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Foraging Behavior and Breeding Performance of Common Loons, *Gavia immer*, Nesting on Lakes in Central Alberta.

by

Beverly Angela Gingras ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

in

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Abstract

In central Alberta, Common Loons, *Gavia immer*, use a variety of lakes which differ in prey base. Loons were monitored on lakes with different prey assemblages to determine if this factor affected behavior and reproductive success. In 1994-1995 foraging behavior of adult loons and chicks was compared between small, shallow lakes that contained small-bodied fish (Minnow Lakes) and fishless lakes. Adult loons made dives of shorter duration and dove more frequently on Fishless Lakes than on Minnow Lakes. Provisioning rates by adults on Minnow Lakes decreased for older chicks (≥ 5 wks), but remained high for chicks on Fishless Lakes. Adults on Fishless Lakes may have been unable to meet their own energy requirements plus those of larger chicks with only invertebrate prey. Breeding surveys (1993-1996) indicated that Minnow Lakes offered good fledging habitats but not good nesting habitats. Fishless Lakes offered good nesting sites but chicks rarely fledged. The number of fledged/territorial pair was similar between the two lake types. Fledging rates on these small lakes were lower than on larger, deeper lakes that contained large-bodied fish species.

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1.1 Introduction

1.1.1 The Relationship Between Breeding Performance and Diet

The annual breeding success of an individual bird can be defined as the number of offspring raised to independence (fledging). Success of a bird within a breeding season may be constrained by a number of factors. These constraints can occur at the : 1) prenesting stage, when birds are finding and securing territories, nesting sites and/or mates and developing gametes; 2) nesting stage, when eggs are laid and incubated; and 3) hatchling-fledgling stage, when chicks hatch and grow. An individual's characteristics, such as age and sex, may influence success at any of these stages. For example, young birds may lack the physiological capacity to produce, and the experience needed to successfully raise, as many young as older birds. An increase in clutch size, nesting success, and/or fledging success with age has been observed in many birds, including Lesser Scaups, *Aythya affinis* (Afton 1984), Yellow-eyed Juncos, *Junco phaeonotus* (Weathers and Sullivan 1989), and Seychelles Warblers, *Acrocephalus sechellenis* (Komdeur 1996).

The environment also places constraints on breeding success. The length of the breeding season can influence the number of young an individual can raise. Depending on the length of the breeding season, renesting after a failed initial attempt may be impossible. Many temperate and arctic birds with short breeding seasons are constrained to laying one clutch during the breeding season. The weather can also influence the breeding success of a bird. For example, severe thunderstorms in east-central Georgia between 1984 and

1989 resulted in drowning of Wood Stork, *Mycteria americana*, eggs and chicks on five occasions (Coulter and Bryan 1995). Periods of cold temperatures during some of the Wood Stork breeding seasons resulted in many instances of prenesting colony abandonment and nest/egg abandonment.

Biotic factors such as competition for available mates and habitat, parasitism of nests, and predation on young can also directly influence breeding success. Competition for resources and mates often results in some individual "floaters" who may be unable to breed (e.g., Purple Gallinules, *Porphyrula martinica*, Hunter 1987). Parasitism by ecto-parasites such as mites, flies, or fleas can lower the nesting success of birds such as the Great Tit, *Parus major* (Oppliger *et al.* 1994), and the Pied Flycatcher, *Ficedula hypoleuca* (Merino and Piotti 1995). Brood parasitism also decreases the nesting and/or fledging success of many birds (e.g., parasitism by Shiny Cowbird, *Molothrus bonariensis*, on Pied Water-Tyrants, *Fluvicola pica,* Cruz and Andrews 1997). Predation on eggs and chicks is often the leading cause of reproductive failure. For example, egg predation by Marsh Wrens (*Cistothorus palustris*), resulted in the failure of 51% of the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) nests in a freshwater marsh near Lake Manitoba in 1993 - 1994 (Picman and Isabelle 1995). Predation by Fish Crows (*Corvus ossifragus*) and rat snakes (*Elaphe obsoleta*) resulted in the failure of greater than 50% of Common Ground-Dove (*Columbina passerina*), Northern Mockingbird (*Mimus polyglottos*), Brown Thrasher (*Toxostoma rufum*), and Northern Cardinal (*Cardinalis cardinalis*) nests in two Florida citrus groves in 1989 (Mitchell *et al.* 1996)

Perhaps the most influential biotic factor on the success of an individual at any stage within the breeding season is the abundance and density, and the caloric and nutritional characteristics of food items. Lack of suitable food in the prenesting stage may result in the delay of the laying date (Wanless and Harris 1992), reduced clutch size (Hussell and Quinney 1987), reduced egg size (Hakkarainen and Korpimäki 1994), and/or reduced or no breeding attempts (Rodenhouse and Holmes 1992). Insufficient food in the incubation stage may result in reduced brood size (Korpimäki 1992) and/or reduced nest attendance or nest abandonment (Bukacinska *et al.* 1996). Lack of food in the hatchling-fledgling stage may result in reduced chick attendance or chick abandonment (Hamer *et al.* 1993) and may result in the starvation and subsequent death of chicks (Rodenhouse and Holmes 1992).

In the past, most researchers examining the relationship between diet and breeding success have focused on the influence of food abundance on breeding success with the expectation that breeding success would be directly related to abundance of preferred food. In some cases, there is strong evidence that reductions in preferred food results in poor reproductive output. Korpimäki (1992) found that common voles (*Microtus epirotics*) in Finland were the main and the preferred prey of Long-eared Owls (*Asio otus*) during a 13 year period (1977-1989). He also found that Long-eared Owl annual breeding density, mean clutch size, and mean brood size were positively correlated with common vole abundance. Watson *et al.* (1992) found that the nesting density of Golden Eagles (*Aquila chrysaetos*) in six areas across Scotland in 1982 - 1985 was positively related to carrion abundance and breeding success (chick fledged per pair) of the eagles was positively related to live prey abundance. Experimental reduction of caterpillars in a 30 ha plot of deciduous forest in New Hampshire resulted in fewer nesting attempts by Black-throated Blue Warblers, *Dendroica caerulescens* (Rodenhouse and Holmes 1992).

Natural caterpillar reduction in the same area during a four year period (1982 - 1985) resulted in reductions in nesting attempts, nestling growth rates, nestling survival, and the number of young fledged per nest.

In other cases, no evidence was found to support a direct link between prey abundance and reproductive success. For example, Adams *et al.* (1994) reduced the number of grasshoppers around Vesper Sparrow (*Pooecetes gramineus*) nests in the Little Missouri National Grassland, North Dakota, but did not manipulate the grasshoppers around control nests. They found no difference in the fledging rate between control and manipulated sites. They suggested that adults in the manipulated sites compensated behaviorally for the reduction by foraging farther away from the nests. These studies indicate that the relationship between diet and breeding success is more complicated than originally perceived.

1.1.2 The Relationship Between the Breeding Success, Foraging Behavior, and Diet of Aquatic Birds

Much of the research examining the relationship between diet and breeding success has focused on aquatic birds, particularly fish-eating aquatic birds. The reasons for using these birds as study species are numerous. Compared to other species, most piscivorous birds are large and conspicuous. Most display some level of parental care which includes chick feeding and many are colonial. Thus, the success and feeding patterns of many individuals can be easily monitored. In addition, many piscivorous birds are thought to concentrate their foraging efforts on one or two species of fishes. These birds are, therefore, thought to be particularly sensitive to changes in fish abundance. This belief has resulted in the proposal that piscivorous birds, particularly their breeding success, can be used as indicators of fish stocks (Anderson *et al.* 1982, Barrett *et al.* 1987).

The possibility that piscivorous birds can be used to monitor fish abundance has been influential in promoting studies examining the relationship between diet and reproductive output of these birds. The resulting research has indicated that the breeding success of some species is highly correlated with fish abundance in the breeding area. For example, the fledging success of Brown Pelicans (*Pelecanus occidentalis*) nesting in southern California from 1970 - 1979 was found to be positively correlated with abundance of the species' major food source in the area, northern anchovies (*Engraulis mordax*; Anderson *et al.* 1982). In 1980 - 1983, Barrett *et al.* (1987) found that Atlantic Puffin (*Fratercula arctica*) fledging success at 12 colonies on the coast of Norway was directly related to herring (*Clupea harengus*) abundance in the area. The proportion of breeding pairs which hatched chicks, the number of eggs hatched per eggs laid, the number of chicks fledged per chicks hatched, and the number of chicks fledged per breeding pair of Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous-winged Gulls (*Larus glaucescens*) in Sitkalidak Strait (Gulf of Alaska) in 1977 - 1978 was positively correlated with pacific sandlance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*) abundance in the area (Baird 1990).

Research on other species indicate that some bird can behaviorally buffer the effects of low food abundance. Change in diet is one way adults may adjust their behavior when preferred food abundance is low. Northern Gannets (*Sula bassana*) increased the number of fish species consumed when their main prey species, sandeel (*Ammodytes marinus*) abundance declined from 1981 - 1988 at a breeding colony on the northwest tip of Shetland (Martin 1989). The broadening of diet resulted in no changes in breeding success during the time of sandeel decline. Adjustments in activity budgets may represent one way birds attempt to compensate for periods of low food abundance (Cairns 1987). For example, a colony of Common Murres (*Uria aalge*) on Shetland experienced a year of high and a year of low food (sandeels) abundance (Uttley *et al.* 1994), but breeding success did not differ between years. Uttley *et al.* (1994) suggested that adults compensated behaviorally for low food abundance by spending more time foraging and by feeding chicks larger prey items.

Buffering attempts are not always successful. Whereas Common Murres were able to adjust their behavior to compensate for low sandeel abundance, Black-legged Kittiwakes in the same area, at that time were unable to behaviorally ameliorate the effects of low food abundance (Hamer *et al.* 1993). Although adult Kittiwakes spent more time feeding in the low food year, no hatchlings survived to fledge in 1990, whereas 85% of chicks hatched in the high food year survived to fledge. If and how a bird responds to changes in prey abundance and composition can be affected by the level of change in abundance. Cairns (1987) suggested that at a certain threshold of low prey abundance, birds may reach a limit in their ability to compensate behaviorally. Further reductions in prey abundance are reflected in reductions in breeding success. The ability to behaviorally ameliorate the effects of low food supply may depend on whether individuals of a species are restricted to certain feeding areas, have rigid or energetically expensive feeding behaviors, or have specialized dietary and nutritional needs (Hamer *et al.* 1993).

Foraging behavior is not only influenced by energetic and nutritional demands; it is also affected by age and sex. For example, differences in foraging behavior between young and adult aquatic birds may be due to differences in experience and physiology (Burger 1986). Differences in body and bill sizes between male and female birds may also result in differences in foraging patterns. The larger body mass, and therefore greater body oxygen storage capacity, of male Western Grebes, *Aechmophorus occidentalis* (Forbes and Sealy 1990) and Red-Throated Loons, *Gavia stellata* (Reimchen and Douglas 1984) enables them to dive for longer periods of time than females and males' larger bills enable them to eat larger prey items than females.

Foraging patterns, such as dive duration and dive rate, are also influenced by diet. Feeding on organisms that differ in terms of caloric, nutritional, and/or behavioral characteristics may require different foraging strategies. For example, the amount of time a diving bird spends underwater is dependent on the time it takes to search for, handle, and consume prey (Ydenberg 1986). Thus, dive duration may be influenced by a prey's mobility, swimming speed and style. Birds that feed on prey that are sessile or slow-moving, and relatively easy to catch, may spend less time underwater per dive than birds that feed on fast moving or erratically swimming prey that are difficult to catch (Ulenaers *et al.* 1992, Barr 1996). Dive duration may also be influenced by the size of prey, as larger prey may be more difficult to handle and consume than smaller prey (Ulenaers *et al.* 1992). Prey that are found deeper in the water column or that hide in vegetation may require dives of longer duration (Bost *et al.* 1994). Dive rate may also be influenced by the distribution of prey items; aggregated prey, schooling fish for example, may be easier to locate and exploit than solitary prey items (Ydenberg 1986). The caloric values of different prey items will influence overall activity budgets as birds may need to devote more time to feeding or to feed more frequently when eating prey of lower caloric value (Obst *et al.* 1995).

The preceding review indicates that past studies on a variety of species have concentrated on the relationship between prey abundance and reproductive success and have focused less on the behavioral aspects involved in this relationship. Recent research (e.g., Cairns 1987, Hamer *et al.* 1993, Uttely *et al.* 1994, Phillips *et al.* 1996) indicates that a complex relationship exists between characteristics of individual birds, prey base characteristics, foraging behavior, and reproductive success.

1.1.3 The Relationship Between Common Loon Breeding Success, Foraging Behavior, and Prey Composition and Abundance

Loons (*Gaviidae*) are holoarctic aquatic birds that are highly adapted morphologically (e.g. webbed feet, legs that are situated far back on body and consist of a short femur and a long tibiotarsus with a cnemial crest that creates extra area for muscle attachment, and reduced pneumaticity in their bones) to living in aquatic habitats. These morphological adaptations cause loons to be extremely awkward on land and thus most of a loon's life is spent in the water. This dependency on aquatic environments, along with a fairly low reproductive output (usually one clutch consisting of 1-2 eggs per year), means that loon populations are sensitive to habitat changes. Declines in loon populations have been attributed to loss of suitable nesting habitat due to shoreline development and to disturbance by recreational activities (Ream 1976, Titus and Van Druff, 1981, Heimberger *et al.* 1983). Declines in prey abundance in breeding areas have also been blamed for poor reproductive success (Alvo *et al.* 1988, Eriksson and Sundberg 1991).

Loons are thought to have narrow dietary requirements, with fish being the main dietary component (McIntyre 1994). Therefore, loon breeding success should be sensitive to any changes in fish abundance. However, studies examining loon reproductive output on lakes with differing fish densities indicate that the relationship between prey composition and abundance, and loon reproductive success is not simple. For example, Eriksson (1986), found no relationship between Swedish Arctic Loon, *Gavia arctica*, productivity and the density of fish in nesting lakes. He suggested that declines in fish density within lakes due to acidification, and the subsequent changes in zooplankton and phytoplankton abundance and composition, resulted in increases in water clarity which increased the ability of loons to detect prey (Eriksson 1985). In addition, he suggested that this increase in detectability of prey fish, in combination with an increase in invertebrate abundance and the ability of Arctic Loons to feed their chicks invertebrates as well as fish, allows Arctic Loons to adjust to some changes in fish populations (Eriksson and Sundberg 1991). Red-throated Loons on the other hand, usually nest on small fishless lakes and import only fish from larger lakes or from the ocean to feed chicks (Reimchen and Douglas 1984, Eriksson *et al.* 1990). The combination of using an energetically expensive method of gathering food for chicks and having a diet restricted to fish may result in the Red-throated Loon breeding success being sensitive to changes in fish populations (Eriksson *et al.* 1990, Eriksson 1994).

The diet of Common Loons (*Gavia immer*) is similar to other species of loons; gut content analysis indicates that, although Common Loons may eat invertebrates and vegetation, the main component of an individual's diet is typically fish (Barr 1996). Large-bodied fish, such as yellow perch (*Perca flavescens*) and white sucker (*Catostomus* *commersoni*), are often found in the stomachs of adult loons during the breeding season. Small-bodied fish (e.g., lake chub, *Couesius plumbeus*, and ninespine stickleback, *Pungitius pungitius*) are also frequently found in stomach contents (Ontario, Barr 1996). However, Common Loons differ from Red-throated Loons as Common Loons do not import fish from sites other than the nesting lake to feed chicks. Thus, all the food required to raise chicks to fledging must come from the natal lake. In addition, it has been estimated that large quantities (423 kg) of fish are needed to support two adult Common Loons and two chicks throughout the breeding season (5.5 months, Barr 1986). Because of dependency on fish and restricted feeding habitats (i.e., the natal lake), Common Loon breeding success is thought to be highly sensitive to changes in fish abundance in breeding lakes.

However, studies investigating the effects changes in diet have on the reproductive output of Common Loons often report contradictory results. For example, Parker (1988) examined the relationship between reproductive success and pH of nesting lakes of Common Loons in the Adirondacks of New York. He found that pH did not influence the breeding success of loons even though lakes with lower pH (e.g., 5.12) had lower fish densities (mean of 2.3 items per minnow trap) than lakes with higher pH (e.g., 5.78, mean of 80.3 items per minnow trap). However, Alvo *et al.* (1988) observed Common Loons nesting on acid-sensitive (little buffering capacity) lakes in the Sudbury region, Ontario and found that alkalinity and pH of the lakes were positively correlated and that high-alkalinity lakes were more likely to have successfully breeding loon pairs (pairs with fledglings) than low-alkalinity lakes. Although the fish populations in the lakes were not directly measured, they attributed the differences in reproductive success to differences in fish biomass as acidified lakes tend to have reduced fish populations (Schindler *et al.* 1985).

Alvo *et al.* (1988) also found that loons nesting on larger, deeper lakes were more successful than loons on smaller, shallower lakes. In fact, many studies have revealed a relationship between lake area and Common Loon breeding success. Researchers in eastern Canada and the United States have found that loons are more likely to successfully fledge young on larger, oligotrophic (as defined by total phosphorus levels < 10 µg/l, Wetzel 1975) lakes: > 100 ha in New Hampshire (Blair 1992); > 40 ha in Nova Scotia (Kerekes 1990); > 40 ha in Ontario (Wayland and McNicol 1990, Barr 1986). Reports indicate that loons may nest on smaller lakes (McIntyre 1994), but Kerekes *et al.* (1996) and Barr (1986, 1996) suggest that small oligotrophic lakes do not have enough total food biomass to support a pair of loons and chicks.

Studies conducted in eastern Canada and the United States indicate that lake area, prey abundance, and breeding success of Common Loons are correlated. However, in 1992, Paszkowski (1994) surveyed waterfowl on 25 lakes in central Alberta and found Common Loons present on a variety of lakes. The lakes are all relatively productive (total phosphorus >10 µg/l, Wetzel 1975), but differ in terms of size, depth, and fish species composition. Based on their morphometry and fish community, these lakes can be categorized into three lake types (Robinson and Tonn 1989): 1) "Pike Lakes" which are usually larger (≥ 40 ha) and deeper (≥ 9 m) and, due to predation upon small-bodied fish, are only populated by large-bodied fish such as northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersoni*); 2) "Minnow Lakes" which are usually small (< 40 ha) and shallow (< 9 m) and, due to low winter oxygen levels, contain only small-bodied fish tolerant of hypoxia such as fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*); and 3) "Fishless Lakes" which are usually small (< 40 ha), shallow (< 9 m) and naturally fishless, most likely due to frequent and prolonged winter hypoxia and the lack of permanent inflow or outflow streams which hampers colonization.

Differences between the breeding success of loons on these different lake types in Alberta may be expected. For example, loons on lakes with reduced or no fish populations may encounter less recreational activity than loons on lakes with fisheries and less predation from aquatic predators such as large fish that may occasionally eat chicks (Yonge 1981). In addition, Barr (1996) found that loons prefer to eat smaller individuals of many fish species (e.g., yellow perch and white sucker), therefore, loons foraging on larger lakes may compete for prey with piscivorous fish. The smaller Minnow and Fishless Lakes may offer protection from fish predators, and may be easier to defend from other avian competitors (Belant 1991), but may lack adequate food supplies (Barr 1996).

The presence of successfully breeding loons on these small lakes suggest that these lakes have sufficient prey biomass to support a pair and chicks, and that Common Loons are more flexible in their diet and behavior then previously thought. Evidence suggests that loons may be able to adjust their behavior when foraging for different prey species. For example, Parker (1988) found that adult loons may compensate for the lack of fish as prey by feeding invertebrates to chicks. In addition, both Parker (1988) and Alvo *et al.* (1988) found that adult loons nesting on acidic, fishless lakes spent considerable time away from the breeding lake, presumably feeding on fish elsewhere. Parker (1985) also observed three instances of a pair of adult loons from a fishless lake flying fish in from other lakes to feed their chicks, a behavior that is unusual for this species.

The presence of loons on the different lake types presented the opportunity to compare the behavior of loons foraging for different prey. In the second and third chapters, I describe how during the summers of 1994 and 1995, I collected behavioral observations on Common Loons nesting on Minnow Lakes and on Fishless Lakes to compare the behavior of loons foraging primarily for fish to that of loons foraging primarily for invertebrates. I chose to compare the behavior of loons foraging on Fishless Lakes to that of loons foraging on Minnow Lakes because Minnow Lakes and Fishless Lakes are generally similar in size and depth. These lakes are small enough that one pair of loons can occupy the entire lake and exclude other avian species that may compete for resources (e.g., Red-necked Grebes, *Podiceps grisegena*). In addition, unlike many Pike Lakes, these lakes experience little recreational activity, and lack fish that may prey on loon chicks or compete with loons for food. From a practical view, these small lakes are advantageous in the sense that all areas of the lake can be observed from a single location.

The presence of loons on the different lake types in Alberta also presented the opportunity to compare the breeding success of individuals of the same species that forage for different prey. In the fourth chapter of my thesis, I present data collected during the summers of 1993 - 1996, on the success of loons in the establishment of territories, nesting, hatching and fledging young on Pike, Minnow, and Fishless Lakes. Comparing the breeding success of loons on the three lake types to each other, and to lakes in other areas of Canada and the United States, allows for the assessment of these lakes as nesting habitat for Common Loons.

In the fifth, and concluding, chapter I explore the relationship between breeding performance, foraging behavior, and diet of Common Loons in central Alberta. I indicate how this study may be applied to current and future research on Common Loons. Finally, the need for and direction of future studies examining the relationship between the environment, behavior, and reproductive success of aquatic birds in general, and of Common Loons specifically, are addressed.

1.2 Literature Cited

Adams, J. S., Knight R. L., McEwen, L. C. and T. L. George. 1994. Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. Condor 96:739-748.

Afton, A. D. 1984. Influence of age and time on reproductive performance of female Lesser Scaup. Auk 101:225-265.

Alvo, R., Hussell, D. J. T., and M. Berrill. 1988. The breeding success of common loons (*Gavia immer*) in relation to alkalinity and other lake characteristics in Ontario. Canadian Journal of Zoology 66:746-752.

Anderson, D. W., Gress, F. and K. F. Mais. 1982. Brown pelicans: influence of food supply on reproduction. Okios 39:23-31.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21:224-235.

Barr, J. F. 1986. Population dynamics of the Common Loon (*Gavia immer*) associated with mercury contaminated waters in northwestern Ontario. Canadian Wildlife Service Occasional Paper No. 56.

Barr, J. F. 1996. Aspects of Common Loons (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321:119-144.

Barrett, R. T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Røv, N. and W. Vader. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980-1983. Ornis Scandinavica 18:73-83.

Belant, J. L. 1991. Territorial activities of Common Loons on single-pairs lakes. Passenger Pigeon 53:299-302.

Blair, R. B. 1992. Lake features, water quality and the summer distribution of Common Loons in New Hampshire. Journal of Field Ornithology 63:1-9.

Bost, C. A., Puetz, K. and J. Lage. 1994. Maximum diving depth and diving patterns of the gentoo penguin *Pygoscelis papua* at the Crozet Islands. Marine Ornithology 22:237-244.

Bukacinska, M., Bukacinska, B., and A. Spaans. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). Auk 113:300-309.

Burger, J. 1986. Effects of Age on Foraging in Birds. *In* Acta XIX Congressus Internatalis Ornithologicus. Ed. Henri Ouellet pp 1128-1139.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5:261-271.

Coulter, M. C. and L. Bryan. 1995. Factors affecting reproductive success of Wood Storks (*Mycteria americana*) in east-central Georgia. Auk 112:237-243.

Cruz, A. and R. Andrews. 1997. The breeding biology of the Pied Water-Tyrant and its interactions with the Shiny Cowbird in Venezuela. Journal of Field Ornithology 68:91-97.

Eriksson, M. O. G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. Ornis Scandinavica 16:1-7.

Eriksson, M. O. G. 1986. Reproduction of Black-throated Diver *Gavia arctica* in relation to fish density in oligotrophic lakes in southwestern Sweden. Ornis Scandinavica 17:245-248.

Eriksson, M. O. G., Blomqvist, D., Hake, M., and O. C. Johansson. 1990. Parental feeding in the Red-throated Diver *Gavia stellata*. IBIS 132:1-13.

Eriksson, M. O. G and P. Sundberg. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. Bird Study 38:135-144.

Eriksson, M. O. G. 1994. Susceptibility to fresh water acidification by two species of loon, Red-throated Loons (*Gavia stellata*) and Arctic Loons (*Gavia arctica*) in southwest Sweden. In: Kerekes, J. J.(ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:439-444.

Forbes, L. S. and S. G. Sealy. 1990. Foraging roles of male and female western grebes during brood rearing. Condor 92:421-426.

Hakkarainen, H. and E. Korpimäki. 1994. Environmental, parental and adaptive variation in egg size of Tengmalm's owl under fluctuating food conditions. Oceologia 98:362-368.

Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P. and M.D. Burns. 1993. The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. IBIS 135:255-263.

Heimberger, M., Euler, D., and J. Barr. 1983. The impact of cottage development on Common Loon reproductive success in central Ontario. Wilson Bulletin 95:431-439.

Hunter, L. A. 1987. Acquisition of territories by floaters in cooperatively breeding purple gallinules. Animal Behavior 35:402-410.

Hussell, D. J. T. and T. E. Quinney. 1987. Food abundance and clutch size of Tree Swallows *Tachycineta bicolor*. IBIS 129:243-258.

Kerekes, J. J. 1990. Possible correlation of summer common loon (*Gavia immer*) population with the trophic state of a water body. Internat. Verein. Limnol. 24: 349-353.

Kerekes, J. J., Duggan, M., Tordan, R., Boros, G., and M. Bronkhorst. 1996. Abundance and distribution of fish-eating birds in Kejimkujik National Park 1988-1995. Lake and Reservior Management 11:156.

Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler. Behavioral Ecology 7:417-425.

Korpimäki, E. 1992. Diet composition, prey choice, and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. Canadian Journal of Zoology 70:2373-2381.

Martin, A. R. 1989. The diet of Atlantic Puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170-180.

McIntyre, J. 1994. Loons in freshwater lakes. In: Kerekes, J. J.(eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:373-413.

Merino, S. and J. Piotti. 1995. Pied Flycatchers prefer to nest in clean nest boxes in an area with detrimental nest ectoparasites. Condor 97:828-831.

Mitchell, M. C., Best, L. B., and J. P. Gionfriddo. 1996. Avian nest-site selection and nesting success in two Florida citrus groves. Wilson Bulletin. 108:573-583.

Obst, B. S., Russell, R. W., Hunt, G. L. Jr., Eppley, Z. A., and N. M. Harrison. 1995. Foraging radii and energetics of Least Auklets (*Aethia pusilla*) breeding on three Bering Sea islands. Physiological Zoology 68:647-672.

Oppliger, A., Richner, H., and P. Christe. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). Behavioral Ecology 5:130-134.

Parker, K. E. 1988. Common loon reproductive and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66:804-810.

Paszkowski, C. A. 1994. Factors affecting aquatic bird assemblages in central Alberta. Proceedings of the 3rd Annual Alberta Lake Management Society 15-19.

Phillips, R. A., Caldow, R. W. G., and R. W. Furness. 1996. The influence of breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*. IBIS 138:140-149.

Picman, J. and A. Isabelle. 1995. Sources of nesting mortality and correlates of nesting success in yellow-headed blackbirds. Auk 122:183-191.

Ream, K. H. 1976. Loon productivity, human disturbance, and pesticide residues in northern Minnesota. Wilson Bulletin 88:427-432.

Reimchen, T.E and S. Douglas. 1984. Feeding schedule and daily food consumption in Red-throated Loons (*Gavia stellata*) over the prefledging period. Auk 101:593-599.

Robinson, C. L. K. and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:81-89.

Rodenhouse, N. L and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. Ecology 73:357-372.

Titus, J. R. and L. W. Van Druff. 1981. Response of the Common Loon to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota. Wildlife Monographs 79:1-60.

Schindler, D. W., Mills, K. H., Malley, D. F., Findlay, D. L., Shearer, J. A., Davies, I. J., Turner, M. A., Lindsey, G. A., and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. Science 228:1395-1401.

Uttley, J. D, Walton, P., Monaghan, P., and G. Austin. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. IBIS. 136:205-213.

Ulenaers, P., J. Van Vessem, and A. Dhondt. 1992. Foraging of the great crested grebe in relation to food supply. Journal of Animal Ecology 61:659-667.

Wanless, S. and M. P. Harris. 1992. Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145-154.

Watson, J., Rae, S. R. and R. Stillman. 1992. Nesting density and breeding success of golden eagles in relation to food supply in Scotland. Journal of Animal Ecology 61:543-550.

Wayland, M. and D. K. McNicol. 1990. Status report on the effects of acid precipitation on common loon reproduction in Ontario: The Ontario Lakes Loons Survey Technical Report Series No. 92. C. W. S., Ontario region.

Weathers, W. W. and K. A. Sullivan. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs 59:223-246.

Wetzel, R. G. 1975. Limnology. W.B. Saunders Co. Toronto.

Ydenberg, R. C. 1986. Foraging by diving birds. *In* Acta XIX Congressus Internatalis Ornithologicus. Ed. Henri Ouellet pp 1832-1843.

Yonge, K. S. 1981. The breeding cycle and annual production of the Common Loon (*Gavia immer*) in the boreal forest region. MS thesis, University of Manitoba, Winnipeg, 141 pp.

Chapter Two

Feeding Behavior of Common Loons Nesting on Lakes With and Without Fish in Central Alberta, Canada

2.1 Introduction

The foraging behavior of aquatic birds is governed by characteristics such as age (Olivaceous Cormorants, *Phalacrocorax olivaceous*, Morrison *et al.* 1978) and sex (Georgian Shags, *Phalacrocorax georgianus*, Wanless *et al.* 1995), but is also influenced by biotic and abiotic environmental conditions such as food supply (Kittiwakes, *Rissa tridactyla*, Hamer *et al.* 1993) and water quality (Arctic Loons, *Gavia arctica*, and Common Mergansers, *Mergus merganser*, Eriksson 1985). The extent to which changes in the environment, particularly changes in food supply, affect aquatic birds is dependent on a species' ability to compensate behaviorally (Burger and Piatt 1990, Forbes and Sealy 1990, Wanless and Harris 1992, Salamolard and Weimerskirch 1993, Monaghan *et al.* 1994, Bukacinska *et al.* 1996). Some species, such as the Red-necked Phalarope (*Phalaropus lobatus*) have specialized dietary requirements and are unable to behaviorally respond to changes abundance of their major prey (Rubega and Inouye 1994). Cairns (1987) suggested that other species may possess the behavioral flexibility required to respond to changes in prey abundance and recent studies indicate that dive rates (Common Murres, *Uria aalge*, Monaghan *et al.* 1994), chick provisioning rates (Kittiwakes, Wanless and Harris 1992), and time budgets (Common Murres, Burger and Piatt 1990) may be adjusted by some species of aquatic birds when prey abundance changes.

Cairns (1987) also suggested that changes in behavior may actually reflect changes in prey availability, in terms of a bird's ability to locate and capture prey, and that most studies simply assume that prey availability is correlated with absolute prey abundance. Birds may respond to a decline in a preferred prey population by feeding on less preferred, but more abundant prey (Kittiwakes and Glaucous-wing Gulls, *Larus glaucescens*, Baird 1990; Cape Gannets, *Morus capensis*, Crawford and Dyer 1995; American White Pelicans, *Pelecanus erythrorhynchos*, Findholt and Anderson 1995; Herring Gulls, *Larus argentatus*, Bukacinska *et al.* 1996). Thus changes in diving rate, provisioning rates, or time budgets may not only be a function of changes in prey abundance, but may also reflect shifts in diet composition (Obst *et al.* 1995).

Feeding on organisms that differ in caloric, nutritional, and/or behavioral characteristics may require different foraging strategies (Rodriguez-Robles and Leal 1993). For example, the amount of time a diving bird spends underwater is dependent on the time it takes to search for, handle, and consume prey (Ydenberg 1986). Thus, dive duration may be influenced by a prey's swimming speed and style. Birds that feed on prey that are sessile or slow-moving, and relatively easy to catch, may spend less time underwater per dive than birds that feed on fast moving or erratically swimming prey that are difficult to catch (Ulenaers *et al.* 1992, Barr 1996). Dive duration may also be influenced by the size of prey, as larger prey may be more difficult to handle and consume than smaller prey (Ulenaers *et al.* 1992). Prey that are found deeper in the water column or that hide in vegetation may require dives longer in duration (Bost *et al.* 1994). Dive rate may also be influenced by the distribution of prey items; aggregated prey, schooling fish for example, may be easier to locate and exploit than solitary prey items (Ydenberg 1986). The caloric values of different prey items will influence overall activity budgets as birds may need to devote more time to feeding when eating prey of lower caloric value (Obst *et al.* 1995).

