Aquatic Habitat Use by North American Moose (*Alces alces*) and Associated Richness and Biomass of Submersed and Floating-leaved Aquatic Vegetation in North-central Minnesota

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ABSTRACT

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Key words: *Alces alces*, herbivory; aquatic vegetation communities, beaver, *Castor canadensis*, habitat, moose.

The North American moose (*Alces alces*) is a species of socio-economic importance that has undergone recent declines in some areas of its range and may be impacted by climate change through effects on physiology or habitat availability. Moose frequently use aquatic habitat during summer but the timing, frequency and reasons for this behaviour are not well understood and appear to vary geographically. My objectives were to: 1) clarify the importance of aquatic habitat to North American moose through a literature review and 2) estimate richness and biomass of submersed and floating-leaved vegetation in lakes and beaver ponds potentially used by moose in north-central Minnesota through a comparative field study. The literature suggests that moose use aquatic habitats to feed and escape biting insects and do not appear to use them to escape predators or ameliorate heat stress, though the latter function may be important at the extreme southern limits of moose range. Richness and biomass of aquatic plants in aquatic areas potentially used by moose in north-central Minnesota was heavily influenced by the presence and damming activity of beaver (*Castor canadensis*). Beaver ponds contained higher richness and biomass of aquatic vegetation compared to lakes. The creation and maintenance of large (> 1 ha) beaver ponds 6-38 years of age facilitate moose in meeting nutritional demands because they allow growth and reproduction of species less competitive but potentially more palatable than the dominant floating-leaved plant *Brasenia schreberi*. The maintenance of beaver populations may be important for moose conservation in north-central Minnesota.

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1.0 GENERAL INTRODUCTION

The moose (*Alces alces*) is a species of socio-economic importance throughout its circumpolar boreal range (Reeves and McCabe 1998; Timmermann and Rodgers 2005). This herbivore is an important aesthetic resource (Cobus 1972) and game species (Crichton 1998; Timmermann and Rodgers 2005). Thus, moose in North America have received much research and management attention in the past century and much is known about their habitat needs (Peek 1998).

Ecologists have suggested that climatic factors may limit the range of moose in North America (Karns 1998). The moose is the largest cervid on Earth (Bubenik 1998), and as such it responds differently to thermal stress when compared to other deer species (Demarchi and Bunnell 1995). The moose's large body size and dark pelage make it ideally suited to cold boreal winters, and therefore the northern range limit of the moose is thought to coincide with decreased forage availability above the tree line as opposed to extreme cold temperatures (Telfer 1984; Karns 1998). Conversely, these adaptations reduce cooling efficiency during the non-winter period, particularly in the early spring when moose still possess winter pelage (Renecker and Hudson 1986; 1989; Dussault et al. 2004). Evidence from captive moose has confirmed that moose are thermally stressed at lower temperatures than have been reported for other cervids (Renecker and Hudson 1986, McCann et al. 2013) and bedding or standing in water may limit the proportion of total energy expenditure devoted to thermoregulation (Renecker and Hudson 1990). Providing insight based on anecdotal observations of moose bedded in shallow streams during hot periods in Alberta, Kelsall and Telfer (1974) suggested that moose populations should not persist in areas where daily summer temperatures frequently exceed 26°C because moose are not capable of cooling themselves to adequately maintain homeostasis. Following their conclusion that moose southern range limits are dictated by warm climates, Kelsall and Telfer (1974) speculated that the existence of thermal refuges (treed wetlands, lakes, ponds, etc.) for moose could allow them to survive at latitudes farther south than would be possible in the absence of these landscape features.

Moose in central North America will almost certainly experience some level of habitat alteration due to climate change (Rempel 2011). Moose at their southern range periphery may also experience dramatic increases in daily summer temperatures, which could cause heat stress that would compromise energy acquisition (Lowe et al. 2010). Over a 45-year observed period, moose populations in Minnesota have declined dramatically and they have been virtually extirpated from the northwest region of the state (Murray et al. 2006; Lenarz et al. 2009). The decline in annual population growth rates in northwestern Minnesota has been correlated with increasing atmospheric temperatures from 1961-2006 (Murray et al. 2006). Researchers have expressed concern that temperature-mediated decreases in survival of moose near the southern periphery of their range (Lenarz et al. 2009) may lead to extirpation from all of Minnesota (Lenarz et al. 2010; McGraw et al. 2010) and other southern parts of their current range (Lowe et al. 2010). Therefore, the importance of aquatic refuges for ameliorating heat stress in moose should be clarified in Minnesota in an effort to identify components of moose habitat where moose are the least thermally stressed during the hottest times of the snow-free period.

Moose feed on submersed, floating-leaved and emergent plants that are present in aquatic areas during the snow-free period (Belovsky and Jordan 1978; Fraser et al. 1980). In some areas, moose consume significant fractions of annual submersed and floating-leaved plant production following spring green-up (Aho and Jordan 1979; Fraser and Hristienko 1983; Morris 2002). It is plausible, then, that aquatic areas are an essential component of moose habitat at southern range limits in North America because they allow moose to ameliorate heat stress and feed simultaneously (Belovsky and Jordan 1978; Belovsky 1981). The hypothesis that moose use aquatic habitat for feeding and cooling implies that moose engage in behavioural thermoregulation leading to selection of aquatic areas, but that has not been consistently detected in North America (e.g., Dussault et al. 2004; Lowe et al. 2010).

The importance of aquatic areas for moose in summer may be a controversial topic among wildlife researchers and managers because proportional use of aquatic habitats is often quite low across North America (Phillips et al. 1973; Kufeld and Bowden 1996; Leptich and Gilbert 1989; Osko et al. 2004; Broders et al. 2012). A biogeographical perspective, similar to that employed by Kelsall and Telfer (1974), may be needed to clarify the importance of aquatic areas to moose during summer. It is possible that different or multiple mechanisms might drive observed aquatic feeding in different areas of the world based on differences in aquatic plant availability and nutritional requirements of moose belonging to different sub-populations (Boonstra and Sinclair 1984; Butler 1986; Jordan 1987). Moose on Isle Royale, for example, have been described as sodium-limited in the spring and early summer (Jordan et al. 1973) and moose in Ontario have been shown to select aquatic forage items with higher sodium concentrations (Fraser et al. 1984). Alternatively, moose living on the Copper River Delta in Alaska appeared to forage in a manner consistent not only with sodium acquisition but also maximization of foraging efficiency (MacCracken et al. 1993).

The central hypothesis of this thesis is that aquatic areas are an essential component of moose habitat in North America because they allow moose to satisfy their metabolic requirements by feeding on aquatic vegetation. My objective was to determine what mechanisms (e.g., heat stress amelioration) might plausibly influence aquatic habitat use by North American moose, particularly in the Great Lakes-St. Lawrence region. To accomplish this objective, I first report a detailed literature review and synthesis that compares the extent of moose aquatic habitat use and the suggested mechanisms driving this use in the Great Lakes-St. Lawrence region relative to areas elsewhere in North America that support moose populations. Following this I report on a field study in northern Minnesota in which I estimated the annual production of important aquatic food items for moose. I further explored local and landscape-level factors that may affect the availability of aquatic forage for moose in lakes and beaver ponds of north-central Minnesota.

2.0 MOOSE AQUATIC HABITAT USE: A REVIEW AND SYNTHESIS

2.1 Moose Aquatic Habitat Use: Hypotheses and Predictions

North American moose (*Alces alces*) use of aquatic areas such as lakes, rivers, ponds, treed wetlands, and other seasonally inundated habitats has long been known (McCabe and McCabe 1928; Murie 1934). Use of aquatic habitats does appear to vary geographically (Peek 1998). Several hypotheses for aquatic habitat use by moose have emerged in the literature: minimization of predation risk, insect avoidance, heat stress amelioration, and nutrition. A greater understanding of the factors driving regional variability in aquatic habitat use by moose should reveal the importance of aquatic areas to moose, particularly at southern range limits (Peek 1998; see general introduction). The objective of this chapter is to evaluate the available evidence supporting or contradicting hypotheses for aquatic habitat use by moose using information from studies in four regions of North America (Alaska-North, encompassing all of moose range north of the prairie provinces of Canada and within Alaska; Mountain-West, encompassing all areas of moose range west of Minnesota that are not present in Alaska-North; Northeast-Maritimes, encompassing all areas of moose range in Canada and the U.S. lying east and south of the lower St. Lawrence River; Great Lakes-St. Lawrence, encompassing all areas of moose range in North America not delineated above). In the following sections, the hypotheses listed above, which are not necessarily mutually exclusive, are summarized and a suite of predictions are generated (Table 1). The predictions are then qualitatively evaluated using information obtained from a literature review of studies of moose aquatic habitat use. Each prediction conformed to one of the following categories: geographic variation in proportional use of aquatic habitat, seasonal variation in aquatic habitat use, diel variation in aquatic habitat use, and summer forage preferences. According to this framework, each of the four hypotheses possessed a unique set of alternative predictions (justified below) that together represented the

Table 1. A hypothetico-deductive framework for examination of mechanisms driving moose use of aquatic habitat in North America. Predictions are separated into four categories (geographic, seasonal or diel variation in aquatic use by moose and forage preferences). Aquatic forage preferences are defined relative to terrestrial forage and relative to other aquatic items differing in their sodium, protein and energy contents.

