates, then these birds should be ingesting more prey matter per unit of time and effort. This would eventually lead to these ducklings growing faster and achieving higher body masses at age 40 days, as was recorded in this study.

5.6. CONCLUSIONS

There were distinct differences in food availability between the 15 occupied wetlands that were examined across the four years of this study, and ponds varied predictably in their annual productivity. Optimal foraging theory predicts that experienced birds should forage in patches that consistently yield the highest energetic and/or nutritional returns and that these birds should continuously gauge their foraging effort by sampling the current profitability of encountered patches (Charnov 1976). Birds found foraging in suboptimal habitats are likely there because of other factors such as competition.

From this study, it can be concluded that prey abundance in brood-rearing wetlands influences Barrow's Goldeneye duckling growth rates, prefledging survival, and first year return rates. However, evidence that prey abundance is directly related to recruitment patterns and therefore fitness variation among females is inconclusive. Regardless, the results of this study predict that females should be sampling local wetlands for their habitat quality and that annual philopatry and territorial defense should be higher on the more productive ponds. I would also predict that birds should attempt to move from the less productive to more productive ponds, although the use of suboptimal habitats is the result of intraspecific competition, where the only alternative is to forego breeding altogether.

This study did not find evidence of an increase in reproductive effort (in terms of clutch size or egg mass) by females on higher quality lakes, in contrast to several other studies. Females nesting on higher quality habitats should invest more resources into increasing clutch size if these lakes are able to support higher duckling densities and enhance survival, thereby increasing a female's lifetime reproductive success. However, the results of this study indicate that offspring recruitment (and hence female fitness) is not necessarily linked to the quality of brood rearing habitat. However, the effects of prey availability may be a subtle one and difficult to detect in short-term studies.

One must be careful in interpreting these associations, and lack of them, as causal, and I suggest that further experimental evidence is necessary. As well, invertebrate biomass values reported here are only an index of wetland productivity levels; these biomass values do not reflect differences in a prey item's availability based on behaviour, size, colour, or capturability (Armstrong and Nudds 1985).

5.7. MANAGEMENT RECOMMENDATIONS

Waterfowl habitats should be managed to maximize the survival of breeding adults and the production of young. Changes in limnological components of wetland ecosystems could have negative impacts on aquatic invertebrate communities, reducing waterfowl prey availability, diversity (Bendell and McNicol 1987), and quality (McAuley and Longcore 1988), and thereby affecting nutrient intake and growth rates of ducklings. Therefore, productive wetlands should be managed in such a way that they provide stable, abundant food supplies for egg laying females and developing young. Also, maintaining suitable brood-rearing habitat near nesting areas will also lessen the likelihood of duckling mortality during overland movements from the nest. Specifically for Barrow's Goldeneye, it is further suggested that managers be particularly sensitive to wetlands in close proximity to cavity nesting habitat, such as mature aspen stands (discussed in Chapter 2).

5.8. LITERATURE CITED

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Table 5.1. Four year means and stardard errors for aquatic invertebrate data, duckling masses, and prefledging survival for 15 lakes studied each year from 1997-2000, Riske Creek, BC. Prefledging survival is defined as the percent of the brood that is alive at age 40 days.

Year	Mean Activity Trap Biomass (g/sample)		Mean Chironomid Biomass (g/sample)		Female Mass (g) at 40 Days of Age		Male Mass (g) at 40 Days of Age		Prefledging Survival (%)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1997	139.2	28.8	2.6	0.9	520.7	10.1	655.4	8.5	52.7	8.0
1998	118.4	20.6	2.2	0.5	526.9	17.3	659.4	12.7	57.1	6.8
1999	96.4	17.2	1.4	0.5	530.6	9.8	656.4	9.9	53.2	7.2
2000	93.2	20.7	--	--	530.1	11.7	653.4	20.2	57.7	7.1

Table 5.2. Univariate regression analysis between hatch dates and female Goldeneye duckling mass, survival, and annual return rates. *N* = 15 lakes followed over four years (1997-2000).

	r	*F* Ratio	*P*	*n*
Female mass day 40	0.01	0.1	0.9	95
Prefledging survival	0.26	3.7	0.06	53
1st year return rates	0.05	0.09	0.8	36
2nd year return rates	0.22	1.8	0.2	36
3rd year return rates	0.21	1.6	0.2	22
4th year return rates	0.22	0.9	0.3	19
Recruitment	0.17	1.1	0.3	38

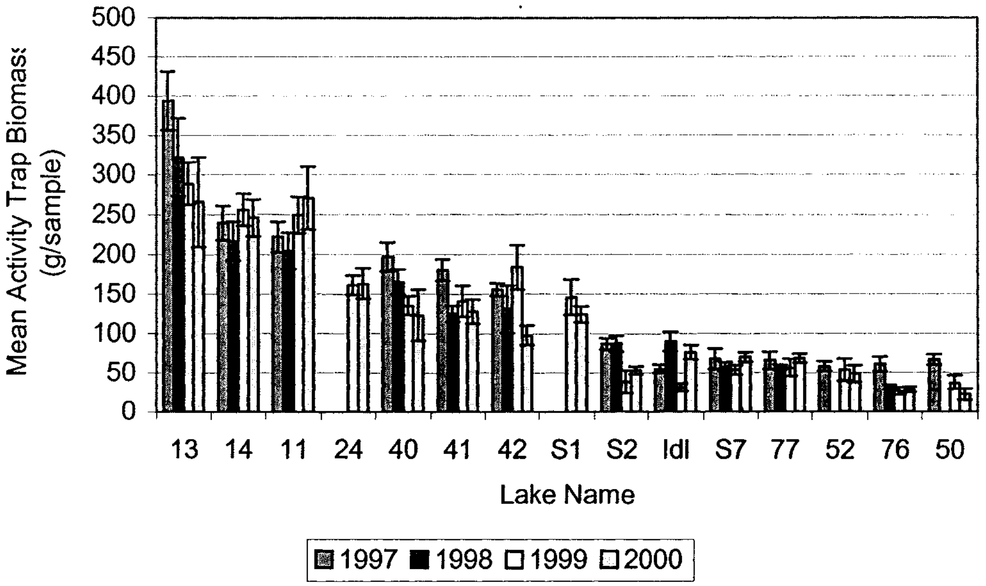
Table 5.3. Number of female Goldeneye ducklings banded and percent that were resighted in each subsequent year, as well as percent seen paired, and average age of first year breeders.

Year Banded	Number of Female Ducklings Banded	Percent Returned 1st Year	Percent Returned 2nd Year	Percent Returned 3rd Year	Percent Returned 4th Year	Percent Seen Paired	Mean Age of New Breeders
1997	79	28	20	15	5	15	3.0 +/- 0.0
1998	87	20	21	8	2	16	2.5 +/- 1.3
1999	60	15	7	8	--	5	2.6 +/- 0.3
2000	103	24	35	--	--	23	2.0 +/- 0.0

Table 5.4. Univariate regression analysis between mean annual return rates of female Goldeneye ducklings and mean activity trap and chironomid biomass. $N = 15$ lakes followed over four years (1997-2000).

	Activity Trap Biomass			**Chironomid Biomass**		
Percent Returned	***r***	***F* Ratio**	***P***	***r***	***F* Ratio**	***P***
1st Year	0.4	6.2	0.02	0.5	7.7	0.01
2nd Year	0.1	0.2	0.6	0.01	0.1	0.9
3rd Year	0.1	0.2	0.7	0.1	0.2	0.6
4th Year	0.01	0.1	0.8	0.1	0.1	0.8
Recruited	0.2	1.9	0.2	0.1	1.4	0.3

a)



b)

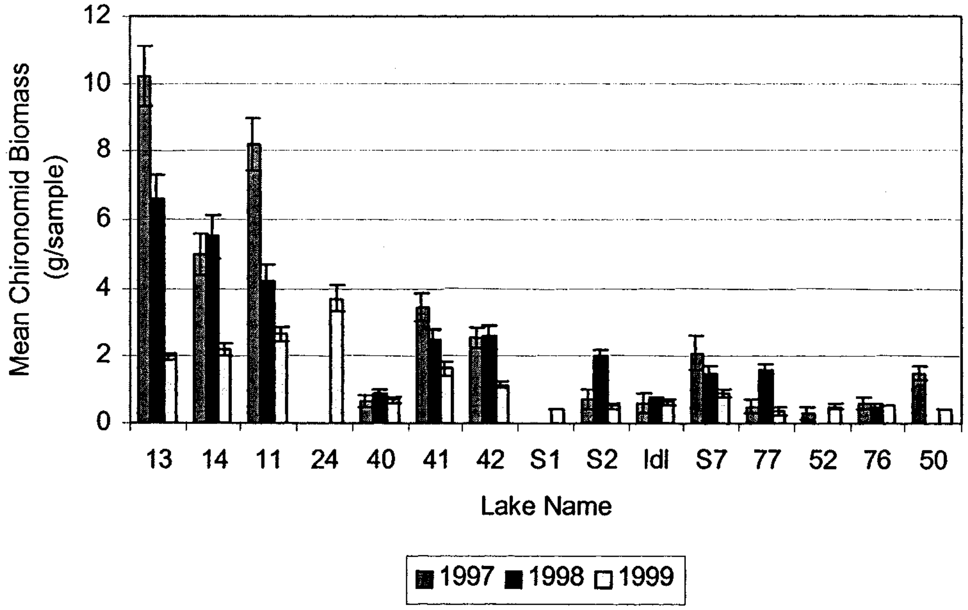


Figure 5.1. Annual mean biomass of a) activity trap (1997-2000), and b) chironomid samples (1997-1999), for 15 lakes at Riske Creek, BC. Error bars are ± 1 SE.

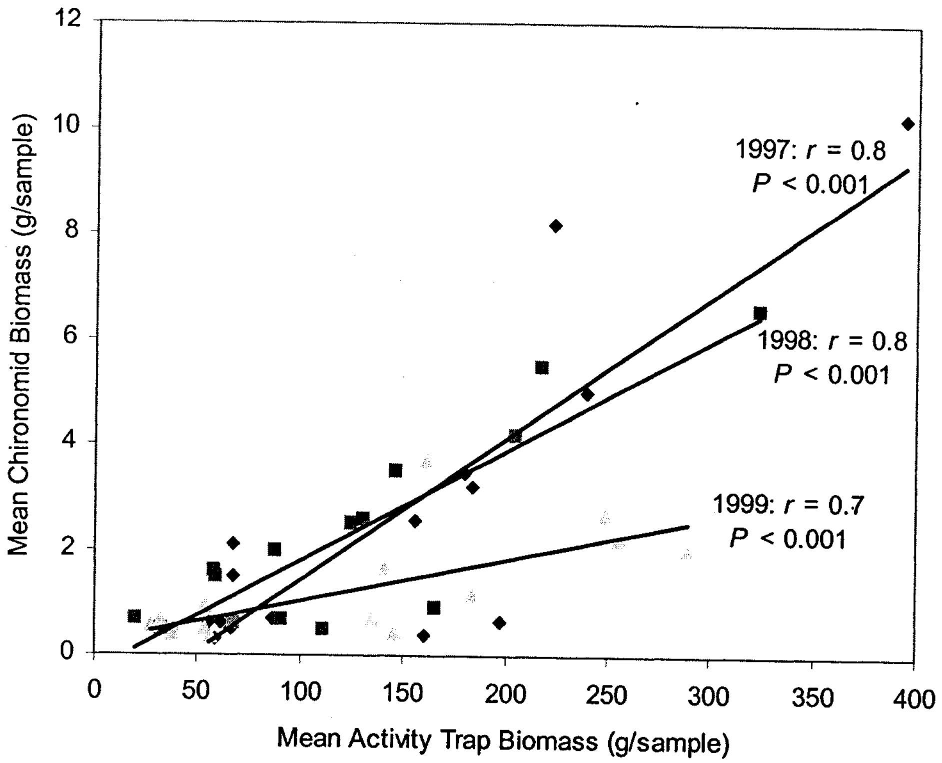


Figure 5.2. Mean chironomid biomass values plotted against mean activity trap biomass values, for 15 lakes (1997-1999).