Common Loons (*Gavia immer*) are highly territorial aquatic diving birds that are thought to have specialized dietary requirements (McIntyre 1988). Gut content analysis indicate that, although loons may eat invertebrates and vegetation, the main component of a loon's diet is typically fish (Barr 1996). Large-bodied fish (e.g., yellow perch, *Perca flavescens*, and white sucker, *Catostomus commersoni*) and small-bodied fish (e.g., lake chub, *Couesius plumbeus*, and ninespine stickleback, *Pungitius pungitius*) are often found in the stomachs of adult loons during the breeding season in Ontario (Barr 1996). In addition, it has been estimated that large quantities (423 kg) of fish are needed to support two adult Common Loons and two chicks during the breeding season (5.5 months, Barr 1986). However, unlike Red-throated Loons (*Gavia stellata*, Reimchen and Douglas 1985) adult Common Loons do not import fish from other lakes to feed chicks and thus are restricted to prey caught from the nesting lake.

Because Common Loons are piscivores and have restricted feeding locations (i.e., nesting lakes), loon populations may be sensitive to changes in fish abundance and species composition. This concern has led to studies examining loon productivity, i.e., the number of fledglings produced, on lakes that have reduced fish populations or have lost fish populations due to human-induced acidification. These reports indicate that the relationship between fish abundance and species composition and the reproductive success of Common Loons is more complex than previously thought. For example, Parker (1988) found no relationship between reproductive success and the pH of nesting lakes of Common Loons in the Adirondacks, New York, although he did find that lakes with lower pH (e.g., 5.12) had lower fish densities (mean of 2.3 items per minnow trap) than lakes with higher pH (e.g., 5.78, mean of 80.3 items per minnow trap).

Parker (1988) suggested that the loons on lakes with reduced or no fish populations may encounter less recreational activity than loons on lakes with fisheries and less predation from aquatic predators, such as large fish, that occasionally eat chicks (Yonge 1981). The absence of these two possible causes of chick mortality may have masked the effects of reduced fish densities on the loon population as a whole. Parker (1988) also suggested that adult loons may have compensated for the lack of fish as prey by feeding invertebrates to chicks. In addition, he found that adult loons nesting on acidic fishless lakes spent considerable time away from the breeding lake, presumably feeding on fish elsewhere. Parker (1985) also observed, on three occasions, adult loons from a fishless lake flying fish in from other lakes to feed their chicks, a behavior that is unusual for this species.

Like Parker (1988), Alvo *et al.* (1988) studied the reproductive success of loons nesting on acid-sensitive (little buffering capacity) lakes. They censused lakes in the Sudbury region of Ontario and found that loons nesting on low-alkalinity lakes were less successful than loons nesting on high-alkalinity lakes. They also found that loons nesting on larger, deeper lakes were more successful than loons on smaller, shallower lakes and suggested that the smaller lakes lacked the prey biomass needed to support a pair of loons and chicks.

Wayland and McNicol (1990) also examined the reproductive success of Common Loons in Ontario, but unlike Alvo *et al.* (1988), they found no relationship between loon productivity and lake pH. They did find a relationship between lake area and the presence and reproductive success of loons. In fact, researchers in eastern Canada and the United States have found that loons are most commonly observed on large, oligotrophic, as defined by total phosphorus levels (<10 µg/l, Wetzel 1975), lakes:

> 100 ha in New Hampshire (Blair 1992); > 40 ha in Nova Scotia (Kerekes *et al.* 1996); > 40 ha in Ontario (Wayland and McNicol 1990 and Barr 1986). Although there are reports that loons nest on smaller lakes (McIntyre 1994), Kerekes *et al.* (1996) and Barr (1986, 1996) suggest that small oligotrophic lakes in eastern Canada do not contain enough prey to support a loon family.

In 1992, Paszkowski (1994) surveyed waterfowl on a 25 lakes in central Alberta and found Common Loons present on a variety of lakes. All of the lakes were relatively productive (total phosphorus >10 µg/l, Wetzel 1975), but differed in size, depth, and fish species composition. In addition to observing loons nesting on larger (≥ 40 ha), deeper (≥ 9 m) lakes that contain populations of large-bodied fish such as northern pike (*Esox lucius*), white sucker, and yellow perch, similar to loon habitat in eastern Canada, she found loons nesting on smaller (< 40 ha), shallow (< 9 m) lakes that contained only small-bodied fish such as the fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*). Like Munro (1945) in British Columbia, she found loons nesting on small (< 40 ha), shallow (< 9 m), naturally fishless lakes.

The ecology of loons on small lakes is not well documented; thus this study was initiated to determine how loons use these "atypical" habitats (i.e., as both feeding and nesting lakes or as nesting lakes only) and to investigate the foraging behavior of loons on fishless lakes and physically similar lakes with small-bodied fish. The presence of loons on lakes that are similar in size and depth, but that differ in prey base composition, also provided the opportunity to compare the behavior of loons foraging primarily for invertebrates to that of loons that may be foraging primarily for fish. In addition, comparing the behavior of loons foraging on fishless lakes to that of loons foraging on lakes with small-bodied fish offered many advantages over comparing the behavior of loons foraging on fishless lakes to that of loons foraging on lakes with large-bodied fish. As mentioned, lakes with small-bodied fish and fishless lakes are similar in size and depth and, unlike lakes with large-bodied fish, these lakes are small enough that one pair of loons can occupy the entire lake and exclude other avian species (e.g. Red-necked Grebes, *Podiceps grisegena*) that may compete for resources. In addition, unlike large lakes that support sport fisheries, these lakes experience little recreational activity, and lack fish that may prey on loon chicks or that may compete with loons for food. From a practical view, these small lakes are advantageous as much of a lake's surface area can be observed from a single location.

During the summers of 1994 and 1995, I collected behavioral observations in central Alberta on Common Loons nesting on small lakes that contain small-bodied fish (referred to as Minnow Lakes hereafter) and that are fishless (referred to as Fishless Lakes hereafter), to compare the behavior of loons on these two different lake types. In addition, studies (Barr 1996, Evers 1994) suggest that differences exist between the diets and foraging behavior of adult male and female loons, and that adult loon behavior may change during the breeding season and as chicks mature. By observing adult loons on the two lake types, I sought to determine if: 1) adult loons on small lakes feed primarily from the nesting lakes, or if they fly elsewhere to feed; 2) time budgets, particularly time spent foraging, and foraging patterns (e.g., dive rate and dive duration) differ between Minnow and Fishless Lakes, and between male and female birds, and at different stages during the breeding period; and 3) dive success differs between Minnow and Fishless Lakes.

Based on studies conducted in other geographic regions (Alvo *et al.* 1988, Parker 1988), which suggest that adult loons nesting on Fishless Lakes fly elsewhere to feed, I predicted that adult loons on Fishless Lakes in Alberta would spend more time away from the nesting lakes than loons nesting on Minnow Lakes. Parker's (1988) study suggests that loons may catch invertebrates with more ease than fish, but that invertebrates may not provide the calories needed to satiate chicks and cause adult loons to feed chicks more frequently in order to compensate. Therefore, I predicted that loons foraging on Fishless Lakes in Alberta would spend less time underwater per dive, have a high percentage of successful dives, and dive more frequently. The adults would also increase the amount of time they devote to foraging to insure that their caloric requirements are met. Loons foraging on Minnow Lakes, on the other hand, were predicted to spend more time underwater pursuing fish per dive and have a lower percentage of successful dives. Adult loons were not expected to dive or feed chicks as frequently, and not devote as much time foraging, as loons nesting on Fishless Lakes.

Because adult male loons are larger (22% heavier on average, Barr 1996) than female loons, they have the physiological capacity to remain underwater for longer periods of time and to consume larger prey than do female loons. Thus, I predicted that the dives of males would be longer in duration than that of female's. In order to compensate for consumption of smaller prey, female loons would dive more frequently. Female loons may spend less time feeding as they are smaller in size and require less food than males.

Based on studies by Evers (1994) and Burger (1986), I predicted that the foraging behavior adult loons on small lakes in Alberta would change during the breeding season. Particularly, adult loons would spend less time foraging when nesting because they would have to incorporate incubation into their time budgets. Adult loons would dive more frequently and their dives would be shorter in duration when they are feeding chicks than before they nest or when they are incubating eggs. As chicks age, their demand for food increases (Barr 1996). Adults may respond by diving for food more frequently (as they feed only one prey item at a time), and/or by feeding larger prey items to chicks.

2.2 Methods

2.2.1 Study Sites

Research was centered at the University of Alberta Meanook Biological Research Station (54°37'N 113°20'W), Athabasca, Canada. In 1994, intensive behavioral observations were conducted on territorial Common Loon pairs on 2 Fishless Lakes and 3 Minnow Lakes (see Appendix 2-1). In 1995, 2 Fishless Lakes and 3 Minnow Lakes were added to the behavioral study, however, loons on 2 Minnow Lakes that were observed in 1994 were not studied in 1995. Therefore, loons on a total of 4 Fishless Lakes and 4 Minnow Lakes were studied in 1995.

The natural vegetation surrounding the lakes is representative of boreal mixedwood forests with the dominant tree species being trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). The shoreline vegetation of each lake was similar in species composition and usually consisted of a number of sedge and grass species, but the total area of the shoreline vegetation varied as some lakes were surrounded by extensive wetlands and others had very little wetland shoreline. The dominant emergent vegetation was common cattail (*Typha latifolia*), and the submergent vegetation included coontail (*Ceratophylum demersum*), and pondweed (*Potamogetan* spp.). The lakes were also characterized by a number of floating-leaved species such as yellow water lily (*Nuphar variegatum*) and smartweed (*Polygonum natas*).

Lakes were similar in morphometry and water chemistry (see Appendix 2-1). The morphometric and chemical characteristics of some of the lakes were first measured in a previous study in 1986 (Prepas *et al.* 1988) and the area and depth of these lakes were remeasured in 1995 with the use of topography maps (Paszkowski, unpubl.). The depth, area, and phosphorous concentrations of the remaining lakes were measured during the summers of 1993, 1994, and 1995 (Paszkowski, unpubl.). Fish populations in some of the lakes were first sampled in 1986 and 1987 (Robinson and Tonn 1989) and resampled in 1993 and 1994 (Tonn and Paszkowski, unpubl.). The remaining lakes were initially sampled during the summers of 1993 and 1994 (Tonn and Paszkowski, unpubl.).

2.2.2 Observation Times and Methods

Observations began in May, when the loons arrived and established territories, and when possible, continued until the birds left the lake to migrate in late August or early September. Observations were made from a canoe or from vantage points on shore using either a spotting scope or binoculars. Elevated (1 m high) platforms (1.5 m x 1.5 m) were used on three lakes in order to view lakes in their entirety. Platforms were not required on the remaining lakes. Blinds were not used as loons are often distracted by them and are less disturbed by a human presence (McIntyre 1988). Lakes were visited at least once each week. During each visit at least one hour of observation was recorded for each member of the loon family present. Observations usually began at 0900 hrs and time budgets were recorded until around 1700 hrs. However, at least once each month I recorded observations at each lake in the early morning, from dawn (0530 hrs - 0630 hrs) until 0900 hrs, and in the late evening, from 1900 hrs until dusk (2130 hrs - 2300 hrs).

At the start of each observation period (hour), the sex of the loon observed (the male being the larger of the loon pair; Barr 1973), the age of any chick present, the breeding stage of the loon, the time of day, and the weather conditions (% cloud cover in 1994 and 1995 and temperature in 1995) were recorded. The breeding period was divided into: 1) the prenesting stage, the period of time when loons arrive and establish territories until they lay 1-2 eggs in mid-May; 2) the nesting stage, from when loons initiate egg laying until eggs hatch 26 - 31 days later; and 3) the postnesting stage, the time from when chicks hatch until all members of the loon family leave the nesting lake for fall migration.

During each observation period, the frequency, duration, and location of all behaviors were recorded on maps of the lakes. Adult behaviors (see McIntyre 1988 for a detailed description of the behaviors) included: 1) territorial behavior, any inter- and intra-specific agonistic behaviors such as vocalization, wing beating, and chasing; 2) reproductive behavior, any behaviors relating to courtship, pair bonding, and copulation; 3) nesting, the laying and incubation of eggs on a nest; 4) sleeping, indicated by the loon placing its head over its back and tucking a foot under a wing; 5) preening, any activities relating to maintenance of feathers such as oiling, bathing, and head rubbing; 6) foraging, any behavior related to the procurement of food and; 7) floating, the loon was on the water surface and not participating in any of the previously mentioned behaviors. Foraging behaviors were "peering" (loons submerge head into the water column, presumably looking for food), foraging dives (loons search for, pursue, and attempt to capture and consume food underwater) and chick provisioning (adults feeding chicks).

Loons dive for other purposes besides foraging, but a foraging dive is the next action following peering and may result in chick provisioning. In addition, foraging dives occur in bouts, where loons dive continuously for periods of time. For example, a typical bout would include 26 dives in 24 minutes, but bouts may range from 5 dives in 4 minutes to 112 dives in 64 minutes. Non-foraging dives are associated with behaviors relating to preening, reproduction, and territory defense and do not usually occur in bouts.

2.2.3 Quantification of Foraging Behaviors

To determine if loons on small lakes feed primarily on their nesting lake and to determine if prey base, sex of a loon, and breeding period influence the amount of time spent on lake, I calculated the total amount of time spent on the lake by each adult member of the resident loon pair during each visit. To determine if time budgets and foraging patterns differ between lake types, between male and female loons, and among breeding periods, from each hour long observation period, I calculated: 1) the percentage of time spent performing each recognized behavior; 2) the dive rate, number of dives per minute while foraging; 3) the mean dive duration, the mean length of time spent under water per dive while foraging; and 4) the percentage of successful dives as defined by the delivery of food to a chick immediately following a dive (postnesting only).

2.2.4 Statistical Analysis

2.2.4.1 Lake Use by Loons

2.2.4.1.1 Loon Presence/Absence on Minnow and Fishless Lakes

Mann-Whitney U tests (Zar 1994) were performed to determine if the percentage of time loons were observed on a lake was influenced by the presence or absence of fish. The analysis was based on the total hours that male and female loons were present and absent on 5 lakes in 1994 and 8 lakes in 1995.

2.2.4.1.2 Male and Female Presence/Absence

Mann-Whitney U tests were performed to determine if the percentage of time loons were observed on a lake differed between males and females. The analysis was based on the total hours present and absent by male and female loons on all 5 lakes in 1994 and 8 lakes in 1995.

2.2.4.1.3 Loon Presence/Absence During the Breeding Season

Kruskal-Wallis One-Way Analysis of Variance (ANOVA) tests were used to determine if the percentage of time loons were present on a lake was influenced by the breeding status of the bird. Data collected on only those loon pairs which completed all stages in the breeding season (loon pairs on 3 lakes in 1994 and 4 lakes in 1995) were included in the analysis.

2.2.4.2 Time Budgets, Dive Rates, and Dive Durations

Repeated hourly observation periods on the same individual were considered to be independent behavioral samples only when separated by at least one hour during which no observations were recorded for the individual. Only those observations considered to be independent were included in analyses. All individual loon data sets collected in 1994 and 1995 including all time budgets, dive rates and mean dive durations per observation period were first tested using One-Sample Kolmogorov-Smirnov tests and were found not to be normally distributed. Thus, the data were analyzed using non-parametric statistical tests. Data analysis was done on a yearly basis because the loons on some lakes were not observed in both years and because it was not known whether the same loons returned to the lakes that served as study sites in both years.

2.2.4.2.1 Loon Behavior on Minnow and Fishless Lakes

The time budgets (time spent foraging), dive rates and mean dive durations of the loon pair on each lake (5 lakes in 1994 and 8 lakes in 1995) during the entire breeding season were compared using Mann-Whitney U tests to determine if the behavior of loons on any of the lakes differed, specifically if the behavior of loons on Fishless and Minnow Lakes differed.

In addition, to determine if the distribution of percentage of time spent foraging, dive rates, and dive durations of loons on Minnow and Fishless Lakes in general differed, cumulative frequency distributions were constructed and compared using Two-Sample Kolmogorov-Smirnov tests. I analyzed all data collected during the breeding period for each individual bird. However, because loon behavior may differ between breeding stages and because loons on more Fishless Lakes nested and hatched chicks than on

Minnow Lakes, I also analyzed the data for each individual bird collected only during the month of May (prenesting period for most birds). The results of the analyses using all data were very similar to the results obtained when using only the data collected in May. The analyses based on all the data will be presented; analyses based on the data collected in May will be discussed only when the results differed between the two data sets.

The Two-Sample Kolmogorov-Smirnov tests often produced significant results in only in one year, but general patterns were similar between years. These patterns are presented in histograms based on all the data collected in both years (both years combined).

2.2.4.2.2 Male and Female Behavior

Mann-Whitney U tests were performed using all data collected during the breeding period for each individual bird to determine if the foraging patterns of the male and the female on each lake differed in 1994 (all 5 lakes) or in 1995 (all 8 lakes). In addition, cumulative frequency distributions of the percentage of time spent foraging, dive rates, and dive durations were constructed and compared between male and female birds using Two-Sample Kolmogorov-Smirnov tests to determine if the distributions differed between male and female loons in general.

2.2.4.2.3 Loon Behavior During the Breeding Season

To determine if foraging behavior changed as the breeding season progressed in 1994 and 1995, the time budgets, dive rates, and mean dive durations of individual loons were compared among the prenesting, nesting, and postnesting breeding periods using Kruskal-Wallis One-Way ANOVA tests. Cumulative frequency distributions of time spent foraging, dive rates, and dive durations of loons in general during the prenesting, nesting, and postnesting periods were constructed and compared using Two-Sample Kolmogorov-Smirnov tests. Only those loons that went through all stages of the breeding season were included in the analyses (3 pairs in 1994, 4 pairs in 1995).

2.2.4.2.4 Adult Behavior as Chicks Mature

Chick ages were combined into two groups (1-35 days old and 36 days and older) based on the fact that the critical survival period for Common Loon chicks appears to occur after 4-5 weeks (Parker 1988). Mann-Whitney U tests were performed to determine if time budgets, dive rates, and dive durations of individual adult loons differed when carrying for younger versus older chicks.

2.2.4.3 Dive Success

Data sets for dive success of loons on each lake were examined using One-Sample Kolmogorov-Smirnov tests and proved not to be normally distributed. Kruskal-Wallis One-Way ANOVAs were performed to determine if the percentage of successful dives per observation period differed between lakes in either 1994 or 1995. In addition, cumulative frequency distributions of the percentage of successful dives per observation period of loons were constructed for each lake and compared using Two Sample

Kolmogorov-Smirnov tests to determine if the distribution of successful dives differed between lakes.

2.3 Results

2.3.1 Lake Use by Loons

2.3.1.1 Loon Presence/Absence on Minnow and Fishless Lakes

Loon pairs were more likely to be present on their territorial lakes than absent (see Appendix 2-2 for the hours present and the total hours visited). In 1994 and 1995, loons on Minnow Lakes and on Fishless Lakes spent a similar percentage of time on their territorial lakes (Table 2-1).

2.3.1.2 Male and Female Presence/Absence

In 1994 and 1995 male loons spent less time on the lakes then female loons (Fig. 2-1); however the difference between the sexes was not significant in both years (Table 2-1).

2.3.1.3 Loon Presence/Absence During the Breeding Season

The percentage of time a loon was observed on a lake was influenced by the stage of the breeding cycle (Fig. 2-2). In both 1994 and 1995 (Table 2-1), during prenesting and most loons spent all of their time on the lakes and it was not until the postnesting stage that loons began to leave the lakes. Except for the cases of chick abandonment, at least one adult was on the lake until chicks were at least one month old. It was not until late in the season, when the chick(s) was able to care for itself (at least eight weeks old) that both adults were absent from a lake simultaneously.

2.3.2 Time Budgets, Dive Rates, Dive Durations

2.3.2.1. Loon Behavior on Minnow and Fishless Lakes

On average, loons engaged in foraging far more often than any other behavior (Fig. 2-3, see Appendix 2-3 for means, standard errors, medians, ranges, and sample sizes). In 1994, there were no significant differences in the time spent foraging among loons on any of the lakes (Table 2-2; see Appendix 2-4 and 2-5 for median, ranges and sample sizes). In 1995, the time spent foraging by loons on Minnow Lakes and Fishless lakes were generally internally consistent (i.e., loons on the Fishless Lakes spent a similar percentage of time foraging per observation period and loons on the Minnow Lakes spent a similar percentage of time foraging per observation period); however, loons on some Fishless Lakes (e.g., Little Buck) spent more time foraging per observation than loons on Minnow Lakes (Fig. 2-4).

The frequency distributions of the percentage of time spent foraging (Fig. 2-5) indicated that loons on Minnow and Fishless Lakes exhibited a similar range of time spent foraging among observation periods. However, loons on Minnow Lakes displayed a greater frequency of observation periods in the higher end of the distribution than loons on Fishless Lakes. This may reflect the fact that loons laid eggs on more Fishless Lakes than on Minnow Lakes. Thus, loons on Fishless Lakes would display a greater proportion of observation periods where they spent all their time incubating and not foraging. In fact, in both 1994 and 1995, the distributions of the time spent foraging in May by loons on Minnow Lakes and by loons on Fishless Lake were not significantly different ($p = 0.166$, $p = 0.969$, respectively). The distributions of the time spent foraging by loons during the entire breeding period on Minnow Lakes and on Fishless Lakes were significantly different in 1995 but not in 1994 (Table 2-3).

Dive rates differed among lakes. In 1994, the dive rates of loons on Joseph Lake (Fishless Lake) were greater than the dive rates of loons on all the other lakes (Table 2-4, Fig 2-4). The dive rates of loons on Tawatinaw Lake (Minnow Lake) were lower than the dive rates of loons on 2 other lakes (Table 2-4, Fig 2-4). Loons on Tawatinaw displayed the lowest dive rates whereas loons on Joseph displayed the highest dive rates (Fig. 2-4). In 1995, the dive rates of loons on all the lakes were similar (Table 2-4), except for Joseph Lake which again differed from 3 Minnow and 2 Fishless Lakes. Frequency distributions indicated that loons on Fishless Lakes and Minnow Lakes exhibited a similar range of dive rates (Fig. 2-5). The dive rate distribution for loons on Minnow Lakes was significantly different from the dive rate distribution for loons on Fishless Lakes (Table 2-3) in 1994 and in 1995. However, dive rates of loons on Minnow Lakes were concentrated in the lower range of dive rates, suggesting that loons on Minnow Lakes dove less frequently than loons on Fishless Lakes.

Differences in dive duration paralleled differences in dive rates. In 1994, the dive durations of the loons on Joseph Lake were lower than in all other lakes (Table 2-5) and the dive duration of loons on Tawatinaw Lake were higher than the dive duration of loons on 2 other lakes (Fig. 2-4). In 1995, mean dive durations were not significantly different among loons across the Minnow Lakes (Table 2-5). The dive durations of loons on 2 Fishless Lakes (Tempo and Little Buck Lakes) were similar to each other but significantly differed from the dive durations of loons on the other Fishless Lakes. A distinct difference between the mean dive durations of loons on Minnow and Fishless Lakes could not be distinguished as mean dive durations of loons on West Baptiste Lake were similar to that of loons on some Fishless Lakes, and dive durations of loons on Tempo Lake and Little Buck Lake were similar to that of loons on many of the Minnow Lakes.

However, the mean dive duration frequency distributions of loons on Fishless Lakes and on Minnow Lakes indicated that although loons on these two lake types exhibited a similar range of mean dive durations (Fig. 2-5), the dive durations of loons on Minnow Lakes were aggregated in the upper range of the distribution, suggesting that loons on Minnow Lakes spent longer under water per dive than loons on Fishless Lakes. The dive duration distribution of loons on Minnow Lakes was significantly different from the dive duration distribution of loons on Fishless Lakes in 1995 but not in 1994 (Table 2-3).

2.3.2.2 Male and Female Behavior

In 1994 and 1995, male and female loons on each lake did not differ in the percentage of time they spent foraging per observation period (Table 2-6). Frequency distributions (Fig. 2-6) indicated that male and female loons exhibited a similar range of the percentage of time spent foraging per observation and the distributions of the were not significantly different from each other in 1994 or in 1995 (Table 2-3).

In 1994, dive rates did not significantly differ between the male and the female loon on any of the 6 lakes and in 1995 dive rates significantly differed between the male and the female loon on 2 of the 8 lakes (Table 2-6). Frequency distributions (Fig. 2-6) indicated that female and male loons exhibited a similar range of dive rates, however the dive frequencies of male loons were aggregated in the lower range of the distribution, suggesting that male loons dove less frequently than female loons. The female and male distributions were significantly different from each other in 1995 but not in 1994 (Table 2-3).

In 1994, mean dive durations did not significantly differ between the male and the female loon on any of the 6 lakes and in 1995, mean dive durations significantly differed between the male and the female loon on 2 of the 8 lakes (Table 2-6). Female and male loons exhibited a similar range of mean dive duration per observation (Fig. 2-6) however, the dive durations of male loons were aggregated in the upper range of dive durations, suggesting that male loons spent longer under water per dive than female loons. The dive duration distribution of male loons was significantly different from the dive duration distribution of female loons in 1995 but not in 1994 (Table 2-3).

2.3.2.3 Loon Behavior During the Breeding Season

The percentage of time spent foraging for 3 of 6 individuals differed significantly among breeding periods in 1994, but for only 1 of 8 individuals in 1995 (Table 2-7). Frequency distributions (Fig. 2-7) indicated that before nesting, loons spent most, if not all, their time foraging; nesting loons did not forage during many observation periods. The prenesting and nesting distributions were significantly different in both years (Table 2-3). More time was devoted to foraging in the postnesting than in the nesting but the nesting and postnesting distributions were significantly different only in 1995. The prenesting and postnesting distributions were not significantly different in either year (Table 2-3).

The dive rate per observation period of 3 out of 6 individuals in 1994 and of 6 out of 8 individuals in 1995 significantly differed among breeding periods (Table 2-7). Generally, in both years, the range of dive rates exhibited by loons were similar between the nesting and postnesting periods but the dive rates were aggregated in the lower range in the nesting period and in the upper range in the postnesting period, suggesting that dive rates increased as the breeding season progressed (Fig 2-7). The dive rate distributions of loons in the prenesting and postnesting periods were significantly different from each other in both years (Table 2-3), but the dive rates of loons in the nesting stage were significantly different from the dive rates in the postnesting stage only in 1994.

Mean dive durations of 4 out of 6 individuals in 1994 and of 5 out of 8 individuals in 1995 differed between breeding periods (Table 2-7). Generally, in both years, the range of dive durations exhibited by loons were similar between the nesting and postnesting periods but mean dive durations were aggregated in the upper range in the prenesting period and in the lower range in the postnesting period, suggesting that dive durations decreased during the breeding season (Fig. 2-7). In 1994 and 1995, the mean dive duration distributions of loons significantly differed between the prenesting and nesting periods and between the prenesting and postnesting period but not between the nesting and postnesting period (Table 2-3).

2.3.2.4 Adult Behavior as Chicks Mature

No trends were observed between the percentage time spent foraging, dive rates, or dive durations of adult loons and chick age (Fig. 2-8). In 1994 and 1995, the percentage of time spent foraging, the dive rates, and the mean dive durations for all adults combined when chicks were 1-35 days old were not significantly different then the percentage of time spent foraging, the dive rates, and the dive durations of adults when chicks were 36+ days old (Table 2-8).

2.3.3 Dive Success

The percentage of successful dives per observation period (see Appendix 2-6 for medians, ranges, and sample sizes) did not significantly differ among lakes in 1994 (Kruskal-Wallis One-Way ANOVA test statistic = 0.219, p = 0.96, df = 2, N = 21 observations) or in 1995 (Kruskal-Wallis One-Way ANOVA test statistic = 1.694, p = 0.429, df = 2, N = 21 observations). In addition, cumulative frequency distributions (Fig. 2-9) of the percentage of successful dives per observation period were similar between loons on two Fishless Lakes and on one Minnow Lake in both years (Table 2-9.)

2.4 Discussion

Unlike Red-Throated Loons (Reimchen and Douglas 1984) and Common Loons observed in New York by Christoff (1979), both members of Common Loon pairs in central Alberta foraged almost exclusively on the small nesting lakes. It was not until the chicks were able to feed themselves for short periods of time that adults began to leave the lakes. In addition, unlike loons nesting on lakes that were fishless due to acidification in Ontario (Alvo *et al.* 1988) and in New York (Parker 1988), loons nesting on the naturally fishless lakes in Alberta spent most of their time foraging on the nesting lake. In contrast to the observations made by Parker (1985), loons in this study did not fly food back to the chicks. Other piscivores (e.g., Kittiwakes, Hamer *et al.* 1993) fly further away from nesting colonies and spend more time feeding and away from chicks when prey abundance is low than when it is high. It appears that the highly productive lakes in Alberta can have a sufficient prey base that allows adults to remain on the natal lakes through most of the breeding season. However, in years where sufficient prey abundances do not exist, adult loons may abandon chicks (Chapter 4), perhaps to forage elsewhere.

Similar to many other studies (Strong 1985, Evers 1994, Barr 1996, Ford and Gieg 1995), loons on these small lakes allocated much of their time to foraging. How much time loons spend foraging on lakes in Alberta is not dependent on whether they are foraging primarily for fish or primarily on invertebrates. Cairns (1987) suggested that the amount of time spent foraging is influenced by prey abundance but is constrained by the time needed for other behaviors. Many studies (e.g., Common Murres, Burger and Piatt 1990; Kittiwakes, Hamer *et al.* 1993) have reported increases in the percentage of time spent foraging when abundance of preferred prey declines. Similar time budgets of loons on the two lake types indicates that the loons either could not adjust time budgets or that the loons did not need to adjust time budgets, i.e., adult loons were able exploit invertebrates effectively and that invertebrates were in large enough quantities to provide sufficient food biomass for the adults. Similarities between the percentage of successful dives by loons on Minnow Lakes and by loons on Fishless Lakes, suggests that invertebrates were as easy to find and catch as minnows (although the actual diet of adult loons on Minnow Lakes is unknown, fish are the main component of the chicks'; Chapter 3).

Adult loons foraging presumably for fish on Minnow Lakes dove less frequently and spent more time underwater per dive than loons foraging solely for invertebrates. Dive duration is related to the amount of time spent traveling, searching and pursing prey but is constrained by the physiological capacity to remain underwater. Dive rates are negatively related to dive durations (Ydenberg and Forbes 1988) but may also be influenced by prey quality. Thus, loons foraging for invertebrates, a food source that perhaps is easier to find, pursue and consume, spend less time underwater per dive than loons foraging for fish which are presumably more difficult to catch and handle. Loons on Minnow Lakes may spend more time underwater consuming aggregated prey items such as schooling minnows than loons in Fishless Lakes that may exploit solitary invertebrates. At the same time, invertebrates, such as leeches (e.g., *Nephelposis obscura*, a common leech found in many of the study lakes, unpubl. data) are of higher energetic content (5344 cal/g, Driver 1981) than a fathead minnow (1072 cal/g, Bryan *et al.* 1996), but may provide less energy per dive as even a large leech (e.g., 0.5 g, Davies and Everett 1976) weighs less than an average fathead minnow (4.3 g, Price *et al.* 1991). Therefore, loons foraging for invertebrates have to eat more prey items and consequently dive more frequently than loons foraging on fish to meet their caloric requirements.

Are adult loons on small Fishless and Minnow Lakes able to meet their daily energetic requirements? Barr (1996) suggests that adult loons need approximately 960 g of food/day. Assuming that Barr (1996) meant 960 g of fish/day, adult loons on Minnow Lakes would need to consume at least 223 fathead minnows (of average weight) per/day. The average dive rate of adult loons on Minnow Lakes was 1.264 dives/min or 75 dives per/h. If we assume that at least 50% of those dives are successful (a conservative assumption based on the dive success of loons found in this study), and that one prey item was eaten per dive, then an adult loon could eat 38 minnows/h. Adult loons on Minnow Lakes would need to forage for 6 hours in order to meet their daily food requirements. This estimate was calculated assuming that loons were only eating fish and that fish were abundant in the lake. However, there are occasions when fish densities in the lakes are low and adult loons probably have to supplement their diet with invertebrates. For example, mark-recapture studies done on Beaver Pond in May 1994 and 1995 indicated that fish were not in sufficient quantities (2407 and 3133 fish respectively, Tonn unpubl.) to feed 2 adult loons for 4 months.