Hypothesis	Predictions			
	Geographic variation	Seasonal variation	Diel variation	Forage preferences
Minimization of direct predation risk	Aquatic use greatest in Great Lakes-St. Lawrence and least in Northeast-Maritimes	Aquatic use greatest in August-September and lowest in April-May	Aquatic use nocturnal (greatest between dusk and dawn)	Preference for aquatic forage items not anticipated
Biting insect avoidance	Could not be determined	Aquatic use greatest mid-June to early-July	Aquatic use crepuscular (peak at dawn and dusk)	Preference for aquatic forage items not anticipated
Heat stress amelioration	Aquatic use greatest in Northeast-Maritimes and Mountain-West. Use least in Alaska-North and Great Lakes-St. Lawrence	Aquatic use greatest in July and August and least in May and June	Aquatic use diurnal (greatest 1100-1959, least 2300-0759)	Preference for aquatic forage items not anticipated
Nutrition (sodium acquisition)	Aquatic use greatest in Great Lakes-St. Lawrence relative to other regions.	Aquatic use greatest in May and June relative to other summer months	Diel variation in aquatic use not anticipated	Terrestrial forage preferred over aquatic forage but aquatic items commonly consumed are higher in sodium than aquatic forage not typically eaten
Nutrition (foraging efficiency)	Aquatic use approximately equal in all regions	Seasonal variation in aquatic use not anticipated	Diel variation in aquatic use not anticipated	Aquatic forage preferred over terrestrial forage. Aquatic items commonly consumed higher in energy and protein than aquatic forage not typically eaten

conditions required for acceptance of a given hypothesis. This framework also provided the opportunity for rejection of hypotheses for which support was completely lacking. Multiple combinations of hypotheses that were partially supported could emerge from this qualitative analysis but it was my intention to first consider, and possibly discount, the most parsimonious explanations for aquatic habitat use by North American moose (i.e., that a single hypothesis might sufficiently explain this behavioural pattern).

Minimization of Predation Risk

Wolves (*Canis lupus, Canis lycaon)* are well adapted for hunting and killing moose (Peterson and Ciucci 2003) and are the principal natural predators of moose in North America (Ballard and Van Ballenberghe 1998). Though predation on moose, particularly calves, by ursids (*Ursus americanus, Ursus arctos*) occurs in North America (Ballard and Van Ballenberghe 1998), I assumed that ursid predation pressure has not been sufficiently consistent and widespread to have caused moose behavioral adaptation (to use aquatic areas) when compared to wolf predation. Thus, predation risk hereafter refers solely to risk of predation by wolves. Risk of predation on moose has potentially led to adaptation to use aquatic areas through natural selection because moose occupying areas in close proximity to water may be better able to escape or avoid attacks by wolves (Stephens and Peterson 1984).

The hypothesis that moose might remain in close proximity to aquatic areas so as to more easily escape attacks by terrestrial predators was not recognized by Peek (1998) as a potential mechanism for use of aquatic areas in Ontario, Isle Royale and Quebec (Great Lakes-St. Lawrence region) or the Copper River Delta of Alaska (Alaska-North).Yet, Eastman and Ritcey (1987) suggested moose in the boreal upland areas of British Columbia (Mountain-West) may use aquatic areas to minimize predation risk. Riverine habitats might be important calving sites in Alaska, presumably because dense stands of willow commonly associated with rivers and streams provide lateral cover that would obscure bedded post-partum cows from potential predators (Lesresche et al. 1974). The majority of active calving sites for moose in Algonquin Provincial Park, Ontario, are located on islands compared to on peninsulas or within landlocked areas and this may be due to the importance of water in deterring predators (Wilton and Garner 1991). Calves consistently occupying small islands off the coast of Isle Royale appeared to have a greater probability of survival relative to calves living on Isle Royale itself (Stephens and Peterson 1984). However, post-partum female moose tended to bed nearer to an island's center than to its shoreline in central Ontario, possibly because cows were avoiding wolves hunting along watercourses (Addison et al. 1990). Wolf-killed moose carcasses tended to be found clustered near aquatic areas on Isle Royale (e.g., beaver ponds, lakes; Bump et al. 2009) and wolves may attack and kill swimming moose (Jordan et al. 2010). Detailed descriptions of moose behaviour in Yellowstone National Park (Mountain-West) were provided by McMillan (1954) who noted that actions indicating wariness (e.g., frequent lifting of the head, ear swiveling, running short distances and stopping) were more frequently observed while moose were in water compared to terrestrial habitats. Moose might be aware of their vulnerability to predator attack in water because of the apparent difficulty moose have in extricating themselves from aquatic substrate (McMillan 1954). Moose movement through aquatic substrates was simulated by Belovsky and Jordan (1978) who found evidence in agreement with McMillan's claim that moose may have difficulty rapidly removing themselves from an aquatic area. In the only detailed field-based study of moose access routes to aquatic areas, Timmermann and Racey (1989) demonstrated that increased substrate solidity and decreased shrub abundance were positively associated with moose access routes to aquatic areas in northwestern Ontario (Great Lakes-St. Lawrence), presumably due to greater ease of entry and extrication at these locations. Therefore, although suggested as a plausible explanation by some studies, evidence contradictory to the minimization of predation risk hypothesis exists in three of four major regions in North America (Mountain-West, Alaska-North, and Great Lakes-St. Lawrence).

The probability of an ungulate being attacked and killed by wolves is related to both direct and indirect sources of predation risk (Hebblewhite et al. 2005; Kittle et al. 2008). Direct predation risk is simply represented by the frequency distribution of predators on the landscape (Fortin et al. 2005; Mao et al. 2005) whereas indirect predation risk is a function of prey susceptibility and predator presence in different habitat types (Hebblewhite et al. 2005). The effects of indirect predation risk on ungulate habitat use are complicated by the existence of factors that might improve fitness in areas of apparent high indirect risk (e.g., deterrence of wolves by human activity, increased forage availability; Hebblewhite and Merill 2007; Kittle et al. 2008). Conversely, direct predation risk constitutes a simple estimate of mortality risk irrespective of landscape-level features and may, in fact, be important in structuring ungulate habitat use at broad spatial scales (Kittle et al. 2008). Direct predation risk (as measured by wolf density) may be a more parsimonious explanation for geographic variation in aquatic habitat use by North American moose compared to indirect predation risk that likely operates at finer spatial scales. Mean wolf density in the Great Lakes-St. Lawrence, Mountain-West, and Alaska-North regions has been estimated at 2.29 (n=6 estimates), 1.66 (n=9 estimates) and 0.71 (n=12 estimates) wolves/100 km^2, respectively (Table 2). Wolves do not appear to inhabit the Northeast-Maritimes region (0.00 wolves/100 km^2; n=2).

Wolves are at their greatest density in the Great Lakes-St. Lawrence region and thus I predicted that proportional use of aquatic habitat by moose would be greatest in this region relative to all other regions. I predicted that moose would display the least proportional use of aquatic habitat in the Northeast-Maritimes region where their primary predator, the wolf, is largely absent. I found considerable differences in wolf numbers among areas of high and low wolf density within the Alaska-North and Mountain-West regions. For these regions, moose use of aquatic areas may be higher in locations supporting denser wolf populations. For example, moose on the Kenai Peninsula may be more inclined to use aquatic areas than moose living in the Northwest Territories. Moose in Yellowstone National Park (where wolf densities are high) might be more inclined toward aquatic habitat use relative to moose living outside the park (where wolf densities are lower).

Seasonal variation in summer activity of wolves is heavily influenced by the reproductive cycle of the breeding female (Mech and Boitani 2003). Denning of wolves in North America begins in April, with breeding animals making increasingly large forays as the summer progresses. In general, breeding animals (and to some extent non-breeders) tend to range farther and farther as the pups age throughout the summer (Packard 2003). The onset of denning in the Alaska-North region occurs near April 13, with parturition expected to occur May 1-May 11 (Ballard et al. 1987). Pups in this study were first seen outside the den on June 1. Two breeding females living in south-central Alaska began making regular hunting excursions May 27-June 5, and increased the length of time spent hunting following June 16 (Ballard et al. 1991). The timing of denning onset appears similar in the Great Lakes-St. Lawrence and Mountain-West regions (but see Mech 2002) with estimated denning dates of April 12-18 in northern Minnesota (Frits and Mech 1981; Fuller 1989) and April 18 in British Columbia and

Table 2. Wolf (*Canis lupus, Canis lycaon*) density (wolves/100 km^2) at 30 locations within 4 geographic regions (Alaska-North, Mountain-West, Great Lakes-St. Lawrence and Northeast-Maritimes) of North America. Where multiple estimates (i.e., references) were used to generate a density for a given location the mean value was used. Each unique location encountered during a literature review of geographic variation in wolf density was included in the table.

Region	Location	Wolves/100 km^2	References
Alaska-North	Northwest Territories	0.32-0.65	Kelsall (1957)
	South-central Alaska	0.35-0.39	Davis (1978);Ballard et al. (1982;1987);Ballard and Miller (1990);Ballard et al. (1990)
	East-central Alaska	0.40	Boertje et al. (1987;1988)
	Northern Alaska and Yukon	0.51-0.65	Stephenson (1975); Singer (1984); Adams and Stephenson (1986);Dale et al. (1995)
	Southern Yukon	0.61	Larsen et al. (1989);Hayes et al. (1991)
	Central Yukon	0.65	Sumanik (1987);Hayes and Harestad (2000a,b)
	Denali National Park, AK	0.71	Murie (1944);Haber (1968;1977) Singer and Dalle-Molle (1985)
	Unit 13, AK	0.77	Rausch (1967)
	Interior Alaska	0.90	Gasaway et al. (1983)

Table 2. *cont'd.*

Region	Location	Wolves per 100 km^2	References
Alaska-North	Southeastern Alaska	1.00-1.54	Atwell et al. (1963)
	Tanana Flats, AK	1.11	Stephenson (1977)
	Kenai Peninsula, AK	1.20	Franzmann et al. (1980);Peterson et al. (1984);Schwartz and Franzmann (1991)
Mountain-West	Greater Yellowstone Area	0.18	Smith et al. (2010)
	Central Idaho	0.30	Smith et al. (2010)
	Jasper National Park, AB	0.44	Carbyn (1974)
	Saskatchewan	0.46-0.96	Banfield (1951)
	Southwestern Montana	0.80	Berger and Geese (2007)
	Northern Alberta	1.27	Fuller and Keith (1980a,b); Oosenburg and Carbyn (1982);Bjorge and Gunson (1989);Gunson (1995)
	Southwestern Manitoba	2.60	Carbyn (1980;1983)
	Yellowstone National Park, WY	4.35	Smith et al. (2004)
	Grand Teton National Park, WY	4.56	Berger et al. (2008)