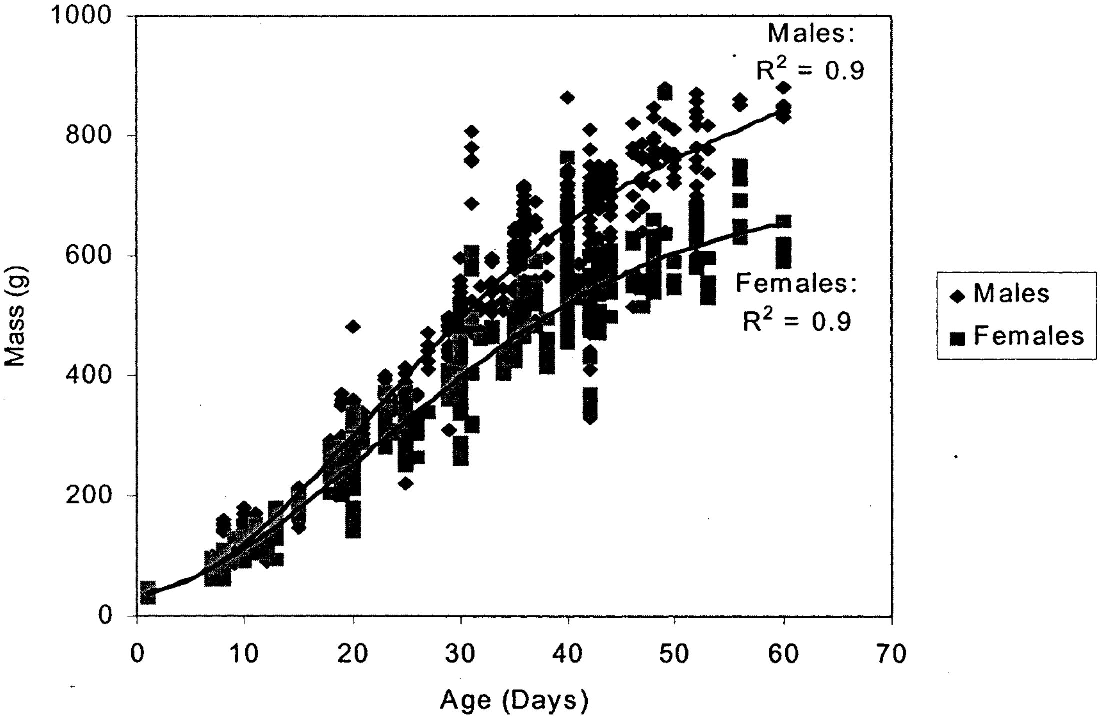


Figure 5.3. Mean growth projections for male and female Barrow's Goldeneye ducklings captured between 1997 and 2000.

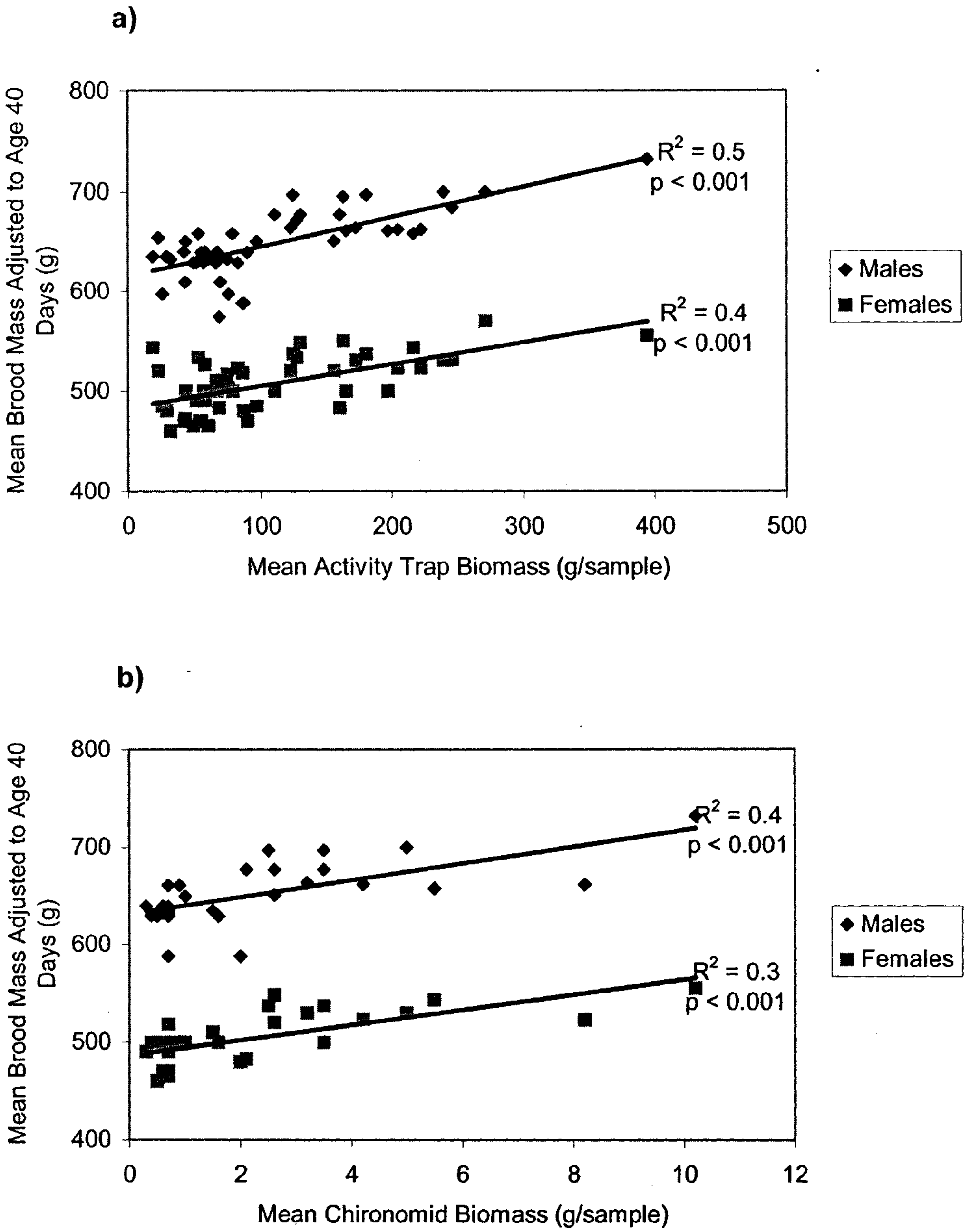


Figure 5.4. Mean brood mass for male and female Barrow's Goldeneye ducklings, adjusted to age 40 days, plotted against mean a) activity trap biomass (1997-2000), and b) chironomid biomass values (1997-1999).

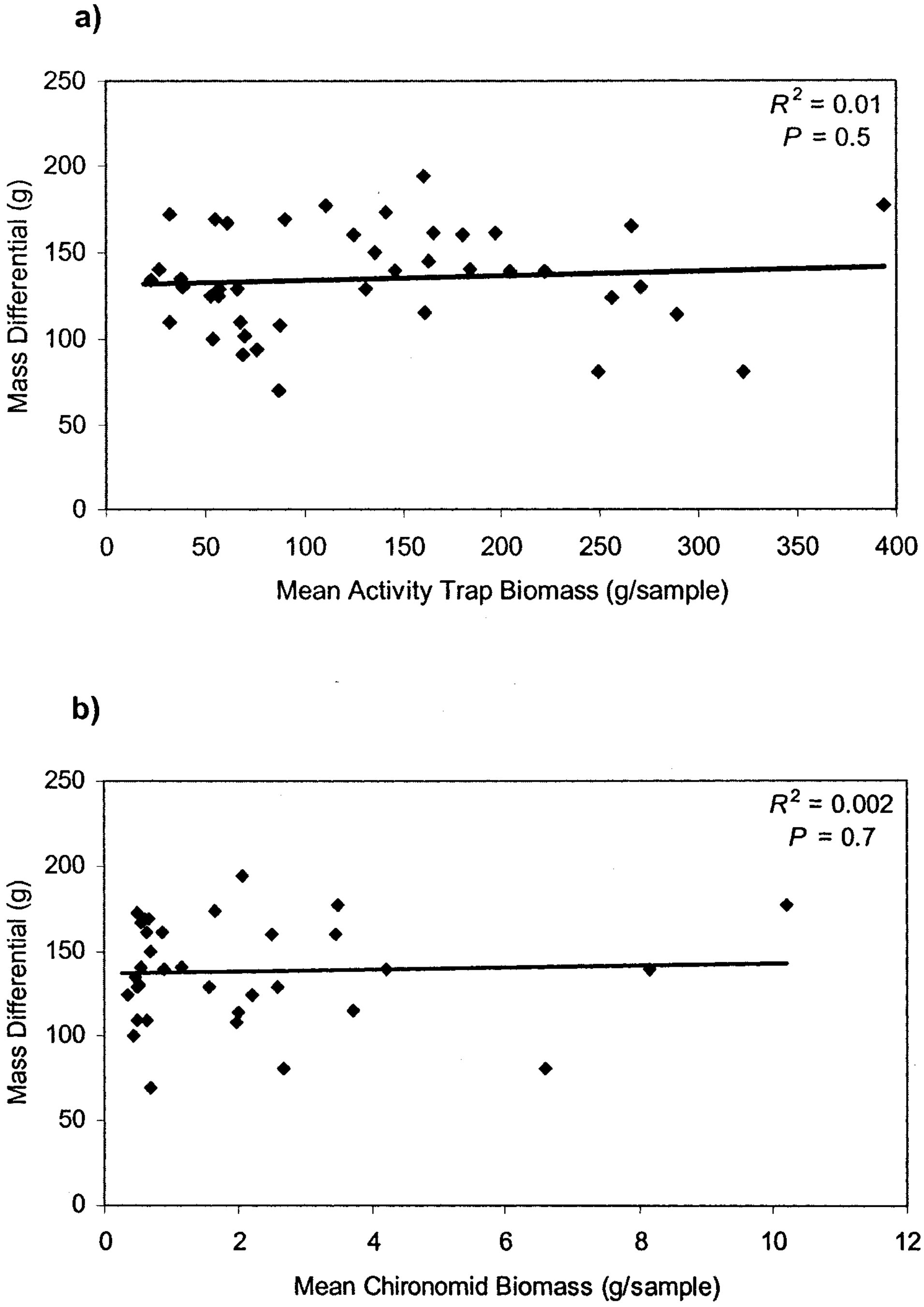


Figure 5.5. Mass differential values between male and female Barrow's Goldeneye ducklings plotted against mean a) activity trap (1997-2000), and b) chironomid biomass values (1997-1999).

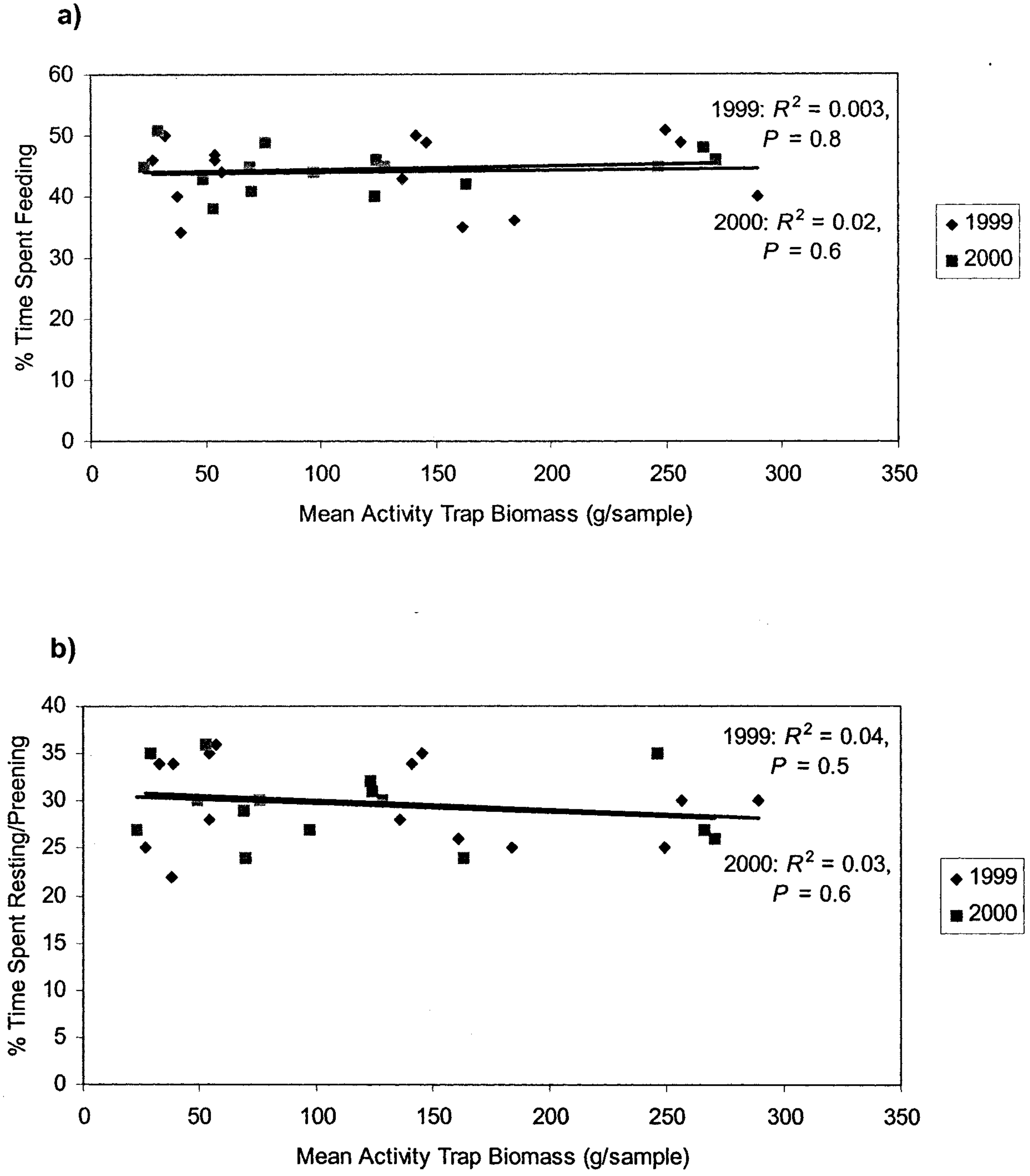
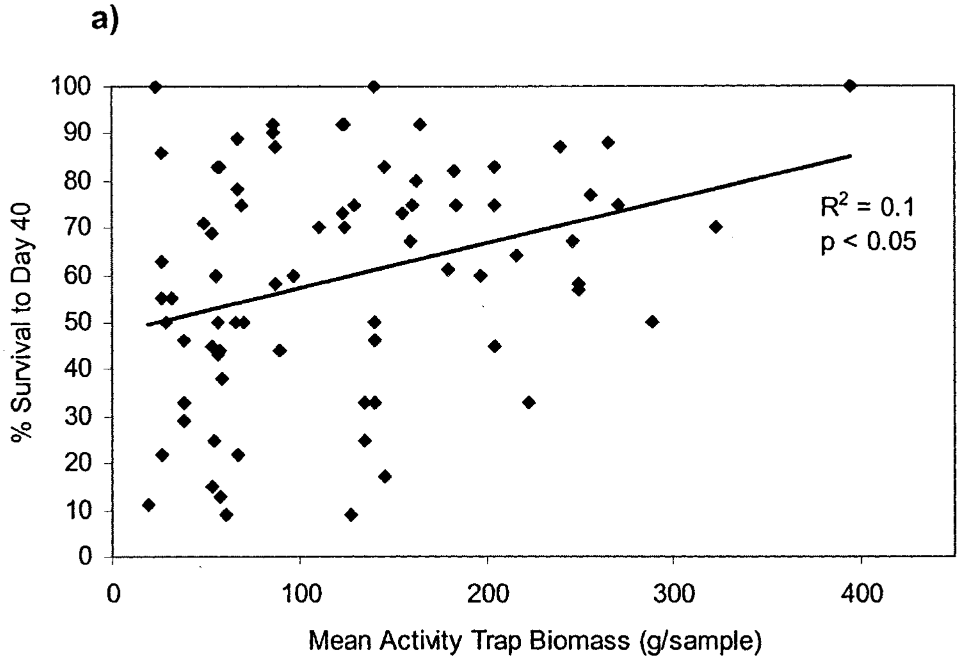