Loons foraging for invertebrates may require less prey biomass to meet their daily requirements. For example, 960 g of minnows equates to 1.029 x 10^6 calories which equates to approximately 193 g of leeches or 551 average sized leeches (0.35 g, Davies and Everett 1976) leeches per day (leeches are used as representative invertebrates because they were found to be the main component of chicks on Fishless Lakes, Chapter 3). The average dive rate of adult loons on Fishless Lakes was 1.432 dives/min or 96 dives/h or 48 large leeches/h (based on a 50% dive success rate and one prey item eaten per dive). Adult loons on Fishless Lakes would need to forage for 11 h/day in order to meet their daily food requirements. Based on these estimates, it is possible that adult loons foraging on Fishless Lakes may have been able to meet their daily energy requirements, but they would have had work harder (in terms of hours spent foraging) than loons on Minnow Lakes. In addition, these rates are calculated assuming that the loons are choosing large macroinvertebrates and that these large macroinvertebrates are abundant. Thus, I may be overestimating the amount of energy gained per dive and underestimating the amount of hours per day loons would have to forage in order to meet their daily energy requirements.

It is important to note that the foraging patterns (time spent foraging, dive durations, and dive rates) of adults on some of the Minnow Lakes were similar to the foraging patterns of adults on Fishless Lakes (e.g. Tempo and Little Buck lakes). This may reflect the fact that although fish make up the largest component of the diet of loons on Minnow Lakes (as indicated by food fed to chicks, Chapter 3), invertebrates are also a large component of their diet. Differences in the diet of loons on the Fishless Lakes may explain why the foraging patterns of adults on the individual lakes differed. For example, although leeches were found to be the largest component of the chick's diet on both Tempo and Joseph Lakes, leeches made up a larger proportion of the chick's diet on Tempo Lake than on Joseph Lake and a larger percentage of small, unidentified invertebrates and vegetation were fed to chicks on Joseph Lake (Chapter 3). This probably reflects differences in abundance of invertebrate species within these lakes as sweep-net samples taken in 1994 and 1995 indicated that leeches were more abundant in Tempo Lake than in Joseph Lake (unpubl. data). Differences in diet may explain differences between the dive patterns of loons on Tempo Lake and Joseph Lake; dives by loons on Joseph Lake were of shorter duration and more frequent than that by loons on Tempo Lake.

As was observed by Evers (1994) in Michigan, on average female and male loons on the small lakes in Alberta spend a similar amount of time foraging per observation period. However, unlike males, females tend to either spend no time foraging or spend all their time foraging per observation period. In addition, when females are foraging they dive more frequently and their dives are shorter in duration than males. This suggests that because females spend less time foraging, perhaps because they spend more time incubating, they must compensate by diving for food more frequently and spending less time underwater per dive. Alternatively, it could suggest that females were foraging for different prey items than males.

Male Western Grebes (*Aechmophorus occidentalis*) are larger than females and forage for larger fish (Forbes and Sealy 1990). Male South Georgian Shags are also larger than females and spend, on average, longer underwater per dive than females (Wanless *et al.* 1995). Wanless *et al.* (1995) suggested that differences in prey size or composition may be responsible for differences in dive duration. The size difference between male and female loons may result in differences in diet and thus differences in foraging behavior. Barr (1996) found in Ontario that crayfish and minnows were more common in female than male loon stomachs and that perch, sucker, and char (e.g. brook trout, *Salvelinus fontinalis* and lake trout, *S. namaycush*) were more common in male than female loon stomachs. Thus, female loons in Alberta may be diving for slower moving prey such as invertebrates and younger and smaller fish that are easier to catch but lower in total caloric content. Females loons may therefore spend less time underwater pursing and handling prey than males. Further studies are needed to determine the diets of adult loons.

Loons also forage differently depending on the stage in the reproductive cycle. As observed by Evers (1994) and Barr (1996), prenesting loons spent much of their time foraging, more so than at any other stage in the breeding period. Prenesting loons perhaps foraged more because they did not have to spend time nesting or caring for chicks and could thus build up energy reserves that were lost during spring migration and that were needed for laying and incubating eggs. When nesting, the percentage of time loons spent foraging decreased. When the chicks hatched, adult loons increased the amount of time they foraged but not to the level as when they first arrived to the lakes. Barr (1996) observed a similar behavioral pattern of a decrease in the time spent foraging in the nesting period followed by an increase in the postnesting period. Evers (1994) observed a steady decrease in the time spent foraging by adults during the breeding season and did not report an increase in foraging in the postnesting period. However, he did not include time spent feeding the chicks in his analysis and this time may account for the differences between our results.

Dive rates increased and dive durations decreased during the breeding season. Dive durations may have decreased in response to seasonal availability of prey. As was found by Mittelbach (1981) in a small lake in Michigan, large macroinvertebrate abundance decreased in the study lakes as the breeding season progressed (unpubl. data). In addition, the size distribution of minnows and stickleback also changes during the season as the older and larger adults die and are "replaced" by younger and smaller juveniles (Price *et al.* 1991). Smaller prey may have resulted in shorter dive durations and thus greater dive rates and may explain the increase in time spent foraging in the postnesting stage.

However, the time spent foraging, dive duration, and dive rates did not change as the chicks aged. If the availability of larger prey was decreasing over the breeding period, the dive durations should have continued to decrease and dive rates should have continued to increase. In addition, it was expected that dive rates would increase as chicks grow and their demand for food increases. Emms and Verbeek (1991) found that the provisioning rates of Pigeon Guillemots (*Cepphus columba*) increased as chicks matured and then declined in the later stages of the nestling period. It was expected that loons would behave in a similar manner; loon chick demand for food increases as the chicks age (Barr 1996) and thus parents should have responded by diving more frequently in order to satiate chicks. The lack of change in the foraging patterns of loons suggests that adult loons: 1) were already at their maximum dive rates and could not increase the number of times they dove per minute or; 2) were feeding younger chicks enough food to satiate the chicks and did not have to increase the amount of food given to chicks; or 3) provisioned chicks more frequently but did not dive more frequently as chicks matured (i.e. increased the number of dives devoted to the procurement of chick food and decrease the number of dives devoted to the procurement of food for themselves, see Chapter 3 for related discussion).

The foraging behavior of Common Loons on small lakes in Alberta is influenced by the prey composition within the nesting lake, the sex of the loon, and the breeding period. Foraging behavior of adult Common Loons appears to be flexible to an extent. Dive durations of adult Common Loons are influenced by the prey base exploited and dive rates can be adjusted in turn. Dive durations of loons foraging for invertebrates are shorter but dive rates are greater. Invertebrates, such as leeches, offer less calories per dive than fish and as a result loons on Fishless Lakes must dive more frequently than loons on Minnow Lakes to insure that their energy requirements are met.

Thus, it appears that adult Common Loons, like some other piscivores, have the ability to behaviorally compensate for differences in prey composition in order to meet their own daily energy requirements (they may not be able to meet their chicks daily requirements; Chapters 3 & 4). This study also indicates that it is important to recognize that changes in preferred prey abundance may result in prey switching and that differences in prey composition may influence behavior. Therefore, if differences exist between the behavior of birds during periods of suspected low preferred prey abundance and periods of adequate prey abundance, it can not be assumed that the differences in behavior are a result of the changes to preferred prey abundance alone. Alternative prey may be abundant but may be of less caloric value and may require different foraging strategies than preferred prey and as a result behavioral changes may not reflect absolute prey abundance per se but prey composition or availability.

Foraging behavior also differs between the sexes and between stages during the breeding cycle. Thus, it is important to keep these differences in mind when studying foraging behavior. The foraging behavior of males of a species may not be representative of the foraging behaviors of females. Changes in prey base may have differential effects on the sexes. In addition, the behavior of birds at one stage in their breeding cycle may not adequately reflect the behavior of birds during other stages in their breeding cycle. Also, changes in prey base may have differential effects depending on the stage of the breeding cycle.

2.5 Literature Cited

Alvo, R., Hussell, D. J. T. and M. Berrill. 1988. The breeding success of common loons (*Gavia immer*) in relation to alkalinity and other lake characteristics in Ontario. Canadian Journal of Zoology 66:746-752.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21:224-235.

Barr, J. F. 1973. Feeding biology of the Common Loon (*Gavia immer*) in oligotrophic lakes of the Canadian Shield. Ph. D. thesis. University of Guelph, Ontario.

Barr, J. F. 1986. Population dynamics of the Common Loon (*Gavia immer*) associated with mercury contaminated waters in northwestern Ontario. Canadian Wildlife Service Occasional Paper No. 56.

Barr, J. F. 1996. Aspects of Common Loons (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321:119-144.

Blair, R. B. 1992. Lake features, water quality and the summer distribution of Common Loons in New Hampshire. Journal of Field Ornithology 63:1-9.

Bost, C.A., Puetz, K., and J. Lage. 1994. Maximum diving depth and diving patterns of the gentoo penguin *Pygoscelis papua* at the Crozet Islands. Marine Ornithology 22:237-244.

Bryan, S. D., Soupir, C. A., Duffy, W. G., and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology 111:153-161.

Bukacinska, M., Bukacinska, B., and A. Spaans. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). Auk 113:300-309.

Burger, A. E. and J. F. Piatt. 1990. Flexible time budgets in Common Murres: Buffers against variable prey abundances. Studies in Avian Biology 14:71-83.

Burger, J. 1986. Effects of Age on Foraging in Birds. *In* Acta XIX Congressus Internatalis Ornithologicus. Ed. Henri Ouellet pp 1128-1139.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5:261-271.

Christoff, M. 1979. A study of the early chick rearing period of the Common Loons (*Gavia immer*). From: McIntyre, J. 1988. The Common Loon. University of Minnesota Press. Minneapolis.

Crawford R. J. M. and B. M. Dyer 1995. Responses of four seabirds to fluctuating availability of Cape anchovy *Engraulis capensis* of South America. IBIS 137:329-339.

Davies, R. W. and R. P. Everett. 1976. The life history, growth, and age structure of *Nephelopsis obscura* Verrill, 1872 (Hirudinoidea) in Alberta. Canadian Journal of Zoology 55:620-627.

Driver E. A. 1981. Calorific values of pond invertebrates eaten by ducks. Freshwater Biology 11:579-581.

Emms, S. K. and N. A. M. Verbeek. 1991. Brood size, food provisioning and chick growth in the pigeon guillemot *Cepphus columba.* Condor 93:943-951.

Eriksson, M. O. G. 1985. Prey detectablility for fish-eating birds in relation to fish density and water transparency. Ornis Scandinavica 16:1-7.

Evers, D. C. 1994. Activity budgets of a marked Common Loon (*Gavia immer*) nesting population. In: Kerekes, J. J.(ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:415-420.

Findholt, S. L. and S. H. Anderson. 1995. Foraging areas and feeding habitat selection of the American White Pelican (*Pelecanus erythrorhynchos*) nesting at Pathfinder Reservoir, Wyoming. Colonial Waterbirds 18:47-57.

Forbes, L. S. and S. G. Sealy. 1990. Foraging roles of male and female western grebes during brood rearing. Condor 92:421-426.

Ford, T. B. and J. A. Gieg. 1995. Winter behavior of the Common Loon. Journal of Field Ornithology 66:22-29.

Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P. and M. D.Burns. 1993. The influence of food supply on the breeding ecology of Kittiwakes Rissa tridactyla in Shetland. IBIS 135:255-263.

Kerekes, J. J. 1990. Possible correlation of summer common loon (*Gavia immer*) population with the trophic state of a water body. Internat. Verein. Limnol. 24: 349-353.

Kerekes, J. J., Duggan, M., Tordan, R., Boros, G., and M. Bronkhorst. 1996. Abundance and distribution of fish-eating birds in Kejimkujik National Park 1988-1995. Lake and Reservoir Management 11:156.

McIntyre, J. 1988. The Common Loon. University of Minnesota Press. Minneapolis.

McIntyre, J. 1994. Loons in freshwater lakes. In: Kerekes, J. J.(eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes.. Hydrobiologia 279/280:373-413.

Mittelbach, G. G. 1981. Patterns of invertebrate size and abundance in aquatic habitats. Canadian Journal of Fisheries and Aquatic Sciences 38:896-904.

Monaghan, P., Walton, P., Wanless, S., Uttley, J. D. and M. D. Burns. 1994. Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. IBIS 136:214-222.

Morrison, M. L., Slack, R. D., and E. Shanley Jr. 1978. Age and the foraging ability relationships of olivaceous cormorants. Wilson Bulletin 90:414-422.

Munro, J. A. 1945. Observations of the loon in the Cariboo Parklands, British Columbia. Auk 62: 38-49.

Obst, B. S., Russell, R. W., Hunt, G. L. Jr., Eppley, Z. A., and N. M. Harrison. 1995. Foraging radii and energetics of Least Auklets (*Aethia pusilla*) breeding on three Bering Sea islands. Physiological Zoology 68:647-672.

Parker, K. E. 1985. Observations of a flying Common Loon carrying a fish. Journal of Field Ornithology 56:412-413.

Parker, K. E. 1988. Common loon reproductive and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66:804-810.

Paszkowski, C. A. 1994. Factors affecting aquatic bird assemblages in central Alberta. Proceedings of the 3rd Annual Alberta Lake Management Society 15-19.

Prepas, E. E., M. E. Dunnigan, and A. M. Trimbee. 1988. Comparison of in situ estimates of chlorophyll a obtained with Whatman GF/F and GF/C glass-fiber filters in mesotrophic and hypereutrophic lakes. Journal of Fisheries and Aquatic Sciences 45:910-914.

Price, C. J., Tonn, W. M., and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. Canadian Journal of Zoology 69:2109-2115.

Reimchen, T. E and S. Douglas. 1984. Feeding schedule and daily food consumption in Red-throated Loons (*Gavia stellata*) over the prefledging period. Auk 101:593-599.

Reimchen, T.E and S. D. Douglas. 1985. Differential contribution of the sexes to prefledged young in Red-throated Loons. Auk 102:198-201.

Robinson, C. L. K. and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:81-89.

Rodriguez-Robles, J. A. and M. Leal. 1993. Effects of prey type on feeding behavior of *Alsophis portoricensis* (Serpentes: Colubridea). Journal of Herpetology 27:163-169.

Rubega, M. and C. Inouye. 1994. Prey switching in Red-necked phalaropes *Phalaropus lobatus*: Feeding limitations, the functional response, and water management at Mono Lake, California, USA. Biological Conservation 70:205-210.

Salamolard, M. and H. Weimerskirch. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wander albatross. Functional Ecology 7:643-652.

Strong, P. I. V. 1985. Habitat selection by Common Loons. Phd thesis. University of Maine, Ornono.

Ulenaers, P., J. Van Vessem, and A. Dhondt. 1992. Foraging of the great crested grebe in relation to food supply. Journal of Animal Ecology 61:659-667.

Wanless, S. and M. P. Harris. 1992. Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145-154.

Wanless, S., Harris, M. P. and J. A. Morris. 1995. Factors affecting daily activity budgets of South Georgian Shags during chick rearing at Bird Island, South Georgia. Condor 97:550-558.

Wayland, M. and D. K. McNicol. 1990. Status report on the effects of acid precipitation on common loon reproduction in Ontario: The Ontario Lakes Loons Survey Technical Report Series No. 92. C. W. S., Ontario region.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Company. Toronto.

Ydenberg, R. C. 1986. Foraging by diving birds. *In* Acta XIX Congressus Internatalis Ornithologicus. Ed. Henri Ouellet pp 1832-1843.

Ydenberg, R. C. and L. S. Forbes. 1988. Diving and Foraging in the Western Grebe. Ornis Scandinavica 19:129-133.

Yonge, K. S. 1981. The breeding cycle and annual production of the Common Loon (*Gavia immer*) in the boreal forest region. MS thesis, University of Mantioba, Winnipeg, 141pp.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. New Jersey.

Table 2-1. Results from Mann-Whitney U tests comparing the proportion of time spent on the study lakes by loons on Fishless and Minnow Lakes and by adult male and female loons, and from Kruskal-Wallis One-Way ANOVA tests comparing loons during the prenesting, nesting, and post nesting breeding periods. N = the number of observations. U = the Mann-Whitney U test statistic. H = the Kruskal-Wallis test statistic. Degrees of freedom for Mann-Whitney U tests = 1. Degrees of freedom for Kruskal-Wallis tests = 2. p = the probability.

		1994			1995	
	N	U	p	N	U	p
Fishless vs Minnow	22	60	1.000	32	103.5	0.566
Male vs Female	22	66	0.623	32	146.5	0.000*
	N	H	p	N	H	p
Breeding Period	18	12.645	0.000*	24	8.919	0.012*

* significant differences

Table 2-2. Results from Mann-Whitney U tests comparing the percentage of time spent foraging per observation period by loons on each study lake in 1995. N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

	Lake	1994 Beaver N	U	p	Bobier N	U	p	Tawatinaw N	U	p	Joseph N	U	p
Minnow	Beaver												
	Bobier	51	162.000	0.794									
	Tawatinaw	51	207.000	0.362	16	38.000	0.528						
Fishless	Joseph	80	825.000	0.774	45	155.000	0.835	45	183.000	0.298			
	Tempo	92	1256.500	0.108	57	251.000	0.202	57	172.000	0.578	86	722.500	0.106

	Lake	1995 Beaver N	U	p	Mystic N	U	p	Two Island N	U	p	West Baptiste N	U	p	Joseph N	U	p	Little Buck N	U	p	Shumaker N	U	p
Minnow	Beaver																					
	Mystic	94	1293.000	0.149																		
	Two Island	60	336.000	0.184	56	270.000	0.642															
	West Baptiste	54	114.000	0.800	50	85.000	0.374	14	17.000	0.234												
Fishless	Joseph	76	677.000	0.866	72	674.000	0.438	38	177.000	0.356	32	65.000	0.896									
	Little Buck	59	171.000	0.134	55	118.500	0.020*	21	83.000	0.048*	15	31.000	0.462	37	102.000	0.255						
	Shumaker	76	870.000	0.023*	72	755.500	0.050	38	124.000	0.425	32	38.000	0.122	54	469.000	0.067	37	64.500	0.015*			
	Tempo	91	1453.000	0.001*	87	656.000	0.014*	53	193.000	0.400	47	52.000	0.065	69	383.000	0.022*	52	76.000	0.002*	69	578.000	0.891

* significant differences

Table 2-3. Calculated probabilities of Two-Sample Kolmogorov-Smirnov tests comparing the cumulative percentage of time spent foraging, dive rate (dive/min), and mean dive duration (s) frequencies of loons on Minnow and Fishless Lakes, male and female loons, and loons in the prenesting, nesting, and postnesting breeding periods in 1994 and 1995.

	1994			1995		
Test	% Foraging	Dive rate	Dive Duration	% Foraging	Dive rate	Dive Duration
Minnow vs Fishless Lakes	0.313	0.032*	0.061	0.009*	0.016*	0.007*
Males vs Females	0.221	0.170	0.274	0.447	0.001*	0.003*
Breeding Periods:						
Prenesting vs Nesting	0.000*	0.025*	0.001*	0.000*	0.000*	0.001*
Nesting vs Postnesting	0.000*	0.003*	0.177	0.302	0.114	0.272
Prenesting vs Posnesting	0.391	0.000*	0.000*	0.143	0.000*	0.000*

* significant differences

Table 2-4. Results from Mann-Whitney U tests comparing the dive rate (dive/min) per observation by loons on each study lake in 1994 and 1995. N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

		1994											
	Lake	Beaver			Bobier			Tawatinaw			Joseph		
		N	U	p	N	U	p	N	U	p	N	U	p
Minnow	Beaver												
	Bobier	42	121.000	0.631									
	Tawatinaw	41	173.000	0.061	15	48.000	0.021*						
Fishless	Joseph	64	290.000	0.003*	38	65.000	0.049*	37	195.000	0.000*			
	Tempo	65	572.000	0.554	39	148.000	0.404	38	143.000	0.194	61	217.000	0.000*

		1995																				
	Lake	Beaver			Mystic			Two Island			West Baptiste			Joseph			Little Buck			Shumaker		
		N	U	p	N	U	p	N	U	p	N	U	p	N	U	p	N	U	p	N	U	p
Minnow	Beaver																					
	Mystic	82	1293.000	0.149																		
	Two Island	51	220.000	0.444	49	246.000	0.088															
	West Baptiste	47	78.000	0.352	45	80.000	0.470	14	8.000	0.053												
Fishless	Joseph	61	186.000	0.001*	59	682.000	0.000*	28	167.000	0.000*	24	75.000	0.051									
	Little Buck	51	186.000	1.000	49	196.000	0.680	18	52.000	0.310	14	14.000	0.257	28	161.000	0.000*						
	Shumaker	57	257.000	0.293	55	224.000	0.151	24	100.000	0.053	20	30.000	0.896	34	193.000	0.080	24	89.000	0.200			
	Tempo	67	568.000	0.577	65	439.000	0.411	34	117.000	0.861	30	42.000	0.254	44	100.000	0.001*	34	102.000	0.682	40	142.000	0.204

* significant differences

Table 2-5. Results from Mann-Whitney U tests comparing the mean dive duration (s) per observation by loons on each study lake in 1994 and 1995. N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

	Lake	1994 Beaver			Bobier			Tawatinaw			Joseph		
		N	U	p	N	U	p	N	U	p	N	U	p
Minnow	Beaver												
	Bobier	42	166.000	0.336									
	Tawatinaw	42	81.000	0.078	16	11.000	0.027*						
Fishless	Joseph	65	776.500	0.001*	39	175.500	0.073	39	30.500	0.001*			
	Tempo	64	513.500	0.962	38	85.000	0.210	38	68.650	0.065	61	703.000	0.001*

	Lake	1995 Beaver			Mystic			Two Island			West Baptiste			Joseph			Little Buck			Shumaker		
		N	U	p	N	U	p	N	U	p	N	U	p	N	U	p	N	U	p	N	U	p
Minnow	Beaver																					
	Mystic	81	837.000	0.865																		
	Two Island	51	152.500	0.367	48	109.500	0.080															
	West Baptiste	47	128.500	0.417	44	124.000	0.326	14	34.000	0.124												
Fishless	Joseph	61	602.000	0.002*	58	207.000	0.000*	28	12.000	0.000*	24	24.500	0.101									
	Little Buck	51	168.000	0.604	48	145.500	0.426	18	31.000	0.399	14	31.000	0.255	28	5.500	0.000*						
	Shumaker	58	460.000	0.031*	55	527.500	0.000*	25	17.500	0.002*	21	24.000	0.185	35	123.500	0.344	25	13.000	0.001*			
	Tempo	68	516.500	0.709	65	602.500	0.200	35	108.500	0.748	31	89.000	0.196	45	391.000	0.001*	35	122.500	0.835	42	312.000	0.007*

* significant differences

Table 2-6. Results from Mann-Whitney U tests comparing the percentage of time spent foraging, dive rate (dive/min), and mean dive duration (s) per observation period of male and female loons on each study lake in 1994 and 1995. N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

	% Foraging			Dive Rate			Dive Duration		
Lake	N	U	p	N	U	p	N	U	p
				1994					
Minnow Lakes									
Beaver	43	248.500	0.649	34	97.000	0.105	34	194.500	0.081
Bobier	8	11.500	0.309	8	4.000	0.248	8	11.500	0.309
Tawatinaw	8	8.000	1.000	7	11.000	0.077	8	5.000	0.381
Fishless Lakes									
Joseph	37	117.000	0.105	30	74.000	0.110	31	126.500	0.797
Tempo	49	334.000	0.491	31	135.000	0.471	30	103.000	0.832
				1995					
Minnow Lakes									
Beaver	49	396.500	0.053	42	87.000	0.001*	42	362.500	0.000*
Mystic	45	212.000	0.385	40	173.000	0.497	39	232.500	0.219
Two Island	11	16.000	0.705	9	10.000	1.000	9	7.500	0.539
West Baptiste	5	5.000	0.248	5	2.000	0.564	5	4.000	0.564
Fishless Lakes									
Joseph	27	98.500	0.713	19	34.000	0.364	19	54.000	0.406
Little Buck	10	17.000	0.285	9	1.000	0.039*	9	17.000	0.037*
Shumaker	27	90.000	0.961	15	27.000	0.908	16	38.500	0.493
Tempo	42	184.000	0.411	25	45.000	0.096	26	108.000	0.185

* significant differences

Table 2-7. Results from Kruskal-Wallis One-Way ANOVA tests comparing the percentage of time spent foraging, dive rate (dive/min), and mean dive duration (s) per observation of each individual adult loon on the study lakes during the prenesting, nesting, and postnesting breeding periods in 1994 and 1995. N = the number of observations. H = the Kruskal-Wallis test statistic. p = the probability. Degrees of freedom for all tests = 2.

		% Foraging			Dive Rate			Dive Duration		
Lake	Sex	N	H	p	N	H	p	N	H	p
					1994					
Minnow Lakes										
Beaver	Male	20	8.588	0.014*	19	5.448	0.066	19	4.682	0.096
	Female	23	10.262	0.006*	15	4.937	0.085	16	7.426	0.024*
Fishless Lakes										
Joseph	Male	17	0.635	0.728	15	10.110	0.006*	15	9.220	0.010*
	Female	20	4.622	0.099	15	7.620	0.022*	17	10.929	0.004*
Tempo	Male	24	2.364	0.307	18	7.691	0.021*	18	6.425	0.040*
	Female	25	15.482	0.000*	13	4.038	0.133	12	3.397	0.183
					1995					
Minnow Lakes										
Beaver	Male	24	1.738	0.419	23	8.165	0.017*	22	13.689	0.001*
	Female	25	7.594	0.022*	19	9.513	0.009*	19	11.127	0.004*
Fishless Lakes										
Joseph	Male	13	17.500**	0.667	8	0.000**	0.025*	8	15.000**	0.021*
	Female	14	2.007	0.367	11	0.000**	0.014*	11	24.00**	0.014*
Shumaker	Male	14	2.867	0.238	7	1.571	0.456	8	2.386	0.303
	Female	13	3.086	0.214	8	5.125	0.077	8	4.500	0.105
Tempo	Male	18	1.182	0.554	10	6.955	0.031*	10	4.282	0.118
	Female	25	3.529	0.171	16	12.904	0.002*	16	11.110	0.004*

* significant differences

** Mann-Whitney U tests performed as data from postnesting period was not gathered (DF =1).

Table 2-8. Results from Mann-Whitney U tests comparing the percentage of time spent foraging, dive rate (dive/min), and mean dive duration (s) per observation of each individual adult loon when chicks are 1-35 days old and 35+ days old on the study lakes in 1994 and 1995. N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

		% Foraging			Dive Rate			Dive Duration		
Lake	Sex	N	U	p	N	U	p	N	U	p
					1994					
Minnow Lakes										
Beaver	Male	8	5.000	0.739	7	0.000	0.053	7	10.000	0.053
	Female	10	9.000	0.508	7	4.000	0.480	8	8.500	0.885
Fishless Lakes										
Joseph	Female	8	11.000	0.232	7	2.000	0.157	8	5.500	0.546
Tempo	Female	9	6.000	0.748	6	8.000	0.064	6	4.000	1.000
					1995					
Minnow Lakes										
Beaver	Male	8	5.000	0.456	7	5.000	0.724	6	2.500	0.376
	Female	12	8.500	0.202	11	6.000	0.131	11	15.500	0.774
Fishless Lakes										
Tempo	Female	10	3.500	0.068	7	5.000	1.000	1	1.500	0.171

Table 2-9. Calculated probabilities of Two-Sample Kolmogorov-Smirnov tests comparing the cumulative percentage of successful dives (as defined by the delivery of food to a chick immediately following a dive) per observation period of loons on the study lakes in 1994 and 1995.

	1994	1995
Dive Success:		
Beaver vsTempo	0.200	0.260
Beaver vs Joseph	0.267	-
Tempo vs Joseph	0.267	-
Beaver vs Shumaker	-	0.636
Tempo vs Shumaker	-	0.714

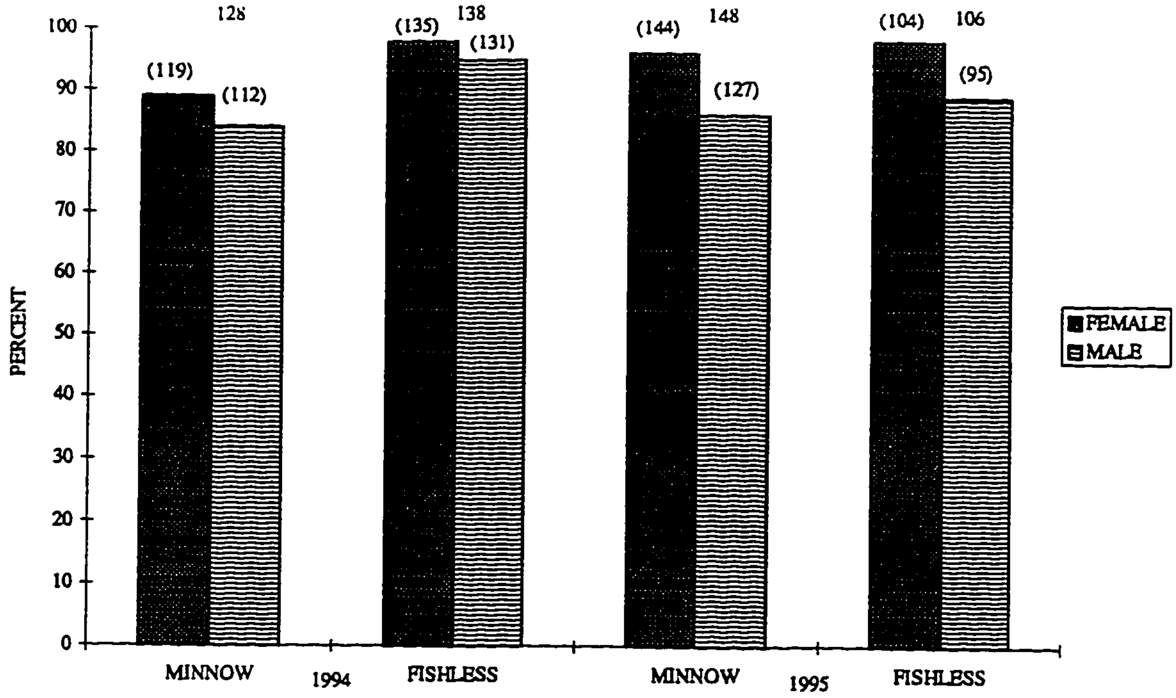

Figure 2-1. The percentage and number (in brackets) of hours loons were present on Minnow and Fishless lakes in 1994 and 1995. The total number of hours visited are also indicated at the top of the figure.