Table 2. *cont'd.*

Region	Location	Wolves per 100 km^2	References
Great Lakes-St. Lawrence	Ontario	0.20-0.38	Pimlott et al. (1969)
	Pukaskwa National Park, ON	1.20	Bergerud et al. (1983)
	Southern Quebec	1.67	Messier (1985a,b);Potvin (1988)
	Minnesota	2.88	Olson (1938);Stenlund (1955);Van Ballenberghe et al. (1975);Berg and Kuehn (1980);Fuller (1989);Frits and Mech (1981);Gogan et al. (2000)
	Algonquin Provincial Park, ON	3.38	Pimlott et al. (1969);Kolenosky (1972);Forbes and Theberge (1995)
	Isle Royale National Park, MI (1959-1994)	4.40	Mech (1966);Jordan et al. (1967);Peterson (1977);Peterson and Page (1988);Peterson et al. (1998)
Northeast-Maritimes	New Brunswick	0	Boer (1988)
	Newfoundland	0	Ballard and Van Ballenberghe (1998)

Montana (Boyd and Pletscher 1999). Females were first located away from dens in northwestern Minnesota on April 18 (Frits and Mech 1981), which coincides approximately with predicted time of parturition (April 29) elsewhere in the region (Mills 2006). The attendance of wolves at the homesites (dens and rendezvous sites) tends to diminish over the course of a summer (Potvin et al. 2004; Ruprecht et al. 2012). Greater distances between breeding females and pups were reported beginning in August (Frits and Mech 1981). The pups in the above study emerged from the den around June and began ranging farther throughout the summer and eventually abandoned homesites by September. Homesites of wolves in northern Minnesota were abandoned by packs starting in early-August (Harrington and Mech 1982). Similarly, detection of wolves by howling and radio tracking in Algonquin Provincial Park was greatest in July (Joslin 1967; Kolenosky and Johnston 1967), possibly owing to reduced movement in July relative to later months. Significant declines in percent homesite attendance by breeding adults was related to various reproductive stages (86.7% preweaning to 21.6% postweaning, with an abrupt decline of approximately 20% immediately following weaning; Ruprecht et al. 2012). Wolves were not located within 0.5 km of homesites by September, suggesting onset of nomadic hunting behavior at this time (Ruprecht et al. 2012). Abandonment of homesites by wolves appears to begin in August, and I surmise that it is at this time that direct risk to large ungulates increases due to increased presence of hunting wolves. If direct predation risk drives aquatic habitat use by North American moose then I predict low use of aquatic areas in April and May with a subsequent increase in August and September concomitant with increased direct predation risk. Indirect predation risk may not necessarily conform to the above seasonal pattern (e.g., direct risk is lowest in April and May but indirect risk may be higher at this time due to, for example, increased vulnerability of cow-calf pairs in different areas; Patterson et al 2013) but, as discussed above, is a less a parsimonious mechanism than direct predation risk.

Wolves in south-central Alaska of the Alaska-North region appeared to show greatest activity near monitored dens (i.e., arriving and departing to hunt) between 0600-0800 and 2100-2300, with very little activity observed from 1300-2000 (Ballard et al. 1991). Wolves in Denali National Park, Alaska, in the Alaska-North region, left dens to hunt most often in the evening, with reported departure times of 1600-2200 (Murie 1944). Similarly, wolves living on the Kenai Peninsula, Alaska, appear to do most of their travelling (and likely hunting) at night. Wolves in Algonquin Provincial Park appeared most active at dusk, and responded to howling slightly more from dusk until dawn than during daylight hours (Joslin 1967). Similarly, maximum activity of radio tracked wolves in Algonquin Park occurred shortly before and after dusk (Kolenosky and Johnston 1967). Wolves in Minnesota were reported to be most active from 2000-0800 (Merill and Mech 2003) and wolves on Isle Royale showed greatest homesite attendance during the day (0600-1800; Potvin et al. 2004). It appears that wolves tend toward nocturnal hunting activity during summer, typically leaving homesites in the evening and returning near dawn. If direct predation risk drives aquatic habitat use by North American moose then I predict that moose use of aquatic areas would be greatest during nighttime hours, between dusk and dawn, when the number of wolves hunting is likely to be highest.

Insect Avoidance

Mosquitoes, black flies and deer flies, and horseflies (culicids, simuliids, and tabanids, respectively) are major biting insect pests of North American moose (Laurian et al. 2008; Renecker and Hudson 1990). Insect avoidance is a potential benefit of aquatic habitat for moose

(Kelsall and Telfer 1974). Moose use of river habitat in Ontario (Great Lakes-St. Lawrence), for example, was suggested as a strategy to escape the biting attacks of simuliids (Flook 1959). The author did not believe that moose were using aquatic habitat for any reason other than insect relief and stated that moose were never observed to be feeding on aquatic vegetation while in water. Although extensive stands of aquatic vegetation existed within the river, Flook (1959) noted that moose were not observed in these areas. Conversely, extensive feeding on aquatic vegetation in northwestern Ontario led to the conclusion that insect relief was a less plausible hypothesis for aquatic habitat use by moose than aquatic feeding (deVos 1958). Moose showed some preference for herbaceous habitats and by extension aquatic areas (11 of 12 herbaceous habitat categories were at least seasonally inundated with water though only 2 of 12 were permanently flooded) in Voyageurs National Park, Minnesota (Cobb et al. 2004). This apparent preference for herbaceous habitat in summer might be related to moose seeking refuge from biting insects in open areas (though aquatic feeding was also mentioned as a possible mechanism; Cobb et al. 2004). Moose in Minnesota used aquatic habitat prior to typical peak densities of large biting insects (e.g., tabanids) but extensive time spent in water by moose during June may have been related to high densities of simuliids and culicids at this time (Peek et al. 1976). Moose using aquatic areas in Minnesota, however, were most often observed with the majority of their bodies above water and thus fully exposed to biting insects (Peek 1971; though not discussed was the possibility of increased wind speed in open habitats providing some insect relief).

Moose living in northern Alaska might make use of stream beds and the open tundra because increased wind speeds in these areas potentially provide relief from biting flies (Mould 1977). Aquatic feeding depth by moose was influenced by the presence of biting insects in

Bowron Lake Park, British Columbia (Ritcey and Verbeek 1969). Moose in that study tended to feed in deeper water when harassment from flies appeared to be at its worst. Moose in the Northwest Territories were observed "submerging to the neck" and this particular behavior was prevalent "especially when the mosquitoes were bad in late June and early July" (Barry 1961). Renecker and Hudson (1989) noted energy expenditures of free-ranging moose in the aspen parklands region of Alberta approximately doubled between May and July, partially due to increased harassment by insects over this period. They later stated that energetic costs associated with insect harassment might be reduced when moose enter aquatic areas (Renecker and Hudson 1990). There does not appear to be much evidence supporting the insect relief hypothesis from the Northeast-Maritimes region, though Koitzsch (2002) included insect relief as one potential benefit of aquatic areas for moose. Dodds (1955) was skeptical of the importance of aquatic areas to moose in Newfoundland and did not observe moose using available aquatic areas for insect relief.

An attempt to determine the extent of geographic variation in the abundance of culicids, simuliids, and tabanids proved problematic due to a relative scarcity of baseline data in the literature (Hocking 1960) and an apparent lack of consistency with respect to sampling protocol (Smith et al. 1970; Downs et al. 1986; Toupin et al. 1996; Deans et al. 2005; Butt et al. 2008). For example, studies in the Alaska-North region reported mean number of sampled mosquitoes per day was 13-19 individuals according to 5-minute landing counts (Downes et al. 1986; Yukon Territory) but 35 mosquitoes per day according to 5-minute vacuum sampling of exposed black cloth (Toupin et al. 1996; Ungava Region of Quebec). Overall, I was unable to locate sufficient information in the literature to determine the extent, if any, of geographic variation of biting insects across North American moose range. I, thus, was unable to predict whether moose might be more inclined to use aquatic areas as refuge from biting insects in one region relative to another.

The activity of biting insects in the Alaska North region was greatest in mid-July and much reduced by the second week of August (Hocking et al. 1950; Miller 1951; Curtis 1953; Hocking and Pickering 1954; Corbett and Danks 1973; Downes et al. 1986; Toupin et al. 1996). Peak activity of biting insects generally occurred earlier and persisted longer outside of the Alaska-North region (mid-June to late July; Beckel and Atwood 1959; Smith et al. 1970; Westwood and Brust 1981; Trueman and Maciver 1986; McElligot and Galloway 1991; Butt et al. 2008; Laurian et al. 2008). If insect avoidance drives aquatic habitat use by North American moose I predict the greatest use of aquatic habitat from mid-June to late-July, with the added caveat that moose living in the Alaska-North region would show a later seasonal peak in aquatic use than moose in other regions owing to a later peak biting insect season.

Biting insect activity of culicids and simuliids generally showed a crepuscular pattern with most studies reporting a primary peak at dusk and a secondary peak near dawn (Haufe 1952; Curtis 1953; Wolfe and Peterson 1960; Happold 1965; Boyer et al. 2013; Downes et al. 1986; Toupin et al. 1996; Trueman and Maciver 1986). Tabanids, in comparison, have a greater tendency to be active during daylight hours, but activity appears to peak closer to the morning than midday (e.g., 0900-1200; Miller 1951). If insect avoidance drives aquatic habitat use by North American moose I predict that moose use of aquatic areas would be greatest near dusk concomitant with a daily peak in biting insect activity.

Heat Stress Amelioration

The southern range limit of moose may be limited by warm summer temperatures because moose have a low upper critical temperature (Kelsall and Telfer 1974; Renecker and Hudson 1986; McCann et al. 2013). It follows that aquatic habitat use by moose may be related to a need for moose to cool themselves by submersing themselves in water (Peek 1998). Feeding time by moose may be constrained by warm ambient temperatures (Belovsky and Jordan 1978; Belovsky 1981; Renecker and Hudson 1992) but this constraint may be relaxed when moose are feeding in water (Belovsky 1978). Peek (1998) implied that, within the Great Lakes-St. Lawrence region, longer periods of aquatic habitat use by moose observed in Minnesota relative to Ontario might be explained by greater mean daily temperatures in the former area. Ackerman (1987) reported that moose on Isle Royale exhibited a greater tendency toward heat-reducing behaviors, including bedding in water, when summer temperatures exceeded 30°C. Moose in the Mountain-West region may experience energy debts as a result of a failure to feed in hot weather (Renecker and Hudson 1992) and this negative effect of high ambient temperature may be ameliorated by moose standing or bedding in water or saturated soil (Eastman and Ritcey 1987; Renecker and Hudson 1990; Demarchi and Bunnell 1995).