Figure 5.6. Percent time spent a) feeding, and b) resting/preening by Barrow's Goldeneye ducklings, plotted against mean activity trap biomass values, 1999 and 2000.



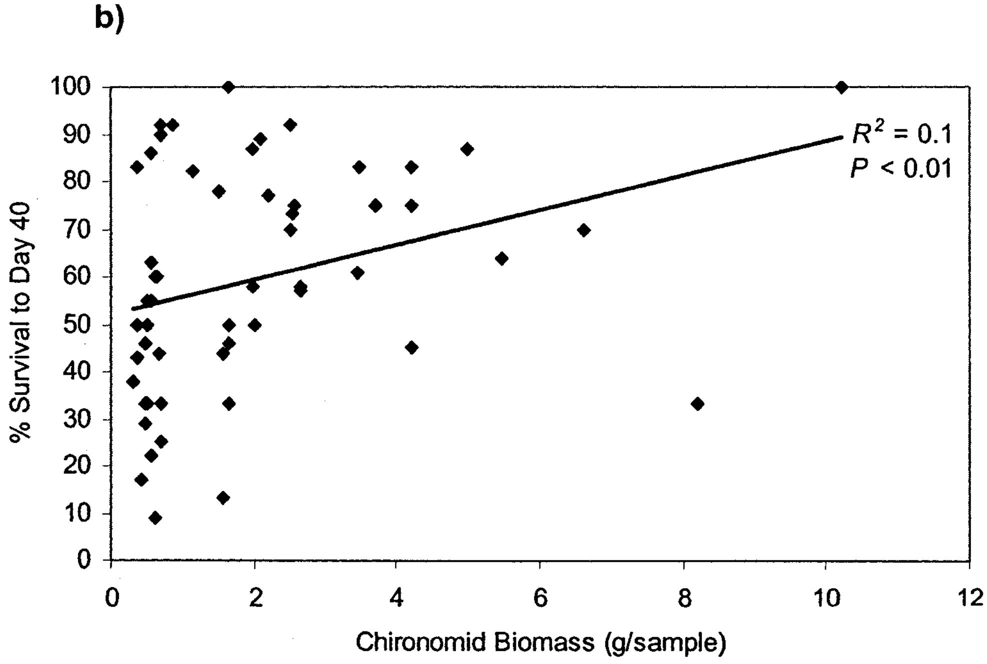


Figure 5.7. Percent Barrow's Goldeneye brood survival to age 40 days plotted against mean a) activity trap (1997-2000), and b) chironomid biomas values (1997-1999).

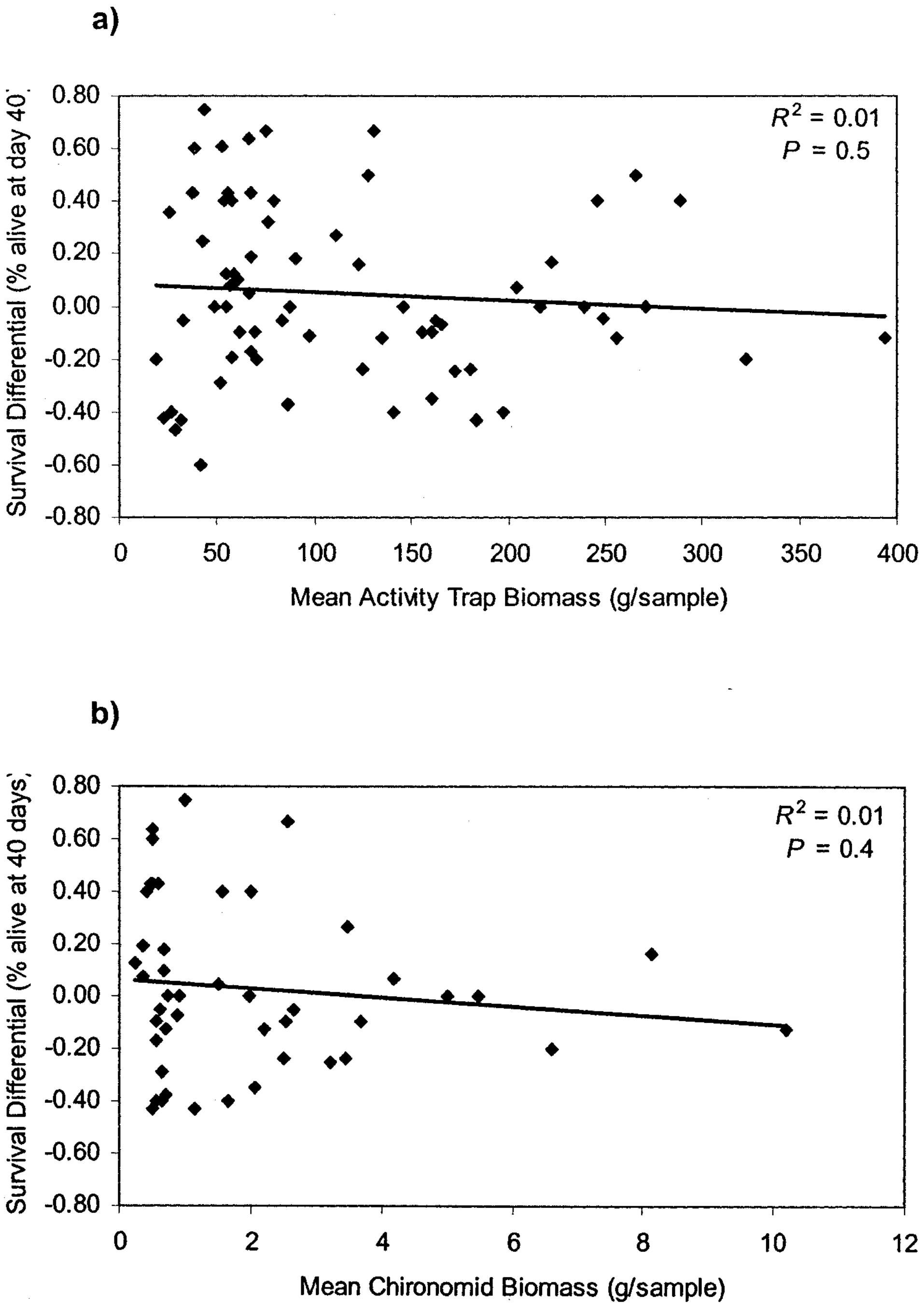
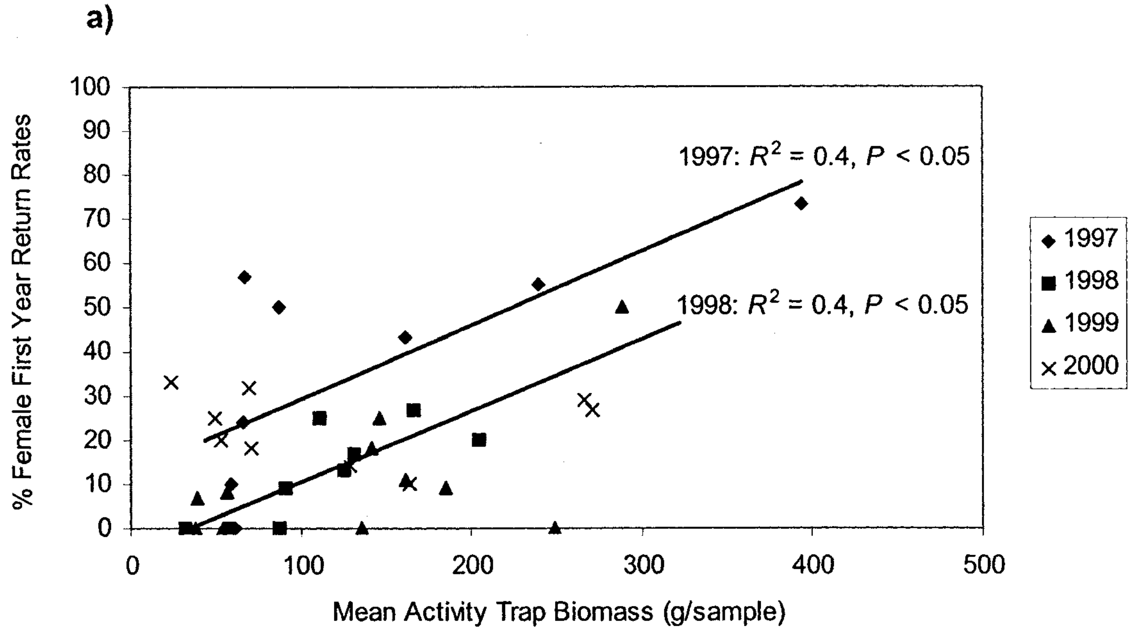


Figure 5.8. Survival differential values between male and female Barrow's Goldeneye ducklings plotted against mean a) activity trap (1997-2000), and b) chironomid biomass values (1997-1999).



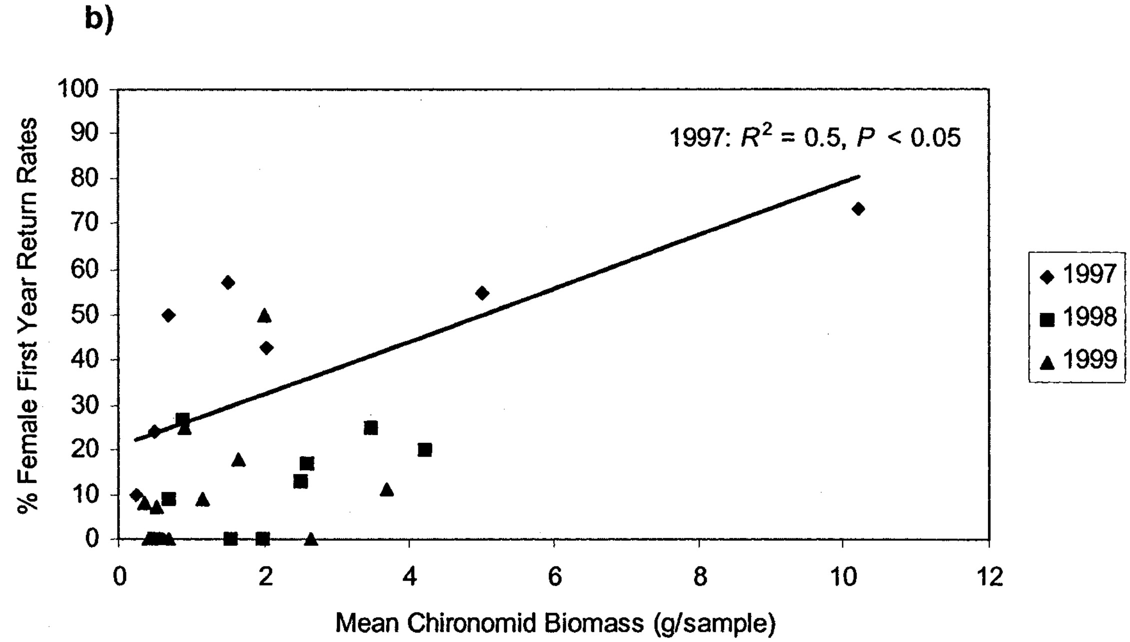


Figure 5.9. Percent first year return rate for female Barrow's Goldeneye ducklings plotted against mean a) activity trap (1997-2000), and b) chironomid (1997-1999) biomass values.