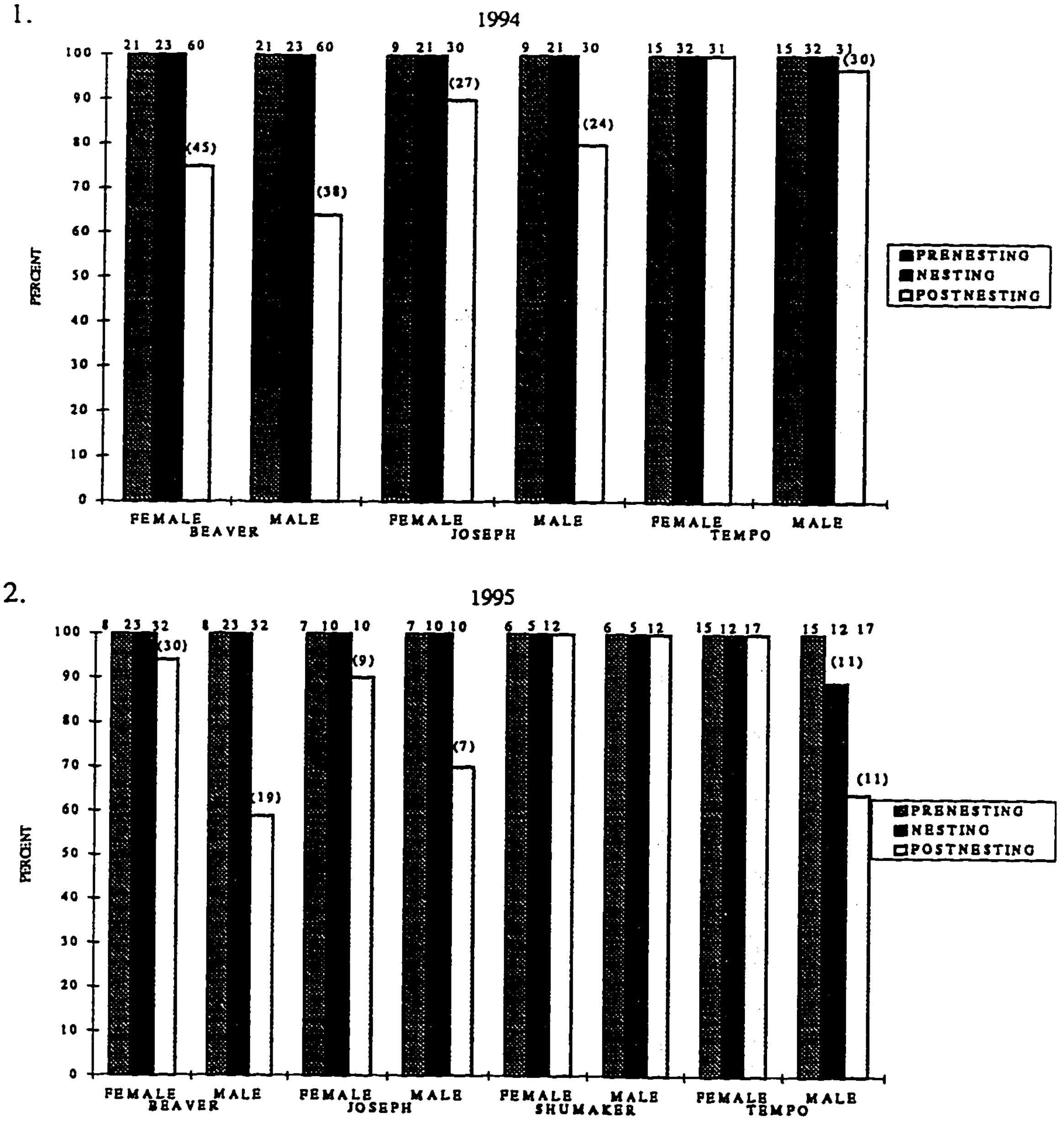

Figure 2-2. The percentage of hours loons were present on lakes during the prenesting, nesting, and postnesting breeding stages in 1994 (1) and 1995 (2). The total number of hours visited and the number of hours loons were present (in brackets) are also indicated on the top of the figures. Beaver is a Minnow Lake, the rest are Fishless Lakes.

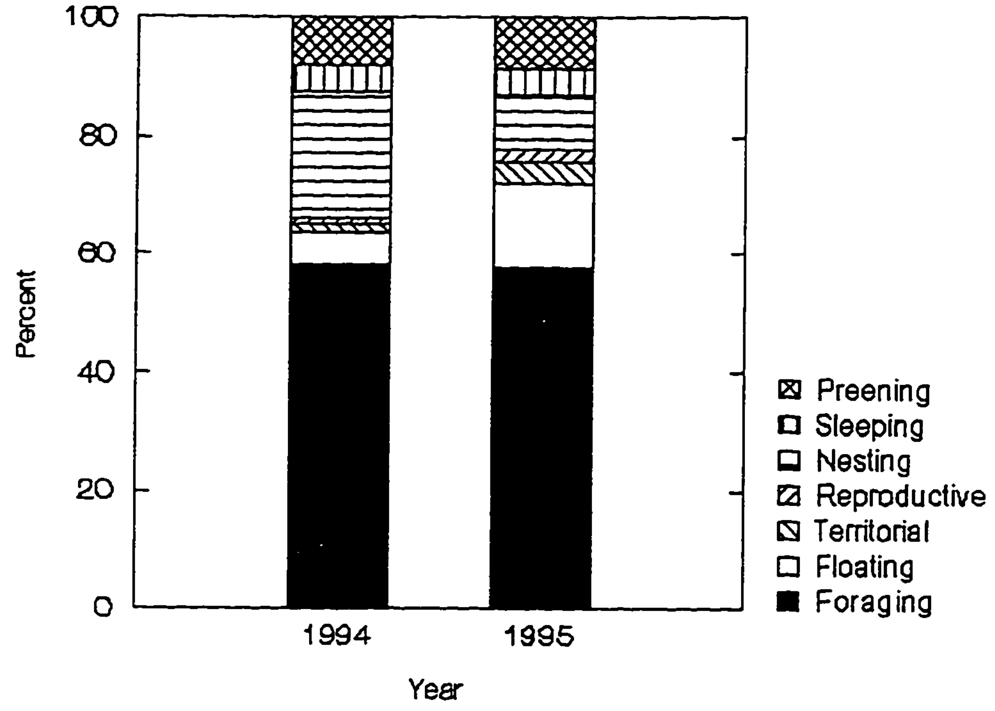

Figure 2-3. The mean percentage of observation time that loons participated in different behaviors during the summers of 1994 and 1995 (based on data collected on all the loons: 10 loons, 145 hours in 1994 and 16 loons, 216 hours in 1995).

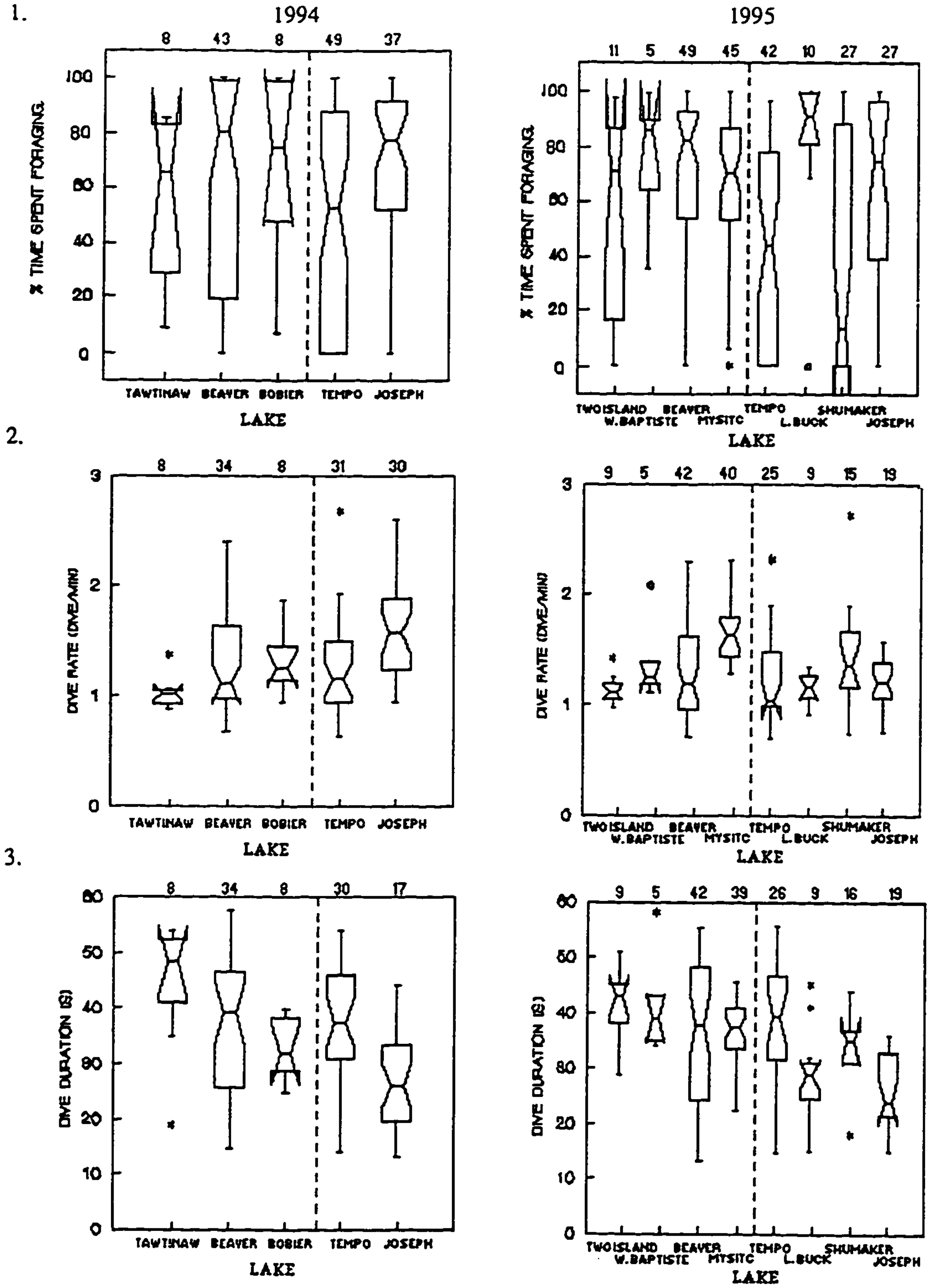

Figure 2-4. Box-whisker plots of the percentage of time spent foraging (1), the dive rate (dive/min) (2), and the mean dive duration (s) (3) per observation period of loons on the study lakes in 1994 and 1995. The box represents the middle 50% of the data, the horizontal line within the box is the median, the extending vertical lines represent the remaining 50% of the data, circles and asterisks represent outliers, and the notches represent 95% confidence intervals. Vertical dashed lines separate Minnow Lakes and Fishless Lakes, respectively. The total number of observations is presented on top of the figure.

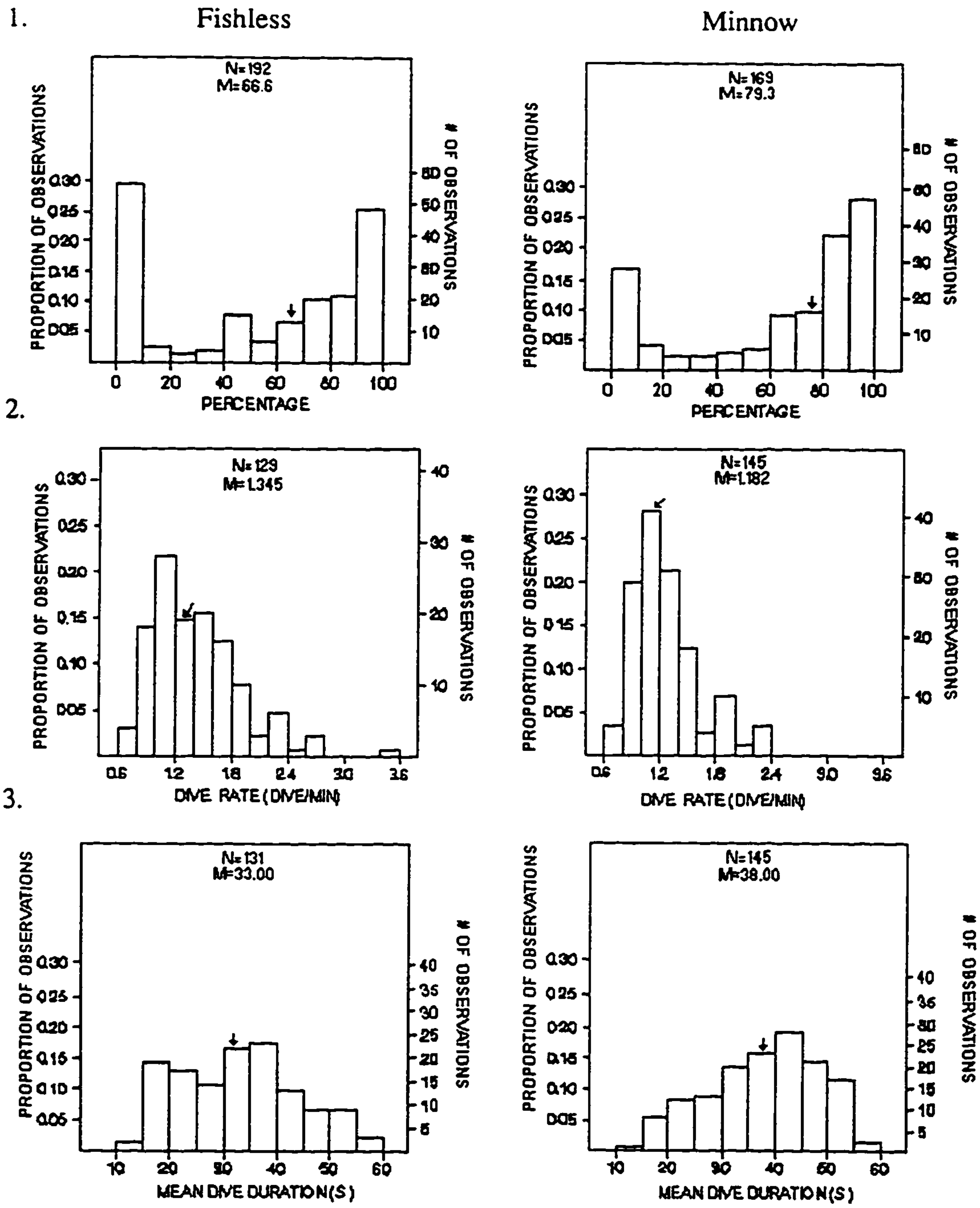

Figure 2-5. Histograms of the percentage of time spent foraging (1), the dive rate (dive/min) (2), and the mean dive duration (s) (3) per observation period by loons on Fishless and Minnow Lakes. N = the total number of observation periods (both years combined). M = the median and the arrows indicate the median.

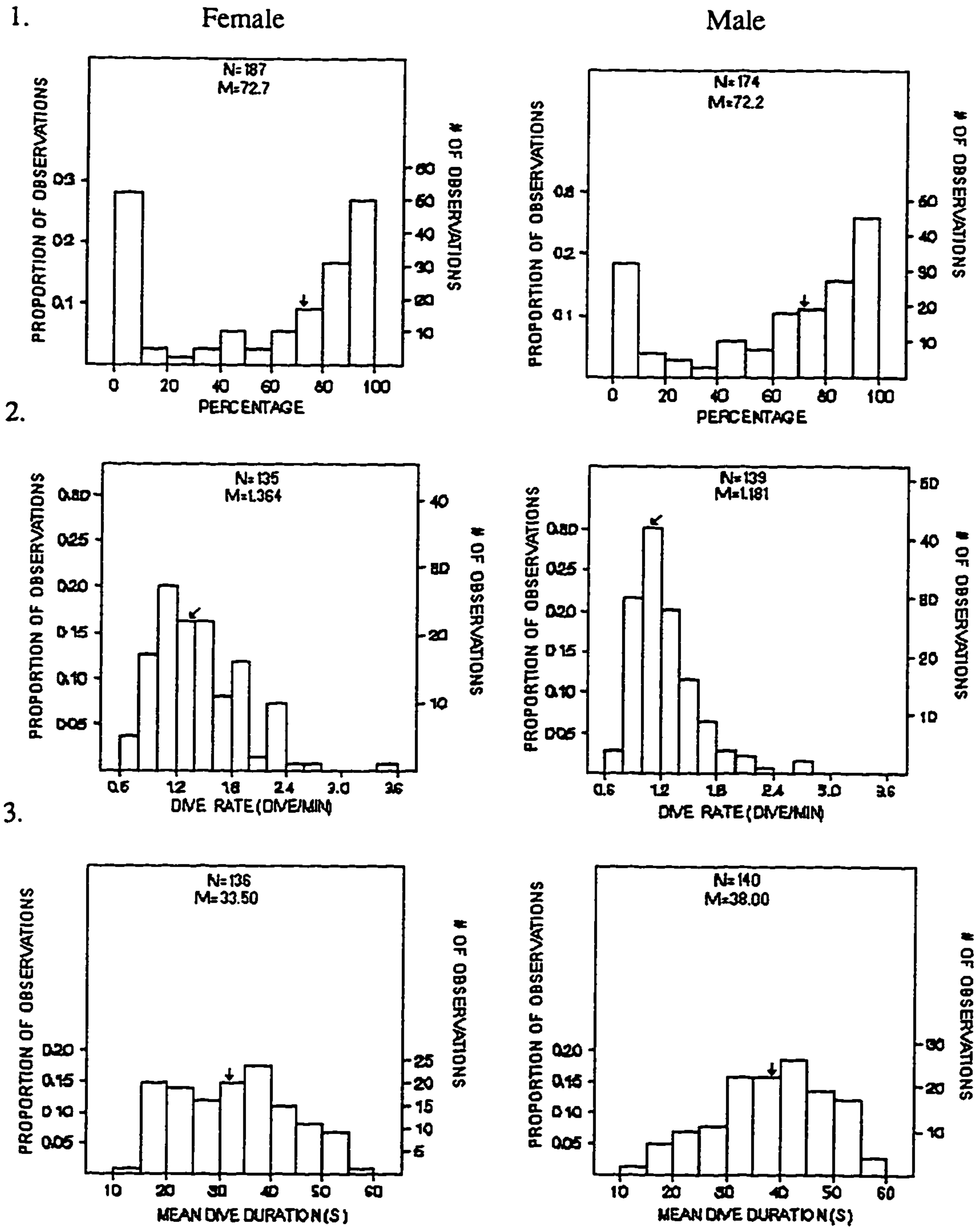

Figure 2-6. The percentage of time spent foraging (1), the dive rate (dive/min) (2), and the mean dive duration (sec) (3) per observation period by adult male and female loons. N= the total number of observations (both years combined). M = the median and the arrows indicate the median.

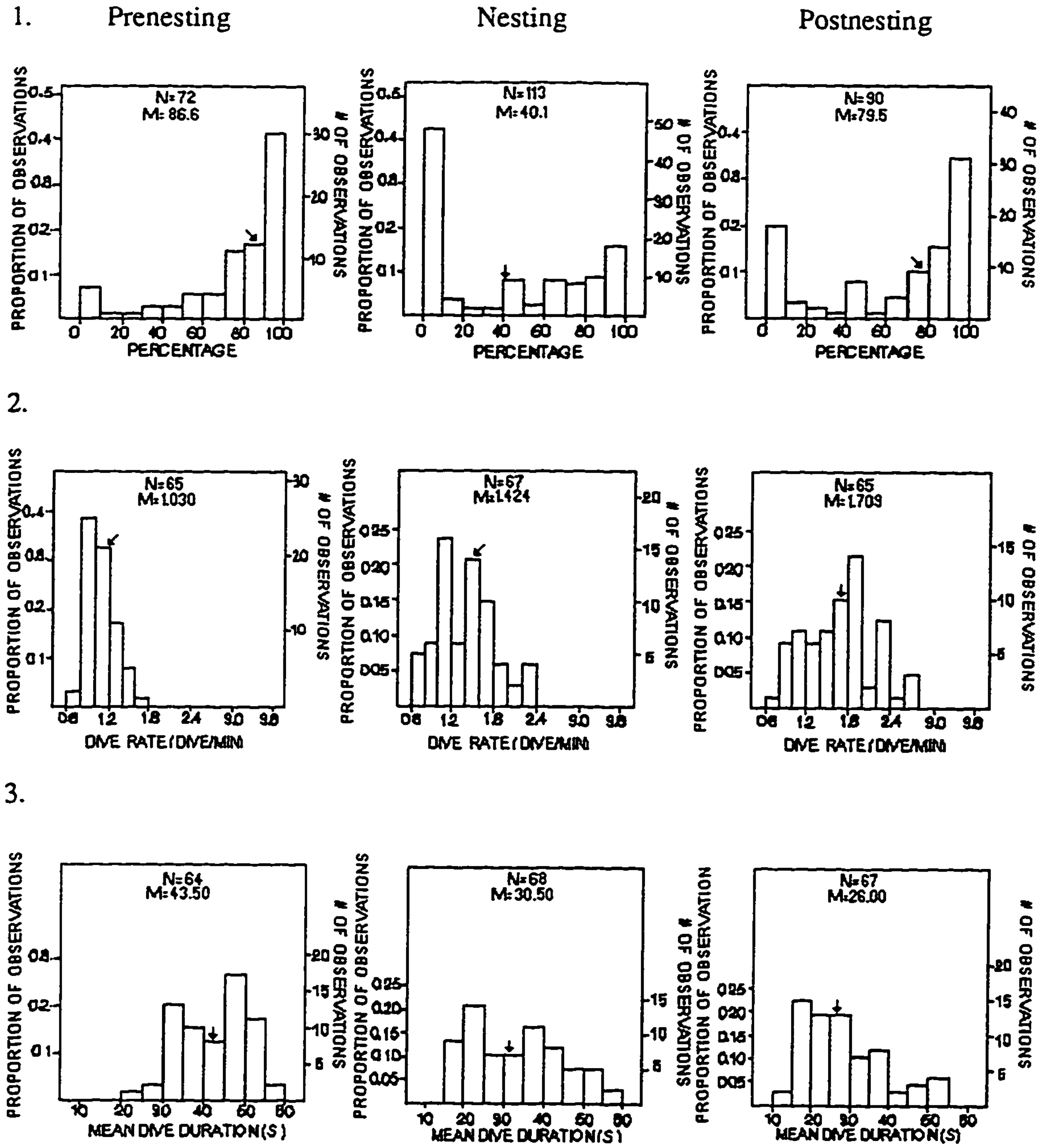

Figure 2-7. The percentage of time spent foraging (1), the dive rate (dive/min) (2), and the mean dive duration (s) (3) per observation by loons during the prenesting, nesting, and postnesting periods of the breeding cycle. N = the total number of observations (both years combined). M = the median and the arrows indicate the median.

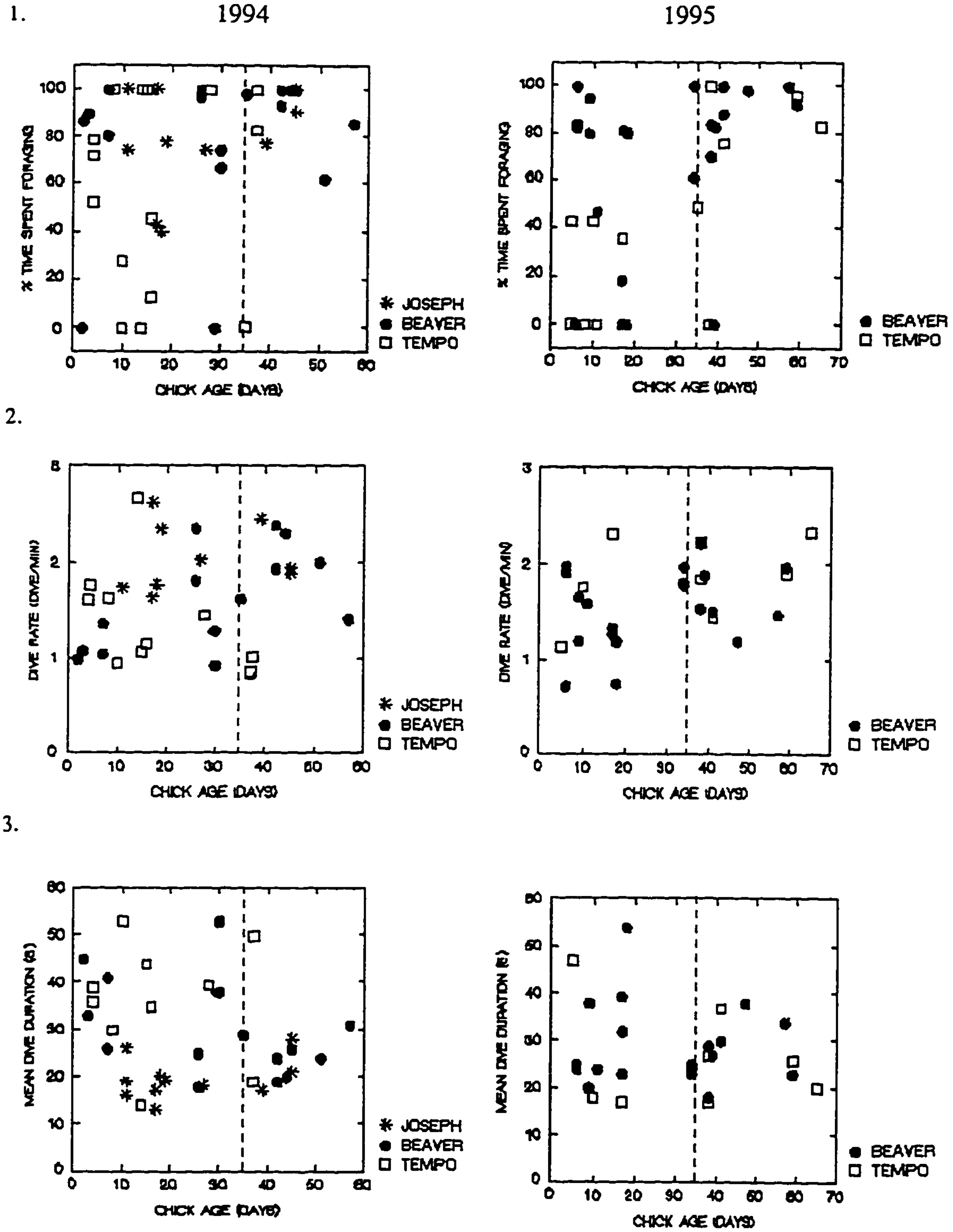

Figure 2-8. The percentage of time spent foraging (1), the dive rate (dive/min) (2), and the mean dive duration (s) (3) per observation period of adult loons on the Beaver Pond, Tempo Lake, and Joseph Lake versus the age of the chicks (days) in 1994 and 1995. The vertical dashed lines indicate chick ages 1-35 days and 36+ days.

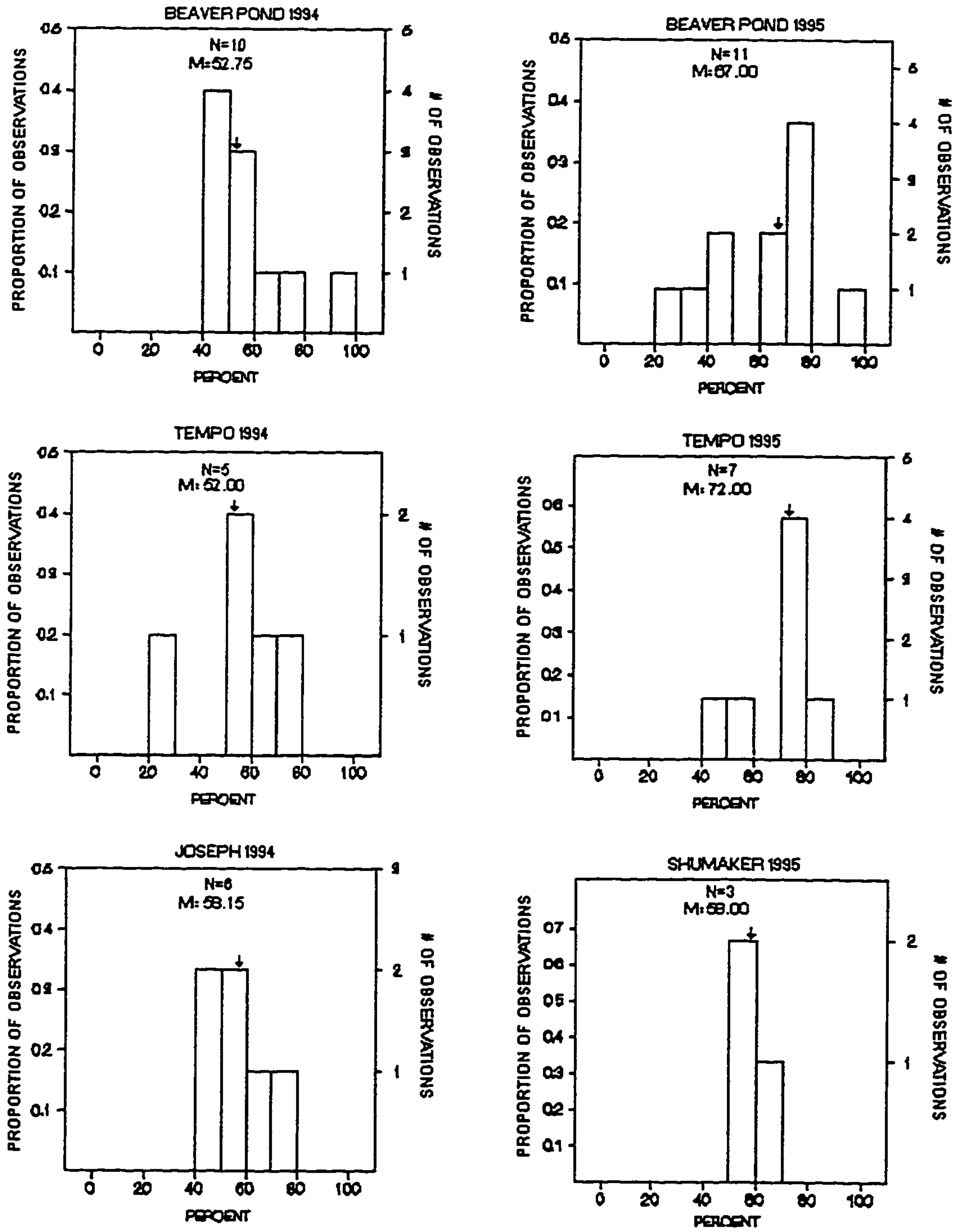

Figure 2-9. The percentage of successful dives (as defined by the delivery of food to a chick immediately following a dive) per observation period by loons on the Beaver Pond, Tempo Lake, and Joseph Lake in 1994 and on the Beaver Pond, Tempo Lake, and Shumaker Lake in 1995. N = the total number of observations. M = the median and the arrows indicate the median.

Appendix 2-1. The location (latitude and longitude), area, maximum depth, and total phosphorus measurements of Fishless Lakes and Minnow Lakes (fathead minnow, *Pimephales promelas*, and/or brook stickleback, *Culaea inconstans*) studied in central Alberta during the summer(s) of 1994 and/or 1995.

Lake	Location	Year	Fish Assembledge	Area (ha)	Max. Depth (m)	Total P (ug/L)
Unnamed-"Tempo"	54°37'N 113°20'W	1994 & 1995	Fishless	9.4	2.50	108.1
Joseph	54°37'N 113°12'W	1994 & 1995	Fishless	12.1	1.50	13.5
Unnamed-"Shumaker"	54°38'N 113°18'W	1995	Fishless	20.0	6.75	36.0
Little Buck	54°41'N 112°32'W	1995	Fishless	51.6	1.10	181.0
Unnamed-"Beaver"	54°38'N 113°35'W	1994 & 1995	*P. promelas*	2.7	4.30	26.2
Bobier	54°33'N 113°10'W	1994	*C. inconstans*	25.2	1.10	86.3
Tawatinaw	54°21'N 113°28'W	1994	*C. inconstans*	47.4	4.30	46.4
Unnamed-"Mystic"	54°23'N 113°21'W	1995	*P. promelas, C. inconstans*	14.3	2.20	42.7
Unnamed-"West Baptiste"	54°44'N 113°40'W	1995	*P. promelas, C. inconstans*	25.3	1.50	80.0
Two Island	54°26'N 113°13'W	1995	*C. inconstans*	57.8	1.00	96.0

Appendix 2-2. The total hours study lakes were visited and the percentage of hours male and female loons were present on the lakes in 1994 and 1995.

		1994		1995		Both Years	
		Total	% Present	Total	% Present	Total	% Present
Minnow Lakes							
Beaver	Female	104	86	63	97	167	90
	Male	104	79	63	79	167	79
	Total	208	82	126	88	334	84
Bobier	Female	24	100	-	-	24	100
	Male	24	100	-	-	24	100
	Total	48	100	-	-	48	100
Mystic	Female	-	-	69	97	69	97
	Male	-	-	69	88	69	88
	Total	-	-	138	93	138	93
Tawatinaw	Female	6	100	-	-	6	100
	Male	6	100	-	-	6	100
	Total	12	100	-	-	12	100
Two Island	Female	-	-	10	80	10	80
	Male	-	-	10	100	10	100
	Total	-	-	20	90	20	90
West Baptiste	Female	-	-	6	100	6	100
	Male	-	-	6	100	6	100
	Total	-	-	12	100	12	100
Minnow Lakes	Total	268	86	296	91	564	88
Fishless Lakes							
Joseph	Female	60	95	27	96	87	95
	Male	60	90	27	92	87	90
	Total	120	93	54	93	174	93
Little Buck	Female	-	-	12	92	12	92
	Male	-	-	12	92	12	92
	Total	-	-	24	92	24	92
Shumaker	Female	-	-	23	100	23	100
	Male	-	-	23	100	23	100
	Total	-	-	46	100	46	100
Tempo	Female	78	100	44	100	122	100
	Male	78	99	44	84	122	93
	Total	156	99	88	92	244	97
Fishless Lakes	Total	276	96	212	94	488	95
All Lakes	Total	544	91	508	92	1052	96

Appendix 2-3. The means, ± 1 standard errors (SE), medians, and ranges (minimum = Min., maximum = Max.) of the percentage of time adult loons performed different behaviors per observation period (N = the number of observation periods) in 1994 and 1995.