Broders et al. (2012) tested the heat stress amelioration hypothesis using GPS data from collared moose in mainland Nova Scotia (Northeast-Maritimes) but did not detect a significant difference in the number of moose locations in water when ambient air temperatures were 20-26°C compared to when temperatures were 10-16°C. It should be noted, however, that moose locations during the most extreme summer temperatures (i.e., > 26°C) were screened from their analysis. Dodds (1955) supported the notion that moose use aquatic areas to cool down in Newfoundland and reported that "edges of bogs were often utilized and not infrequently moose would lie in water to a depth of 2”-6” on warm days.” The availability of aquatic habitat that might provide thermal relief may be an important determinant of summer habitat quality in Maine (Thompson et al. 1995), Vermont (Koitzsch 2002), Massachusetts (Wattles and DeStefano 2013a; 2013b) and upstate New York (Haase and Underwood 2013).

I determined geographic variation in maximum summer (May-August) temperatures in Canada and USA from two open-access online databases of climatological data (Environment Canada and the National Oceanic and Atmospheric Administration, respectively; http://climate.weather.gc.ca/; http://www.ncdc.noaa.gov/). Temperature data were obtained for each location where quantitative data on proportional use of aquatic habitat by North American moose were available (see RESULTS below). If monitoring stations were not present within an author’s study area, the nearest monitoring station to the study area was used. I computed an 11-year average centered on 1992 (the median year of all above mentioned proportional use studies) in order to prevent bias associated with inter-annual variation in mean temperatures across broad spatial scales (e.g., El Nino events).

The lowest mean maximum summer temperature occurred in the Alaska-North region (16.2°C; n=2; Table 3). Mean maximum summer temperatures in Alaska-North ranged from 15.2°C at Cordova Airport, AK to 17.2°C in Petersburg, AK. The second lowest mean maximum summer temperature occurred in the Great Lakes-St. Lawrence region (21.6°C; n=5). Mean maximum summer temperatures in the Great Lakes-St. Lawrence region ranged from 17.9°C in Grand Marais, MN to 24.5°C in Agassiz Refuge, MN. Mean maximum summer temperatures were higher in the Mountain-West and Northeast-Maritimes region than the Alaska-North and Great Lakes-St. Lawrence regions. Mean maximum summer temperature in the Mountain-West region was 22.2°C (n=5). Mean maximum summer temperatures in the Mountain-West region ranged from 20.3°C in Red Rock, MT to 27.1°C in Fort Howes, MT. Mean maximum summer temperature in the Northeast-Maritimes region was 22.3°C (n=5). Mean maximum summer temperatures in the Northeast-Maritimes region ranged from 18.2°C in Corner Brook, NL to 26.1°C in Amherst, Massachusetts. If moose are using aquatic areas to minimize the effects of heat stress during temperature maxima then I predict the lowest proportional use of aquatic habitat in the Alaska-North and Great Lakes-St. Lawrence regions, as these areas have the lowest mean maximum summer temperatures. I also predict moose should show the highest proportional use of aquatic habitat in the Northeast-Maritimes and Mountain-West regions, as these areas have the highest mean maximum summer temperatures.

Mean maximum temperatures in North America increased from May to June and from June to July and August (Table 3). The mean maximum temperature in May was 16.6°C (n=16). Mean maximum temperatures in May ranged from 12.2°C in Corner Brook, NL to 21.3°C in Amherst, MA. The mean maximum temperature in June was 21.6°C (n=16). Mean maximum temperatures in June ranged from 15.2°C in Cordova, AK to 28.1°C in Fort Howes, MT. The mean maximum temperature in July was 23.8°C (n=16). Mean maximum temperatures in July ranged from 16.6°C at Cordova Airport, AK to 29.3°C in Fort Howes, MT. The mean maximum temperature in August was 23.4°C (n=16). Mean maximum temperatures in August ranged from 16.8°C at Cordova Airport, AK to 30.2°C in Fort Howes, MT. If moose are using aquatic areas as a means to ameliorate heat stress then I predict greater use of aquatic habitat in July and August relative to May and June, as the former months would appear to present greater thermal challenges for moose than the latter. I also predict lower intensity of use in May relative to other months, as May appears to be the least thermally stressful month in all regions. I used a subset of

Table 3. Summary of mean maximum temperatures during May-August at 16 locations within 4 geographic regions where North American moose use aquatic habitat. Data from Environment Canada and NOAA online databases (http://climate.weather.gc.ca/; http://www.ncdc.noaa.gov/). All numerical values represent an 11-year average centered on 1992 (the median year of all proportional use studies) except where otherwise indicated. The mean value given is the temperature value for each location averaged across all 4 months and represents an estimate of mean maximum summer temperature in that location. The references indicated are those for which the temperature data were collected. If a temperature monitoring station was not present in an author's study area then the nearest monitoring station was used.

Region	Location	Month				Mean	References
		May	June	July	August		
Alaska-North	Cordova Airport, AK	12.4	15.2	16.6	16.8	15.2	MacCracken et al. (1997)
	Petersburg, AK	14.6[a]	17.2[b]	18.7[b]	18.2[b]	17.2	Doerr (1983)
Great Lakes-St. Lawrence	Grand Marais, MN	12.4	17.2	20.3	21.8	17.9	Lenarz et al. (2011)
	North Bay, ON	16.3	22.0	24.1	22.5	21.3	Kearney and Gilbert (1976)
	Isabella, MN	17.4	22.8	23.7	23.2	21.8	Peek et al. (1976)
	Huntsville, ON	17.8	23.1	25.4	24.1	22.6	Lowe et al. (2010)

[a] =1987-1996

[b] =1987-1995

[c] =1988-1997

Table 3. *cont'd.*

Region	Location	Month				Mean	References
		May	June	July	August		
Great Lakes-St. Lawrence	Agassiz Refuge, MN	20.4	25.3	25.9	26.3	24.5	Phillips et al. (1973)
Mountain-West	Red Rock, MT	14.2[c]	19.4[c]	23.8[c]	24.0[c]	20.3	Dorn et al. (1970)
	Edmonton, AB	17.4	20.6	22.2	21.5	20.4	Renecker and Hudson (1990)
	Fort Nelson, BC	16.8	21.4	22.7	21.7	20.7	Gillingham and Parker (1990)
	Butte, MT	16.6	21.9	26.0	25.9	22.6	Knowlton (1960)
	Fort Howes, MT	20.9[c]	28.1[c]	29.3[c]	30.2[c]	27.1	Van Dyke et al. (1995)
Northeast-Maritimes	Corner Brook, NL	12.2	17.5	21.6	21.7	18.2	Dodds (1955)
	Truro, NS	15.7	21.1	24.3	24.1	21.3	Broders et al. (2012)
	Colebrook, NH	18.1	23.1	25.1	23.8	22.5	Miller and Litvaitis (1992)
	Berlin, NH	18.4	23.9	25.9	25.1	23.3	Scarpitti et al. (2005)

[a]=1987-1996

[b]=1987-1995

[c]=1988-1997

Table 3. cont'd.

Region	Location	Month				Mean	References
		May	June	July	August		
Northeast-Maritimes	Amherst, MA	21.3	26.6	29.0	27.6	26.1	Wattles and deStefano (2013a;b)

[a]=1987-1996

[b]=1987-1995

[c]=1988-1997

references appearing in Table 3 to determine diel variation in air temperature (°C) among 8 sequential daily time periods (1=1100 to 1359, 2=1400-1659…8=0800-1059). Hourly temperature data were used to determine an average air temperature for each time period (e.g., mean of temperatures at 1100, 1200, and 1300, for time period 1). For the five studies conducted in the USA, I utilized the 30-year running average hourly climate normals (1981-2010) available through NOAA (http://www.ncdc.noaa.gov/). I selected a single day (the 16th) of each month (May-August) and calculated the mean value for each daily time period across all four months (Table 4). Hourly climate normals were available for fewer stations in the USA than were monthly temperature data and thus in some cases a new station had to be selected to represent a study area (e.g., Petersburg, AK in Table 3 became Juneau, AK in Table 4). Environment Canada does not provide hourly climate normals for the same 30-year period and only began providing hourly data in 1990. Subsequently, average values for each hour at Canadian locations were computed for the same day (the 16th) in all four months (May-August) for the years 1995-1997 (i.e., centered on the median, 1996, of the 30-year period for which the USA climate normals were calculated,1981-2010). I then calculated the mean for each daily time period across all four months, as above (Table 4). At all locations, the warmest air temperatures occurred in time periods 1-3 (1100-1959), with time period 2 exhibiting the highest mean temperatures (Table 4). Mean temperatures during time periods 1, 2 and 3 for all locations combined were 17.4°C, 18.1°C and 17.1°C, respectively. The coolest air temperatures occurred in periods 5-7 (2300-0759), with time period 6 exhibiting the lowest mean temperatures (Table 4). Mean temperatures during time periods 5, 6 and 7 for all locations combined were 11.9°C, 10.5°C and 11.2°C, respectively. Air temperatures intermediate to those above occurred during time period 4 (13.8°C; 2000-2259) and time period 8 (14.6°C; 0800-1059). If moose are using aquatic areas as a means to ameliorate heat stress then I predict that intensity of aquatic habitat use would be greater during time periods 1-3 (the hottest period of the day) than time periods 5-7.

Nutrition

Aquatic feeding by moose has long been observed throughout North America (McCabe and McCabe 1928; Peterson 1955; Denniston 1956; Leresche and Davis 1973; Aho and Jordan 1979; Joyal and Scherrer 1978; Fraser et al. 1980; Crete and Jordan 1982; MacCracken 1992; Morris et al. 2002) and there are two leading hypotheses that attempt to explain aquatic feeding by moose based on nutritional requirements: sodium acquisition and improved foraging efficiency in aquatic versus terrestrial habitats. Moose are thought to have been responsible for marked declines in biomass of aquatic vegetation on Isle Royale (Murie 1934; Krefting 1951) and evidence from exclosure experiments in Isle Royale, Ontario and Maine supports the notion that moose in some areas consume significant fractions of the annual production of aquatic vegetation (Aho and Jordan 1979; Fraser and Hristienko 1983; Morris et al. 2002; Quarnemark and Sheldon 2004).