Chapter 6

EFFECTS OF INTERSPECIFIC COMPETITION AMONG BARROW'S GOLDENEYE, BUFFLEHEAD, AND OTHER SPECIES OF DIVING DUCKS

6.1. Abstract: Breeding Barrow's Goldeneye (*Bucephala islandica*) and Bufflehead (*B. albeola*) exhibit intraspecific and interspecific aggression, defending well delineated territories from which they exclude other individuals. Typically, the larger, more aggressive Barrow's Goldeneye exclude Bufflehead and other duck species. Food has been proposed as the most likely defended resource responsible for interspecific territoriality. Beyond behaviour, we lack an understanding of what effect interspecific interactions have on Barrow's Goldeneye and Bufflehead abundance.

Numbers of goldeneye were reduced experimentally to determine if the absence of this competitor results in positive fitness consequences for Bufflehead measured as increased number of broods seen, and higher fledging success. I predicted that there are fitness costs associated with coexistence and these costs are incurred primarily by the subordinate Bufflehead.

Blocking goldeneye nest sites resulted in a drastic decline in the number of goldeneye broods produced, but not a decrease in the number of territories occupied by goldeneye breeding pairs. There were no changes in the number of breeding pairs or broods of Bufflehead and other diving duck species, perhaps because of the continued presence of the territorial goldeneye pairs. Explanations for the continued presence of territorial goldeneye pairs on treatment lakes are speculative, but may reflect the long-term value of a site in a saturated environment.

The absence of goldeneye broods on treatment lakes did not result in increased brood survival for other species. These results suggest that either, 1) goldeneye do not have a direct effect on the brood survival rates of other species, 2) the ecological interactions between these species are complex and changes in response variables, such as reproductive success of subordinate species, may not be detected in such a short term study, or 3) there are other costs of coexistence that were unmeasured in this study.

6.2. INTRODUCTION

The effects of interspecific competition on species abundance and richness is a central concept in population and community ecology (Lotka 1925, Volterra 1926, Schoener 1974, Tilman 1982, Wiens 1989). Inter- and intraspecific competition is widespread, and is typically asymmetrical, with one species preventing another, either directly or indirectly, from having access to resources necessary for reproduction and survival. The degree to which species overlap in their resource requirements dictates the degree to which they compete, taking into account the density-dependent availability of that resource (Newton 1998). Competition influences the abundance of one or all species involved, particularly if they are resource limited (e.g., availability of food or nest sites). In such cases where species have identical resource needs they should be unable to persist in the same area indefinitely (Gause 1934). Despite being a major focus, studies of interactions between guild members rarely measure fitness-related consequences of coexistence (Wiens 1983, Martin and Martin 2001).

When it is economically advantageous to defend a limiting resource, a species may adopt forms of interference competition, such as territoriality, to maximize their efficiency in acquiring the resource. Brown (1964) first proposed the concept of economic defensibility, viewing spacing patterns as a result of cost-benefit trade-offs experienced by individuals. The potential costs associated with aggressive interactions include increased metabolic rates and energy expenditure, and the risk of injury (Hogstad 1987). However, successful defense and acquisition of limited resources necessary for survival and reproduction confers fitness benefits, normally assessed on the basis of lifetime reproductive success. For example, male Song Sparrows (*Melospiza melodia*) that acquired a territory and a mate in their first year produced twice as many offspring in their lifetimes compared to males unable to obtain territories until their second year (Smith and Arcese 1989). Central to Brown's theory is the requirement that a defended resource must be limited in its availability (usually in a density-dependent fashion), and exist in a predictable spatial and temporal manner (Brown 1964). Resources that are most often defended with profitable pay-offs include food, mates, and nest sites.

Waterfowl exhibit a diverse range of spacing patterns and strikingly different intensities of interspecific competition, ranging from non-territorial species such as Mallard (*Anas platyrhynchos*), scaup (*Athya* sp.), Canvasback (*Aythya valisneria*), and Northern Pintails (*Anas acuta*), to the extremely territorial goldeneye (*Bucephala islandica*, *B. clangula*), Bufflehead (*B. albeola*), and shelducks (*Tadorna* sp.). Each strategy has its own set of costs and benefits for the individual involved and is often closely associated with feeding and mating behaviour. For instance, most dabbling duck species occupying seasonal and semipermanent wetlands with unpredictable food supplies, have large overlapping foraging sites and are, therefore, not territorial (Nudds and Ankney 1982, Talent et al. 1982, Duebbert and Frank 1984). Conversely, species such as goldeneye and Bufflehead, which breed on stable, predictable wetlands, aggressively exclude competitors from well defined territories (Savard 1982, 1986, Gauthier and Smith 1987).

Barrow's Goldeneye and Bufflehead are closely related sympatric species that compete for nest sites (tree cavities) and food. Despite markedly different body sizes, these species are remarkably similar in their ecological strategies associated with nesting, foraging, habitat selection, and avoidance of predators (Savard 1986, Gauthier 1985). The degree of diet overlap between these species is high, and competition for food is likely the most important selective factor for interspecific aggression between them (Savard 1982, Gauthier and Smith 1987, Eadie et al. 1995). Access to foraging locations on wetlands involves aggressively defended Type 3 breeding pair and brood territories (Nice 1941), and the larger bodied goldeneye is most often the dominant species (Savard 1982, Gauthier and Smith 1987). Interspecific aggression by goldeneye and Bufflehead is also directed towards other waterfowl species with high diet overlaps (Savard 1982), and therefore the presence of these birds should affect the local composition of the waterfowl community as a whole.

The previous chapters of this thesis have dealt with environmental limiting factors such as nest site availability and food abundance. The purpose of this chapter is to examine the effects of asymmetrical interference competition between Barrow's Goldeneye and Bufflehead, in terms of its impact on the abundance of Bufflehead pairs and broods, and duckling survival rates. This will be assessed by experimentally reducing goldeneye breeding pairs and broods from a portion of the study site and determining any changes in Bufflehead numbers or reproductive success, compared to those on several control lakes. I will also monitor the effects of goldeneye removal on other waterfowl species. I predict that the presence of goldeneye breeding pairs and females with broods negatively affects the abundance, reproductive success, and spatial distribution of Bufflehead pairs and broods, as well as those of other diving duck species.

A secondary motivation for this study is to examine the potential effects of increasing goldeneye populations through artificial nest box programs. Although nest boxes have been proven to be a useful conservation tool to target species-specific concerns, we lack a general understanding of the effects of artificially increasing goldeneye numbers on the rest of the waterfowl community.

6.3. METHODS

6.3.1. Study Area

This study took place at Riske Creek, B.C., from April-August 1999-2002. General details of the study area are provided in Chapter 1.

6.3.2. Goldeneye Removal Experiment via Blocking Nest Box Entrances

I attempted to reduce goldeneye breeding pairs by blocking access to all goldeneye nest boxes and known goldeneye cavities in an isolated portion of the study site, in 2001 and 2002. The treatment location was chosen because it had been extensively searched for tree cavities in 1997-2000 and was known to have very few. By blocking nest sites, I attempted to force goldeneye pairs to leave this portion of the study area in search of nest sites elsewhere, and thus, also intended to reduce, or eliminate, goldeneye broods.

All nest boxes (n = 52), and known cavities (n = 6) were blocked on 15 experimental lakes. Fifteen control lakes of similar size and habitat characteristics were established in another area.

6.3.3. Population Surveys

Weekly ground-based population surveys of all waterfowl species were conducted on the 15 experimental and 15 control lakes from mid-April to mid-August, one year prior to treatment (2000), the first year of treatment (2001), and a second year of treatment (2002). Surveys of the treatment and control lakes were performed one day apart. All birds were counted and classified based on species, age (adult, juvenile, or duckling size class as in Taber 1969), gender, and whether they were alone, paired, or in a group. Approximately 70% of adult female goldeneye, and 30% of adult female Buffleheads, in the study area were marked with nasal tags allowing for individual identification. I assumed unmarked females with broods to be the same individuals if they were found in the same brood territory locations as the previous visit. Brood survival was defined as the number of ducklings within a brood that survived until the age of 40 days. This age was arbitrarily chosen because Bufflehead ducklings begin flying at 40-50 days of age (Eadie et al. 1995), at which time it becomes difficult to determine if changes in brood numbers are due to mortalities, or movements to other lakes.

Because goldeneye are aggressive towards other species of diving ducks, but not dabblers, four common species of diving ducks were considered in this study: Ruddy Ducks (*Oxyura jamaicensis*), Lesser Scaup (*Aythya affinis*), Ring-necked Ducks (*Aythya collaris*), and Redheads (*Aythya americana*).

6.3.4. Species Diversity

Because I could confidently enumerate all species present in my study area, I used 'species richness' as a measure of waterfowl species diversity.

6.3.5. Statistical Analysis

The experimental design of this study followed a Before/After and Control/Impact experiment (BACI, Green 1979) with repeated sampling before and after treatment (Underwood 1991). It was an area-by-time factorial design and I used two-factor analysis of variance (ANOVA) to test for area-by-time interactions. Three tests are associated with this analysis, corresponding to the two main effects (before-after and control-treatment), and the interaction between these. Significant interactions indicate treatment effects. The treatment (blocking of boxes) was considered a fixed factor. The two treatment years (2001 and 2002) were compared to the 'before treatment' year (2000), separately.

Each year, a mean value was calculated for each response variable (number of pairs, broods, other species, and mean brood survival rates), for each of the 15 treatment and 15 control lakes. These mean values were used in all subsequent analyses. Therefore, the analysis was designed to test for differences in the means, between sites (treatment and control lakes), before and after treatment (as suggested by Bernstein and Zalinski 1983). The survey data had a skewed distribution, and was transformed with a square root transformation. Because the data contained zeros, 0.5 was added to each data point before transformation (Steel and Torrie 1980).

All levels of significance were 95% ($\alpha = 0.05$) unless Bonferroni adjustments were necessary, in which case the significance level was determined by dividing $\alpha = 0.05$ by the number of comparisons made.

6.4. RESULTS

6.4.1. Breeding Pairs

BACI analysis showed no significant changes in the number of goldeneye and Bufflehead pairs between treatment and control lakes, before and after the boxes were blocked (Table 6.1. and Figure 6.1.). Goldeneye pairs remained on all treatment lakes in all three years of the study, and actually increased slightly in years two and three. These birds aggressively defended pair territories and were seen copulating, but no active nest sites (natural cavities) were found. Bufflehead pair abundance also increased slightly on treatment lakes, but this increase was matched on control lakes.

Pooled as a group, the four 'other diving duck species' also showed no significant differences in pair abundance, between control and treatment areas, in either treatment year (Figure 6.1). Similar results where found when these four species were examined individually (Table 6.2, Figure 6.2). Although Lesser Scaup pair abundance increased on treatment lakes in 2001, this result was not significant (Table 6.2).

6.4.2. Brood Numbers

Despite the continued presence of territorial pairs on the treatment lakes, the number of goldeneye broods decreased significantly in the first year of treatment, and remained equally low during the second year (Figure 6.3). The treatment was thus effective at reducing nesting by goldeneye. However, no significant changes in the number of Bufflehead broods were found for either treatment years. The number of broods of the four other diving species also remained unchanged through all three years of the experiment (Figures 3 and 4).

Goldeneye broods that did appear on the experimental lakes in 2001 ($n = 4$ broods, on two lakes) and 2002 ($n = 5$ broods, on three lakes), presumably hatched in unknown natural cavities. Female goldeneye with broods established and actively defended brood territories. These lakes were excluded from the brood survival analysis, discussed below.

6.4.3. Brood Survival Rates

Even though goldeneye broods were absent from treatment lakes used in this analysis, treatment lakes showed no increases in Bufflehead brood survival rates, with treatment and control lakes showing nearly identical patterns over three years (Figure 6.5). Analysis of survey data collected since 1995, also showed no relationship between Bufflehead brood survival rates and the absence/presence of goldeneye broods (Figure 6.6).