	1994						1995					
Behavior	Mean	SE	Median	Min.	Max.	N	Mean	SE	Median	Min.	Max.	N
Foraging	59.1	3.2	74	0	100	145	57.7	2.1	70.7	0	100	216
Preening	7.6	1.0	0	0	54.5	145	8.6	0.8	2.2	0	64.6	216
Floating	7.6	1.6	0	0	100	145	14.8	1.7	2.8	0	100	216
Sleeping	4.7	1.5	0	0	100	145	4.1	0.9	0	0	97.7	216
Territorial	1.6	0.7	0	0	71.9	145	3.7	0.9	0	0	100	216
Reproductive	0.9	0.5	0	0	61.6	145	1.7	0.4	0	0	43.7	216
Nesting	18.5	3.1	0	0	100	145	9.5	1.9	0	0	100	216

Appendix 2-4. The medians and ranges (minimum = Min. and maximum = Max.) of the percentage of time spent foraging, dive rate, and mean dive duration per observation period (N = the number of observation periods) and the total number of recorded dives by male and female adult loons on the study lakes in 1994.

		% Foraging				Dive Rate (dive/min)				Dive Duration (s)				Total
		Median	Min.	Max.	N	Median	Min.	Max.	N	Median	Min.	Max.	N	Dives
Minnow Lakes														
Beaver	Female	85.8	0.0	100	23	1.396	0.825	2.368	16	32	15	58	16	1177
	Male	78.8	0.0	100	20	1.028	0.674	2.395	18	44	19	53	18	953
Bobier	Female	48.7	7.1	100	4	1.399	1.072	1.868	4	29	25	40	4	148
	Male	88.8	67.2	100	4	1.213	0.945	1.364	4	35	30	40	4	253
Tawatinaw	Female	65.4	18.9	84.0	4	0.903	0.868	1.002	3	52	19	54	4	108
	Male	60.2	8.8	85.5	4	1.030	0.925	1.350	4	47	35	51	4	112
Fishless Lakes														
Joseph	Female	84.4	0.0	100	20	1.889	0.951	3.429	15	25	16	43	16	1279
	Male	70.3	0.0	100	17	1.459	0.976	2.617	15	28	13	44	15	917
Tempo	Female	64.6	0.0	100	25	1.171	0.797	1.709	13	38	19	50	12	449
	Male	60.4	0.0	100	24	1.174	0.862	2.682	18	36	14	54	18	636

Appendix 2-5. The medians and ranges (minimum = Min. and maximum = Max.) of the percentage of time spent foraging, dive rate, and mean dive duration per observation period (N = the number of observation periods) and the total number of recorded dives by male and female adult loons on the study lakes in 1995.

		% Foraging				Dive Rate (dive/min)				Dive Duration (s)				Total
		Median	Min.	Max.	N	Median	Min.	Max.	N	Median	Min.	Max.	N	Dives
Minnow Lakes														
Beaver	Female	80.1	0.0	100	25	1.595	0.807	2.279	19	25	13	54	20	1238
	Male	87.9	0.0	100	24	1.044	0.700	1.978	23	47	23	55	22	1182
Mystic	Female	74.5	0.0	100	25	1.245	0.777	1.593	22	35	23	46	21	795
	Male	65.3	0.0	96.5	20	1.211	0.849	1.491	18	40	30	45	18	740
Two Island	Female	60.4	15.6	85.9	4	1.123	0.957	1.228	4	43	38	51	4	128
	Male	75.2	0.0	97.5	7	1.093	9.69	1.394	5	43	29	50	5	206
West Baptiste	Female	61.2	35.8	86.5	2	1.634	1.186	2.082	2	27	18	37	2	103
	Male	89.7	64.8	99.6	3	1.251	1.103	1.385	3	35	31	44	3	146
Fishless Lakes														
Joseph	Female	75.1	0.0	100	14	1.654	1.308	2.286	11	24	15	36	11	838
	Male	70.5	0.0	100	13	1.595	1.265	2.184	8	26	22	33	8	497
Little Buck	Female	86.4	0.0	98.6	4	1.364	1.271	1.369	3	34	34	37	3	218
	Male	96.5	68.5	100	6	1.107	0.934	1.291	6	42	35	58	6	272
Shumaker	Female	39.9	0.0	98.6	13	1.442	0.733	2.720	8	28	15	41	8	343
	Male	9.3	0.0	100	14	1.274	0.915	1.899	7	29	22	45	8	348
Tempo	Female	45.6	0.0	95.8	24	1.210	0.880	2.336	15	38	15	51	15	743
	Male	41.9	0.0	91.9	18	1.021	0.713	1.561	10	44	15	56	11	323

Appendix 2-6. The medians and ranges (minimum = Min. and maximum = Max.) of the percentage of successful dives (as defined by the delivery of food to a chick immediately following a dive) per observation period (N = the number of observation periods) and the total number of recorded dives of loons (successful and unsuccessful) on the study lakes where chicks were present in 1994 and 1995.

Lake	Median	Min.	Max.	N	Total Dives
			1994		
Minnow Lakes					
Beaver	53.00	43	98	10	983
Fishless Lakes					
Joseph	58.00	44	73	6	634
Tempo	52.00	25	71	5	886
Minnow Lakes			1995		
Beaver	67	20	91	11	840
Fishless Lakes					
Shumaker	58	56	61	3	276
Tempo	72	42	85	7	591

Chapter Three

Foraging Behavior, Begging Rates, and Provisioning Rates of Common Loon, *Gavia immer*, Chicks on Lakes With and Without Fish in Central Alberta, Canada

3.1 Introduction

When first hatched, many young birds lack the neural development, experience and foraging skills needed to feed themselves and thus must rely on adults to provide most of their nourishment. However, chicks can behaviorally influence how much and perhaps what they are fed. Chick begging has been found to influence provisioning rates by adults. Specifically, high levels of begging induces high chick provisioning rates (e.g., Glaucous-winged Gulls, *Larus glaucescens*, Henderson 1975; Great Tits, *Parus major*, Bengtsson and Ryden 1983; European Starlings, *Sturnus vulgaris*, Cotten *et al.* 1996). Begging rates are governed by chick hunger, and chick hunger is influenced by the type of food given to chicks and frequency of feedings (Bengtsson and Ryden 1983). Low provisioning rates and poor quality of food fed to chicks results in chick hunger and high begging rates (e.g., Yellow-headed Blackbirds, *Xanthocephalus xanthocephalus*, Price and Ydenberg 1995). Provisioning patterns are influenced by prey availability. Low preferred prey abundance may result in increased provisioning rates of low quality prey (e.g., Western Grebes, *Aechmophorus occidentalis*; Forbes and Sealy 1990), or an increase in the size or amount of less preferred prey fed per feeding episode (e.g., Common Murres, *Uria aalge*, Uttley *et al.* 1994). Thus, a relationship exists between prey availability, the behavior of chicks (begging rates), and the behavior of adults (chick provisioning rates).

The foraging behavior of chicks is dictated by prey availability but is also influenced by their own foraging skills. As chicks mature, they learn and develop the skills needed to forage efficiently (Burger 1986). In addition, as chicks grow they are anatomically able to consume larger prey items and chicks may forage for different prey items as they age. Therefore, the foraging patterns of young chicks are often very different from the foraging patterns of older chicks (e.g., American Coots, *Fulica americana*, Desrochers and Ankney 1986).

The energetic demands of chicks often increase and then plateau as chicks to adult size (e.g., Storm Petrels, *Hydrobates pelagicus*, Bolton 1995). Parents may respond to this demand by increasing provisioning rates (e.g., Pigeon Guillemot, *Cepphus columba*, Emms and Verbeek 1991), by increasing the amount of food per visit (Bolton 1995), or by changing the kinds of food given to chicks (e.g., Common Murres, Hatchwell 1991). This growth period is a critical time for chicks and if parents are unable to respond to the chick's nutritional demands, chick starvation and death may result (e.g., Herring Gulls, *Larus argentatus*, Pierotti and Murphy 1987, Kittiwakes *Rissa tridactyla*, Wanless and Harris 1992). Once chicks have reached a certain size and maturity level, their dependence on adults for food lessens and provisioning rates decrease (Desrochers and Ankney 1986). Thus, provisioning rates and begging rates are often at the highest levels when chicks are young.

Thus, there exists a complex relationship between chick growth and energetic needs, chick provisioning rates, begging rates, foraging patterns, and prey availability. This relationship is particularly sensitive in birds that are thought to have specialized dietary requirements such as the Common Loon, *Gavia immer* (McIntyre 1988). Adult Common Loons are monogamous through the breeding season, hatch one or two chicks, and exhibit high levels of parental care which includes chick provisioning. Loons are thought to be strict piscivores (Barr 1986, McIntyre 1988). This view has been based on gut content analysis that indicate that the main component of a loon's diet is typically large-bodied fish, such as yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersoni*), and small-bodied species, such as lake chub (*Couesius plumbeus*) and ninespine stickleback (*Pungitius pungitius*) (Ontario, Barr 1996). The absence of loons on lakes low in fish abundance (Barr 1986, Kerekes 1990, Wayland and McNicol 1990) has also reinforced the traditional view that loons are dependent on fish as a prey source.

However, recent studies indicate that loon behavior and diet is more flexible then originally perceived. Alvo and Berrill (1992) found that invertebrates were a large component of young loon chicks' diet in the Sudbury region of Ontario. As chicks matured, adult loons switched from feeding invertebrates to feeding fish to chicks. In addition, Alvo *et al.* (1988) found loons in the Sudbury region nesting on lakes where fish populations were reduced or lacking due to cultural acidification. However, adult loons on these lakes were less successful at raising chicks to fledgling than loons on lakes with abundant fish populations.

On the other hand, Parker (1988) found that loons nesting on acidic lakes with low or no fish populations in the Adirondacks of New York were able to raise chicks on diets of invertebrates. Neither of the studies intensively examined the foraging behavior (e.g., time spent foraging, dive rates, and dive durations) of chicks on these lakes so it is difficult to determine if and how differences in prey base influenced the behavior of chicks and if differences in behavior resulted in differences in fledging success. Parker (1988) did examine the time adult loons spent feeding chicks (min/observation) and found that adults feeding invertebrates to chicks spent more time provisioning than adults feeding fish to chicks. Parker (1988) also observed that a chick on a fishless lake begged frequently. However, Parker (1988) did not compare the provisioning behaviors of adult loons or the begging behaviors of chicks on lakes of low pH to that of adults and chicks on "healthy lakes".

In 1992, Paszkowski (1994) surveyed waterfowl on 25 lakes in central Alberta and found Common Loons present on lakes that were all relatively productive, as defined by total phosphorus levels (> 10 μg/l, Wetzel 1975), but that differed in terms of size, depth, and fish species composition. Paszkowski (1994) found loons nesting on larger (≥ 40 ha), deeper (≥ 9 m) lakes that contain populations of large-bodied fish such as northern pike (*Esox lucius*), white sucker, and yellow perch, similar to loon habitat in eastern Canada, as well as on small (< 40 ha), shallow (< 9 m) lakes that contained only small-bodied fish such as fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*), referred to as Minnow Lakes hereafter. Like Munro (1945) found in British Columbia, she found loons nesting on small (< 40 ha), shallow (< 9 m), naturally fishless lakes, referred to as Fishless Lakes hereafter.

The presence of loons on lakes that are similar in size and depth, but that differ in prey base, provided the opportunity to compare the behavior of loons foraging primarily for invertebrates to that of loons foraging primarily for fish. In conjunction with a study on the behavior of adult Common Loons on these Minnow and Fishless Lakes (see Chapter 2), I examined the provisioning rates, begging rates, and foraging patterns of chicks on the lakes. During the summers of 1994 and 1995, I collected behavioral observations in central Alberta on Common Loon chicks on one Minnow Lake and on two Fishless Lakes to determine if: 1) time budgets, particularly time spent foraging, differ between chicks on Minnow and Fishless Lakes and change as chicks mature; 2) foraging patterns (e.g., dive rate and dive duration) differ between chicks on Minnow and

Fishless Lakes and change as chicks mature; 3) begging rates and provisioning rates differ between chicks on Minnow and Fishless Lakes and change as chicks mature; and 4) prey items fed to chicks differ between Minnow and Fishless Lakes and change as chicks mature.

The comparison between the behavior of loons on Minnow and on Fishless Lakes was chosen, as opposed to comparing loons on lakes with large-bodied fish and on Fishless Lakes, for a number of reasons. Minnow and Fishless Lakes are similar in size and depth and, unlike lakes with large-bodied fish, these lakes are small enough that one pair of loons will occupy the entire lake. In addition, unlike large lakes that support sport fisheries, these lakes experience little recreational activity, and lack fish that may prey on loon chicks or that may compete with loons for food. From a practical view these small lakes are advantageous in the sense that much of a lake's surface area can be observed from a single location. Although adult behavior was examined on a larger number of lakes (Chapter Two), the number of lakes examined here is small because not all territorial loon pairs attempted to nest or did not hatch eggs.

3.2 Methods

3.2.1 Study Sites

Research was centered at the University of Alberta Meanook Biological Research Station (54°37'N 113°20'W), Athabasca, Canada. The behavior of five chicks on three lakes in 1994 and three chicks on three lakes in 1995 was examined. All the lakes were similar in morphometry and in water chemistry (see Appendix 3-1). The morphometry and chemical characteristics were measured during the summers of 1993-1995. The fish populations were sampled in 1993 and 1994 (Tonn and Paszkowski unpubl.). The riparian vegetation and vegetation within the lakes are described elsewhere (Chapter 2).

3.2.2 Observation Times and Methods

Observations began when the chicks hatched (usually in June) and, when possible, continued until the fledglings left the lake to migrate in late August or early September. Observations were made from vantage points on shore using either a spotting scope or binoculars. Elevated (1m high) platforms (1.5m x 1.5m) were used on Tempo and Joseph Lakes (Fishless Lakes) in order to view lakes in their entirety. Platforms were not required on Beaver Pond (Minnow Lake). Blinds were not used as loons are often distracted by them and are less disturbed by a human presence (McIntyre 1988). Observation periods lasted one hour and during each observation period, the frequency, duration, and location of all behaviors were recorded on maps of the lakes. Behaviors (see McIntyre 1988 for a detailed description of the behaviors) included: 1) territorial behavior, any inter- and intra-specific agonistic behaviors such as vocalization, wing beating, and chasing; 2) back-riding, chick(s) carried on parent's back; 3) sleeping, indicated by the loon placing it's head over its back and tucking a foot under a wing; 4) preening, any activities relating to maintenance of feathers such as oiling, bathing, and head rubbing; 5) foraging, any behavior related to the procurement of food and; 6) floating, the loon was on the water surface and not participating in any of the previously mentioned behaviors. Foraging behaviors included "peering" (loons submerge head into the water column, presumably looking for food), foraging dives (loons search for, pursue, and attempt to capture and consume food underwater), begging for food by chicks (as indicated by the chick pecking at the adult's bill or neck) and it also included chick provisioning episodes which involved chicks waiting for and accepting food from the adults. Loons dive for purposes other than foraging, but a foraging dive is the next action following peering. In addition, foraging dives occur in bouts, when loons dive continuously for periods of time. Non-foraging dives are associated with behaviors relating to preening and do not usually occur in bouts.

In addition to recording behavior, I also attempted to identify food items fed to chicks. Adult loons usually consume food underwater; I never observed an adult swallow prey at the water surface. Identification was therefore restricted to food given to chicks by adults. Food items were identified as vegetation, invertebrate, or fish. I also tried to identify, to the lowest taxonomic level possible, the invertebrates fed to chicks. Occasionally, I was unable to identify very small invertebrates that were swallowed very quickly. In those cases, prey were classified as "unidentified invertebrates". Cases where prey could not be identified as vegetation, invertebrate, or fish were classified as "unidentified".

3.2.3 Quantification of Foraging Behaviors

In order to determine if time budgets and foraging patterns of chicks on Fishless Lakes differ from those of chicks on Minnow Lakes and to determine if time budgets, foraging patterns and prey items fed to chicks on different lakes types change with age, I calculated the: 1) percentage of time spent performing each recognized behavior; 2) dive rate, the number of dives per minute while foraging per observation (minutes of foraging behavior summed per observation and divided by foraging dives per observation); 3) mean dive duration, the mean length of time spent under water per foraging dive for each observation period; 4) chick provisioning rate, the number of times the chick was given food per minute of observation; 5) chick begging rate, the number of times the chick begged (pecked at adults) for food per minute of observation and; 6) percentage of fish, vegetation, and identified and unidentified invertebrates fed to chicks during observations.

3.2.4 Statistical Analysis

3.2.4.1 Chicks

Statistical analysis of the chick data was complicated by the fact that no chicks fledged on either Fishless Lake in 1994 and that 1 chick fledged on the Tempo Lake but not on Joseph Lake in 1995. To circumvent this problem, comparisons were made on chicks during a similar age span (maximum age based on the age of death of chicks on Tempo and Joseph lakes and the availablility of data collected at similar dates). Thus, the behavior of chicks 1-42 days old on the Beaver Pond (2 chicks fledged in 1994 and 1 chick fledged in 1995) was compared to the behavior of chicks 1-41 days old on Tempo Lake and to the behavior of chicks 1-39 days old on Joseph Lake. Repeated hourly observation periods on the same individual were considered to be independent behavioral samples only when separated by at least one hour during which no observations were taken on the individual. Only those observations considered to be independent were included the data sets. The behavioral data sets for chicks on each lake (1994 and 1995 combined due to small sample sizes) were first examined for departures from a normal distribution using the One-Sample Kolmogorov-Smirnov test. None of the data sets were found to have a normal distribution, therefore Kruskal-Wallis One-Way Analysis of Variance (ANOVA) tests were used to determine if significant behavioral differences existed among lakes.

In addition, in order to determine if behavior changed as chicks matured, chick ages were combined into two groups (1-35 days old and 36 days and older) based on the fact that the critical survival period for Common Loon chicks appears to occur around the 5th week after hatching (Parker 1988). Mann-Whitney U tests were used to determine if the behavior of any of the chicks differed at 1-35 days old and at 36+ days old.

3.2.4.2 Prey

To determine if the proportion of fish (where applicable), vegetation, identified invertebrates (leeches, odonate/coleopteran larvae, and amphipods), and unidentified invertebrates fed to chicks on each lake differed between chicks age 1-35 days and 36+ days old and if the proportion of prey fed to chicks on each lake differed between years, Pearson Chi-Square tests for independence were performed. Pearson Chi-Square tests were also performed to determine if the proportion of leeches, odonate/coleopteran larvae, amphipods, and small, unidentified invertebrates fed to chicks differed between lakes (1994 and 1995 data combined).

3.3 Results

3.3.1 Chicks

3.3.1.1 Time Budgets

Common Loons chicks devoted a large percentage of their hourly time budgets to foraging or being fed (54.5% ± 5.6, n = 35 observations). In both 1994 and 1995 chicks spent more time feeding than any other behavior (see Appendix 3-2 for means, standard errors, medians, ranges and sample sizes).

The percentage of time chicks spent per observation period accepting food from their parents differed significantly among lakes (Table 3-1). Chicks on Joseph Lake spent a greater percentage of time per observation period accepting food from their parents than chicks on Beaver Pond and on Tempo Lake; this difference was significant for Beaver Pond (see Table 3-2 for analysis and Appendix 3-3 for medians, ranges, and sample sizes). The percentage of time chicks accepted food from their parents varied as chicks grew (Fig. 3-1). Chicks at 1-35 days old on Joseph Lake spent significantly more time per observation period accepting food from their parents than chicks at 36+ days old (Table 3-3). The time spent being fed by parents decreased, although not significantly, as chicks matured on Beaver Pond (Fig. 3-1). No pattern was distinguishable for the chicks on Tempo Lake.

The percentage of time chicks foraged for themselves per observation period did not differ significantly between lakes (Table 3-1). Chicks on Beaver Pond spent more time foraging as they grew older (Fig. 3-1) and chicks 36+ days old spent significantly more time foraging for themselves than chicks 1-35 days old (Table 3-3). The percentage of time loon chicks on Joseph and Tempo spent foraging did not change significantly between 1-35 days old and 36+ days old.

3.3.1.2 Begging and Provisioning Rates

The begging rates of chicks were not significantly different between lakes (Table 3-1), although begging rates of chicks on Beaver Pond were higher than that of chicks on Fishless Lakes of a similar age (Appendix 3-3). Although no significant differences were detected between the begging rates of chicks 1-35 days old and chicks 36+ days old on any of the lakes (Table 3-3), the general trend was an increase in begging rates as chicks grew older (Fig. 3-2). However, begging rates peaked at Beaver Pond when chicks were 40 - 45 days old and declined thereafter (Fig. 3-2).

The provisioning rates of chicks did not differ significantly among lakes (Table 3-1). However, provisioning rates were greater on the Fishless Lakes than on Beaver Pond (see Appendix 3-3). On no lake did the provisioning rates of chicks 1-35 days old differ significantly from chicks 36+ days old (Table 3-3). However, the provisioning rates of chicks peaked when chicks were approximately 35 - 40 days old on Beaver Pond followed by a decline in the rate as chicks grew older (Fig. 3-2). The provisioning rates of chicks on Tempo and Joseph Lakes did not follow this pattern. Generally, provisioning rates on the Fishless Lakes remained high.

3.3.1.3 Dive Rate

Dive rates did not significantly differ among chicks (Table 3-1). However, the dive rates of chicks on Joseph Lake and Beaver Pond tended to be higher than that of chicks on Tempo Lake (Fig 3-3). The dive rates of chicks 1-35 days old and chicks 36+ days old on Fishless Lakes were not significantly different, but the dive rates of the chicks 1-35 days old on Beaver Pond were significantly lower than that of chicks 36+

days old (Table 3-3). The general trend for chicks on Beaver Pond was an increase in dive rate as the chicks grew older (Fig. 3-3), a pattern not apparent for the chicks on Tempo and Joseph Lake.

3.3.1.4 Dive Duration

The dive durations of chicks on Beaver Pond and Tempo Lake were higher than that of chicks on Joseph Lake (Fig 3-4), but this difference was not statistically significant (Table 3-1). Mean dive duration of chicks on the Beaver Pond (Fig. 3-4) increased with age of the chick; chicks 1-35 days old made significantly shorter dives than chicks 36+ days old (Table 3-3). This pattern was not apparent for the chicks on Tempo and Joseph Lakes.

3.3.2 Prey

3.3.2.1 Lakes

The proportion of various prey items fed to chicks on the Beaver Pond differed significantly between 1994 and 1995 (Table 3-5). In both 1994 and 1995 fish comprised most of the known prey items fed to chicks on Beaver Pond (Table 3-4), although more fish were fed in 1995 than in 1994. Mark-recapture estimates done in May of 1994 and 1995 suggest that fish were more abundant in 1995 (Tonn unpubl.). Chicks were also fed invertebrates and vegetation. Leeches were the most common invertebrate fed to the chicks in both 1994 and 1995 (Table 3-5). Odonate/coleopteran larvae and unidentified invertebrates made up a larger component of the chicks diet in 1994 than in 1995. Amphipods were rarely fed to chicks in either year.

Most of the known food items fed to chicks on Tempo Lake were invertebrates (Table 3-4). The proportion of prey items fed to the chicks differed significantly between years (Table 3-4). In both years leeches were the main component in the diet on Tempo Lake. However, the proportion of leeches fed to the chicks was significantly greater in 1995 than in 1994. In 1994, amphipods were the second largest component of the chicks diet where as, in 1995, odonate/coleopteran larvae held this rank.

Invertebrates were the main food item fed to chicks on Joseph Lake (Table 3-4). As seen on Tempo Lake, leeches were the most common food item. Odonate/coleopteran larvae were the second and unidentified invertebrates were the third most common invertebrate items fed to chicks.

The proportion of leeches, odonate/coleopteran larvae, amphipods, and unidentified invertebrates fed to chicks significantly differed among lakes (Table 3-5). Chicks on Beaver Pond were fed leeches and amphipods less frequently than chicks on the Fishless Lakes. Leeches and amphipods were more common and small unidentified invertebrates were less common in the diet of chicks on Tempo Lake than on Joseph Lake (Table 3-5).

3.3.2.2 Age Groups

The diet of chicks on each lake at 1-35 days old was different than the diet at 36+ days old (Table 3-4 and Table 3-5). The proportion of fish fed to chicks at 1-35 days old on Beaver Pond was lower (but not significantly) than the proportion of fish fed to chicks 36+ days old (Table 3-4). Correspondingly, the amount of vegetation and invertebrates fed declined as chicks grew older. Of the invertebrates fed to chicks, the proportion of leeches increased as chicks aged, whereas the proportion of the remaining invertebrates declined (Table 3-5).

The proportion of invertebrates fed to chicks on Tempo Lake and on Joseph Lake increased as chicks aged (Table 3-4). In addition, the proportion of the various invertebrate prey items significantly differed as the chicks aged on both Tempo Lake and on Joseph Lake (Table 3-4). Leeches were the main component in the diet of chicks at ages 1-35 days and at 36+ days old on both lakes and the proportion of leeches fed to the chicks on both lakes increased as chicks grew older (Table 3-5). The second most common food item of chicks on Tempo Lake, for both ages groups, was odonate/coleopteran larvae, but the overall proportion of insect larvae fed to chicks decreased as chicks aged. A similar proportion of insect larvae, unidentified invertebrates, and vegetation were fed to chicks at ages 1-35 days on Joseph Lake. However, the proportion of insect larvae fed increased as chicks grew older, where as the proportion of unidentified invertebrates and vegetation fed decreased as the chicks aged.

3.4 Discussion

Studies investigating the relationship between chick behavior and prey have focused on begging rates and provisioning rates (e.g., Bengtsson and Ryden 1983, Hatchwell 1991, Price and Ydenberg 1995) Few studies have examined time budgets or foraging patterns of chicks in relation to prey base. In addition, those studies that have looked at the relationship between begging rates, provisioning rates and prey have focused on behavioral responses to changes in absolute prey abundance and not on responses to changes in prey composition. These studies have reported that chicks begged more when hungry and, as a consequence, were fed more (e.g., Rock Doves, *Columba livia*, Mundloch 1995; Yellow-headed Blackbirds, Price and Ydenberg 1995).

My study indicates that chick behaviors are influenced by prey composition. Many Foraging behaviors of Common Loon chicks 1 - 41 days old that were fed invertebrates tended to differ from those of chicks of similar age that were fed primarily fish. Generally, loon chicks on Fishless Lakes spent more of their time accepting food from their parents than loon chicks on the Minnow Lake. Chicks on Tempo Lake spent most of their time being fed and very little time foraging for themselves. Chicks on Joseph Lake spent most of their time being fed by their parents or feeding themselves. In addition, provisioning rates of chicks on Fishless Lakes were higher than that of chicks on Beaver Pond and chicks on Fishless Lakes did not beg frequently, presumable because they were always being fed.

Dive rates were similar between chicks on Joseph Lake and Beaver Pond and were higher than on Tempo Lake, probably owing to the fact that chicks on Tempo Lake rarely fed themselves. However, when chicks on Tempo Lake did dive, the duration of the dives were similar to that of chicks on Beaver Pond. The dive durations of chicks on

Joseph Lake were much shorter than that of chicks on the other two lakes. Differences in dive duration may reflect differences in prey composition.

This study confirms reports by Alvo and Berrill (1992) that adult Common Loons, like Arctic Loons (Eriksson and Sundberg 1991), feed invertebrates to chicks even when fish are available. As suspected by Barr (1973), leeches are a large part of a chicks diet, especially on Fishless Lakes. Leeches (e.g., *Nephelopsis obscura*, a common leech found in many of the study lakes, unpubl. data) have high caloric values (e.g., 5344cal/g, Driver 1981) and can grow quite large (e.g., 3.26 g Peterson 1983) and thus may be an important alternative prey source for loons. Leeches made up a larger proportion of the chick's diet on Tempo Lake than on Joseph Lake. In addition, a greater percentage of amphipods were fed to chicks on Tempo Lake than to chicks on Joseph Lake, while a larger percentage of small, unidentified invertebrates and vegetation were fed to chicks on Joseph Lake. This probably reflects the composition and abundance of invertebrate species within these lakes as sweep-net samples taken in 1994 and 1995 indicated that leeches and amphipods were more abundant in Tempo Lake than in Joseph Lake (unpubl. data). Differences between invertebrate composition of the lakes may explain the differences between the behavior of chicks on Tempo and Joseph lakes (e.g., shorter dive duration of chicks on Joseph Lake).

Research on the foraging behavior and diet of Common Loon chicks foraging on lakes that contain fish in other geographic regions (e. g., Ontario, Alvo and Berrill 1992) indicated that when loon chicks are between 0 and 4 weeks, invertebrates and vegetation are the main components of their diet, but between weeks 4 and 6, fish become the main component of their diet. In observing the foraging behavior of hand-reared Common Loon chicks, Barr (1996) found that the chicks consumed food and grew at exponential rates during this period but the rates began to level off when the chicks were 8 weeks old. He also found that at 8 weeks chicks were dependent on adults for approximately half of their food intake and suggested that 8 weeks of age was the transition period for attaining independence from the adults.

The behavior of chicks on Beaver Pond appeared to develop in a similar manner as described by Alvo and Berrill (1992) and Barr (1996). Generally, begging rates and provisioning rates peaked when chicks on Beaver Pond were approximately 6 weeks old and then declined as the chicks matured. The adults responded to an increase in the demand for food (as indicated by begging rates) by feeding more fish to the chicks. Dive rates and dive durations of chicks increased as they grew and became less adults for food and foraged for themselves more frequently.

On the other hand, adults continued to provide the bulk of the chick's diet on Fishless Lakes and chicks did not often forage for themselves as they grew. Adult loons on Fishless Lakes increased the amount of leeches fed to chicks as chicks matured. However, they did not change their provisioning rates. This suggests provisioning rates were at their highest possible levels and that the loons could not increase feeding rates. Therefore, adult loons feeding primarily invertebrates to chicks could only maintain their provisioning rates and not decrease the rates as they would if fish were available. However, caution must be used in interpreting these results as they are based on observations on 3 lakes in 2 years. In addition, data sets are incomplete as chicks on Fishless Lakes did not often survive to fledge (see Chapter 4).

It appears that Common Loons have the capacity to behaviorally respond to differences in prey composition. Can Common Loons in Alberta foraging on small lakes adequately adjust their behavior to insure that their energy requirements are met? Barr

(1996) suggests that loons chicks eat approximately 53 kg of food in 15 weeks. A young chick (1-35 days old) consumes less than half that of an older chick (Barr 1996). Thus, at 5 weeks a chick will have ate 10600 g of fish (303 g of fish/day or 3.284×10^5 cal/day; based on the caloric value of an averaged sized fathead minnow, 1072 cal/g, Bryan *et al.* 1996), and from week 5 - 15 weeks a chick will have ate 42400 g of fish (606 g of fish/day or 6.496×10^5 cal/day)

The average provisioning rate when chicks were 1-35 days old on Beaver Pond was 0.579 feedings/min (feeding = chick receiving prey from parent) or 35 feedings/hr. Based on my observations, 66% of those feeding episodes involved fish and 34% involved invertebrates and vegetation. For simplicity, I assumed that leeches of an average size (e.g., 0.35 g, *Nephelopsis obscura*, Davies and Everett 1976) were the only invertebrate fed and that one prey item was eaten per provisioning episode. Thus, loon chicks were fed 23 minnows/h and 12 leeches/h or 1.285×10^5 cal/h (based on the caloric content of minnows and of leeches, 5344cal/g, and the average weight of a minnow, 4.3 g Price *et al.* 1991, and the average weight of a leech). Therefore, the daily caloric requirements of young loon chicks on Beaver Pond were being met given the time budgets, provisioning rates and diet of the chicks. (Because dive rates of young chicks were low and because of the difficulty in estimating dive success at that age, these were not factored into the calculation).