It has been hypothesized that moose on Isle Royale are sodium limited (Jordan et al. 1973; Jordan 1987) and as a result consumed large quantities of aquatic vegetation that contained significantly higher sodium concentrations than terrestrial browse (Botkin et al. 1973). Similarly, the sodium content of aquatic vegetation consumed by moose in northwestern Ontario and Maine is at least an order of magnitude greater than the sodium content of terrestrial vegetation in the same areas (Fraser et al. 1984; Crossley 1985). Furthermore, moose in Ontario tended to consume aquatic plants with the highest concentrations of sodium (Fraser et al. 1984).

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Table 4. Summary of mean summer air temperatures for 8 sequential daily time periods (Time 1=1100-1359, 2=1400-1659…8=0800-1059) at 8 locations within 4 geographic regions where North American moose use aquatic habitat. Data were obtained from Environment Canada and NOAA online databases (http://climate.weather.gc.ca/; http://www.ncdc.noaa.gov/). Numerical values for USA locations represent the mean of hourly climate normals (1981-2010) for the 16th of each month in May-August (n=4) for each time period. Values for Canadian locations were computed as above, but due to a lack of data were restricted to a three-year period, 1995-1997, centered on the median of 1981-2010.

Region	Location	Time Period							
		Time 1	Time 2	Time 3	Time 4	Time 5	Time 6	Time 7	Time 8
Alaska-North	Juneau, AK	14.4	13.6	14.2	11.7	10.1	8.0	10.0	12.6
	Valdez, AK	13.0	14.2	13.5	11.4	9.5	7.2	8.6	10.7
Great Lakes-St. Lawrence	Duluth, MN	19.2	20.1	18.5	14.8	12.9	11.9	12.6	16.6
	North Bay, ON	18.0	19.2	18.3	15.4	14	13.1	12.9	15.3
Mountain-West	Fort Nelson, BC	14.2	14.9	14.4	11.9	10.9	9.7	9.9	12.6
	Helena, MT	21.3	23.5	22.2	17.4	14.1	11.7	11.4	16.4
Northeast-Maritimes	Concord, NH	23	23.9	21.8	17.3	14.8	13.3	14.2	19.5
	Corner Brook, NL	15.7	15.6	13.5	10.8	9.2	8.8	10.2	13.4

The primary mechanism driving aquatic feeding by moose in northern Maine was presumed to be a need to acquire sodium (Morris 2002), but close proximity to the Atlantic Ocean, and therefore airborne salt, casts some level of doubt on this interpretation. For example, the very low level of aquatic feeding exhibited by a tame moose living in Newfoundland might be explained by an absence of sodium limitation in moose living in close proximity to airborne salt (Butler 1986). Also somewhat contradictory to the sodium limitation hypothesis is the existence and extensive use of a mineral lick on Isle Royale that should obfuscate a moose's need to feed on aquatics if the drive to use aquatic areas results simply from sodium limitation (Risenhoover and Peterson 1986).

Increased foraging efficiency in aquatic habitats relative to terrestrial habitats was potentially responsible for observed patterns of aquatic use on the Copper River Delta in Alaska (MacCracken 1992). Aquatic plants consumed by moose tended to be more digestible and contained greater crude protein levels than terrestrial vegetation. Available biomass of aquatic forage was also greater than available biomass of terrestrial forage. Peak use of aquatic plants by moose occurred well in advance of peak aquatic plant biomass in the author's study area, as has been reported in Ontario and Minnesota (Peterson 1955; Peek et al. 1976; Fraser et al. 1982). Moose on the Copper River Delta exhibited shortened feeding bouts when feeding on aquatic vegetation relative to terrestrial vegetation, implying that the increased quality and availability of aquatic vegetation relative to terrestrial vegetation led to increased foraging efficiency (MacCracken et al. 1993). Sodium concentrations were not thought to be an important driver of aquatic feeding by moose in their study area. It should be noted that, as discussed above, the proximity of the North Pacific Ocean to the Copper River Delta might eliminate any sodium limitation characteristic of interior sub-populations of moose, such as those in the Great Lakes-

St. Lawrence region. Aquatic forage items represented up to 37% of moose summer diet on Isle Royale and contained greater crude protein levels and lower C:N ratios (used as an index of digestibility) than terrestrial forage species (Tischler 2004). Aquatic feeding by moose might be part of a larger strategy to minimize heat loss and acquire essential minerals while simultaneously maximizing diet quality in a relatively nutrient-poor boreal ecosystem (Tischler 2004).

If the sodium limitation hypothesis were correct I predict that moose belonging to interior sub-populations (i.e., within the Great Lakes-St. Lawrence region) would exhibit greater proportional use of aquatic areas relative to other regions, as these populations are the furthest distance from ocean-derived salt and thus sodium limitation in these populations is more likely than elsewhere in North America. I also predict, under the sodium limitation hypothesis, that aquatic habitat use by moose would be greatest in early spring (May and June) when sodium hunger is greatest due to ionic imbalances resulting from both a shift from woody to herbaceous food and a sodium debt incurred overwinter (Jordan 1987). Under the sodium limitation hypothesis, substantial diel variation in moose aquatic habitat use would not exist if the drive to use aquatic areas is solely to acquire sodium, since mineral concentrations are very unlikely to differ over the course of a 24-hour period. I also expected that moose should exhibit preferences for aquatic plants with higher sodium concentrations relative to aquatic plants with lower sodium concentrations. Under the sodium limitation hypothesis I do not predict moose to exhibit stronger preferences for aquatics than terrestrial forage since aquatic plant ingestion would primarily serve to satisfy sodium, but not necessarily energy or protein requirements.

A different set of predictions results from the hypothesis that aquatic feeding represents a more efficient foraging strategy relative to terrestrial feeding. I predict that moose throughout

North America would seek to maximize foraging efficiency through aquatic feeding and thus proportional use of aquatic areas by moose would not vary with respect to geographic region. I also expected, under the foraging efficiency hypothesis, that substantial seasonal and diel variation in aquatic habitat use by moose would not be readily apparent since moose would seek to maximize foraging efficiency throughout the summer season and over the course of 24-hour cycles. This prediction, however, is complicated by the possibility that aquatic plants in early summer are more palatable (presumably due to greater energy or protein content; Fraser et al. 1984) and that moose might restrict feeding bouts to cooler portions of the day (Belovsky and Jordan 1978; Renecker and Hudson 1992; Dussault et al. 2004). Thus, the existence of seasonal and diel variation in aquatic habitat use by moose would not necessarily allow for discounting of the importance of foraging efficiency. I predict that, under the foraging efficiency hypothesis, moose would show preferences for aquatic forage over terrestrial forage and that moose would feed most often on aquatic plants with higher crude protein and digestible energy values relative to aquatic plants with lower energy and protein values, irrespective of sodium content.

2.2 Literature Search Methods

A detailed literature review was conducted to acquire the data needed to test the above predictions (i.e., data mining). This literature review focused on gaining information pertaining to both the extent and timing of aquatic habitat use and aquatic feeding by moose in North America. Specifically, articles were selected for their capacity to provide information pertaining to the following topics: seasonal and diel variation in peak use of aquatic habitat by moose, proportion of all summer moose locations (as obtained from visual observation, VHF telemetry, or satellite tracking) within aquatic habitats, number and identity of aquatic plant taxa consumed, relative preferences for aquatic plant species relative to other aquatics in the diet or terrestrial vegetation, and sodium concentrations, crude protein levels, and digestible energy values of aquatic vegetation available to moose. I used a modified search method similar to that used by Klassen and Rea (2008; see Fig. 1 within) in their review of nocturnal activity of moose.

I first reviewed the summary volume “Ecology and Management of the North American Moose” (Franzmann and Schwartz 1998), searching systematically through the entirety of the book for any mention of aquatic habitat use or feeding. Any references, based on their title and potential for providing useful information (as indicated by Franzmann and Schwartz 1998), were considered ‘potentially useful.’ ‘Potentially useful’ references were also identified by systematically searching the online article database of the journal *Alces*. Hard copies of the journal, or summary books containing papers from proceedings of the annual North American Moose Conference and Workshop and International Symposia on moose ecology and management (e.g. volume 101 of Naturaliste Canadienne), were also used where available. Finally, ‘potentially useful’ articles were found with Boolean operators and keywords in the online search engine, Thomson Reuters Web of Science (formerly ISI Web of Science), as in Klassen and Rea (2008). This search was designed to be intentionally very broad initially, and the keywords selected for the literature search were chosen accordingly. I utilized the words “moose,” “Alces” or ungulate* as the “moose term” in three separate literature searches. These literature searches took the following general form: (moose term) AND habitat* OR (moose term) AND home range* OR (moose term) AND activit* OR (moose term) and movement* OR (moose term) AND time-energy budget* OR (moose term) AND behavio(u)r OR (moose term) AND forag* OR (moose term) AND food* OR (moose term) AND diet* OR (moose term) AND feed*. I assumed that, given the broad nature of the searches conducted and the detail in which

Franzmann and Schwartz (1998) was examined, all references pertinent to stage 1 of the data mining procedure were located.

As suggested by Klassen and Rea (2008), the abstracts of ‘potentially useful’ articles were scanned and if it became immediately clear that useful data or anecdotal evidence would not be obtained from the article it was discarded and not used as part of this literature review. If the article was not discarded, the introduction and methods were read and the usefulness of the article was reassessed and discarded as above if it did not contain pertinent information. Finally, the results section was read and any pertinent information was recorded. If data or other information were obtained, the article was read in its entirety and any cited articles within were also assessed for their potential usefulness.