There were also no significant changes in the brood survival rates of other species of diving ducks (Figure 6.5 and 6.7). Ring-necked Ducks did show a decline in survival rates on treatment lakes in 2001, but this result was not significant after a Bonferroni adjustment ($\alpha = 0.5/2 = 0.025$).

6.4.4. Species Richness

The overall number of waterfowl species present did not change on treatment lakes over the three years of this study (Table 6.1, Figure 6.8).

6.5. DISCUSSION

The experimental removal of goldeneye nest sites did not result in a decrease in the number of goldeneye breeding pairs, and therefore, few conclusions can be made about this portion of the study. There were also no observed changes in the number of breeding pairs of Bufflehead and other diving duck species, a result that is likely the consequence of the continued presence of territorial adult goldeneye. Since the number of Bufflehead and other species' breeding pairs remained unchanged, it was not surprising to see the number of broods for these species remain unchanged as well.

Explanations for the continued presence of territorial goldeneye pairs on treatment lakes are speculative, but may reflect the long-term value of a site in a saturated environment. Several of these birds were marked with nasal tags and were seen on treatment lakes in all three years of the experiment, indicating a high degree of site-faithfulness, even when nest sites were removed for two years. It is possible that some females may have found nest sites elsewhere, but none of these marked birds were found incubating clutches on other lakes in the study area, despite an excess of nest sites on these lakes, and none were seen with broods. Although it was previously concluded that goldeneye breeding pairs at Riske Creek are limited by nest site availability (Savard 1988), it may be that they are also limited by access to foraging territories near nest sites, like Bufflehead (Gauthier and Smith 1987). Regardless, it is likely that the presence of these goldeneye inhibited any changes in Bufflehead pair abundance, as well as those of other species, and therefore, the number of broods produced.

The blocking of goldeneye nest sites resulted in a drastic decline in the number of goldeneye broods produced. However, this did not result in increased brood survival for other species, suggesting that either, 1) goldeneye presence does not have a direct effect on other species' brood survival rates, or 2) the ecological interactions between these species are complex and changes in response variables, such as reproductive success of subordinate species, may not be detected in a short term study. Or, there are other costs of coexistence that were unmeasured in this study, manifested through other components of fitness, such as adult condition and ability to produce a clutch, and juvenile growth, development, and postfledging survival.

In Chapter 4, I discussed how Bufflehead may be forced to establish territories on a wider variety of wetland quality, as the dominate goldeneye occupy habitat with higher food abundance. This may reflect a tradeoff between competitive ability and tolerance to environmental conditions that differ between closely-related territorial birds (Morse 1974). Occupying these seemingly suboptimal lakes may have higher fitness payoffs for individual Bufflehead females, compared to remaining on lakes with high goldeneye densities (e.g. Ideal Despotic Distribution; Fretwell and

Lucas 1970, Parker and Stuart 1976). This pattern has been found in other closely-related species, from a wide variety of taxa including reef fish (*Embiotica*; Hixon 1980), bumblebees (*Bombus*; Bowers 1985), barnacles (*Balanus* and *Chthamalus*; Connell 1961), salamanders (*Plethodon*; Jaeger 1971), and chipmunks (*Eutamias*; Chappell 1978).

Page 190 (Chapter 6).

Competition theory states that without ecological segregation, two species cannot co-exist together as complete competitors if resources are limiting (Rosenzweig 1981). For goldeneye and Bufflehead to remain sympatric, then either, 1) these two species are not competing for similar resources (e.g., tree cavities, prey, territorial space), 2) resources are not limiting for these two species, or 3) their territorial behaviour is to be considered as spatial segregation, and therefore ecological segregation.

The first two possibilities are unlikely. There is ample evidence showing that goldeneye and Bufflehead are indeed interspecific competitors (Erskine 1972, Savard 1982, Savard and Smith 1987, Gauthier and Smith1987, Mallory et al. 1999, also see Figures 4.3 and 4.8, this study), and it is doubtful that their co-existence does not come at a cost for at least one of these species, particularly the behaviorally subordinate Bufflehead. Although I showed in Chapter 3 that goldeneye and Bufflehead were not competing for similar sized cavities, it has been previously shown that they have a high diet overlap (Erskine 1972, Savard 1982, Eadie et al. 1995). Several aspects of goldeneye and Bufflehead behavior suggest the adaptive value of territories centers around securing a food supply for female mates, and for ducklings (Donaghey 1975, Savard 1982, Savard and Smith 1987, Gauthier and Smith1987).

Persistent interspecific competition is possible in simple habitats with little ecological divergence (Orians and Wilson 1964). The alkaline wetlands of this study site have little aquatic plant diversity, are commonly devoid of fish, and have a relatively reduced diversity of aquatic invertebrate prey (Savard 1982). Thus, there is little opportunity for goldeneye and Bufflehead to exploit different resources (Savard 1982). Spatial separation of territories would allow these closely related species to inhabit separate, but adjoining foraging and brood-rearing areas, even though they have such similar ecology. Both intra- and interspecific territoriality would also limit population sizes and, therefore, regulate resource exploitation (Wynne-Edwards 1962).

Finally, it has been suggested that waterfowl are not resource limited in the breeding season, but are in fact in an evolutionary equilibrium with resource levels (Nudds 1980). Nudds' conclusion highlights the need to quantitatively determine exactly what resource goldeneye and Bufflehead are competing for, and at what degree of intensity. Conclusive diet analysis is needed to determine if these birds are foraging on identical prey items, or if territorial space is the limiting factor.

One of my interests in performing this experiment was to be able to comment on the consequences of increasing goldeneye populations, through nest box programs. Although the results of this study do not allow comment on this issue, other studies suggest that due to their competition for space and for food, the presence of goldeneye limits Bufflehead numbers (Savard 1982). Barrow's Goldeneye and Bufflehead, are obviously strong interspecific competitors, and continue to co-exist by virtue of either resource differentiation, or spatial separation, or both, and it is assumed that both species would expand their abundance in the absence of each other. It is possible that these birds are in a state of competitive equilibrium, and changes in either species' abundance could result in equal, but opposite, changes in the other, particularly for the behaviorally subordinate Bufflehead. Therefore, species-specific nest box programs aimed at increasing goldeneye populations could have negative consequences for Bufflehead numbers.

Future experiments should employ techniques that actively remove Barrow's Goldeneye breeding pairs, and follow fitness components of Bufflehead and other species for more than two years.

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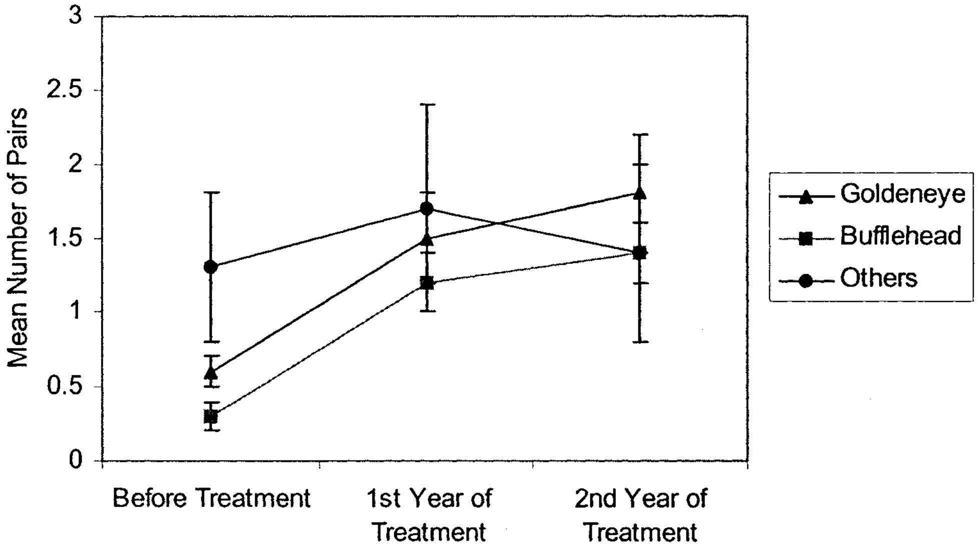
Table 6.1. Results of BACI analysis for Barrow's Goldeneye, Bufflehead, and four other diving spec (Ruddy Ducks, Lesser Scaup, Ring-necked Ducks, and Redheads) observed on 15 treatment and 15 control lakes, one year before treatment (2000), the first year of treatment (2001), and second year o treatment (2002). For all comparisons *df* = 59, except for brood survival analysis where df = 57 in 2 and 56 in 2002.

	Goldeneye		**Bufflehead**		**Other Species**	
Number of Pairs	1st Year of Treatment	2nd Year of Treatment	1st Year of Treatment	2nd Year of Treatment	1st Year of Treatment	2nd Year of Treatment
F Ratio	0.9	3.0	0.3	0.01	0.6	0.9
P	0.3	0.1	0.6	0.9	0.2	0.2
Number of Broods						
F Ratio	6.2	7.2	1.7	0.01	0.3	0.3
P	0.02	0.01	0.2	0.9	0.4	0.5
Brood Survival						
F Ratio	--	--	0.3	0.3	0.8	0.2
P	--	--	0.6	0.6	0.7	0.9
Species Richness						
F Ratio	--	--	--	--	1.0	0.02
P	--	--	--	--	0.3	0.9

Table 6.2. Results of BACI analysis for Ruddy Ducks (RUDU), Lesser Scaup (LESC), Ring-necked Ducks (RNDU), and Redheads (REHE) observed on 15 treatment and 15 control lakes, one year before treatment (2000), the first year of treatment (2001), and the second year of treatment (2002). For all comparisons *df* = 59, except for brood survival analysis where df values are given in the tal

	RUDU		**LESC**		**RNDU**		**REHE**	
Number of Pairs	1st Year of Treatment	2nd Year of Treatment	1st Year of Treatment	2nd Year of Treatment	1st Year of Treatment	2nd Year of Treatment	1st Year of Treatment	2nd Year of Treatment
F Ratio	1.1	1.2	1.1	0.7	0.8	0.6	0.6	0.7
P	0.6	0.6	0.09	0.2	0.6	0.5	0.4	0.2
Number of Broods								
F Ratio	0.2	0.3	0.9	1.1	0.5	0.6	0.1	0.2
P	0.7	0.7	0.2	0.3	0.8	0.3	0.8	0.8
Brood Survival								
F Ratio	0.5	0.1	0.1	0.1	3.8	0.4	1.1	0.7
P	0.7	0.8	0.7	0.9	0.01	0.7	0.6	0.2
df	34	32	34	31	9	13	19	23

a) Treatment Lakes



b) Control Lakes

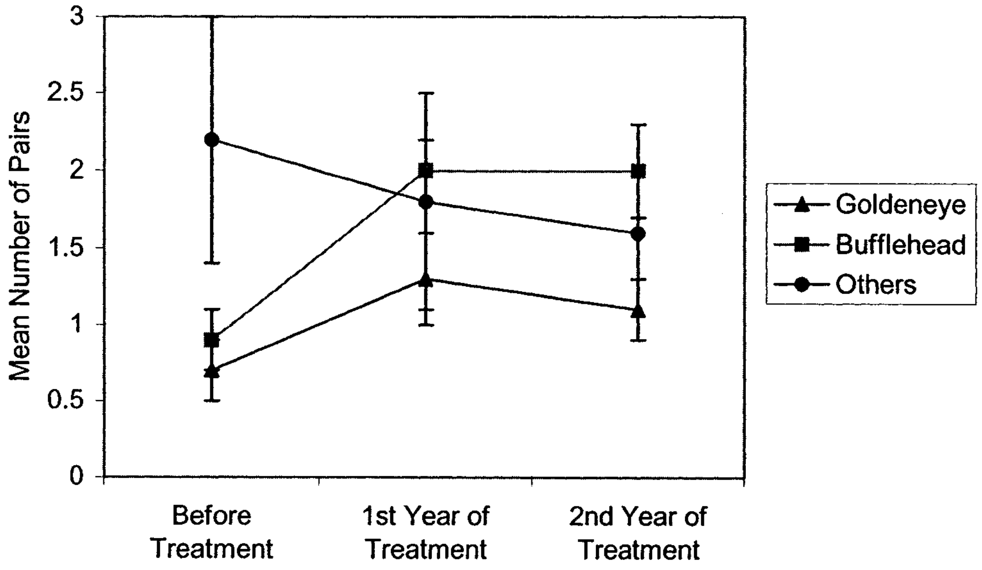
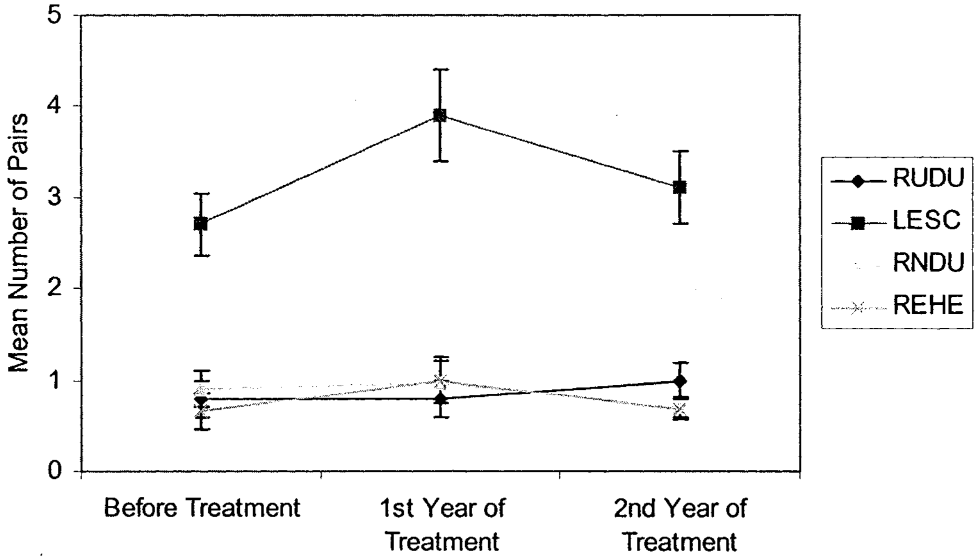