The average provisioning rates when chicks were 36+ days old on Beaver Pond was 0.273 feedings/min or 16 feedings/hour. Based on my observations, 78% of those feeding episodes were fish and 22% were leeches. Therefore, loon chicks would have been fed 12 minnows/h and 4 leeches/h, which equates to 6.280×10^4 cal/h. The dive rate of a chick at this age was 0.540 dives/min or 32 dives/h. Dive efficiency of a chick at 6 weeks is estimated to be 14% increasing to 51% at 9 weeks (Barr 1996) and if we use an estimate in the middle of this range (32%), a loon chick would have fed itself 10 times/hr. This equates to 8 minnows and 2 leeches/h or 4.062 x 10^4 cal/h. Older loon chicks were therefore fed 1.034 x 10^5 cal/h. Thus, the daily caloric requirements of older loon chicks on Beaver Pond were being met given the time budgets, provisioning rates and diet of the chicks.

The average provisioning rates when chicks were 1-35 days old on a Fishless Lake (e.g. Tempo Lake) was 1.022 feedings/min or 61 feedings/h. Most of those feeding episodes were invertebrates and for simplicity, it is assumed that leeches of an average size were the only food eaten and that one leech was eaten per provisioning episode. Loon chicks were therefore fed 61 leeches/h or 1.141 x 10^5 cal/h which is very similar to the estimated amount of calories per day ingested by loon chicks on Beaver Pond.

The average provisioning rates when chicks on Fishless Lakes were 36+ days old was 1.001 feedings/min or 60 feedings/h which equates to 1.122 x 10^5 cal/h. The average dive rate of a chick at this age was 0.022 dives/min or 1 dive/h. Older loon chicks were therefore fed 1.140 x 10^5 cal/h. Thus, the daily caloric requirements of older loon chicks on Fishless Lakes were probably being met but the adult loons would have to work harder (i.e., provision more frequently) than loons on Minnow Lakes to meet these requirements. However, these estimates were made assuming leeches were the only prey in the diet. It does not take into account the smaller food items fed to chicks. Although other invertebrates are of high caloric values (e.g., Odonata larvae: *Lestes dryas*, 5394 cal/g; Coleoptera larvae: *Dytiscus spp.*, 5288 cal/g; Heteroptera larva: *Callicorixa audeni*, 5464 cal/g; Driver 1981), they may not reach a maximum weight similar to that of a leech such as *N. obscura*. Therefore, I could be underestimating the daily caloric intake of chicks on Tempo Lake. In addition, because a greater percentage of smaller prey items were fed to the chicks on Joseph Lake, I believe that the adults there had a difficult time meeting the chicks requirements as the chicks aged.

The low reproductive success of loons on Fishless Lakes (Chapter 4) suggests that it is difficult to raise chicks on a diet of invertebrates. At least one chick fledged on Beaver Pond 4 out of 5 years of monitoring (1992-1996). Adult loons on Tempo Lake fledged one chick 3 out of the 5 years. Although at least one chick was observed on the lake every year of the survey, a chick never survived to fledge on Joseph Lake. Differences between invertebrate composition and abundance in Tempo and Joseph lakes may be responsible for the differential fledging success between the Fishless Lakes.

Thus, despite adjustments to behavior, an "acute" effect of being raised on a diet of invertebrates can be the death of a Common Loon chick. The possible long-term effects of being raised on a diet of invertebrates is unknown. To evaluate the effects we should determine if juvenile loons from Fishless Lakes are in the same body condition (e.g., weight) of juvenile loons from lakes where fish are present. It would also of value to determine if and how being raised on and learning to forage only for invertebrates influences foraging behavior of Common Loons in the wintering areas.

3.5 Literature Cited

Alvo, R. and M. Berrill. 1992. Adult Common Loon feeding behavior is related to food fed to chicks. Wilson Bulletin 104:184-185.

Alvo, R., D. J. T. Hussell, and M. Berrill. 1988. The breeding success of common loons (*Gavia immer*) in relation to alkalinity and other lake characteristics in Ontario. Canadian Journal of Zoology 66:746-752.

Barr, J. F. 1973. Feeding biology of the Common Loon (*Gavia immer*) in oligotrophic lakes of the Canadian shield. Ph.D. University of Guelph, Ontario.

Barr, J. F. 1986. Population dynamics of the Common Loon (*Gavia immer*) associated with mercury contaminated waters in northwestern Ontario. Canadian Wildlife Service Occasional Paper No. 56.

Barr, J. F. 1996. Aspects of Common Loons (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321:119-144.

Bengtsson, H. and O. Ryden. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*: An experimental study. Behavioral Ecology and Sociobiology 12:243-251.

Bolton, M. 1995. Food delivery to nestling storm petrels: Limitation or regulation? Functional Ecology 9:161-170.

Bryan, S. D., Soupir, C. A., Duffy, W. G., and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology: 111:153-161.

Burger, J. 1986. Effects of Age on Foraging in Birds. *In* Acta XIX Congressus Internatalis Ornithologicus. Ed. Henri Ouellet pp 1128-1139.

Cotten, P. A., Kacelnik, A. and J. Wright. 1996. Chick begging as a signal: are nestlings honest? Behavioral Ecology 7:178-182.

Davies, R. W. and R. P. Everett. 1976. The life history, growth, and age structure of *Nephelopsis obscura* Verrill, 1872 (Hirudinoidea) in Alberta. Canadian Journal of Zoology 55:620-627.

Desrochers, B. A. and C. D. Ankney. 1986. Effect of brood size and age on the feeding behavior of adult and juvenile American coots (*Fulica americana*). Canadian Journal of Zoology 64:1400-1406.

Driver E. A. 1981. Calorific values of pond invertebrates eaten by ducks. Freshwater Biology 11:579-581.

Emms, S. K. and N. A. M. Verbeek. 1991. Brood size, food provisioning and chick growth in the pigeon guillemot *Cepphus columba*. Condor 93:943-951.

Eriksson, M. O. G and P. Sundberg. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. Bird Study 38:135-144.

Forbes, L. S. and S. G. Sealy. 1990. Foraging roles of male and female western grebes during brood rearing. Condor 92:421-426.

Hatchwell, B. J. 1991. The feeding ecology of young guillemots *Uria aalge* on Skomer Island, Wales. IBIS 133:153-161.

Henderson, B. A. 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. Condor 77:488-492.

Kerekes, J. J. 1990. Possible correlation of summer common loon (*Gavia immer*) population with the trophic state of a water body. Internat. Verein. Limnol. 24: 349-353.

McIntyre, J. 1988. The Common Loon. University of Minnesota Press. Minneapolis.

Mundloch, C. J. 1995. Chick hunger and begging affect parental allocation of feedings in pigeons. Animal Behavior 49:601-613.

Munro, J. A. 1945. Observations of the loon in the Cariboo Parklands, British Columbia. Auk 62:38-49.

Parker, K. E. 1988. Common loon reproductive and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66:804-810.

Paszkowski, C. A. 1994. Factors affecting aquatic bird assemblages in central Alberta. Proceedings of the 3rd Annual Alberta Lake Management Society 15-19.

Peterson, D. L. 1983. Life cycle and reporduction of *Nephelopsis obscura* Verrill (Hirudinea: Erobdellidae) in permanent ponds of northwestern Minnesota. Freshwater Invertebrate Biology 2: 165-172.

Pierotti, R., and E. C. Murphy. 1987. Intergenerational conflicts in gulls. Animal Behavior 35:435-44.

Price, C. J., Tonn, W. M., and C. A. Paszkowski. 1991. Intraspecific patterns of resource use by fathead minnows in a small boreal lake. Canadian Journal of Zoology 69:2109-2115.

Price, K. and R. Ydenberg. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behavioral Ecology and Sociobiology 37:201-208.

Uttley, J. D., Walton, P., Monaghan, P. and G. Austin. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. IBIS 136:205-213.

Wanless, S. and M. P. Harris. 1992. Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145-154.

Wayland, M. and D. K. McNicol. 1990. Status report on the effects of acid precipitation on common loon reproduction in Ontario: The Ontario Lakes Loons Survey Technical Report Series No. 92. C. W. S., Ontario region.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Company. Toronto.

Table 3-1. Results from Kruskal-Wallis One-Way ANOVA tests comparing the percentage of time chicks were fed by their parents, the percentage of time chicks foraged for themselves, the feeding rate (# of times chick is given food by parents/min), the begging rate (# of times chick pecks at parents for food/min), the dive rate (dive/min), and the mean dive duration (s) per observation of chicks on Beaver, Joseph, and Tempo lakes (1994 & 1995 combined). N = the number of observations. H = the Kruskal-Wallis test statistic. p = the probability. Degrees of freedom for all tests = 2.

Foraging Pattern	N	H	p
% Time Fed by Parents	23	8.013	0.018*
% Time Foraging For Self	23	0.440	0.803
Begging Rate	35	1.271	0.53
Provisioning Rate	36	4.382	0.112
Dive Rate	23	2.561	0.278
Dive Duration	14	4.185	0.123

* significant difference

Table 3-2. Results from Mann-Whitney U tests comparing the percentage of time chicks on Beaver, Joseph, and Tempo Lakes were fed by parents per observation period (1994 & 1995 combined). N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

Lake		Beaver			Joseph	
	N	U	p	N	U	p
Beaver						
Joseph	16	5.000	0.010*			
Tempo	18	23.000	0.156	12	6.000	0.061

* significant difference

Table 3-3. Results from Mann-Whitney U tests comparing the percentage of time chicks were fed by their parents, the percentage of time chicks foraged for themselves, the feeding rate (# of times chick is given food by parents/min), the begging rate (# of times chick pecks at parents for food/min), the dive rate (dive/min), and the mean dive duration (s) per observation of chicks 1-35 days old and 35+ days old on Beaver, Joseph, and Tempo lakes (1994 & 1995 combined). N = the number of observations. U = the Mann-Whitney U test statistic. p = the probability. Degrees of freedom for all tests = 1.

Lake	% Time Fed by Parents			% Time Foraging For Self			Begging Rate		
	N	U	p	N	U	p	N	U	p
Beaver	21	65.500	0.301	21	13.000	0.004*	36	101.000	0.193
Joseph	7	12.000	0.032*	7	4.000	0.463	7	3.000	0.285
Tempo	7	8.000	0.480	7	9.000	0.271	11	8.000	0.199

	Provisioning Rate			Dive Rate			Dive Duration		
	N	U	p	N	U	p	N	U	p
Beaver	27	200.000	0.053	21	21.500	0.027*	17	0.500	0.001*
Joseph	7	6.000	1.000	7	5.000	0.714	4	1.000	0.564
Tempo	11	14.000	0.855	7	7.000	0.696	3	1.000	1.000

* significant differences

Table 3-4. The number and percentage of fish, invertebrates (Invert.) and vegetation (Veg.) fed to chicks on the study lakes in both years, in 1994 and 1995 separately, and at 1-35 days old and 36+ days old. Also presented are the results of Pearson Chi-Square tests comparing the percentage of different prey items fed to chicks between 1994 & 1995 and between chicks aged 1-35 days and 36+ days (both years combined). Chi-Square = the Pearson Chi-Square test statistic. df = the degrees of freedom (df of 5 includes fish, all 4 invertebrate categories, and vegetation; df of 4 includes all 4 invertebrate categories and vegetation) . p = the probability.

Lake		Prey items			Total	Test		
		Fish	Invert.	Veg.		Chi-Square	df	p
Beaver	Both	242	70	28	340			
		71%	21%	8%				
	1994	106	52	22	180	38.13	5	0.000*
		59%	29%	12%				
	1995	136	18	6	160			
		85%	11%	4%				
	1-35	123	47	17	187	0.074	5	0.074
		66%	25%	9%				
	36+	119	23	11	153			
		78%	15%	7%				
Tempo	Both	0	331	15	346			
		0%	96%	4%				
	1994	0	111	11	122	42.432	4	0.000*
		0%	91%	9%				
	1995	0	220	4	224			
		0%	98%	2%				
	1-35	0	273	15	288	20.192	4	0.000*
		0%	95%	5%				
	36+	0	58	0	58			
		0%	100%	0%				
Joseph	1994	0	215	28	243			
		0%	88%	12%				
	1-35	0	129	27	156	40.217	4	0.000*
		0%	83%	17%				
	36+	0	86	1	87			
		0%	99%	1%				

*significant differences

Table 3-5. The number and percentage of amphipods (Amph.), odonate/coleopteran larvae (Insects), leeches (Leech), and unidentified invertebrates (Unident.) that are the main components of the known invertebrates fed to chicks on the study lakes in 1994 and 1995 and at 1-35 days old and 36+ days old. Also presented are the results of Pearson Chi-Square tests comparing the percentage of different invertebrates fed to chicks on Beaver Pond and Tempo Lake (1), on Tempo and Joseph Lakes (2), and on Joseph Lake and Beaver Pond (3). # = denotes comparison. Chi-Square = the Pearson Chi-Square test statistic. df = the degrees of freedom. p = the probability.

Lake	Year	Prey items					Test			
		Amph.	Insects	Leech	Unident.	Total	#	Chi-Square	df	p
Beaver	Both	1	19	34	16	70	1	61.778	3	0.000*
		1%	27%	49%	23%					
	1994	1	16	19	16	52				
		2%	31%	37%	31%					
	1995	0	3	15	0	18				
		0%	17%	83%	0%					
	1-35	1	14	19	13	47				
		2%	30%	40%	28%					
	36+	0	5	15	3	23				
		0%	22%	65%	13%					
Tempo	Both	36	77	209	9	331	2	24.324	3	0.000*
		11%	23%	63%	3%					
	1994	25	22	57	7	111				
		23%	20%	51%	6%					
	1995	11	55	152	2	220				
		5%	25%	69%	1%					
	1-35	36	68	160	9	273				
		13%	25%	59%	3%					
	36+	0	9	49	0	58				
		0%	16%	84%	0%					
Joseph	1994	12	58	117	28	215	3	10.751	3	0.014*
		6%	27%	54%	13%					
	1-35	8	26	67	28	129				
		6%	20%	52%	22%					
	36+	4	32	50	0	86				
		5%	37%	58%	0%					

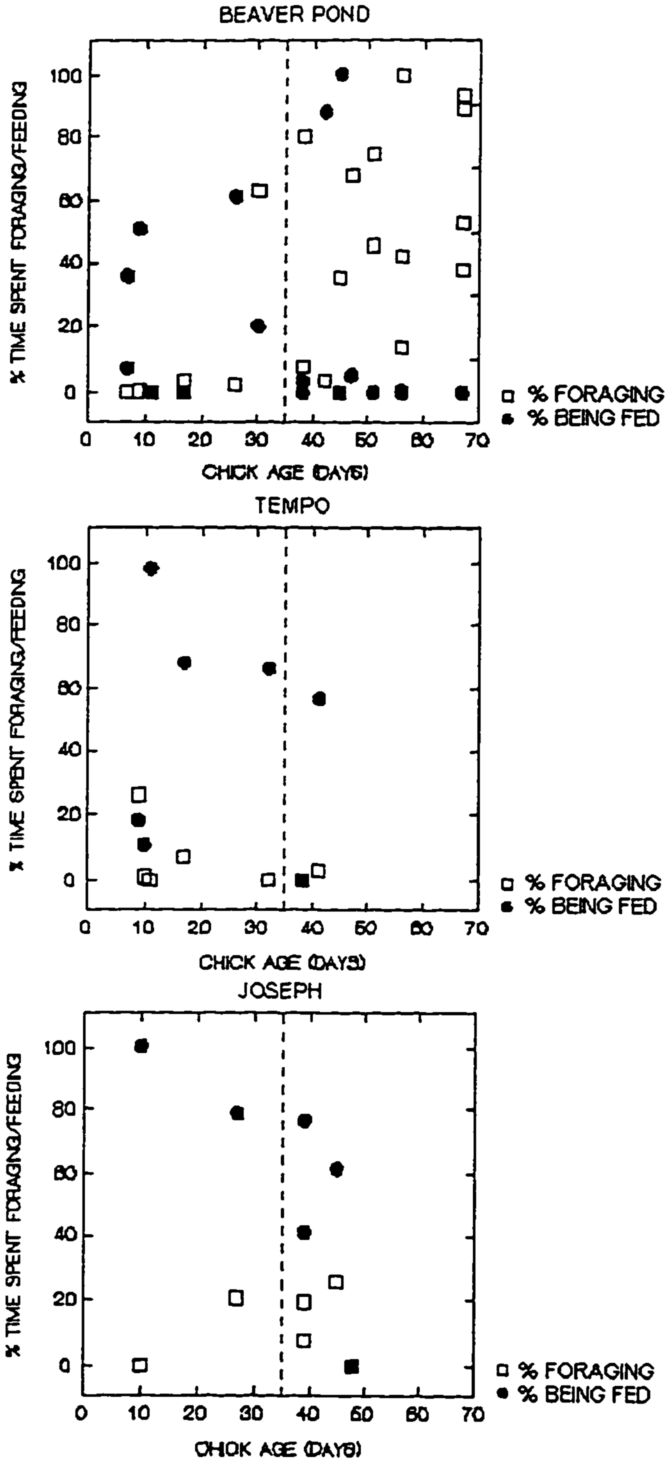

Figure 3-1. The percentage of time loon chicks on the Beaver Pond, Tempo Lake, and Joseph Lake spent foraging for themselves and were fed by their parents per observation period versus chick age (days) in 1994 and 1995 (combined). (A dark square is the result of both rates occupying the same point on the graph.)

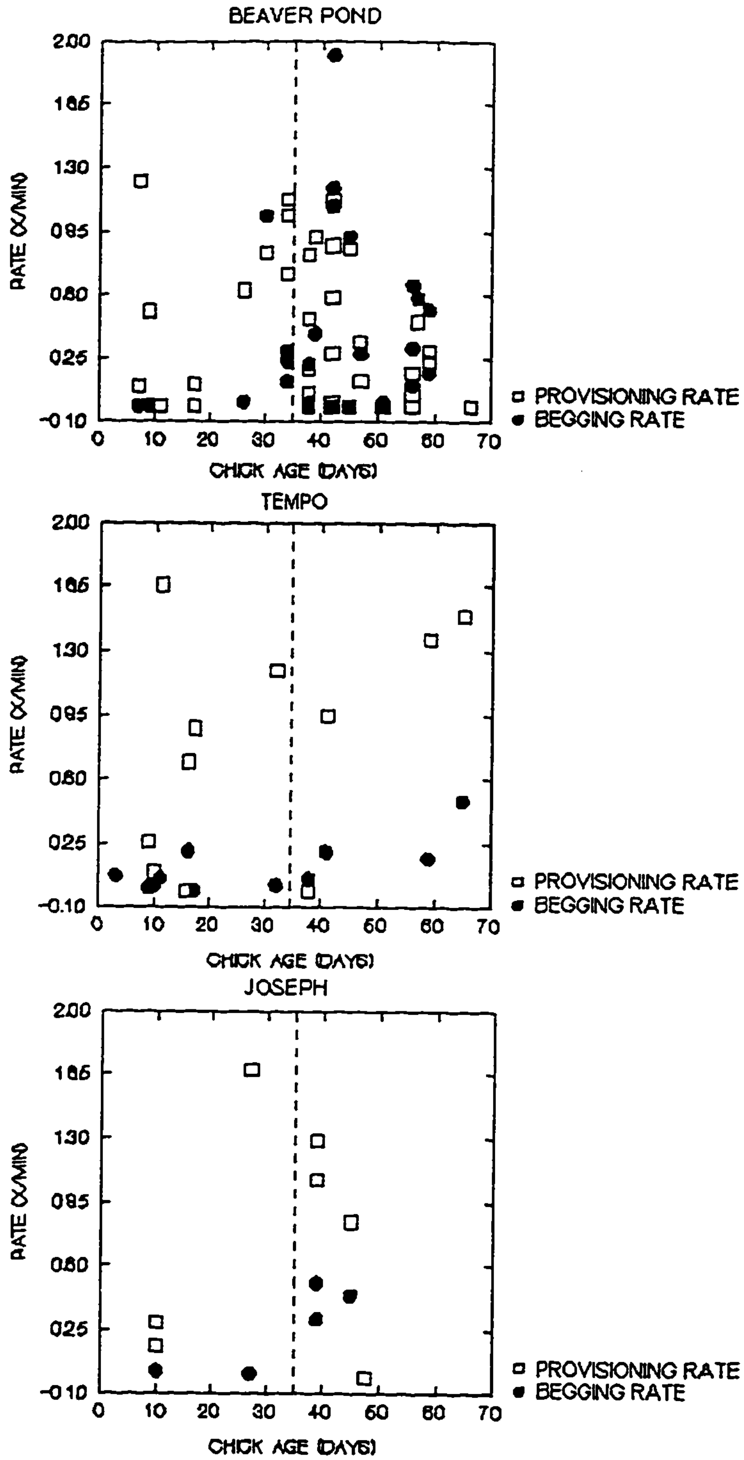

Figure 3-2. The provisioning rates (the # of times chicks accepted food from parents/min) and the begging rates (the # of times chicks pecked at their parents for food/min) per observation period of loon chicks on the Beaver Pond, Tempo Lake, and Joseph Lake versus chick age (days) in 1994 and 1995 (combined). (A dark square is the result of both rates occupying the same point on the graph.)

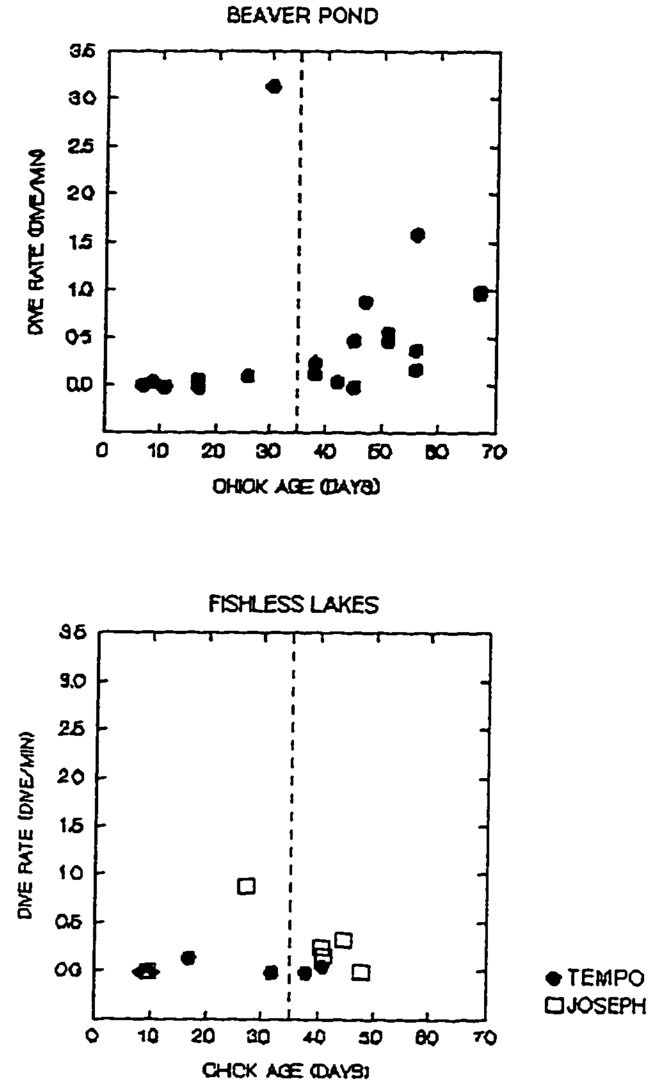

Figure 3-3. The dive rate (dive/min) per observation period of loons chicks on the Beaver Pond, Tempo Lake, and Joseph Lake versus chick age (days) in 1994 and 1995 (combined).

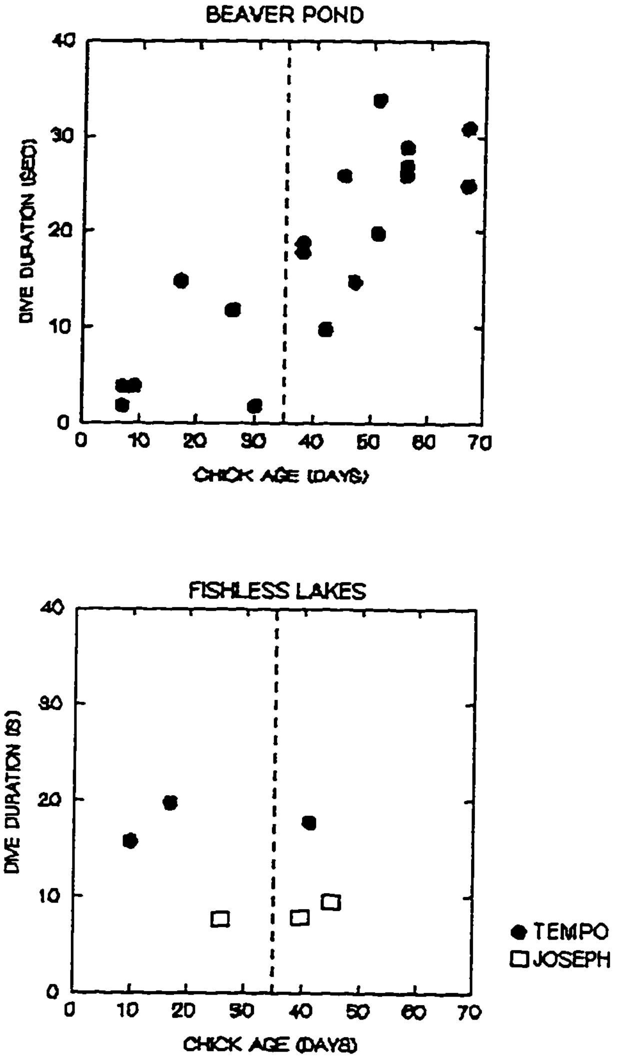

Figure 3-4. The mean dive duration (sec) per observation period of loons chicks on the Beaver Pond, Tempo Lake, and Joseph Lake versus chick age (days) in 1994 and 1995 (combined).

Appendix 3-1. The location (latitude and longitude), area, maximum depth, and total phosphorus measurements of the Fishless Lakes and the Minnow Lake (fathead minnow, *Pimephales promelas*) studied in central Alberta during the summer(s) of 1994 and/or 1995.

Lake	Location	Fish Assembledge	Area (ha)	Max. Depth (m)	Total P (ug/L)
Unnamed-"Tempo"	54°37'N 113°19'W	Fishless	9.4	2.50	108.1
Joseph	54°37'N 113°12'W	Fishless	12.1	1.50	13.5
Unnamed-"Beaver"	54°38'N 113°35'W	*P. promelas*	2.7	4.30	26.2

Appendix 3-2. The means, ± 1 standard errors (SE), medians, and ranges (minimum = Min. and maximum = Max.) of the percentage of time loon chicks performed different behaviors per observation period (N = the number of observation periods).

Behavior	Mean	SE	Median	Min.	Max.	N
Foraging/being fed	57.0	6.1	64.3	0	100	35
Preening	10.1	2.1	4.5	0	42.7	35
Floating	15.7	4.0	2.6	0	85.8	35
Sleeping	11.4	4.3	0	0	100	35
Territorial	0.1	0.1	0	0	2.3	35
Riding	5.7	3.3	0	0	92.4	35

Appendix 3-3. The median and ranges (minimum = Min. and maximum = Max.) of the percentage of time chicks were fed by their parents, the percentage of time chicks foraged for themselves, the feeding rate (# of times chick is given food by parents/min), the begging rate (# of times chick pecks at parents for food/min), the dive rate (dive/min), and the mean dive duration (s) per observation period (N = the number of observation periods) by loon chicks on Beaver Pond, Tempo Lake, and Joseph Lake in 1994 and 1995 combined. All data includes every observation period recorded and 1-approx. 41 days old, 1-35 days old and 36+ days old includes observation periods recorded during those time spans.

		% Time Fed by Parents				% Time Foraging for Self				Begging Rate			
Lakes		Median	Min.	Max.	N	Median	Min.	Max.	N	Median	Min.	Max.	N
Beaver	All data	0.2	0.0	100.0	21	14.3	0.0	99.4	21	0.070	0.000	1.930	36
	1-42	7.6	0.0	88.1	11	2.6	0.0	80.4	11	1.700	0.000	1.930	21
	1-35	14.2	0.0	61.7	8	0.2	0.0	63.2	8	0.000	0.000	1.048	11
	36+	0.0	0.0	100.0	13	46.4	0.0	99.4	13	0.180	0.000	1.930	25
Tempo	All data	57.0	0.0	97.9	7	0.9	0.0	26.7	7	0.067	0.000	0.494	11
	1-41	57.0	0.0	97.9	7	0.9	0.0	26.7	7	0.067	0.000	0.250	9
	1-35	43.6	11.2	97.9	4	4.2	0.0	26.7	4	0.050	0.000	0.250	6
	36+	57.0	0.0	66.5	3	0.0	0.0	3.1	3	0.182	0.033	0.494	5
Joseph	All data	76.9	0.0	100.0	7	8.0	0.0	26.4	7	0.050	0.000	0.517	7
	1-39	78.9	41.7	100.0	5	8.0	0.0	21.1	5	0.050	0.033	0.517	5
	1-35	100.0	78.9	100.0	3	0.0	0.0	21.1	3	0.033	0.033	0.050	3
	36+	51.7	0.0	76.9	4	14.0	0.0	26.4	4	0.383	0.000	0.517	4

Appendix 3-3. Continued

Lakes		Provisioning Rate				Dive Rate				Dive Duration				Total
		Median	Min.	Max.	N	Median	Min.	Max.	N	Median	Min.	Max.	N	Dives
Beaver	All data	0.134	0.000	1.233	37	0.183	0.000	3.145	21	19	2	34	17	572
	1-42	0.558	0.000	1.233	22	0.050	0.000	3.145	11	8	2	19	8	182
	1-35	0.636	0.000	1.233	11	0.034	0.000	3.145	8	4	2	15	6	156
	36+	0.067	0.000	1.131	26	0.483	0.000	1.600	13	26	15	34	11	416
Tempo	All data	0.950	0.000	2.517	11	0.000	0.000	0.150	7	18	16	20	3	15
	1-41	0.883	0.000	2.517	9	0.000	0.000	0.150	7	18	16	20	3	15
	1-35	0.792	0.000	2.517	6	0.017	0.000	0.150	4	18	16	20	2	11
	36+	1.200	0.000	1.501	5	0.000	0.000	0.067	3	18	-	-	1	4
Joseph	All data	0.850	0.000	1.683	7	0.200	0.000	0.833	7	7	7	9	4	106
	1-39	1.083	0.167	1.683	5	0.200	0.000	0.833	5	7	7	7	3	81
	1-35	0.300	0.167	1.683	3	0.000	0.000	0.833	3	7	-	-	1	50
	36+	0.967	0.000	1.300	4	0.258	0.000	0.417	4	7	7	9	3	56

Chapter Four

Common Loon, *Gavia immer*, Breeding Performance on Lakes With Three Different Fish Assemblages in Central Alberta

4.1 Introduction

The role aquatic birds play in food webs has been the focus of many recent studies (e. g., Gere and Andrikovics 1994, Lovvorn 1994, McKinnon and Mitchell 1994). Researchers are acknowledging the influence birds can have on aquatic systems in terms of nutrient addition (Manny *et al.* 1994, Marion *et al.* 1994) and biomass removal (Winfield 1990, Madenjian and Gabrey 1995). In addition, there is an increasing awareness of how changes in lower trophic levels affect bird populations (DesGranges and Gagnon 1994, Wanink and Goudswaard 1994). For example, fish may compete with ducks for invertebrate food sources (Eriksson 1979, Eadie and Keast 1982). Thus, decreases in fish populations, and subsequent increases in invertebrate abundance (Andersson *et al.* 1978, Eriksson *et al.* 1980, Bendell and McNicol 1987) can increase the foraging success and survival of young of duck species such as Common Goldeneye, *Bucephala clangula* (Eadie and Keast 1982), Tufted Duck, *Aythya fuligula* (Giles 1994), and American Black Duck, *Anas rubripes* (Hunter *et al.* 1986).

On the other hand, decreases in fish populations may have adverse effects on piscivorous birds. Considerable evidence indicates that declines in fish supplies can result in declines in breeding success of some-fish eating birds (Anderson *et al.* 1982, Cairns 1987, Baird 1990, Wanless and Harris 1992). However, some birds possess the ability to compensate behaviorally for changes in food supply. These birds may respond to a decline in a preferred prey population by switching to feeding on less preferred, but more abundant, prey (Blacklegged Kittiwakes, *Rissa tridactyla*, and Glaucous-wing

Gulls, *Larus glaucescens* Baird 1990; Cape Gannets, *Morus capensis*, Crawford and Dyer 1995; American White Pelicans, *Pelecanus erythrorhynchos*, Findholt and Anderson 1995; Herring Gulls, *Larus argentatus*, Bukacinska *et al.* 1996). Other species are unable to behaviorally ameliorate the effects of low food supply as they have restricted feeding areas (Brown Pelicans, *Pelecanus occidentalis*, Anderson *et al.* 1982), rigid or energetically expensive feeding habits (Thin-billed Prion, *Pachyptila belcheri*, Weimerskirch *et al.* 1995), or specialized dietary and nutritional needs (Red-necked Phalaropes, *Phalaropus lobatus*, Rubega and Inouye 1994).