2.3 Results

Seventeen studies provided information pertaining to the proportional use of aquatic habitats by moose during summer and early fall (April – October). Data were expressed as a percentage of total summer aquatic habitat use relative to use of other habitats within a given study area (Table 5). Percent aquatic habitat use values appearing in Table 5 were calculated by pooling proportional use data for all seasons, sexes and study sites within each individual study. Areas with saturated soils during summer but without standing water, including treed wetlands, were classed as Bog/Meadow habitat. Pond/Marsh areas included all non-lake or non-river/stream areas containing standing water during some portion of the annual cycle. “Other” wetland habitats included any areas described by the authors as wetlands or aquatic habitat that did not fit within the above categories. Also included in the “Other” category were studies in which all aquatic habitats were pooled into a single category by the original authors. Overall, the mean percent aquatic habitat use by North American moose during summer and early fall (April – October) was 9.16% (n=28 estimates of use).

Mean percent use of aquatic habitat by moose in summer as reported in studies utilizing direct observation, VHF telemetry or GPS collaring was 20.63% (n=6), 5.35% (n=13), and 7.02% (n=9), respectively (Table 5). Unadjusted mean percent use of Lake, Stream/River, Pond/Marsh, Bog/Meadow and Other wetland habitat by moose in summer was 0.5% (n=2), 11.15% (n=2), 3.0% (n=2), 16.25% (n=10), 5.39% (n=12), respectively. However, visual observation of moose in aquatic areas may have provided overestimates of proportional habitat use as both VHF and GPS-based studies reported percent use of aquatic habitat to be much lower than visual sighting-based studies. This bias might arise from the ease of observation of moose in open aquatic areas such as lakes, ponds and rivers relative to forested habitats. Overall, aquatic habitat use was lowest in areas with open water such as lakes and ponds, although this finding relies on just two estimates. Aquatic habitat use was higher in rivers, streams, bogs, and treed wetlands. Stream habitats are often associated with riparian shrub stands (e.g., willow) and thus the result may be confounded by a desire for moose to seek out these areas for lateral cover and/or terrestrial browse (Barry 1961; Boonstra and Sinclair 1961) and not some suite of limnological attributes per se.

Mean percent use of aquatic habitats by moose in summer in Alaska-North, Mountain-West, Great Lakes-St. Lawrence, and Northeast-Maritimes regions was 0.46% (n=5), 9.24% (n=7), 7.29% (n=8), and 17.31% (n=8), respectively Table 5). Percent use of aquatic habitats was greatest in the Northeast-Maritimes region, but this interpretation may be biased by a single large estimate based on visual observation of moose in a single aquatic area (80%; Dodds 1955). If this outlier is removed, the resultant value for Northeast-Maritimes becomes a more conservative

Table 5. Summer and early fall (April – October) aquatic habitat use by moose in North America expressed as percent use of different aquatic habitat types relative to other habitat within a given study area. Percent aquatic habitat use values were calculated by pooling proportional use data for all seasons, sexes and study sites within each individual study. Areas with saturated soils during summer but without standing water, including treed wetlands, were classed as Bog/Meadow habitat. Pond/Marsh areas include all non-lake or non-river/stream areas containing standing water during some portion of the annual cycle. "Other" wetland habitats include any areas described by the authors as wetlands or aquatic habitat that do not fit within the above categories. Also included in the "Other" category are studies in which all aquatic habitats were pooled into a single category by the original authors.

Method	Technique	Region	Type	Reference	Percent use
VHF	Percentage of aerial survey fixes	Alaska-North	Bog/Meadow	Doerr (1983)	1.16
VHF			Lake	Doerr (1983)	0
VHF			Pond/Marsh	Doerr (1983)	0
VHF			Other	Doerr (1983)	1.16
VHF			Stream/River	Doerr (1983)	0
VISUAL	Percentage of moose pellet plots	Great Lakes-St. Lawrence	Bog/Meadow	Kearney and Gilbert (1976)	2.3
VHF	Percentage of ground survey fixes		Pond/Marsh	Berg and Phillips (1974)	6
VHF	Percentage of aerial survey fixes (third order selection)		Bog/Meadow	Lenarz et al. (2011)	15
VHF	Percentage of aerial survey fixes (second order selection)		Bog/Meadow	Lenarz et al. (2011)	17

Table 5. *cont'd.*

Method	Technique	Region	Type	Reference	Percent Use
VHF	Percentage of aerial survey fixes (third order selection)	Great Lakes-St. Lawrence	Other	Lenarz et al. (2011)	5.00
VHF	Percentage of aerial survey fixes (second order selection)		Other	Lenarz et al. (2011)	6.00
VHF	Percentage of aerial/ground survey locations		Other	Phillips et al. (1973)	2.00
GPS	Percentage of utilization distributions		Other	Lowe et al. (2010)	5.00
VISUAL	Percentage of sightings	Mountain-West	Bog/Meadow	Dorn (1970)	6.00
VISUAL	Percentage of sightings		Lake	Dorn (1970)	1
VISUAL	Percentage of sightings		River/Stream	Knowlton (1960)	22.30
VISUAL	Percentage of sightings		Bog/Meadow	Renecker and Hudson (1992)	12.15
VHF	Percentage of aerial/ground survey locations		Bog/Meadow	Van Dyke et al. (1995)	14.70

Table 5. *cont'd.*

Method	Technique	Region	Type	Reference	Percent Use
GPS	Percentage of fixes at 6 hr interval	Mountain-West	Bog/Meadow	Gillingham and Parker (2008)	4.25
GPS	Percentage of fixes at 6 hr interval		Other	Gillingham and Parker (2008)	4.31
VISUAL	Percentage of sightings	Northeast/Maritimes	Bog/Meadow	Dodds (1955)	80.00
VHF	Percentage of aerial/ground survey locations		Other	Miller and Litvaitis (1992)	1.50
GPS	Percentage of fixes at 2-4 hr intervals		Other	Broders et al. (2012)	6.35
GPS	Percentage of minimum convex polygons		Other	Scarpitti et al. (2005)	7.00
GPS	Percentage of utilization distributions		Other	Wattles and de Stefano (2013a)	9.00
GPS	Percentage of minimum convex polygons		Other	Wattles and deStefano (2013a)	12.00
GPS	Percentage of fixes at 0.75-2.25 hr intervals		Bog/Meadow	Wattles and deStefano (2013b)	9.92
GPS	Percentage of fixes at 0.75-2.25 hr intervals		Other	Wattles and deStefano (2013b)	5.33

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estimate of 6.86%. Aquatic habitat use by moose in summer appeared lowest in Alaska-North relative to other regions of North-America.

Sixteen studies provided information pertinent to seasonal variation in aquatic habitat use by North American moose. Of these sixteen studies, four contained quantitative information sufficient to estimate the proportion of peak use of aquatic areas by moose during different portions of the summer (Dunn 1976, Brusnyk and Gilbert 1983, Van Dyke et al. 1995, Scarpitti et al. 2005). Nine studies providing non-quantitative data stated or made reference to the perceived peak in aquatic habitat use during the summer within their study areas (Dodds 1955, Barry 1961, Boonstra and Sinclair 1984, deVos 1958, Dodds 1960, Simkin 1963, Van Ballenberghe and Peek 1971, Kearney and Gilbert 1976, Renecker and Hudson 1989). Three studies provided anecdotal information regarding seasonal variation in aquatic habitat use by North American moose (Goddard 1970; Dodds 1973; Belovsky and Jordan 1978). Anecdotal information followed a trend toward peak aquatic habitat use by moose in mid-summer. Late summer declines were mentioned twice. Dodds (1973) observed a “late summer” decline in aquatic habitat use in Newfoundland, presumably referring to intensity of use by moose. Goddard (1970) stated that aquatic vegetation fed upon by moose in Geraldton, Ontario, was present from late June to early July and thought that peak use of aquatic habitats could be attributed to the seasonal availability of aquatic plants. Belovsky and Jordan (1978) observed a mid-summer minimum (July 13 - August 3) in diversity of deciduous leaves in moose diets and attributed this to the relatively high proportion of aquatic plants in the diet at this time (~18%). A “dropping off” of aquatic habitat use was observed from August 4 – September 15, with a coincident increase in deciduous leaf diversity in the diet (Belovsky and Jordan 1978).

To standardize non-quantitative yet discrete information on seasonal peaks of aquatic habitat use by moose in North America I divided the snow-free period of the annual cycle into 11 discrete 2-week time periods, ranging from April 1- April 14 (Time 1) to September 1-14 (Time 11) and compared peaks in aquatic habitat use reported by different authors (Table 6). Peak use occurred solely within the month of June in the Northwest Territories, northern Ontario and Newfoundland (Barry 1961, Kearney and Gilbert 1976, Dodds 1960). Peak use overlapped the month of June in northeastern Minnesota (May 1 – June 30; Van Ballenberghe and Peek 1971), northern Ontario (June 15 – August 14; deVos 1958, and northern Alberta (June 15 – August 31; Renecker and Hudson 1989). De Vos (1958) reported an extended period of peak aquatic habitat use in Ontario beyond that reported in other studies in that geographic area (Simkin 1963; Kearney and Gilbert 1976). The longest span of reported peak aquatic habitat use was from a study on free-ranging moose in the aspen parklands of Alberta (Renecker and Hudson 1989).

I used the same time periods for quantitative data, whereby some ‘moose-use metric’ of aquatic habitat use provided by the authors was converted to a percentage of peak seasonal use for each time period (Table 7). From each of the four quantitative studies I extracted data from tables and figures, using the mean value of the ‘moose-use metric’ in situations where more than one estimate of moose-use was provided within a time period. If data collection by the authors spanned more than one of the above time periods I used the median date of data collection to determine the relevant time period. Each reported percentage of peak use represented the proportion of the ‘moose use metric’ at that time period divided by the maximum value of the ‘moose use metric’ reported in that study. These data suggest that geographic region influences timing of peak aquatic habitat use, as peak use occurred anywhere from Time 2 (late April in

Table 6. Timing of peak seasonal aquatic habitat use by moose from 9 studies at 6 different locations in North America.