Figure 6.1. Mean number of Barrow's Goldeneye, Bufflehead, and other species' breeding pairs observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

a) Treatment Lakes



b) Control Lakes

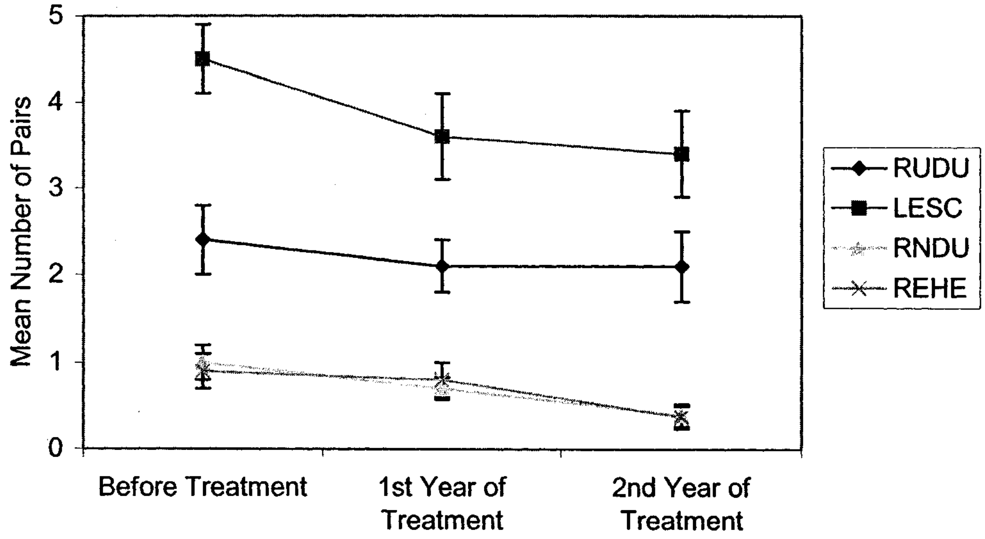
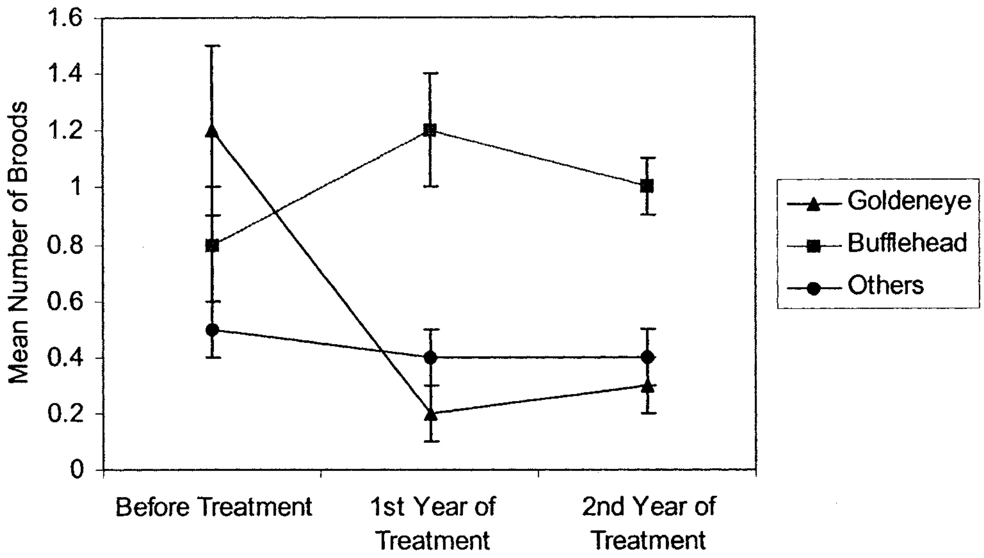


Figure 6.2. Mean number of Ruddy Duck (RUDU), Lesser Scaup (LESC), Ring-necked Duck (RNDU), and Redhead (REHE) breeding pairs observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

a) Treatment Lakes



b) Control Lakes

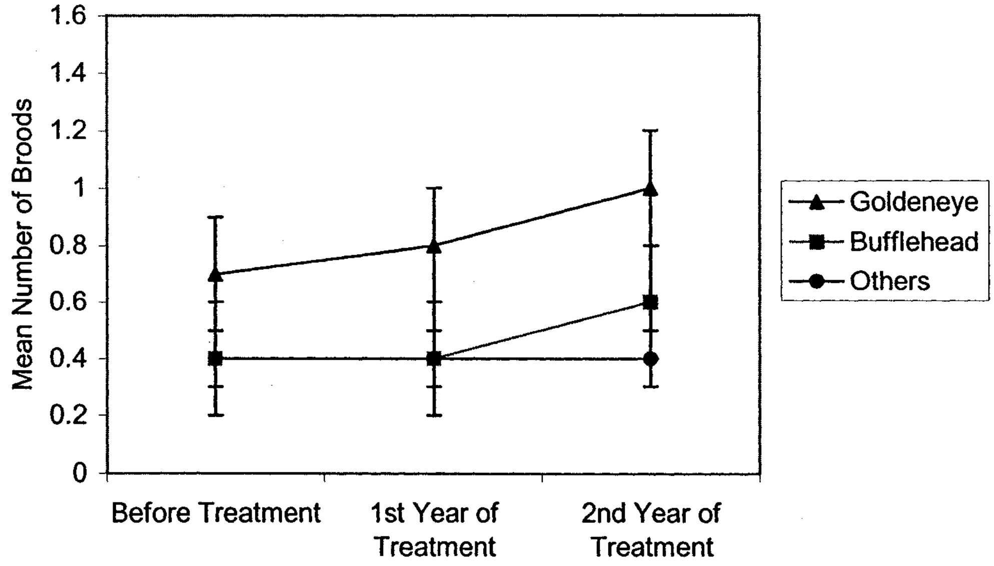
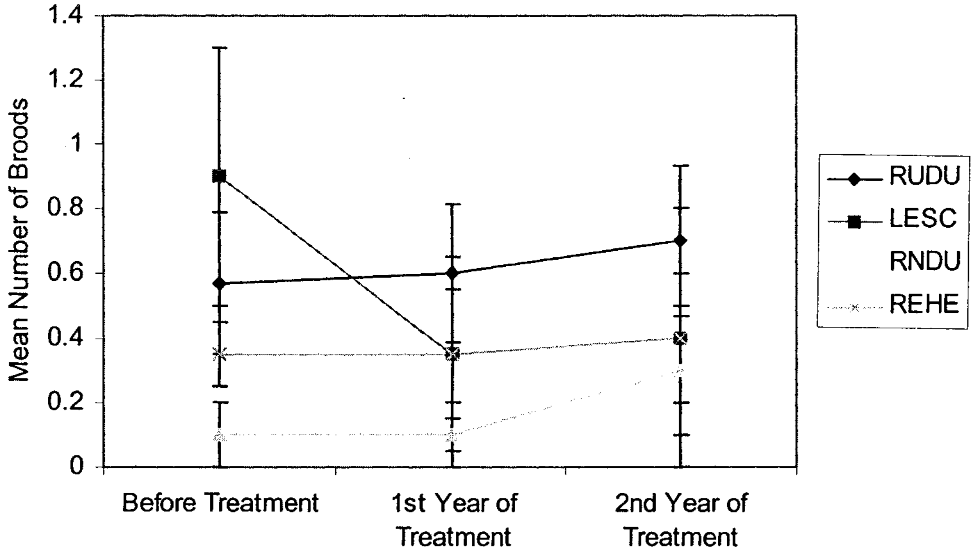


Figure 6.3. Mean number of Barrow's Goldeneye, Bufflehead, and other species' broods observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

a) Treatment Lakes



b) Control Lakes

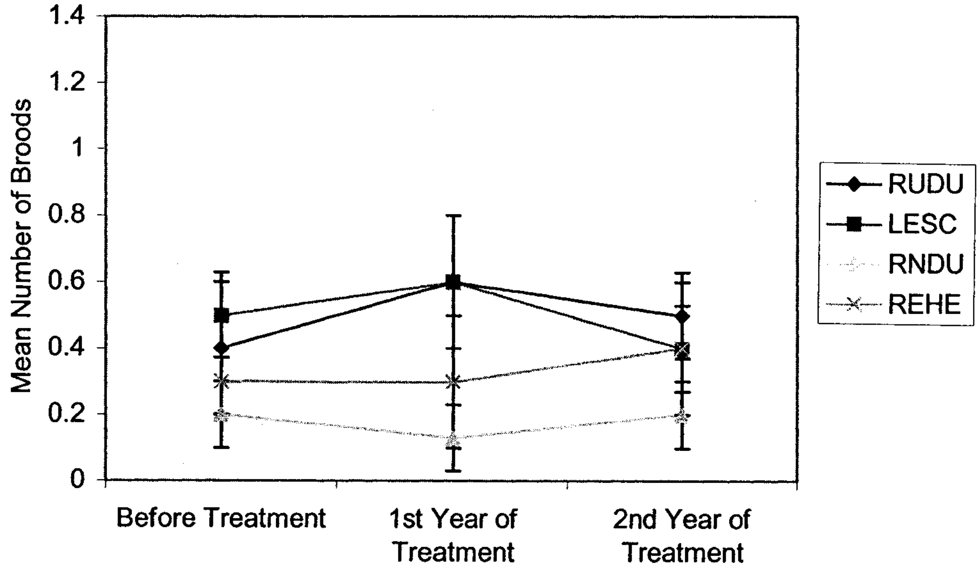
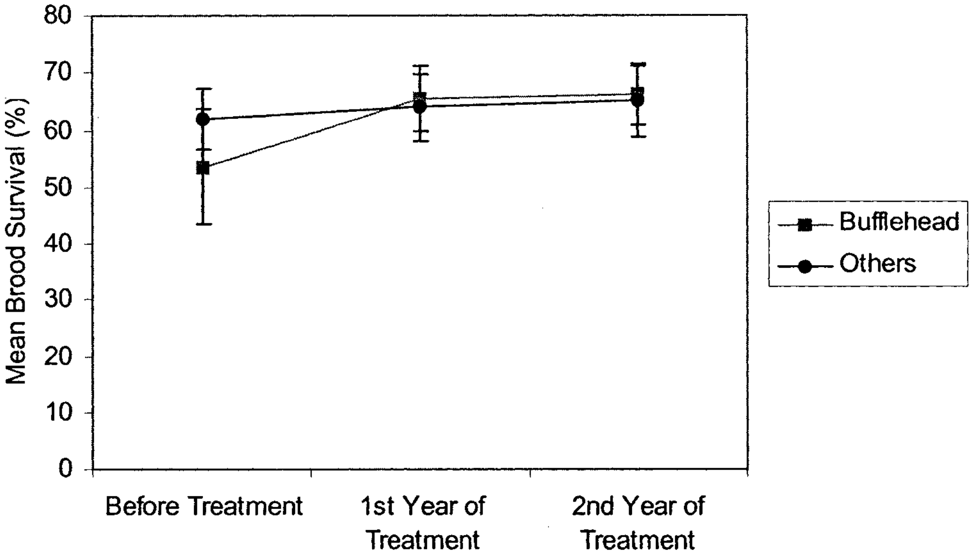