Loons (*Gaviidae*) are aquatic diving birds that are thought to feed mainly on fish (McIntyre 1994). Therefore, loon productivity, measured in terms of the number of fledglings produced, should be sensitive to any alterations in trophic webs linked to changes in fish abundance and species composition. However, studies examining loon production on lakes with differing fish densities suggest that the relationship between prey composition and abundance and loon reproductive success is complex. For example, Eriksson (1986), found no relationship between Swedish Arctic Loon, *Gavia arctica*, productivity and the density of fish in nesting lakes. He suggested that declines in fish density within lakes due to acidification, and the subsequent changes in zooplankton and phytoplankton abundance and composition, resulted in increases in water clarity which increased the ability of the loons to detect prey (Eriksson 1985). In addition, he suggested that increases in prey detectability, in combination with increases in invertebrate abundance and the ability of Arctic Loons to feed their chicks invertebrates as well as fish, allows Arctic Loons to adjust to some changes in fish populations (Eriksson and Sundberg 1991). Red-throated Loons, *Gavia stellata*, on the other hand, usually nest on small fishless lakes and import fish from larger lakes or from the ocean to feed chicks (Reimchen and Douglas 1984, Eriksson *et al.* 1990). The combination of using an energetically expensive method of gathering food for chicks and having a restricted diet may contribute to the sensitivity of the Red-throated Loon to changes in fish populations (Eriksson *et al.* 1990, Eriksson 1994).

Adult Common Loons, *Gavia immer*, are thought to feed primarily on fish (McIntyre 1994, Barr 1996), but have been observed feeding fish, invertebrates, and plants to chicks (Alvo and Berrill 1992). In addition, adults normally feed chicks prey from the nesting lake, and according to Barr (1996), 423 kg of fish is needed to support two adult Common Loons and two chicks throughout the breeding season (5.5 months). However, the influence of fish abundance on the reproductive success of Common Loons is not fully understood. For example, Alvo *et al.* (1988) studied the breeding success of loons nesting on acid-sensitive lakes in the Sudbury region of Ontario and found that low-alkalinity lakes were less likely to have successfully breeding loon pairs (pairs with fledglings) than high-alkalinity lakes and that alkalinity was positively correlated with pH. Although fish abundance was not directly measured, they attributed the differences in reproductive success to differences in fish biomass as acidified lakes tend to have reduced fish populations (Schindler *et al.* 1985). However, Parker (1988) found no relationship between reproductive success and the pH of nesting lakes of Common Loons in the Adirondacks of New York. He did find that lakes with lower pH (e.g. 5.12) had lower fish densities (mean of 2.3 individuals per minnow trap) than lakes with higher pH (e.g. 5.78, mean of 80.3 individuals per minnow trap). Parker (1988) suggested that loons adjusted to changes in fish biomass by incorporating more aquatic invertebrates into their diets.

Wayland and McNicol (1990) examined the reproductive success of Common Loons in Ontario and found no relationship between loon productivity and lake pH. They did find a relationship between lake area and loon success. In fact, researchers in eastern Canada and the United States have found that loons are more likely to successfully fledge young on larger, oligotrophic lakes (as defined by total phosphorous levels <10 µg/l, Wetzel 1975): > 100 ha in New Hampshire (Blair 1992); > 40 ha in Nova Scotia (Kerekes *et al.* 1996); > 40 ha in Ontario (Wayland and McNicol 1990, Barr 1986). Although there are reports that loons nest on smaller lakes (McIntyre 1994), Kerekes (1990) and Barr (1986, 1996) suggest that small oligotrophic lakes do not have enough total food biomass to support a pair of loons and chicks.

In 1992, Paszkowski (1994) surveyed waterfowl on 25 lakes in central Alberta and found Common Loons present on a variety of lakes. The lakes are all relatively productive (total phosphorus >10 µg/l, Wetzel 1975), but they differ in terms of size, depth, and fish species composition. Based on their morphometry and fish community these lakes can be categorized into three types (Robinson and Tonn 1989): 1) "Pike Lakes" which are usually larger (≥ 40 ha) and deeper (≥ 9 m) and, due to predation upon small-bodied fish, are populated only by large-bodied fish such as northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersoni*); 2) "Minnow Lakes" which are usually small (< 40 ha) and shallow (< 9 m), and due to low winter oxygen levels, contain only small-bodied fish such as fathead minnow (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*); and 3) "Fishless Lakes" which are usually small (< 40 ha), shallow (< 9 m), and naturally fishless, most likely due to frequent and prolonged winter hypoxia and the lack of permanent inflow or outflow streams.

The fledging success of loons on these different lake types in Alberta is unknown, but it may related to loon foraging success on different prey bases. For example, Barr (1996) found that loons prefer to eat smaller individuals (5 - 15g) of many fish species (e.g., yellow perch and white sucker); therefore loons foraging on larger lakes may compete for prey with larger piscivorous fish. In addition, loon chicks may be prey for larger fish (Yonge 1981). The smaller Minnow and Fishless Lakes may offer protection from fish predators, and may be easier to defend from other avian competitors (Belant 1991), but may lack adequate food supplies (Barr 1996). However, the presence of successfully breeding loons on these small lakes indicates that the lakes contain enough prey biomass to support one loon pair and chicks and that Common Loons are more flexible in their dietary requirements (i.e., supplement diet with invertebrates) and in behavior than previously thought.

Thus, Paszkowski's (1994) initial survey raised questions concerning loon production and success on small lakes that are not traditionally considered typical loon habitat. This study was initiated to address some of these questions, specifically: 1) to examine the presence and absence of territorial loons, nesting loons, and fledglings on lakes in central Alberta to determine the use by loons of Fishless, Minnow, and Pike Lakes; 2) to examine the percentage of Fishless, Minnow, and Pike Lakes where territorial loons, nesting loons, and fledglings were present every year, at least in one year, and in no years of the survey to determine if some lakes offer a more reliable loon territory, nesting, and/or fledging habitat than others; 3) to examine closely the reproductive patterns of loons on Fishless and Minnow Lakes (atypical habitats) to determine patterns behind reproductive success or failure and; 4) to compare the fledge rate (the number of fledged chicks per territorial loon pair, a common indicator of Common Loon breeding success), of loons present on the three lake types to that of loons nesting in other areas of Canada and the United States.

Comparing the reproductive patterns and success of loons on the three lake types to each other and to that of lakes in other areas of North America allows for the assessment of these lakes as Common Loon nesting habitat. In addition, because events such as heavy rainfall causing nest flooding may affect loons on all lake types and mask the influence of lake type differences on reproductive success, and because loon pairs do not attempt to nest every year (McIntyre 1994), it was essential to examine reproductive patterns across multiple years in order to provide a more accurate description of Common Loon reproduction on lakes in central Alberta.

4.2 Methods

4.2.1 Study Sites

From 1993 - 1996, I conducted a census for Common Loons on 18-41 lakes in the area around the Meanook Biological Research Station (54°37'N 133°20') in central Alberta, Canada. The lakes varied with respect to area, maximum depth, and prey base (see Appendix 4-1). The morphometry and chemical characteristics of some of the lakes were first measured in a previous study in 1986 (Prepas *et al.* 1988) and the area of these lakes were remeasured in 1995 with the use of topography maps (Paszkowski, unpubl.). The depth, area, and phosphorous concentrations of the remaining lakes were measured during the summers of 1993, 1994, and 1995 (Paszkowski, unpubl.). The fish populations in some of the lakes were first sampled in 1986 and 1987 (Robinson and

Tonn 1989) and resampled in 1993 and 1994 (Tonn and Paszkowski, unpubl.). Remaining lakes were sampled during the summers of 1993 and 1994 (Tonn and Paszkowski, unpubl.).

The natural vegetation surrounding the lakes was representative of boreal mixedwood forests with the dominant tree species being trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). The shoreline vegetation of the lakes usually consisted of a number of sedge and grass species. However, the shorelines of some lakes were grazed by cattle. The dominant emergent vegetation was common cattail (*Typha latifolia*), and the submergent vegetation included coontail (*Ceratophylum demersum*) and pondweed (*Potamogetan* spp.). The lakes were also characterized by a number of floating-leaved species such as yellow water lily (*Nuphar variegatum*) and smartweed (*Polygonum natas*).

4.2.2 Survey Methods

Large lakes were censused from a canoe using binoculars; smaller lakes were censused from shore using a spotting scope. In 1992, Paszkowski (1994) surveyed 25 lakes once to determine the general distribution of Common Loons in the Athabasca area. In 1993, I added 16 lakes to the initial survey for a total of 41 lakes (8 Fishless Lakes, 18 Minnow Lakes, 15 Pike Lakes), and a coarse-scale evaluation of use of the lake types was achieved by noting the presence or absence of territorial loon pairs during May or June visits (e.g., May 23 - June 8 in 1994) to each lake. If territorial loon pairs were observed, the lake was again visited in July (e.g. July 6 - 19 in 1994) to check for the presence or absence of chicks. If chicks were present, the lake was visited again in late August (e.g., August 16 - 25 in 1994) to determine the presence or absence of fledglings.

Chicks at least eight weeks old (McIntyre 1988) in late August were considered to be fledglings. When the exact age of the chick was unknown, the size of the chick (similar to adult size) and presence of juvenile feathers were used as an approximation (Barr 1973).

In 1994, I visited 31 (7 Fishless Lakes, 15 Minnow Lakes, 9 Pike Lakes) of the lakes censused in 1993, allowing for the location of the nest of individual pairs, as well as the monitoring of chick survival and fledgling production. The reproductive patterns of individual loon pairs on 6 of the Fishless Lakes and 8 of the Minnow Lakes that were visited in 1994, were closely monitored in 1995 (1 Minnow Lake was visited once in 1995), and 7 of the Pike Lakes were visited once in late August to check for the presence of fledglings (21 lakes in total were surveyed). In 1996, 18 lakes (4 Fishless Lakes, 7 Minnow Lakes, 7 Pike Lakes) were visited once in late August to determine if any loon pairs on the lakes fledged young.

4.2.3 Quantification and Analysis of Survey Data

4.2.3.1 Phosphorus Concentration and Morphometry Differences Between Lake Types

Based on the 41 lakes surveyed in 1993, one-way Analysis of Variance (ANOVA) tests were performed to determine if Fishless, Minnow, and Pike Lakes differed in terms of area, depth, and phosphorus concentrations. If significant differences were found, Tukey Honestly Significant Difference (HSD) Multiple Comparison tests were performed to determine which lake types differed from each other.

4.2.3.2 Presence/Absence of Loons on Lakes From 1993-1996.

The presence/absence of Common Loons on the survey lakes data were examined to determine if loons were more or less likely to be present on Fishless, Minnow or Pike Lakes. Using the 1993 and 1994 survey data, 2 X 2 contingency tables (Minnow vs Fishless, Minnow vs Pike, and Pike vs Fishless) were analyzed using Fishers Exact tests to determine if the proportion of lakes with territorial pairs, evidence of breeding (nest and/or chicks), and fledglings differed among Fishless, Minnow, and Pike Lakes. Because lakes were visited less frequently in 1995 and 1996 only a subset of these comparisons could be made. Due to the small sample sizes used in many of the contingency tables (more then 20% of the cells had a frequency of less then five), Fishers Exact tests were used to analyze the tables because these tests are more robust with low sample sizes (Zar 1984).

The percentage of Fishless, Minnow, and Pike Lakes, that were surveyed each year, with territorial loons present, nesting pairs present, and fledglings present in every year, in at least in one year, and in no years of the survey was calculated to examine year to year variation of loon presence on lakes and between lake types.

Also presented are the yearly reproductive patterns (presence of territorial pairs, number of eggs, number of chicks, number of fledglings) of loons on the Minnow and Fishless Lakes that were visited in every year of the survey. These detailed examinations were done to determine possible causes of variation in the reproductive patterns of loons among years and among lakes. In addition, many of these small lakes were visited frequently in conjunction with other studies in the area (e.g., loon behavior, Chapters 2 and 3), and, as a consequence, the reproductive status of loons on the small lakes were followed much more closely than on Pike Lakes.

The yearly and average (3 year means, 1993-1995) fledge rates of loon pairs on Fishless, Minnow, Pike Lakes were compared to determine if the number of young fledged per territorial pair differed between the lake types and to determine if the rates differed from that of loons in other geographic areas.

4.3 Results

4.3.1 Phosphorus Concentration and Morphometry Differences Between Lake Types

Phosphorus concentrations, a measure of productivity in lake systems, of the 3 lake types were not significantly different from each other. As expected, the lake types differed in terms of area (ANOVA $F_{2,38} = 12.598$, $p < 0.05$; Fishless Lakes $N = 8$, $\overline{x} = 25.9$ ha ± 7.8 ha; Minnow Lakes $N = 18$, $\overline{x} = 51.8$ ha ± 12.9 ha; Pike Lakes $N = 15$, $\overline{x} = 147.9$ ha ± 22.6 ha) and depth (ANOVA $F_{2,38} = 14.986$, $p < 0.05$; Fishless Lakes $N = 8$, $\overline{x} = 2.3$ m ± 0.7 m; Minnow Lakes $N = 18$, $\overline{x} = 2.7$ m ± 0.5 m; Pike Lakes $N = 15$, $\overline{x} = 12.6$ m ± 2.3 m). Pike Lakes were significantly different from Minnow Lakes (area = Tukey HSD Multiple Comparison $p < 0.05$; depth = Tukey HSD Multiple Comparison $p < 0.05$) and Fishless Lakes (area = Tukey HSD Multiple Comparison $p < 0.05$; depth = Tukey HSD Multiple Comparison $p < 0.05$) but Minnow Lakes and Fishless Lakes were not significantly different from each other in terms of size or depth (area = Tukey HSD Multiple Comparison $p = 0.662$; depth = Tukey HSD Multiple Comparison $p = 0.986$)

4.3.2 Presence/Absence of Loons on Lakes From 1993-1996

4.3.2.1 Territorial Pairs

Territorial loons were present on most of the lakes surveyed in 1993 - 1995 (Table 4-1 and Appendices 4-2, 4-3, and 4-4). The proportion of surveyed Fishless and Minnow Lakes with territorial loons present varied between years but was, on average (Table 4-1), similar between the two lake types. In fact, the proportion of Fishless Lakes with territorial loons present was not significantly different from the proportion Minnow Lakes with territorial loons present in any year of the survey (Table 4-2).

The proportion of Pike Lakes with territorial loons present was similar between 1993 and 1994 (Table 4-1). The proportion of Pike Lakes where territorial loons were present was, on average, greater than the proportion of Fishless Lakes or Minnow Lakes (Table 4-1) but was only significantly greater than Minnow Lakes in 1993 and not significantly different than Fishless Lakes in either year (Table 4-2).

Territorial loons were consistently found on most Fishless Lakes and all Pike Lakes monitored every year of the survey (Table 4-3). Territorial loons were present every year on half of the Minnow Lakes surveyed but were present at least once during the survey for most of the Minnow Lake censused.

4.3.2.2 Nesting Pairs

Territorial loons failed to nest on some lakes during each census year (Table 4-1). Although many territorial loons on Minnow Lakes did not attempt to nest, the overall proportion of Fishless and Minnow Lakes where nest or chicks were observed was similar between the two lake types each year (Table 4-1). In fact, the proportion of Fishless Lakes with nesting loons present was not significantly different from the proportion of Minnow Lakes with nesting loons present in any year of the survey (Table 4-2).

Each year the proportion of Pike Lakes with nesting loons present was greater than that of Fishless or Minnow Lakes (Table 4-1). However, the proportion of Pike Lakes with nesting loons present was not significantly different from the proportion of Fishless Lakes or the proportion of Minnow Lakes with nesting loons present in either year (Table 4-2).

Nests were observed on most of the Pike and Fishless Lakes surveyed each year (Table 4-3) and loon pairs that nested on these lake types usually hatched chicks. Nesting loons were present each year on only one Minnow Lake, Beaver Pond, and nests or chicks were never observed on half the Minnow Lakes surveyed. Causes of egg loss (Table 4-4) included predation, abandonment, or drowning (falling into water accidentally or possibly removed from nest by adults).

4.3.2.3 Fledglings

The percentage of Fishless Lakes and Minnow Lakes with fledglings present did not vary greatly between 1993 - 1995 (Table 4-1). However, in 1996, chicks were present in late August on 75% of the Fishless Lakes; the highest percentage in any year. Many of the chicks observed in late August were small and downy (Table 4-4) and could not be designated, with confidence, as fledglings. No chicks were present in late August of 1996 on any Minnow Lake, the poorest result in all the years of the survey for this lake type. On average, the percentage of Fishless Lakes and the percentage of Minnow Lakes with fledglings were similar (Table 4-1). The proportion of Fishless Lakes with fledglings present was not significantly different from the proportion of Minnow Lakes with fledglings present in any year of the survey (Table 4-2).

The percentage of surveyed Pike Lakes with fledglings varied among years (Table 4-1). However, a greater percentage of Pike Lakes had fledglings present on them each year of the survey, and overall, than Fishless and Minnow Lakes (Table 4-1). In addition, the proportion of Pike Lakes with fledglings present was significantly greater than the proportion of Minnow Lakes with fledglings present, 2 of the 4 years of the survey (Table 4-2). The proportion of Pike Lakes with fledglings present was significantly greater than the proportion of Fishless Lakes with fledglings present, once during the 4 years of the survey (Table 4-2).

Two Pike Lakes were the only lakes to have fledglings present in all 4 years of the survey (Table 4-3) and only one Pike Lake failed to produce a fledging in at least one year of the survey. Most Fishless Lakes and Minnow Lakes surveyed each year, never produced a fledgling (Table 4-3). However, loons that hatched chicks on Minnow Lakes also fledged young. On the other hand, chicks hatched on Fishless Lakes often disappeared (presumed dead) at 3- 7 weeks of age (Table 4-4).

4.3.2.4 Fledge Rate: Young Fledged/Territorial Pair

Each year, the fledge rate of loon pairs on Fishless Lakes was less then that of the fledge rate of loon pairs on Minnow and Pike Lakes (Table 4-5). In fact, on average (3 year mean), less then 0.1 young were fledged per loon pair on Fishless Lakes. Six times as many young were fledged per loon pair on Pike Lakes than on Fishless Lakes (Table 4-5). Twice as many young were fledged per loon pair on Minnow Lakes than on

Fishless Lakes and twice as many young were fledged per loon pair on Pike Lakes than on Minnow Lakes.

4.4 Discussion

Unlike Vermeer (1973) who found Common Loons present only on larger (> 150 ha) lakes in Alberta, I found territorial loon pairs present on a variety of lakes in central Alberta including smaller lakes (some < 10 ha), with and without fish, as well as larger lakes with game fish. This finding also differs from that of Kerekes (1990) who found that no lake < 20 ha in Kejimkujik National Park, Nova Scotia was occupied by territorial loons and from that of Ruggles (1994) who never observed Common Loons on lakes < 12 ha in Alaska. Although loons are often present on the small lakes in Alberta, the larger Pike Lakes ($\bar{x}$ =147.9 ha) are more likely to be occupied by territorial loon pairs, nesting loon pairs, and fledglings than the smaller lakes (Fishless Lakes $\bar{x}$ = 25.9 ha; Minnow Lakes $\bar{x}$ = 51.8 ha). On the other hand, although some studies suggest that loons will not attempt to nest on fishless lakes (Barr 1986) or that fledglings cannot survive on fishless lakes (Alvo *et al.* 1988), the presence or absence of fish in lakes of similar size in this study did not influence the presence of territorial loons, nesting loons, or fledglings.

Although loons are generally more successful on Pike Lakes than on Fishless or Minnow Lakes, the smaller lakes are not without value. Fishless and Minnow Lakes offer good habitats for territorial loons as the smaller lakes may be easier to defend (Belant 1991). In addition, the small lakes may be important feeding areas for loons that are unable to find mates or that do not nest or hatch chicks. Foraging observations (Chapter 2) suggest that adult Common Loons can meet their daily caloric needs by feeding on invertebrates and/or small-bodied fish.

Although loons nested on only a small percentage of Fishless and Minnow Lakes, these lakes consistently had nesting loons year after year. These lakes appear to have shorelines that offer appropriate nest site locations: cover from predators and easy access for adults (McIntyre 1983). Lakes where territorial loons do not attempt to nest (e.g., many of the Minnow Lakes) often have many floating beds of *Typha* and/or steep banks that make access to land impossible. These lakes also have grazed shorelines lacking in structural cover.

Nesting loons on all the Fishless Lakes and most of the Minnow Lakes managed to hatch at least one chick. Although not a frequent occurrence, causes of nests failure in this study, were similar to that found by Fox *et al.* (Hanson Lake, Saskatchewan; 1980) and Croskery (40 lakes in northwestern Ontario; 1991), and included egg depredation by mammalian predators, abandonment of the egg on the nest, and egg drowning.

Although Common Loons frequently nest and hatch chicks on some Fishless Lakes, chicks rarely survive to fledge. It does appear that some lakes (e.g., Tempo Lake) are more likely to fledge young than other lakes (e.g., Joseph Lake). The causes of the year to year reproductive variation within and between lakes may be related to man-made disturbances or predation or may involve the abundance of suitable prey within the lake. The leading cause of chick death in Croskery's (1991) study was fish and avian predation. In addition, recreational boaters on the lakes in Croskery's (1991) study often separated chicks from adults. Without the protection of their parents, chicks were susceptible to avian predators. Noise created by the cutting of trees in the riparian areas around two of the Fishless Lakes in this study may have played a role in the death of the chicks on the lakes in 1994. Before the cutting, Joseph and Tempo lakes experienced little man-made disturbance. The constant and loud noise created by the cutting appeared to agitate the adult loons and the adults abandoned the chicks shortly after the disturbances began. The chicks disappeared from the lake soon after abandonment.

Predation could have been responsible for the death of chicks on the Fishless Lakes; however chicks' bodies were never recovered, so the causes of death are unknown. A chick disappeared on Joseph Lake in 1994 prior to any disturbance and in 1995 without the influence of any disturbance. Thus, it is difficult to determine the role the disturbance played in abandonment. All chicks that disappeared on Fishless Lakes were between 3 and 7 weeks old. Four weeks after hatching appears to be a critical time for chicks as they experience an exponential increase in growth (Parker 1988). Typically, adult loons respond to this increase demand by switching from a primarily invertebrate diet to that of fish (Alvo and Berrill 1992). Evidence (Chapters 3 & 2) suggests that adults feeding on invertebrates may have a difficult time meeting their own energy requirements plus those of larger chicks. Rather than risking their own health and their future reproductive success, adult loons may abandon their chicks if meeting the energetic needs of the chicks proves to be too difficult. In this regard, adult loons behave similar to many other long-lived species (e.g., Antarctic Petrel, *Thalassoica antarctica*, Saether *et al.* 1993, Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Mauck and Grubb 1995, Arctic Skuas, *Stercorarius parasiticus*, Phillips *et al.* 1996).

The ability of the adults on Fishless Lakes to meet their chicks energy requirements may be influenced by the availability of large macroinvertebrates, such as leeches, that offer many calories per provisioning episode. Adults on lakes, such as Tempo Lake, that feed mainly large leeches to their chicks (Chapter 3), are more likely to fledge young than adults on lakes, such as Joseph Lake, that feed mainly smaller invertebrates to chicks. The ability of adults to feed large invertebrates to their chicks may depend on the abundance of these species within the lake. For example, invertebrate sampling suggests that leeches were more abundant in Tempo Lake than in Joseph Lake (unpubl. data). In addition, leeches in Tempo Lake were more abundant in 1995 than in 1994. Correspondingly, a chick was fledged on Tempo Lake in 1995 but not in 1994, suggesting that year to year variation of invertebrate abundance may be responsible for yearly variation of fledging success on these lakes.

Some Minnow Lakes may not offer suitable nesting habitat, but loons that do nest on Minnow Lakes usually hatch chicks and fledge young. Evidence suggests that adult loons are able to meet the daily energetic needs of older chicks by feeding mostly small-bodied fish to chicks (Chapter 3). The ability of adults to provide chicks with enough calories per day may depend on the availability of fish within the lakes. For example, at least one chick fledged on the Beaver Pond in every year of the survey except for 1996. Correspondingly, the fathead minnow population in 1996 was estimated to be much lower (360 minnows), than in previous years (e.g. 23,500 in 1993, W. M. Tonn, unpublished data).

In comparison to other regions, the mean fledge rate of loons on the surveyed lake types in central Alberta from 1993 -1995 (0.40 young fledged/territorial pair) is lower then that found for loon populations of the U.S.A. (12 - 15 years of monitoring, 59 - 1546 territorial pairs, mean fledge rate of 0.51 - 0.59 young fledged/territorial pair, McIntyre 1994) and of that of a relatively stable population of over 100 territorial loon pairs on one large lake in Saskatchewan (1973-1974, mean fledge rate of 0.53 young fledged/territorial pair, Fox *et al.* 1980). The general consensus is that a fledge rate of approximately 0.50 young fledged/territorial pair will maintain a stable loon population (McIntyre 1994). The low fledge rate from my study probably reflect the inclusion of a variety of lakes in the survey. The mean fledge rate of loons on Pike Lakes in central Alberta from 1993 -1994 (0.53 young fledged/territorial pair) is similar to rates found elsewhere. The mean fledging rate of loons on Minnow Lakes (0.22 young fledged/territorial pair) and on Fishless Lakes (0.08 young fledged/territorial pair) is considerably less than that of loons on Pike Lakes in Alberta and of loons elsewhere.

Thus, smaller lakes, especially Fishless Lakes, appear to be "sub-optimal habitats" for Common Loons in Alberta. The question remains as to why loons continue to nest on lakes where they never or rarely fledge young. As I did not band loons in my study area, I do not know if the same loon pairs returned each year to a particular lake. The presence of loon pairs on these lakes each year may suggest that loons cannot "assess" the future quality, in terms of reproduction, of the lakes they occupy. It could also indicate that lakes in central Alberta are saturated with loons; loon pairs may be forced to nest on lower quality habitats or not nest at all. However, the absence of loon pairs on many lakes suggests does not support this explanation. The presence of returning loons on these lakes may indicate that lake/nest site fidelity is a strong and perhaps an inflexible behavior of Common Loons. Some other long-lived species exhibit similar nest fidelity but not to the same degree as loons. For example, Buffleheads (*Bucephala albeola*) that successfully hatch young are more likely to return to the same nest site (Gauthier 1990) than unsuccessful breeders. On the other hand, Furness and Monaghan (1987) suggest that many colonial seabirds (e.g., Shags, *Phalacrocorax aristotelis*, Aebischer 1995) are very site tenacious once they have initially bred in a colony and will return to the colony in subsequent breeding seasons regardless of food conditions in the area.

The lower fledge rates of loons on Minnow Lakes and on Fishless Lakes does not indicate that these type of lakes are not valuable loon habitats. For example, Minnow and Fishless Lakes that do fledge young are more productive in terms of fledglings produced/ha (e.g., 0.74 young fledge/ha on the Beaver Pond in 1994) than the larger Pike Lakes (e.g., a maximum of 0.03 young fledged/ha). In addition, one Minnow Lake, Beaver Pond, was the smallest lake (2.69 ha) in the survey but loons there consistently produced fledglings. Fledglings were also observed on Tempo Lake, which is naturally fishless, three of the five years (1992 - 1996) of the survey. Less than 30% of Pike Lakes surveyed every year of the study produced chicks in all four years of the survey. Croskery (1990) found that only 4.5% of 254 loon territories on 21 lakes in northwestern Ontario produced chicks all 4 years of his study. Kerekes (1996) also noted that not even the largest lakes produced chicks every year of his 7 year study monitoring loons on 25 lakes Nova Scotia. Thus, the prevalence and success of loon on smaller lakes with prey bases such as invertebrates and small-bodied fish, indicates that Common Loons are much more flexible in their nesting and dietary requirements than traditionally thought and that these “atypical” lakes should not be ignored in Common Loon breeding surveys.

4.5 Literature Cited

Aebischer, N. J. 1995. Philopatry and colony fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. IBIS 137:11-18.

Alvo, R. and M. Berrill. 1992. Adult Common Loon feeding behavior is related to food fed to chicks. Wilson Bulletin 104:184-185.

Alvo, R., Hussell, D. J. T. and M. Berrill. 1988. The breeding success of common loons (*Gavia immer*) in relation to alkalinity and other lake characteristics in Ontario. Canadian Journal of Zoology 66:746-752.

Anderson, D. W., Gress, F. and K. F. Mais. 1982. Brown pelicans: influence of food supply on reproduction. Okios 39:23-31.

Andersson, G., Berggren, H., Cronberg, G. and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59:9-15.

Baird, P. H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scandinavica 21:224-235.

Barr, J. F. 1973. Feeding biology of the Common Loon (*Gavia immer*) in oligotrophic lakes of the Canadian Shield. Ph. D. thesis. University of Guelph,Ontario.

Barr, J. F. 1986. Population dynamics of the Common Loon (*Gavia immer*) associated with mercury contaminated waters in northwestern Ontario. Canadian Wildlife Service Occasional Paper No. 56.

Barr, J. F. 1996. Aspects of Common Loons (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321:119-144.

Belant, J. L. 1991. Territorial activities of Common Loons on single-pairs lakes. Passenger Pigeon 53:299-302

Bendell, B. E. and D. K. McNicol 1987. Fish predation, lake acidity and the composition of aquatic insect assemblages. Hydrobiologia 150:193-202.

Blair, R. B. 1992. Lake features, water quality and the summer distribution of Common Loons in New Hampshire. Journal of Field Ornithology 63:1-9.

Bukacinska, M., Bukacinska, B. and A. Spaans. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). Auk 113:300-309.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5:261-271.

Crawford, R. J. M. and D. M. Dyer 1995. Responses of four sea birds to fluctuating availability of Cape anchovy *Engraulis capensis* of South America. IBIS 137:329-339

Croskery, P. R. 1990. The importance of individual territories to the long term production of Common Loons, *Gavia immer,* in northwestern Ontario. Canadian Field-Naturalist 104:557-560.

Croskery, P. R. 1991. Common Loon, *Gavia immer,* nesting Success and young survival in northwestern Ontario. Canadian Field-Naturalist 105:45-48.

DesGranges, J. L. and C. Gagnon. 1994. Duckling response to changes in the trophic web of acidified lakes. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:207-221

Eadie, J. and A. Keast. 1982. Do goldeneye and perch compete for food? Oecologia 55:225-330.

Eriksson, M. O. G. 1979. Competition between freshwater fish and goldeneyes *Bucephala clangula* (L.) for common prey. Oecologia 41:91-107.

Eriksson, M. O. G., Henrikson, L., Nilsson, B. I., Nyman, G., Oscarson, H. G. and A. E. Stenson. 1980. Predator-prey relations important for the biotic changes in acidified lakes. Ambio 9:248-249.

Eriksson, M. O. G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. Ornis Scandinavica 16:1-7.

Eriksson, M. O. G. 1986. Reproduction of Black-throated Diver *Gavia arctica* in relation to fish density in oligotrophic lakes in southwestern Sweden. Ornis Scandinavica 17:245-248.

Eriksson, M. O. G., Blomqvist, D., Hake, M. and O. C. Johansson. 1990. Parental feeding in the Red-throated Diver *Gavia stellata.* IBIS 132:1-13.

Eriksson, M. O. G and P. Sundberg. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. Bird Study 38:135-144.

Eriksson, M. O. G. 1994. Susceptibility to fresh water acidification by two species of loon, Red-throated Loons (*Gavia stellata*) and Arctic Loons (*Gavia arctica*) in southwest Sweden. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:439-444.

Findholt, S. L. and S. H. Anderson. 1995. Diet and prey use patterns of the American White Pelican (*Pelecanus erythrorhynchos*) nesting at Pathfinder Reservoir, Wyoming. Colonial Waterbirds 18:47-57.

Fox, G. A., Yonge, K. S. and S. G. Sealy. 1980. Breeding performance, pollutant burden and eggshell thinning in Common Loons Gavia immer nesting on a Boreal Forest lake. Ornis Scandinavica 11:243-248.