Region	Location	Peak Seasonal Use	Reference
Alaska-North	Northwest Territories	June 1 - June30	Barry (1961)
Mountain-West	Northern British Columbia	May 1 - May 31	Boonstra and Sinclair (1984)
	Northern Alberta	June 15 - August 31	Renecker and Hudson (1989)
Great Lakes-St. Lawrence	Northern Ontario	July 1- July 14	Simkin (1963)
	Northeastern Minnesota	May 1 – June 30	Van Ballenberghe and Peek (1971)
	Northern Ontario	June 15 – June 30	Kearney and Gilbert (1976)
	Northern Ontario	June 15 – August 14	deVos (1958)
Northeast-Maritimes	Newfoundland	July 15 – July 31	Dodds (1955)
	Newfoundland	June 1 –June 30	Dodds (1960)

Table 7. Seasonal variation in aquatic habitat use by moose from 4 studies in 4 separate study areas within North America expressed as the percentage of peak daily use in 11 2-week time periods. Time periods correspond to the following portions of the snow-free period: Time 1= April 1- April 14; Time 2 = April 15- April 30; Time 3 = May 1 – May 14; Time 4 = May 15 – May 31; Time 5 = June 1 – June 14; Time 6 = June 15 – June 30; Time 7 = July 1 - 14; Time 8 = July 15 – July 31; Time 9 = August 1 -14; Time 10 = August 15 – August 31; Time 11 = Sept 1 – Sept 14. Peak values for each study area are shown in bold.

Region	Location	Time Period											Reference
		1	2	3	4	5	6	7	8	9	10	11	
Mountain-West	Montana		**100%**						42%				Van Dyke et al. (1995)
Northeast-Maritimes	New Hampshire			75%					**100%**				Scarpitti et al. (2005)
	Maine					22.5%	35%	**97.5%**	82.5%	35%			Dunn (1975)
Great Lakes-St. Lawrence	Northern Ontario				33.3%	43.3%	**100%**	71.3%	37.8%	24.5%	40%	24.5%	Brusnyk and Gilbert (1983)

Montana) to Time 8 (July 15 – July 31 in New Hampshire; Table 7). It appeared that peak use occurred earlier in northern Ontario (Time 6) than in Maine (Time 7) and New Hampshire (Time 8; Table 7). Overall, the quantitative data agree generally with the non-quantitative information presented above in that the greatest intensity of aquatic habitat use by moose in North America, with some exceptions, appears to occur during the months of June and July in a variety of geographic areas.

Thirteen studies provided information pertinent to diel variation in aquatic habitat use by North American moose. Of these thirteen studies, only three contained quantitative information sufficient to estimate the proportion of peak use of aquatic areas by moose during different portions of the daily cycle (deVos 1958; Ackerman 1987; Cobus 1972). Of the ten studies providing pertinent non-quantitative information, five contained some statement regarding peak daily use of aquatic areas that could be attributed to a discrete time period (Denniston 1956; Simkin 1963; Saunders and Williamson 1972; Dunn 1976; Joyal and Scherer 1978). The remaining five studies provided purely anecdotal information on diel variation in aquatic habitat use by moose (McCabe and McCabe 1928; Dodds 1955; Goddard 1970; Fraser et al. 1980; Renecker and Hudson 1992b).

Overall, moose in North America appear to exhibit crepuscular patterns in aquatic habitat use, with some exceptions. Anecdotal information from Newfoundland indicated sightings of moose in aquatic areas near midday were rare (Dodds 1955). Goddard (1970) and Fraser et al. (1980), working in northwestern Ontario, reported greater frequency of moose sightings and aquatic feeding during twilight hours (early morning and late evening). McCabe and McCabe (1928) indicated that moose would enter aquatic areas to feed within the Bowron Lake region of British Columbia but stated that moose "leave the water with the sun or shortly thereafter" except “during periods of intense heat”. Conversely, Renecker and Hudson (1992) found that feeding on cattails and sedges in semi-aquatic meadows by moose appeared restricted to the middle of the day in the aspen-parklands of Alberta.

To standardize non-quantitative yet discrete information on daily peaks of aquatic habitat use by moose in North America I divided the 24-hr cycle into 8 discrete 3-hr time periods, ranging from 1100-1359 (Time 1) to 0800-1059 (Time 8). I used the same time periods for quantitative data, whereby some ‘moose-use metric’ of aquatic habitat use provided by the authors was converted to a percentage of peak daily use for each time period (availability of data permitting). From each of the three quantitative studies I extracted data from tables and figures, using the mean value of the ‘moose-use metric’ in situations where more than one estimate of moose use was provided within a time period. This provided information on primary and secondary daily peaks of aquatic habitat use by moose as well as apparent daily minimums of aquatic habitat use.

Non-quantitative data regarding diel variation in aquatic habitat use by moose suggested that daily peaks in aquatic habitat use are somewhat variable in North America (Table 8). A single study from Wyoming reported a daily peak between 0200 and 1059 hours but this was the only study that reported a peak in use within two hours after midnight. Each of the remaining non-quantitative studies gave peaks no earlier than 0500 in the morning and no later than 2259 at night. Studies from western Quebec and northern Maine suggested that aquatic habitat use peaks between 1100 and 1659 whereas two studies from northern Ontario suggested a crepuscular pattern in aquatic habitat use with daily peaks at 0500-0759 and 2000-2259. Thus, the non-quantitative data on diel variation in aquatic habitat use by moose suggested that moose most often use aquatic areas during the day or in the early evening.

Table 8. Timing of peak daily summer aquatic habitat use by moose reported in 5 studies from 4 different locations in North America.

Region	Location	Peak Daily Use	Reference
Mountain-West	Wyoming	0200 – 1059	Denniston (1956)
Great Lakes-St. Lawrence	Northwestern Ontario	0500 – 0759 and 2000-2259	Simkin (1963)
	Northwestern Ontario	0500 – 0759 and 2000-2259	Saunders and Williamson (1972)
	Western Quebec	1100 – 1659	Joyal and Scherer (1978)
Northeast-Maritimes	Northern Maine	1100 –1659	Dunn (1976)

Table 9. Diel variation in aquatic habitat use by moose reported in 3 studies from 3 separate study areas within the Great Lakes-St. Lawrence region expressed as the percentage of peak daily use in 8 3-hr time periods. Parentheses denote mean values of the measurement indicated for each time period. Time periods correspond to the following portions of the 24-hr cycle: Time 1= 1100-1359; Time 2 = 1400-1659; Time 3 = 1700 – 1959; Time 4 = 2000 – 2259; Time 5 = 2300 = 0159; Time 6= 0200-0459; Time 7 = 0500 – 0759; Time 8 = 0800 – 1059. Peak values for each study area are shown in bold.

Region	Location	Time Period								Measure	Reference
		1	2	3	4	5	6	7	8		
Great Lakes-St. Lawrence	Isle Royale, MI	26.3% (0.25)	28.4% (0.27)	42.1% (0.40)	**100%** **(0.95)**	30.5% (0.29)	32.6% (0.31)	71.6% (0.68)	33.7% (0.32)	Moose visits/hr	Ackerman (1987)
	Sibley, ON	26.8% (1.02)	48.2% (1.83)	50.8% (1.93)	**100%** **(3.80)**			97.9% (3.72)	50.8% (1.93)	# moose present	Cobus (1972)
	Chapleau, ON		44.5% (0.15)		**100%** **(0.35)**			90.1% (0.31)		Moose seen/hr	deVos (1958)

The quantitative data regarding diel variation in aquatic habitat use clarified somewhat the pattern described above, with aquatic habitat use by moose showing a consistent peak between 2000 and 2259 (Table 9). The number of moose visits per hour (0.95; Ackerman 1987), number of moose present (3.80; Cobus 1972) and number of moose seen per hour (0.35; deVos 1958) in aquatic habitats were all greatest between 2000 and 2259 compared to all other time periods. A secondary peak in aquatic habitat use was reported for all studies from 0500-0759. It should be noted that only Ackerman (1987) conducted observations during nighttime (2300-0459) but reported relatively low use of aquatic habitat at these times (30.5%-32.6% of peak aquatic habitat use). Therefore, quantitative data on diel variation in aquatic habitat by moose appeared to show the greatest intensity of use in the evening (2000-2259) with a secondary peak in the early morning (0500-0759). These data indicated a crepuscular pattern in aquatic habitat use by moose that agreed with non-quantitative observations from the Great Lakes-St. Lawrence region.

Very little information was available for all geographic locations with respect to the proportion of aquatics in the summer diet. Using isotopic analysis of moose hooves on Isle Royale, Tischler (2004), estimated the percentage of aquatics in the summer diet of moose at 14-37%. Conversely, Dungan and Wright (2005) estimated the percentage of aquatics in the summer diet of moose at less than 1% according to bite-count and fecal analyses. On the Kenai Peninsula in Alaska, 3% of summer bites (July and August, n = 28 423 bites) taken by 3 tame moose occurred while feeding on aquatics (Leresche and Davis 1973). It appears plausible moose consume a greater proportion of aquatic forage in the Great Lakes – St. Lawrence region than elsewhere in North America (e.g., Mountain – West and Alaska – North).

Thirty-one studies reviewed provided information pertaining to the number of aquatic plant taxa consumed by moose in different geographic areas. These ordinal data were partitioned according to five commonly recognized functional groups (submersed, emergent, floating-attached, floating unattached, wetland forbs; Cronk and Fennessy 2008; Newmaster et al. 1997). In many cases a single or no estimate was available in the literature for a given functional group in a certain geographic region. Conversely, as many as eight studies contributed to a given functional group within a certain geographic region (i.e., submersed plants in Ontario). In the latter cases, the mean number of taxa reportedly consumed by moose was used as the estimate for the plant functional group in that region.

Greater than one third of all studies on consumption of aquatic plant taxa derived from Ontario, Isle Royale and Quebec (11 of 31), with Ontario most strongly represented (Table 10). Moose appeared to consume greater numbers of submersed and emergent taxa in all geographic areas, followed by floating-attached, floating-unattached, and wetland forb plants, respectively. Consumption of wetland forbs was reported only in Alaska, Colorado, and Ontario. Consumption of floating-unattached plants (commonly referred to as duckweeds) occurred only in Montana, Wyoming and Isle Royale, though moose in Wyoming and Isle Royale were thought to be consuming primarily algae (likely *Spirogyra* spp.) rather than duckweeds (Denniston 1956; Belovsky and Jordan 1978). A low diversity of floating-attached plants in the diet was consistently observed in Colorado, Wyoming, Ontario, Quebec, and Newfoundland. Moose on Isle Royale were not observed to commonly consume floating-attached aquatic vegetation (only a single study reported its consumption; Botkin et al. 1973), though the possibility of historic extirpation of these types of plants has been suggested elsewhere (Murie 1934; Krefting 1974). Overall, submersed and emergent aquatic plants seem to be a fairly consistent component of

Table 10. The number of aquatic plant taxa consumed by North American moose at 11 geographic locations. Information was partitioned according to aquatic plant type. Parentheses denote the number of studies which contributed to each mean number of consumed taxa (rounded to the nearest whole value).