Figure 6.4. Mean number of Ruddy Duck (RUDU), Lesser Scaup (LESC), Ring-necked Duck (RNDU), and Redhead (REHE) broods observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

a) Treatment Lakes



b) Control Lakes

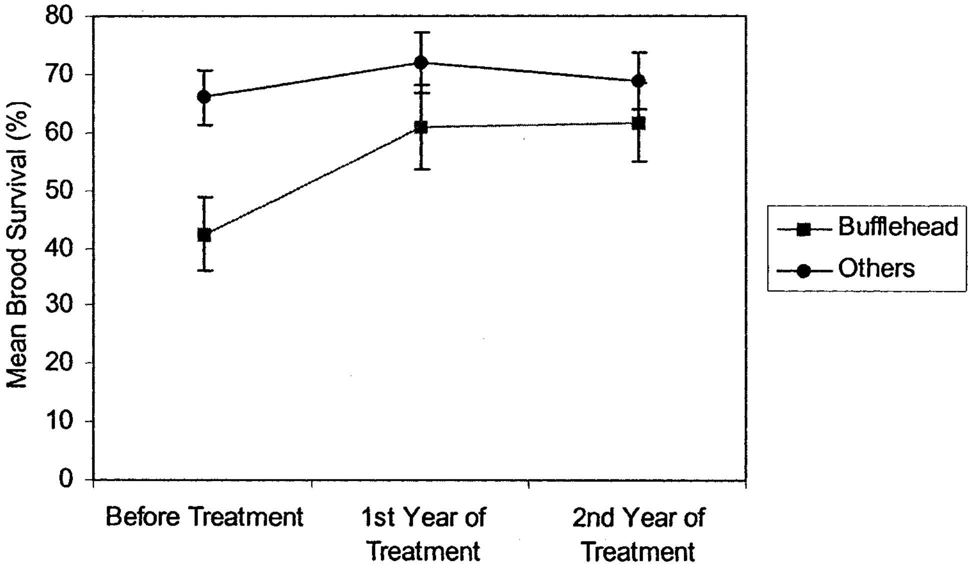


Figure 6.5. Mean brood survival rates (%) for Bufflehead, and other species' broods observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

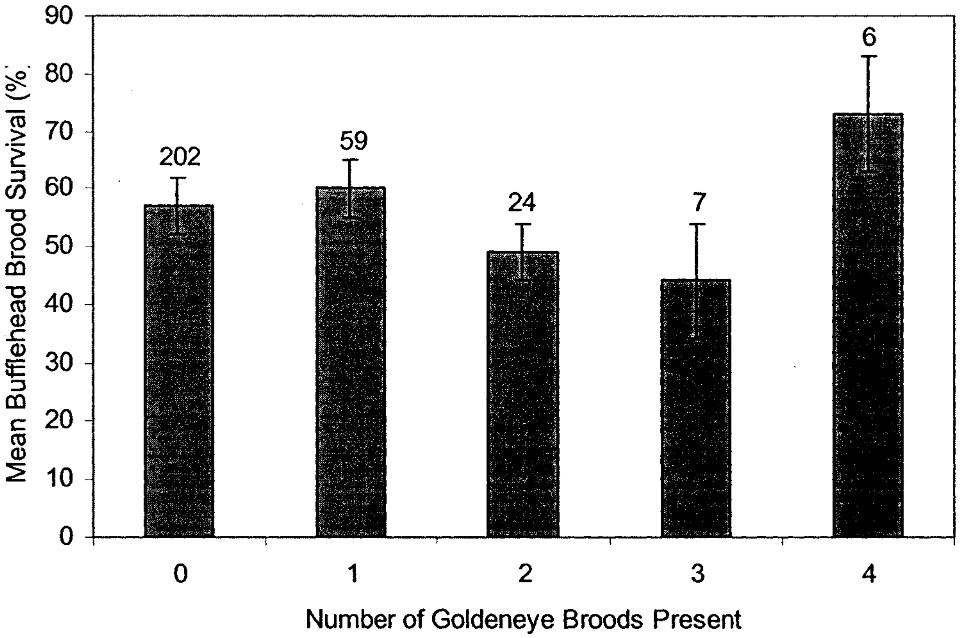
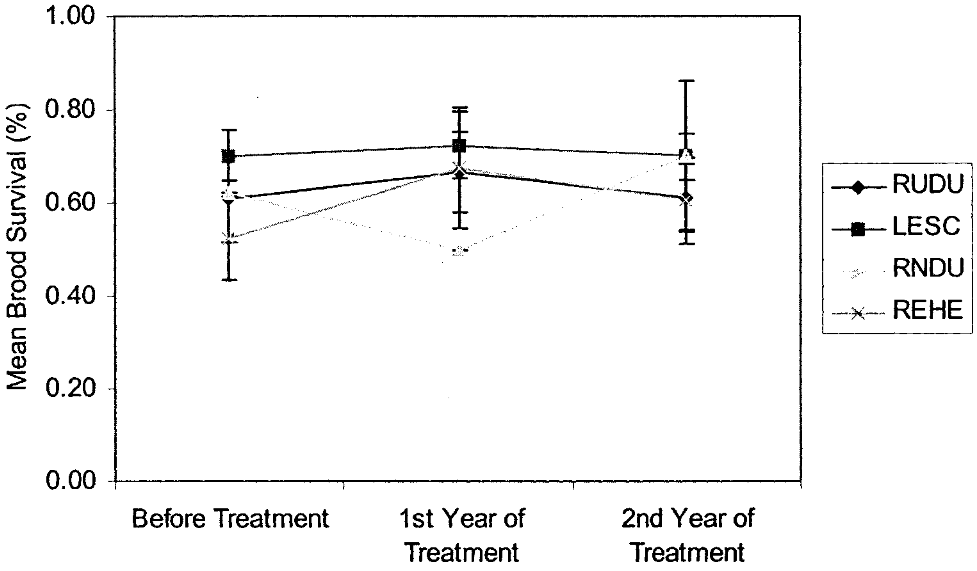


Figure 6.6. Mean Bufflehead brood survival rates (%) on lakes that had 0-4 Goldeneye broods (1995-2000). Numbers above columns indicate sample size of Bufflehead broods in each category. Error bars are ± 1 SE.

a) Treatment Lakes



b) Control Lakes

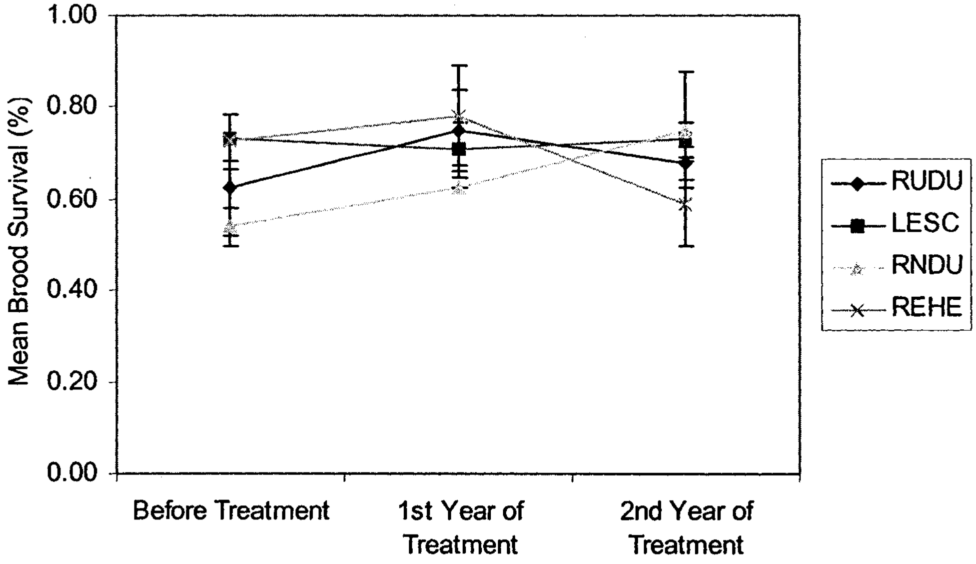


Figure 6.7. Mean brood survival of Ruddy Duck (RUDU), Lesser Scaup (LESC), Ring-necked Duck (RNDU), and Redhead (REHE) broods observed on a) 15 treatment, and b) 15 control lakes one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

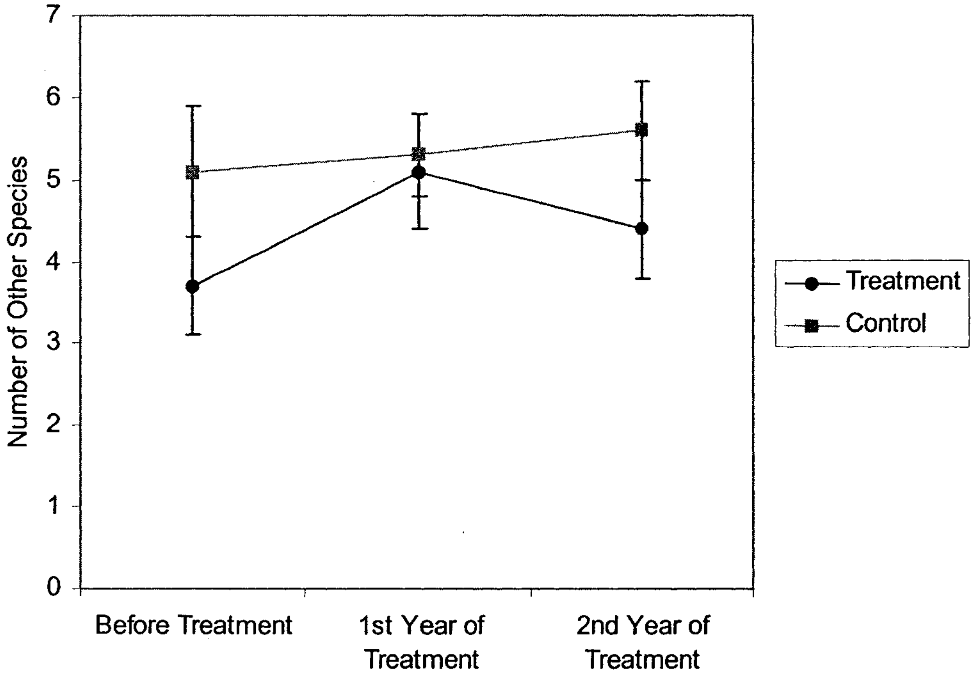


Figure 6.8. Maximum number of waterfowl species observed on 15 treatment and 15 control lakes, one year before treatment (2000), one year after (2001), and two years after treatment (2002). Error bars are ± 1 SE.

Chapter 7

THESIS SUMMARY AND MANAGEMENT RECOMMENDATIONS

The loss and degradation of wetland habitat is a major concern currently facing waterfowl management in North America. Wetlands in the boreal forest of Canada have become an increasingly important area for continental waterfowl populations as prairie wetlands disappear due to agricultural drainage. However, wetlands of the boreal forest are now affected by factors such as forestry, particularly in British Columbia where forestry is the major industry in these regions.

To successfully manage waterfowl populations, we must first have an understanding of their breeding biology, as well as the various abiotic and biotic components of wetland ecosystems that influence waterfowl abundance and distribution. Breeding habitat must offer a complex of ecological resources, including nest sites, suitable wetland space with adequate food supplies for egg-laying females and developing young, and cover that provides protection from predators and adverse weather (Kaminski and Weller 1992).

In this thesis, I focused on the selection of natural cavities and brood-rearing habitat by Barrow's Goldeneye and Bufflehead. For these species, reproduction and the subsequent survival and recruitment of offspring into the breeding population depend on 1) the availability of nest cavities for females to lay eggs; and 2) the quality and availability of brood-rearing habitat and its effect on the growth and survival of ducklings. No conclusive results were found when examining the influence of interspecific competition on the settlement patterns and breeding success of Bufflehead, but it is assumed that co-existence with goldeneye has negative ecological consequences that were unmeasured in this study.

7.1. Natural Cavity Selection and Nest Box Programs

Cavity-nesters are potentially sensitive to habitat alteration such as logging, which could have important population consequences. Knowledge of the biophysical characteristics of nest sites, and preferences exhibited by nesting females, should help forest managers conserve potential nest trees.

In Chapter 2, I determined that Barrow's Goldeneye primarily used abandoned Pileated Woodpecker cavities located in aspen trees with a DBH greater than 35 cm. Active nest sites were typically higher above ground, had relatively larger entrance diameters and floor areas, and had relatively higher canopies, compared to inactive cavities. Bufflehead selected abandoned Northern Flicker cavities which were also most commonly in aspen trees, and with a DBH larger than 25 cm. Bufflehead cavities had larger entrance diameters than unused cavities, and smaller floor areas. For both species, there were no differences in distances to the nearest body of water for used and unused cavities, suggesting that there is an ample supply of cavities near water. I found 3.4 goldeneye cavities per hectare in aspen stands, and 0.2 cavities/ha in mixed stands. Bufflehead cavity density was 6.7 cavities/ha in aspen stands, and 1.6 cavities/ha in mixed stands. More than 90% of these cavities were located within 200 m of a body of water.