Furness, R. W. and P. Monaghan. 1987. Seabird Ecology. Blackie and Son Ltd. Glasgow.

Gauthier, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in buffleheads. Auk 107:126-132.

Gere, G. and S. Andrikovics. 1994. Feeding of ducks and their effects on water quality. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:157-161.

Giles, N. 1994. Tufted Duck (*Aythya fuligula*) habitat use and brood survival increases after fish removal from gravel pit lakes. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:387-392.

Hunter, M. L, Jr., Jones, J. J., Gibbs, K. E. and J. R. Moring. 1994. Duckling response to lake acidification: do black ducks and fish compete? Okios 47:26-32.

Kerekes, J. J. 1990. Possible correlation of summer common loon (*Gavia immer*) population with the trophic state of a water body. Internat. Verein. Limnol. 24: 349-353.

Kerekes, J. J., Duggan, M., Tordan, R., Boros, G. and M. Bronkhorst. 1996. Abundance and distribution of fish-eating birds in Kejimkujik National Park 1988-1995. Lake and Reservoir Management 11:156.

Lovvorn, J. R. 1994. Biomechanics and foraging profitability: an approach to assessing trophic needs and impacts of diving ducks. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:223-233.

Madenjian, C. P. and S. W. Gabrey. 1995. Waterbird predation on fish in western Lake Erie: a bioenergetics model application. Condor 97:141-153.

Manney, B. A., Johnson W. C. and R. G. Wetzel. 1994. Nutrient additions by waterfowl to lakes and reservoirs: predicting their effects on productivity and water quality. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:121-132.

Marion, L., Clergeau, P., Brient, L. and F. Bertru. 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. In:

Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:133-147.

Mauck, R. A. and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. Animal Behavior 49:999-1008.

McKinnon, S. L. and S. F. Mitchell. 1994. Eutrophication and black swan (*Cygnus atratus* Latham) populations: tests of two simple relationships. In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:163-170.

McIntyre, J. W. 1983. Nurseries: A consideration of habitat requirements during the early chick-rearing periods in Common Loons. Journal of Field Ornithology 54:247-253.

McIntyre, J. 1988. The Common Loon. University of Minnesota Press. Minneapolis.

McIntyre, J. 1994. Loons in freshwater lakes. In: Kerekes, J. J.(eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:373-413.

Parker, K. E. 1988. Common loon reproduction and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66:804-810.

Paszkowski, C. A. 1994. Factors affecting aquatic bird assemblages in central Alberta. Proceedings of the 3rd Annual Alberta Lake Management Society 15-19.

Phillips, R. A., Caldow, R. W. G. and R. W. Furness. 1996. The influence of breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*. IBIS 138:140-149.

Prepas, E. E., Dunnigan, M. E. and A. M. Trimbee. 1988. Comparison of in situ estimates of chlorophyll a obtained with Whatman GF/F and GF/C glass-fiber filters in mesotrophic and hypereutrophic lakes. Journal of Fisheries and Aquatic Sciences 45:910-914.

Reimchen, T. E. and S. Douglas. 1984. Feeding schedule and daily food consumption in Red-throated Loons (*Gavia stellata*) over the prefledging period. Auk 101:593-599.

Robinson, C. L. K. and W. M. Tonn. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. Canadian Journal of Fisheries and Aquatic Sciences 46:81-89.

Rubega, M. and C. Inouye. 1994. Prey switching in Red-necked phalaropes *Phalaropus lobatus*: Feeding limitations, the functional response, and water management at Mono Lake, California, USA. Biological Conservation 70:205-210.

Ruggles, A. K. 1994. Habitat selection by loons in southcentral Alaska. In: Kerekes, J. J. (eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:421-430.

Saether, B-E, Andersen, R. and H. C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird: An experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antarctica.* Behavioral Ecology and Sociobiology 33:147-150.

Schindler, D. W., Mills, K. H., Malley, D. F., Findlay, D. L., Shearer, J. A., Davies, I. J., Turner, M. A., Lindsey, G. A. and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. Science 228:1395-1401.

Vermeer, K. 1973. Some Aspects of the nesting requirements of Common Loons in Alberta. Wilson Bulletin 85:429-435.

Wanink, J. H. and K. Goudswaard. 1994. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria, East Africa, on the diet of Pied Kingfishers (*Ceryle rudis*). In: Kerekes, J. J. (ed.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:367-376.

Wanless, S. and M. P. Harris. 1992. Activity budgets, diet and breeding success of Kittiwakes *Rissa tridactyla* on the Isle of May. Bird Study 39:145-154.

Wayland, M. and D. K. McNicol. 1990. Status report on the effects of acid precipitation on common loon reproduction in Ontario: The Ontario Lakes Loons Survey Technical Report Series No. 92. C. W. S., Ontario region.

Weimerskirch, H. Chastel, O. and L. Ackermann. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion, *Pachyptila belcheri*. Behavioral Ecology and Sociobiology 36:11-16.

Wetzel, R. G. 1975. Limnology. W.B. Saunders Co. Toronto.

Winfield, I. J. 1990. Predation pressure from above: observations on the activities of piscivorous birds at a shallow lake. In: P. Biro and J. F. Talling (eds.) Trophic Relationships in Inland Waters. Hydrobiologia 191:223-231.

Yonge, K. S. 1981. The breeding cycle and annual production of the Common Loon (*Gavia immer*) in the boreal forest region. MS thesis, University of Manitoba, Winnipeg.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Inc. New Jersey.

Table 4-1. The number and percentage () of Fishless, Minnow, and Pike Lakes and the total lakes with territorial loons, nests and/or chicks, and fledglings present in 1993-1996. Also presented are percentage means (± 1 standard error, with more than 2 yearly percentages).

	Total lakes	Fishless	Minnow	Pike
1993				
	41	8	18	15
territories	30 (73)	5 (63)	11 (61)	14 (93)
nest/chicks	15 (37)	3 (38)	4 (22)	8 (53)
fledglings	8 (20)	0 (0)	2 (11)	6 (40)
1994				
	31	7	15	9
territories	24 (77)	4 (57)	11 (73)	9 (100)
nest/chicks	14 (45)	2 (29)	5 (33)	87 (78)
fledglings	8 (26)	0 (0)	2 (13)	6 (67)
1995				
	20	6	8	7
territories	NA	4 (67)	3 (38)	NA
nest/chicks	NA	3 (50)	2 (25)	NA
fledglings	7 (37)	1 (17)	1 (13)	5 (71)
1996				
	18	4	7	7
fledglings	7 (39)	1 (25)	0 (0)	4 (57)
Means and Standard Errors				
territories		62% ± 3%	57% ± 10%	97%
nest/chicks		39% ± 6%	27% ± 3%	66%
fledglings		11% ± 6%	9% ± 3%	59% ± 7%

Table 4-2. Probability values of Fishers Exact tests performed on 2x2 contingency tables based on the presence/absence of territorial Common Loon pairs, nesting pairs, and fledglings.

Territorial Pairs				Nesting Pairs				Fledglings			
Year	Fishless vs. Minnow	Minnow vs. Pike	Fishless vs. Pike	Year	Fishless vs. Minnow	Minnow vs. Pike	Fishless vs. Pike	Year	Fishless vs. Minnow	Minnow vs. Pike	Fishless vs. Pike
1993	1.000	0.046*	0.103	1993	0.635	0.083	0.667	1993	1.000	0.101	0.058
1994	0.334	0.266	0.063	1994	1.000	0.089	0.126	1994	1.000	0.021*	0.011*
1995	0.592	-	-	1995	0.58	-	-	1995	1.000	0.041*	0.103
1996	-	-	-	1996	-	-	-	1996	0.364	0.07	0.454

Table 4-3. The number () and percentage of Fishless, Minnow, and Pike Lakes where territorial pairs and nests/chicks were observed in all 3 years, at least 2 years, at least 1 year, or not in any year of the 1993-1995 survey. Also presented is the percentage of lakes where fledglings were present in all 4 years, at least 3 years, at least 2 years, at least 1 year, or not in any year of the 1993-1996 survey. The total number of lakes visited every year of the survey is indicated in bold type.

No. of Years Present	**Fishless**	**Minnow**	***Pike**	**Total Lakes**
	5	**8**	**7**	**20**
Territioral Pairs				
3 years	80% (4)	50% (4)	NA	NA
2 years	80% (4)	75% (6)	100%	85% (17)
1 year	80% (4)	75% (6)	100%	85% (17)
0 year	20% (1)	25% (2)	0	15% (3)
Nest/chicks				
3 years	60% (3)	12.5% (1)	NA	NA
2 years	60% (3)	25% (2)	85.7% (6)	60% (12)
1 year	60% (3)	50% (4)	85.7% (6)	70% (14)
0 year	40% (2)	50% (4)	14.3% (1)	65% (13)
Fledglings				
4 years	0	0	28.6% (2)	15% (3)
3 years	20% (1)	12.5% (1)	57.1% (4)	30% (6)
2 years	20% (1)	12.5% (1)	71.4% (5)	30.5% (6)
1 year	20% (1)	12.5% (1)	85.7% (6)	40% (8)
0 year	80% (4)	87.5% (7)	14.3% (1)	60% (12)

* nests and chicks monitored in 1993 and 1994

Table 4-4. A detailed account of the reproductive patterns (presence of a territorial pair and the number of eggs, chicks, and fledglings) of loons on Fishless Lakes and Minnow Lakes in central Alberta from 1992 -1996. Some lakes were not visited in 1992 and/or in 1996. Question marks indicate that the exact number of eggs laid or chicks hatched is unknown. Dashes indicate that the presence of eggs or chicks is unknown.

Lake	Year	Events				Comments
		Territorial Pair	Eggs	Chicks	Fledglings	
Fishless Lakes						
Tempo	1992	Yes	?	?	1	
	1993	Yes	?	1	0	
	1994	Yes	2	1	0	1 egg found floating in water; the chick was abandoned @ 4 weeks
	1995	Yes	1	1	1	
	1996	Yes	?	?	1	1 large chick was observed with 2 adults
Joseph	1992	Yes	?	1	0	
	1993	Yes	?	1	0	
	1994	Yes	2	2	0	both chicks disappeared @ 4 & 7 weeks
	1995	Yes	2	1	0	1 egg abandoned; the chick was abandoned @ 3 weeks
	1996	Yes	?	1	?	1 small chick observed in late August, no adults present
Shumaker	1992	Yes	2	0	0	
	1993	Yes	-	0	0	
	1994	Yes	0	0	0	
	1995	Yes	2	2	0	2 chicks hatched late (mid-July), no fledglings in late August
	1996	Yes	?	2	?	small chicks observed in late August, 2 adults present
Little Buck	1993	Yes	-	0	0	
	1994	Yes	0	0	0	
	1995	Yes	0	0	0	
Hutterite	1992 - 1996	No				loons present in 1992, 1993, and 1994 but not territorial loons absent in other years

Table 4-4. Continued

Lake	Year	Events				Comments
		Territorial Pair	Eggs	Chicks	Fledglings	
Minnow Lakes						
Beaver Pond	1992	Yes	2	2	2	
	1993	Yes	1	1	1	initial clutch of 2 eggs destroyed, possibly by a mammal predator
	1994	Yes	2	2	2	
	1995	Yes	2	1	1	1 egg abandoned on nest after other egg hatched
	1996	Yes	-	-	0	
Mystic Lake	1993	Yes	-	0	0	
	1994	Yes	0	0	0	
	1995	Yes	-	0	0	pair observed copulating and looking for nest sites
	1996	Yes	-	-	0	
Two Island	1992	Yes	-	0	0	
	1993	Yes	?	1	0	
	1994	Yes	?	1	0	
	1995	Yes	0	0	0	
	1996	Yes	-	-	0	
Bobier	1992	Yes	-	0	0	
	1993	Yes	-	0	0	
	1994	Yes	0	0	0	
	1995	No				loons absent

Table 4-4. Continued

Lake	Year	Events				Comments
		Territorial Pair	Eggs	Chicks	Fledglings	
Minnow Lakes continued						
Turkawski	1992	No				loons absent
	1993	No				loons absent
	1994	Yes	2	0	0	clutch destroyed, possibly by a mammal predator
	1995	No				loons absent
	1996	Yes				present but reproductive status was unconfirmed
Growchowski	1992	Yes	?	2	0	
	1993	No				loons present but not territorial
	1994	Yes	0	0	0	
	1995	No				loons absent
	1996	No				loons present but not territorial
Rochester	1992 - 1996	No				loons present every year, but not territorial
Gilbert	1992 - 1996	No				loons present in 1994 and 1995 but not territorial loons absent in other years

Table 4-5. The number of territorial loon pairs present, the number of young fledged and the fledge rate (young fledged/territorial pair) on Fishless, Minnow, and Pike Lakes in 1993-1995. Also presented are the 2 year fledge rate mean (Pike Lakes) and 3 year fledge rate mean (Fishless and Minnow Lakes).

	1993		
	Fishless	Minnow	Pike
Territorial pairs	5	15	25
Total young fledged	0	2	15
Young fledged/territorial pair	**0**	**0.13**	**0.60**

	1994		
	Fishless	Minnow	Pike
Territorial pairs	4	14	20
Total young fledged	0	3	9
Young fledged/territorial pair	**0**	**0.21**	**0.45**

	1995		
	Fishless	Minnow	Pike
Territorial pairs	4	3	13
Total young fledged	1	1	8
Young fledged/territorial pair	**0.25**	**0.33**	**NA**

	Means and Standard Errors		
fledge rate	0.08	0.22 ± 0.06	0.53

Appendix 4-1. The location (longitude and latitude), area (ha), maximum depth (m), and total phosphorus (ug/l) measurements of Fishless Lakes, Minnow Lakes, and Pike Lakes censused for loon production in central Alberta. Lake names presented in quotes are not officially recognized by the province.

Lake	Location	Area (ha)	Maximum Depth (m)	Total Phosphorus (ug/l)
Fishless Lakes				
"Tempo"	54°37'N 113°19'W	9.44	2.50	108.1
Spear	54°44'N 113°10'W	9.83	2.00	41.1
"Bambi"	54°40'N 112°30'W	10.41	0.60	75.0
Joseph	54°37'N 113°12'W	12.05	1.50	13.5
"Shumaker"	54°38'N 113°18'W	19.96	6.75	36.0
"Hutterite"	54°48'N 113°31'W	27.56	2.20	89.0
Little Buck	54°39'N 112°30'W	51.60	1.10	181.0
Jumping Deer	54°50'N 113°12'W	66.37	1.70	20.6
Minnow Lakes				
"Beaver Pond"	54°38'N 113°35'W	2.69	4.30	26.2
"Bilsky"	54°41'N 113°36'W	8.32	9.00	36.5
"Neilson"	54°39'N 113°38'W	9.11	2.80	360.0
Gilbert	54°30'N 113°10'W	12.81	1.15	48.3
"Turkawski"	54°29'N 113°08'W	13.81	1.50	70.0
"Mystic"	54°23'N 113°21'W	14.31	2.20	42.7
"Rochester"	54°23'N 113°19'W	14.81	1.75	86.3
Bobier	54°33'N 113°10'W	25.21	1.10	86.3
"West Baptiste"	54°44'N 113°40'W	25.26	1.50	80.0
"North Tiperary"	54°26'N 113°12'W	27.97	1.10	38.5
Tawatinaw	54°21'N 113°28'W	47.38	4.30	46.4
"Grochowski"	54°28'N 113°19'W	54.78	1.50	110.0
Two Island	54°26'N 113°13'W	57.84	1.00	96.0
Tiperary	54°27'N 113°14'W	76.90	1.50	113.6
"Orrin"	54°25'N 113°20'W	98.01	2.60	71.7
Canoe	54°37'N 113°08'W	105.04	2.40	500.0
Duggans	54°13'N 113°23'W	123.00	2.40	37.3
Jackfish	54°49'N 113°06'W	214.69	6.00	21.4

Appendix 4-1. Continued

Lake	**Location**	**Area (ha)**	**Maximum Depth (m)**	**Total Phosphorus (ug/l)**
Pike Lakes				
"Teen"	54°29'N 113°43'W	33.76	8.40	28.0
"Pike"	54°32'N 113°42'W	36.83	4.00	48.0
Lofty	54°43'N 112°29'W	70.38	5.50	139.1
North Crooked	54°56'N 113°33'W	71.03	3.10	49.6
Lower Chain	54°58'N 113°30'W	84.22	9.50	12.0
Middle Chain	54°59'N 113°30'W	87.96	10.50	15.5
Narrow	54°37'N 113°37'W	111.59	38.00	11.0
South Crooked	54°54'N 113°32'W	123.41	9.00	66.3
Jenkins	54°55'N 113°36'W	160.18	15.80	52.8
Ghost	54°53'N 113°36'W	196.38	12.00	34.6
Long Island	54°41'N 113°36'W	205.89	14.90	19.3
God's	54°39'N 113°38'W	217.03	4.50	43.0
Lodge	54°43'N 112°27'W	242.81	22.80	18.4
Hope	54°39'N 112°40'W	273.01	16.50	16.1
Chump	54°39'N 112°35'W	304.76	13.70	22.3

Appendix 4-2. The breeding survey results of Fishless, Minnow, and Pike Lakes in central Alberta in 1992 and 1993. Lake names presented in quotes are not officially recognized by the province. The status of loons during 1992: A = absent, P = present, no evidence of breeding, B = present, evidence of breeding, X = not visited.

Lake	1992 Status	1993 No. of Territories	No. of Breeding Attempts	No. of Chicks	No. of Fledglings
Fishless Lakes					
"Tempo"	B	1	1	1	0
Spear	A	0	0	0	0
"Bambi"	X	1	1	1	0
Joseph	B	1	1	1	0
"Shumaker"	B	1	0	0	0
"Hutterite"	P	0*	0	0	0
Little Buck	X	1	0	0	0
Jumping Deer	X	0*	0	0	0
Minnow Lakes					
"Beaver Pond"	B	1	1	1	1
"Bilsky"	P	1	0	0	0
"Neilson"	X	1	0	0	0
Gilbert	A	0	0	0	0
"Turkawski"	A	0	0	0	0
"Mystic"	X	0*	0	0	0
"Rochester"	P	0*	0	0	0
Bobier	P	1	0	0	0
"West Baptiste"	B	1	0	0	0
"North Tiperary"	X	1	0	0	0
Tawatinaw	A	1	0	0	0
"Grochowski"	B	0*	0	0	0
Two Island	P	1	1	1	0
Tiperary	X	0	0	0	0
"Orrin"	P	2	1	2	1
Canoe	P	0	0	0	0
Duggans	X	3	1	2	0
Jackfish	P	2	0	0	0

* loons present but not territiorial

Appendix 4-2. Continued

Lake	1992 Status	1993 No. of territories	No. of Breeding Attempts	No.of Chicks	No. of Fledglings
Pike Lakes					
"Teen"	X	1	0	0	0
"Pike"	B	0	0	0	0
Lofty	P	1	0	0	0
North Crooked	P	1	0	0	0
Lower Chain	X	2	2	3	2
Middle Chain	X	1	1	2	2
Narrow	X	2	2	4	2
South Crooked	P	2	0	0	0
Jenkins	P	2	0	0	0
Ghost	B	2	1	0	0
Long Island	X	3	3	6	6
God's	B	2	1	1	0
Lodge	X	2	2	4	2
Hope	X	3	0	0	0
Chump	X	3	1	1	1

Appendix 4-3. The breeding survey results of Fishless, Minnow, and Pike Lakes in central Alberta in 1994. Lake names presented in quotes are not officially recognized by the province.

Lake	No. of Territories	No. of Breeding Attempts	No. of Chicks	No. of Fledglings
Fishless Lakes				
"Tempo"	1	1	1	0
Spear	0	0	0	0
"Bambi"	0	0	0	0
Joseph	1	1	2	0
"Shumaker"	1	0	0	0
"Hutterite"	0*	0	0	0
Little Buck	1	0	0	0
Minnow Lakes				
"Beaver Pond"	1	1	2	2
"Bilsky"	1	1	1	1
Gilbert	0*	0	0	0
"Turkawski"	1	1	0	0
"Mystic"	1	0	0	0
"Rochester"	0*	0	0	0
Bobier	1	0	0	0
"West Baptiste"	1	1	0	0
"North Tiperary"	0*	0	0	0
Tawatinaw	1	0	0	0
"Grochowski"	1	0	0	0
Two Island	1	1	0	0
"Orrin"	2	0	0	0
Canoe	0*	0	0	0
Duggans	3	0	0	0
Pike Lakes				
Lofty	1	0	0	0
Lower Chain	2	1	1	1
Middle Chain	2	2	2	1
Narrow	3	3	6	4
South Crooked	1	1	1	1
Jenkins	3	0	0	0
Ghost	3	1	0	0
God's	2	1	2	1
Chump	3	3	5	1

*loons present but not territiorial

Appendix 4-4. The breeding survey results of Fishless, Minnow lakes, and Pike lakes in central Alberta in 1995 and 1996. Lake names presented in quotes are not officially recognized by the province. The X indicates the lake was not visited. The ? indicates that the presence and exact numbers of loons on the lake is unconfirmed. Pike Lakes were visited only once in 1995 and all lakes were visited once in 1996 so although loons may have been present at that time, the exact number of territories, breeding attempts, and chicks is unkown.

	1995					1996	
Lake	**No. of Territories**	**No. of Breeding Attempts**	**No. of Chicks**	**No. of Fledglings**	**No. of Pairs with Fledglings**	**No. of Fledglings**	**No. of Pairs with Fledglings**
Fishless Lakes							
"Tempo"	1	1	1	1	1	1	1
"Bambi"	0	0	0	0		X	
Joseph	1	1	1	0		0**	1
"Shumaker"	1	1	2	0		0***	1
"Hutterite"	0	0	0	0		0	
Little Buck	1	0	0	0		X	
Minnow Lakes							
"Beaver Pond'	1	1	1	1	1	0	
Gilbert	0*	0	0	0		0	
"Turkawski"	0	0	0	0		X	
"Mystic"	1	1	0	0		0	
"Rochester"	0*	0	0	0		0	
Bobier	0*	0	0	0		X	
"West Baptiste"	1	X	X	X		X	
"Grochowski"	0	0	0	0		0	
Two Island	1	0	0	0		0	
Canoe	X	X	X	X		0	
Pike Lakes							
Lower Chain	?	?	?	2	1	2	1
Middle Chain	?	?	?	2		0***	1
Narrow	?	?	?	2	1	5	3
South Crooked	?	?	?	0		0	
Jenkins	?	?	?	0		0	
Ghost	?	?	?	1	1	2	1
God's	?	?	?	1	1	2	1

*loons present but not territiorial

**one chick (less than eight weeks old) present in late August

***two chicks (less than eight weeks old) present in late August

Chapter Five

Thesis Conclusions

5.1 Conclusions

The reproductive success of Common Loons, *Gavia immer*, in central Alberta is influenced by prey composition and abundance within the breeding lakes. Generally, loons are more likely to fledge young on Pike Lakes than on Fishless or Minnow Lakes. However, territorial loons are present on many Minnow Lakes. Daily caloric intake estimates suggest that adult loons on Minnow Lakes are able to satisfy their energy requirements. Territorial loons attempt to nest on only a few of these lakes, but those loons that do nest usually hatch chicks and fledge young. Daily caloric intake estimates suggest that adult loons feeding primarily fish to chicks are able to provide a sufficient amount of food needed to meet the daily energy requirements of chicks. The low overall fledge rate of territorial loons on these lakes is therefore related to a failure to nest, perhaps due to a lack of appropriate nest site on many of the lakes, and may not be related to prey base composition (i.e., small-bodied fish) within Minnow Lakes. However, this research suggests that fledging success variation between years may be related to yearly variation of fish abundance within Minnow Lakes.

Territorial loons are present on many Fishless Lakes. Territorial loons on Fishless Lakes exhibit dives of shorter duration and dive more frequently than loons on Minnow Lakes and are able to meet their daily energetic requirements on a diet of invertebrates. Most of the territorial loons on Fishless Lakes nest and hatch chicks, but only one lake produces fledglings on an irregular basis. Daily caloric intake estimates indicate that, although adult loons on Fishless Lakes have higher provisioning rates than loons on

Minnow Lakes and do not decrease these rates as chicks mature, adult loons feeding only invertebrates to older chicks may have a difficult time meeting the caloric requirements of the chick. Adult loons on Fishless Lakes often abandon their chicks; perhaps behaving similar to other long-lived species (e.g., Antarctic Petrel, *Thalassoica antarctica*, Saether *et al.* 1993, Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Mauck and Grubb 1995, Arctic Skuas, *Stercorarius parasiticus*, Phillips *et al.* 1996), which when food conditions are poor, shunt the costs of reproduction to their chicks rather than risk their own future reproductive success

However, in Alberta, by adjusting their foraging behavior, loons on some small lakes can successfully raise chicks on a diet composed entirely of invertebrates. Differences in fledgling success between Fishless Lakes and between years may be related to the availability of large macroinvertebrates, such as some leeches, that offer a high amount of calories per provisioning episode. This study indicates that the behavioral plasticity of loons is greater than previously described (e.g., Barr 1996).

Thus, this study further illustrates the importance of examining behavior when looking at the relationship between diet and reproductive success. For example, Anderson *et al.* (1982) and Barrett *et al.* (1987) have suggested that breeding success of piscivores can be used as an indictor of fish abundance. However, some piscivores have the ability to behaviorally buffer changes in fish abundance, and depending on the severity of prey decline, they are able to ameliorate the effects. Reproductive success will only be affected when food abundances are at very low levels and the birds reach their behavioral buffering capacity and can not make any more adjustments (Cairns 1987, Hamer *et al.* 1993, Phillips *et al.* 1996). Thus, the behavioral flexibility of piscivores can not be ignored. One method of behavioral compensation may involve prey switching and, as observed in this study and others (Pierotti and Annett 1990, Watanuki 1992), feeding on different prey may influence foraging patterns (dive durations and dive rates) and may also influence reproductive success. Therefore, it is also necessary to examine prey composition as well as abundance

Many studies have described the nesting habitat requirements of loons as being large lakes that contain sport fisheries (Blair 1992, Barr 1996, Kerekes *et al.* 1996). Contrary to those studies, which have mainly been conducted on loons in eastern Canada and the United States, loons in Alberta nest successfully on lakes of a variety of sizes with a variety of fish assemblages. This study suggests that it is not the size of the lake or the presence of fish per se that determines the success of loons on a lake; rather, it may be the presence of suitable nest sites and the amount of suitable prey in the lake that determines the success of loon on a lake. Small oligotrophic lakes in eastern Canada and the United States may not contain enough prey biomass to support a loon family and loons are therefore more likely to nest on larger lakes in these areas (Kerekes 1990).

The differences between lakes and subsequent differences between loons in eastern and western areas of Canada, highlight the fact that the information on individuals of a species in one geographic area may not be applicable to individuals in other areas. Loons in other regions may behave differently from loons in Alberta, and thus researchers should not assume, as Vermeer (1973) did in his study of the nesting requirements of loons in Alberta, that loons will only be present only on "typical loon habitat" and ignore smaller lakes. In addition, the presence of loons on fishless lakes should no longer be thought of as "exceptional" (Caron and Robinson 1994). This study and studies by Munro (1945) and Parker (1988) indicate that loons can and do raise young on fishless lakes.

When evaluating and making conservation decisions concerning the habitat of a species, it is important to consider the dietary needs, the behavioral flexibility, and the reproductive patterns of the species. For example, although loons are more likely to fledge young on Pike Lakes, Minnow Lakes and Fishless Lakes may be important for conserving Common Loons. Some of the smaller lakes consistently produce fledglings and although many lakes do not produce fledglings, they may serve as important feeding areas for loons that do not nest. Because loon are highly territorial, resident nesting loons do not allow intruder loons to feed in their territories; thus non-nesting loons require areas, like small lakes, to feed during the breeding season. Thus, the preservation of small lakes may be needed to insure the preservation of loons.

This study also indicates the importance of examining the diet, behavior and reproductive patterns of individuals when examining the effect habitat manipulation may have on a species. For example, research is being conducted to determine the influence of methylmercury exposure on loons (Scheuhammer and Blancher 1994, Meyer *et al.* 1995). Barr (1986) determined that methylmercury concentrates in prey greater than 0.3 $\mu g\ g^{-1}$ wet weight may hinder Common Loon reproductive behavior and success. However, a negative relationship exists between the availability of methylmercury and the pH of lakes (Miskimmin *et al.* 1992). A positive relationship between pH and the abundance and species composition of fish and invertebrates of lakes has also been observed (Schindler *et al.* 1985). Given the results of this study and the inter-relationship between Hg, pH, and prey, it would be difficult to attribute any behavioral or breeding differences observed strictly due to mercury exposure and not due to differences in prey base.

A complex interaction exists between the diet, behavior and reproductive success of an individual. In the past, research has focused on the relationship between prey abundance and reproductive success. This study indicates that species, even those considered "specialists", may have the ability to behaviorally compensate for changes in their environment, including changes in preferred prey abundance. Future studies, especially those concerning conservation issues, should consider the behavioral flexibility of a species, as well as the dietary needs, when examining factors that influence reproductive success.

5.2 Literature Cited

Anderson, D. W., Gress, F. and K. F. Mais. 1982. Brown pelicans: influence of food supply on reproduction. Okios 39:23-31.

Barr, J. F. 1986. Population dynamics of the Common Loon (*Gavia immer*) associated with mercury contaminated waters in northwestern Ontario. Canadian Wildlife Service Occasional Paper No. 56.

Barr, J. F. 1996. Aspects of Common Loons (*Gavia immer*) feeding biology on its breeding ground. In: Proc Hydrobiologia 321:119-144.

Barrett, R. T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Rov, N. and W. Vader. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980-1983. Ornis Scandinavica 18:73-83.

Blair, R. B. 1992. Lake features, water quality and the summer distribution of Common Loons in New Hampshire. Journal of Field Ornithology 63:1-9.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5:261-271.

Caron, J. A. and W. L. Robinson. 1994. Responses of breeding common loons to human upper activity in upper Michigan. In: Kerekes, J. J.(eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280: 431-438.

Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P. and M. D. Burns. 1993. The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. IBIS 135:255-263.

Kerekes, J. J. 1990. Possible correlation of summer common loon (*Gavia immer*) population with the trophic state of a water body. Internat. Verein. Limnol. 24: 349-353.

Kerekes, J. J., Duggan, M., Tordan, R., Boros, G. and M. Bronkhorst. 1996. Abundance and distribution of fish-eating birds in Kejimkujik National Park 1988-1995. Lake and Reservoir Management 11:156.

Mauck, R. A. and T. C. Grubb, Jr. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. Animal Behavior 49:999-1008.

Meyer, M. W., Evers, D. C., Daulton, T. and W. E. Braselton. 1995. Common loons (*Gavia immer*) nesting on low pH lakes in northern Wisconsin have elevated blood mercury content. Water, Air, and Soil Pollution 80:871-880.

Miskimmin, B. M, Rudd, J. W. M. and C. A. Kelly. 1992. Influence of dissolved organic carbon, pH, and microbial respiration rates on mercury methylation and demethylation in lake water. Canadian Journal of Fisheries and Aquatic Sciences 49:17-32.

Munro, J. A. 1945. Observations of the loon in the Cariboo Parklands, British Columbia. Auk 62: 38.49.

Parker, K. E. 1988. Common loon reproductive and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66:804-810.

Phillips, R. A., Caldow, R. W. G. and R. W. Furness. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*. IBIS 138:410-419.

Pierotti, R. and C. A. Annett. 1990. Diet and reproductive output in seabirds. BioScience 40:568-574.

Saether, B-E, Andersen, R. and H. C. Pedersen. 1993. Regulation of parental effort in a long-lived seabird: An experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antarctica*. Behavioral Ecology and Sociobiology 33:147-150.

Scheuhammer A. M. and P. J. Blancher. 1994. Potential risk to common loons (*Gavia immer*) from methylmercury exposure in acidified lakes. In: Kerekes, J. J.(eds.) Proc. Symp. Aquatic Birds in the Trophic Web of Lakes. Hydrobiologia 279/280:445-455.

Schindler, D. W., Mills, K. H., Malley, D. F., Findlay, D. L., Shearer, J. A., Davies, I. J., Turner, M. A., Lindsey, G. A. and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. Science 228:1395-1401.

Vermeer, K. 1973. Some aspects of the nesting requirements of Common Loons in Alberta. Wilson Bulletin 85:429-435.

Watanuki, Y. 1992. Individual diet difference, parental care, and reproductive success in slaty-backed gulls. Condor 94:159-171.