By determining patterns of nest site selection by these birds it may be possible to minimize the loss of nest trees during forest removal. Because 60% of the world's population of Barrow's Goldeneye breed in British Columbia (McKelvey et al. 1989), a province where forestry is a major industry, it becomes particularly important to understand their nesting habitat requirements. My results indicate that aspen groves located within 100 m of productive wetlands, should be managed by foresters to assure the protection of nest sites for these birds. Forest management should also protect primary cavity-nesting species, particularly Pileated Woodpeckers and Northern Flickers, because it is the cavities of these species that are used by goldeneye and Bufflehead.

To optimize the commercial utilization of timber, stands are usually harvested at an age preceding the onset of decay, thereby affecting the availability of older stands that are so important to many wildlife species. In managed forests and tree plantations, cavity-nesting species are often found in low numbers due to shortages in nest sites (Newton 1994). Silvicultural prescriptions should consider perpetuating old-growth aspen and other timber types to insure a supply of cavities for ducks and other species. Preventing the removal of dead or dying trees, trees that typically offer nest sites, would favor those species reliant on cavities. Managers should conserve existing and potential cavity-trees, particularly large aspen in early-to-late stages of decay (decay classes 1-4) and Douglas-firs in late stages of decay (decay classes 4-6). For cavity nesting waterfowl it is imperative that aspen stands near water be maintained, and at least one stand for each body of water. It is further recommended that aspen trees be protected as patches to guard against blow-down. Protecting entire aspen stands will also aid in keeping cavities less conspicuous to predators, and allow young trees to replace older, fallen trees and ensure a continuous supply of cavities over time. The results of this study are specific to the Cariboo-Chilcotin region of British Columbia and areas similar to it.

In Chapter 3, I compared the nesting ecology of goldeneye and Bufflehead using natural cavities versus nest boxes. I concluded that, in some respects, studies of Barrow's Goldeneye that use nest boxes may not be representative of birds nesting in natural cavities, whereas those of Bufflehead are more likely to be so. I found larger clutch sizes, lower nesting success, and different major predators (primarily black bears) for Barrow's Goldeneyes nesting in boxes versus those nesting in natural cavities, but few differences for Bufflehead. These differences were attributed to the location and physical differences between Barrow's Goldeneye nest boxes and natural cavities that affect their conspicuousness to predators and conspecific nest parasites. Goldeneye boxes were concentrated in highly visible locations such as trees at water or forest edge. Natural cavity nests, on the other hand, were often abandoned Pileated Woodpecker cavities dispersed throughout the forest interior and concealed under dense canopy cover. Bufflehead natural cavity nests were typically closer to edges, which may account for their similarity with boxes.

Nest box programs are normally considered an effective conservation tool, particularly for cavity-nesting waterfowl (Eriksson 1982, Fredga and Dow 1984, Savard 1986). However, there may be hidden costs to these programs. Extrapolating from my results, I speculate that nest box programs may in fact create population sinks for Barrow's Goldeneye, attracting large numbers of breeding birds that experience unnaturally high levels of bear predation, and nest parasitism. As such, recommendations for future nest box programs under similar circumstances include installing predator guards (specifically, bear deterrents) and placing boxes in less conspicuous locations, farther from ponds or forest edges, in locations similar to those of natural cavities.

Managers must also be aware that nest box programs used to increase goldeneye abundance may have negative consequences for the rest of the waterfowl community. Considering the extremely aggressive territorial behavior of goldeneye, particularly towards congeners such as Bufflehead (Savard 1986), species-specific nest box programs could change the abundance and distribution of other species. Although well intentioned, nest box programs often occur without consideration for the entire bird community. Few studies have examined the effects of increasing the abundance of selected species on the breeding ecology of other species (Hogstad 1975, Bock et al. 1992). Clearly, more comparative studies involving nest box programs are warranted.

Conserving mature and old growth aspen stands within 100 m of adequate brood-rearing wetlands, will help maintain nest sites for cavity-nesting waterfowl populations. Where suitable aspen stands exist, I think that an approach that encourages development of natural cavities will have distinct advantages over the provision of nest boxes. Managing timber for cavity production would favor a diverse ecosystem with a rich community of cavity-nesting birds.

7.2. Wetland Selection

The continued loss of wetland habitat in North America has given rise to increased efforts to preserve threatened areas and restore damaged ones, in hope to conserve waterfowl production levels. To achieve these objectives, we must identify habitat characteristics that influence lake selection by breeding waterfowl.

In Chapter 4, I assessed the role of biotic and abiotic characteristics of wetlands associated with goldeneye and Bufflehead. I found lake occupancy to be influenced by a complex of factors including the lake's physical characteristics, food supply, water chemistry, and to a lesser degree, aquatic vegetation. Lake size was the most important factor influencing lake occupancy by both species' breeding pairs and broods. Lake depth was also an important feature for breeding pairs, but not for broods, and the abundance of invertebrate prey influenced lake usage by goldeneye pairs and broods, but not Bufflehead. Water chemistry properties such as dissolved oxygen and specific conductivity were highly correlated to these factors.

Variations between species' morphological and behavioral traits have likely resulted in different habitat requirements, probably related to dietary requirements (Sedinger 1992). This study focused only on Barrow's Goldeneye and Bufflehead; other species have other preferences and, therefore, different management needs. However, a large number of waterfowl species rely heavily on invertebrate prey items, and the protection of productive lakes would benefit them as well. Levels of primary production within a lake, including trophic structure and total biomass throughout the aquatic food web, are mediated by a host of interacting physical and chemical factors (Wetzel 1975). Subtle changes in the aquatic environment will result in associated changes in trophic relationships with waterfowl, affecting prey availability, foraging efficiency, nutrient intake rates, and thereby potentially affecting waterfowl populations. Finally, since several studies, including this one, have demonstrated strong correlations between limnological variables and aquatic bird abundance, I suggest these options as a more efficient and less expensive way for managers to assess lake habitat quality, rather than the labour intensive methods of sampling invertebrates.

Habitat selection decisions affect a bird's reproductive success. For juvenile birds, both environmental and maternal factors influence growth patterns, affecting survival and future reproductive output. Several studies have shown that food abundance, quality and availability during the brood-rearing period is a major determinant of growth rates, body size, and body condition in precocial bird species. These, in turn, affect first-year survival, age of first breeding, clutch size, and ultimately adult fecundity, survival, and population dynamics.

In Chapter 5, I examined the relationship between food density and the following reproductive parameters of Barrow's Goldeneye: egg size, clutch size, hatching date, duckling growth rate, prefledging survival, and recruitment. Although it is commonly reported that prey abundance influences juvenile growth and survivorship, few studies have actually examined this relationship due to the difficulty in 1) associating nutrition and waterfowl survivorship, and 2) estimating survivorship and future fecundity.

I found positive correlations between invertebrate levels within a wetland and Barrow's Goldeneye duckling masses at day 40, prefledging survival, and first year return rates. The masses of incubating females did not differ between sampled lakes, nor did nest initiation dates, clutch sizes, or mean egg masses, suggesting that older, more experienced females were not nesting disproportionately on high quality lakes.

I concluded that prey abundance influences Barrow's Goldeneye duckling growth rates, prefledging survival, and first year return rates. However, evidence that prey abundance is directly related to recruitment patterns and, therefore, fitness variation among females remained inconclusive. Regardless, the results of this study predict that females should be sampling local wetlands for habitat quality and that annual philopatry and territorial defense should be higher on the more productive ponds. The use of suboptimal habitats is likely the result of intraspecific competition, where the only alternative is to forego breeding altogether.

Waterfowl habitats should be managed to maximize the survival of breeding adults and the production of young. This study has shown the importance of invertebrates to duckling growth and prefledging survival. This underscores the need to maintain wetland habitats that are rich in invertebrate numbers to meet the nutrient needs of breeding adults and developing young. Changes in limnological components of wetland ecosystems from agricultural practices (e.g., drainage, insecticides), logging, and acid rain, have severely reduced aquatic invertebrate populations in many areas (McNicol et al. 1987, DesGranges and Houde 1989, Krapu and Reinecke 1992). A resulting reduction in waterfowl prey availability, diversity (Bendell and McNicol 1987), and quality (McAuley and Longcore 1988) would affect nutrient intake and growth rates of ducklings. Therefore, productive wetlands should be managed in such a way that they provide stable, abundant food supplies for egg laying females and developing young. Also, maintaining suitable brood-rearing habitat near nesting areas will lessen the likelihood of duckling mortality during overland movements from the nest. For cavity nesting waterfowl, it is further suggested that managers be particularly sensitive to wetlands in close proximity to cavity nesting habitat, such as mature aspen clumps (discussed in Chapter 2).

7.3. Interspecific Competition with Barrow's Goldeneye

In Chapter 6, I attempted to reduce goldeneye pair and brood abundance on 15 experimental lakes, to examine whether co-existence results in negative fitness consequences for Bufflehead.

However, the removal of all known goldeneye nest sites (both boxes and cavities) did not result in a decrease in the number of goldeneye breeding pairs. There were also no observed changes in the number of breeding pairs or broods of Bufflehead and other diving duck species, a result that is likely the consequence of the continued presence of territorial goldeneye. The continued presence of territorial goldeneye pairs on treatment lakes may be a result of these birds' inability to establish territories in other areas. Although blocking goldeneye nest sites resulted in a drastic decline in the number of broods produced, this did not result in increased brood survival for other species. These results suggest that either, 1) goldeneye do not have a direct effect on other species' brood survival rates, or 2) the ecological interactions between these species are complex and changes in response variables, such as reproductive success of subordinate species, may not be detected in such a short term study, or 3) there are other costs of coexistence that were unmeasured in this study.

Regardless, Barrow's Goldeneye and Bufflehead exhibit intense interspecific aggression, with the larger, more aggressive Barrow's Goldeneye successfully excluding Bufflehead and other species from well delineated territories (Savard 1982). Food and/or mates have previously been proposed as the most likely defended resources behind these encounters. Unfortunately, this study was unable to provide conclusive results. We still lack a comprehensive, qualitative understanding of what population effect interspecific, density-dependent interactions have on Barrow's Goldeneye and Bufflehead numbers.

Regardless, it is likely that the presence of goldeneye pairs inhibited any changes in Bufflehead pair abundance, as well as those of other species, and therefore, the number of broods produced. In Chapter 4, I showed Bufflehead may be forced to establish territories on lower quality habitat, as the dominant goldeneye occupy higher quality sites. This may reflect a tradeoff between competitive ability and tolerance to environmental conditions that differ between these territorial birds (Morse 1974). Occupying these seemingly suboptimal lakes may have negative fitness consequences for Bufflehead, such as decreased juvenile growth and post-fledging survival rates. Therefore, the realized fitness costs incurred by Bufflehead, and other species that compete with goldeneye, may be higher than those demonstrated by measuring brood survival only. Barrow's Goldeneye and Bufflehead continue to co-exist by virtue of either resource differentiation, or spatial separation, or both, and it is assumed that Bufflehead would expand their abundance in the absence of goldeneye. It is possible that these birds are in a state of competitive equilibrium, and changes in either species' abundance could result in equal, but opposite, changes in the other, particularly for the behaviorally subordinant Bufflehead. Therefore, species-specific nest box programs aimed at increasing goldeneye populations could have negative consequences for Bufflehead. Future experiments should employ techniques that actively remove Barrow's Goldeneye breeding pairs, and follow fitness components of Bufflehead and other species for more than two years.

7.4. Future Research Needs and Opportunities

This study was largely a correlational study, and therefore does not empirically prove cause-and-effect in the relationships discussed herein. There are still remarkably few experimental studies that have manipulated wetland habitat when examining habitat selection by wetland birds. I suggest that direct experimental approaches are necessary to determine the effects of certain land use practices (e.g., forestry) on the food resources of breeding waterfowl. The importance of macroinvertebrates as a protein source for breeding waterfowl has been well documented (Krapu and Reinecke 1992). However, our knowledge of the nutrition of ducklings is limited, and hinders our ability to make conclusive statements relating habitat characteristics to waterfowl productivity. To better understand brood biology and their habitat requirements, additional studies of the diets, nutrient requirements, and rates of food intake are necessary.

Winter habitat and resource supplies of migratory birds also affect survival and recruitment (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Weller 1988). Wintering grounds can be particularly important to goldeneye and Bufflehead since that is where juvenile birds mature, and where pair formation occurs (Eadie et al. 1995). Therefore, future research and conservation efforts should also be directed at ensuring the preservation of habitat components throughout these birds' annual cycle and range (including migration stop-over sites and molting areas).

North American's cavity nesting waterfowl species are diverse and widespread, and include: Barrow's Goldeneye, Common Goldeneye, Bufflehead, Wood Ducks, Hooded and Common Mergansers (*Lophodytes cucullatus* and *Mergus merganser*), and Black-bellied Whistling Ducks (*Dendrocygna autumnalis*). It is important that biologists do not simply assume that cavity nesting waterfowl are limited by nest site availability, because other factors such as food abundance, access to breeding pair and brood habitat, territoriality, and even winter mortality likely contribute to these species' population dynamics.

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