Region	Location	Submersed	Emergent	Floating Attached	Floating Unattached	Wetland Forb	References[a]
Alaska - North	Alaska	2 (2)	5 (2)	1 (1)		2 (3)	22,24,26,35
Mountain - West	British Columbia	3 (1)	3 (2)				14,27,33
	Alberta		1 (1)				32
	Colorado	1 (1)	1 (1)	1 (1)		1 (1)	12,13
	Montana				1 (1)		23
	Wyoming	4 (2)	1 (1)	1 (1)	1 (1)		8,28
Great Lakes – St. Lawrence	Ontario	4 (8)	4 (5)	2 (7)		1 (1)	3,6,11,15,16,18,19,29
	Isle Royale	3 (3)		1 (1)	1 (2)		1,2,4,31
	Quebec	1 (2)	1 (2)	2 (1)			5,7,21
	Minnesota	1 (1)	1 (1)				30
Northeast - Maritimes	Newfoundland	3 (1)	5 (2)	2 (2)			9,10

[a] 1 = Aho and Jordan (1979), 2= Belovsky and Jordan (1978), 3= Berube (2000), 4 = Botkin et al. (1973), 5 = Boudreau and Bisson (1983), 6 = Cobus (1972), 7 = Crete and Jordan (1981), 8=Denniston (1956), 9 = Dodds (1955), 10 = Dodds (1960), 11 = DeVos (1958), 12 = Dungan and Wright (2005), 13 = Dungan et al. (2010), 14 = Eastman and Ritcey (1987), 15 = Fraser and Hristienko (1983), 16 = Fraser et al. (1980), Fraser et al. (1982), 18 = Fraser et al. (1984), 19 = Goddard (1970), 20 = Joyal (1987), 21 = Joyal and Scherrer (1978), 22= Kielland (2001), 23 = Knowlton (1960), 24 = Leresche and Davis (1973), 25 = Linn et al. (1973), 26 = MacCracken et al. (1993), 27 = McCabe and McCabe (1928), 28 = McMillan (1953), 29 = Peterson (1953), 30 = Phillips et al. (1973), 31 = Quarnemark and Sheldon (2004), 32 = Renecker and Hudson (1985), 33 = Ritcey and Verbeek (1969), 34 = Tischler (2004), 35 = Van Ballenberghe et al. (1989).

moose summer diets throughout North America, with some exceptions (e.g., Alberta and Montana).

Twenty-nine of 31 studies reviewed provided information pertaining to the identity of the aquatic plant species consumed by moose in North America. Thirteen studies reviewed provided information sufficient to attempt an understanding of the relative levels of consumption for many aquatic plant taxa. I used standard competition ranking to generate whole values representing the relative contributions of each species, where possible, relative to other aquatic forage items in the diet. A rank of 1 represented the highest possible rank, and was indicative of a greater level of consumption for a given aquatic plant relative to all other aquatic plants in the diet. In cases where multiple estimates of relative consumption were available for a given species in a certain geographic region the mean rank was used. Though presenting means is typically not suitable for ranked data, I believe that the low number of instances where the number of relative consumption estimates exceeded two (this occurred once, with *Potamogeton alpinus* having three estimates from Ontario) led this to be an effective technique in this case. A further five studies provided information sufficient to generate estimates of aquatic plant consumption relative to all summer food items.

Studies from Alberta, Colorado and Montana identified a very low number of consumed taxa but those identified tended toward higher consumption ranks (Table 11). A single study from Minnesota reported a low number of aquatic taxa (2) consumed by moose and it was not possible to generate consumption ranks for these taxa. Conversely, studies from Ontario and Isle Royale identified the greatest number of aquatic plant taxa consumed by moose. Ontario studies demonstrated a wider range of preference ranks than Isle Royale, with the latter area seeming to have high consumption ranks for a fewer number of species. Studies from British Columbia,

Table 11. Identity and consumption rankings of aquatic forage items consumed by North American moose at 11 geographic locations. Ranked values are shown relative to other aquatics in the diet and relative to all summer food items, where available, at 10 geographic locations. Standard competition ranking was used in all cases, with 1 representing the highest possible level of consumption by moose. In the event that multiple studies within the same geographic location were used to generate ranks, the mean value was taken. Bolded rows demonstrate an apparently consistent decrease in consumption rank when all summer forage items were used in the standard competition ranking procedure. Specific content of sodium and crude protein, expressed as a percentage of 1 g dry matter, were included where available. Energy contents of individual plant taxa represent caloric content per g of dry matter. In the event that multiple studies within the same geographic location gave different values for sodium, protein, or caloric content, the mean value was taken.

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Alaska-North	Alaska	*Carex spp.*			0.02	4.90[b]		24,26
		Drosera rotundifolia						24
		Eriophorum angustifolium						24
		Eriophorum russeolum						24
		Equisetum spp.			0.09	7.70[b]		24,26
		Nuphar polysepalum						24
		Menyanthes trifoliate			0.09	9.20[b]		24,26

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Alaska-North	Alaska	*Pedicularis palustris*						22
		Petasites sp.	1.0	12.0				35
		Potamogeton spp.						22
		Potamogeton epihydrus						24
		Potamogeton perfoliatus						24
		Potentilla palustris			0.06	2.80 [b]		24,26
		Ranunculus reptans						24
		Rubus chamaemorus						24
Mountain-West	British Columbia	*Carex spp.*	4.0					14
		Chara sp./ Nitella sp. (Characeae)	8.0					33

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Mountain-West	British Columbia	*Equisetum spp.*	1.0					33
		Menyanthes trifoliata	5.0					33
		Nuphar spp.						27
		Potamogeton spp.	3.0					27,33
		Potentilla palustris	6.0					33
		Ranunculus spp.	6.0					27,33
		Sparganium spp.	2.0					33
	Alberta	*Typha latifolia*						32
	Colorado	*Nuphar spp.*	2.5	9.0				12,13
		Rumex aquaticus	1.5	6.5				12,13

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Mountain – West	Montana	*Lemna trisulca*	1.0	10.0				23
	Wyoming	*Carex spp.*		8.0				8
		Chara sp.	6.0	19.0				28
		Heteranthera dubia	1.0	3.0				28
		Myriophyllum spp.	2.0	4.0				28
		Nymphaea spp.						8
		Potamogeton alpinus	5.0	13.0				28
		Potamogeton pectinatus	4.0	6.0				28
		Potamogeton spp.						8
		unknown algae						8

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Mountain-West	Wyoming	*Utricularia spp.*	3.0	5.0				28
Great Lakes – St. Lawrence	Ontario	*Brasenia schreberi*						29
		Carex spp.						29
		Chara sp./ Nitella sp. (Characeae)	2.0		0.30	14.00	2961	15
		Eleocharis spp.	10.0		0.23	11.69	4271	3,17,18,29
		Equisetum spp.	9.0		0.22	13.60	3896	11,16,17,18,29
		Glyceria borealis						11
		Juncus spp.						29
		Menyanthes trifoliata						11
		Myriophyllum spp.	1.0		0.97	15.69	3965	3,17,18

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Ontario	*Nuphar spp.*	5.7		0.50	17.71	4507	3,6,11,16,17,18,19,29
		Nymphaea spp.						29
		Pontedaria cordata						29
		Potamogeton alpinus	4.5		0.64	18.10	3832	15,18
		Potamogeton amplifolius	14.0		0.34	13.80	4416	6,11,17,18
		Potamogeton epihydrus	2.0		0.65	16.00	4429	11,15,17,18
		Potamogeton filliformis	1.0		0.78	16.20	4552	6,17,18
		Potamogeton foliosus	2.5		0.83	20.30	4536	15,18
		Potamogeton gramineus	1.0		0.61	14.40	4363	11,17,18
		Potamogeton natans	11.0		0.42	14.55	4491	11,17,18

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Ontario	*Potamogeton perfoliatus*						11
		Potamogeton praelongus	13.0		0.26	15.80	4581	17,18
		Potamogeton pusillus						11
		Potamogeton richardsonii						11
		Potamogeton robinsii	10.5		0.52	15.50	4511	16,18
		Potamogeton zosteriformis	12.0		0.41	18.80	4436	6,18
		Sagittaria spp.	4.0					11,16,29
		Scirpus spp.	1.0		0.63	17.00	4423	11,18,29
		Sparganium angustifolium	4.0		0.65	16.25	4160	3,16,17,18
		Sparganium fluctuans						29

Table 11.*cont'd*.

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Ontario	*Typha latifolia*	2.0		0.25	13.10	4400	16,17
		Utricularia spp.	1.0		1.35	14.32	3740	3,17,18
		Vallisneria Americana						11,19,29
		Zizania sp.						11
Great Lakes – St. Lawrence	Isle Royale	*Carex spp.*	4.0		0.07	5.80		2,4
		Chara sp./Nitella sp. (Characeae)	2.0		0.10	6.80		2,4
		Eleocharis spp.	6.0		0.14	13.00		2,4
		Equisetum fluviatile	5.0		0.16	9.60		2,4
		Lemna minor	2.0			13.80		1
		Myriophyllum spp.	4.0		0.48	14.00		4,31

Table 11. *cont'd*.

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Isle Royale	*Potamogeton pusillus*	2.5					1,31
		Potamogeton richardsonii	3.0		0.72			4,31
		Potamogeton spirillus	4.0					31
		Potamogeton spp.	3.0			15.30		2
		Sagittaria spp.	4.0			14.80		31 2
		Spirogyra spp.	1.0					
		Nuphar spp.			0.94	22.90		4
	Quebec	*Brasenia schreberi*						21
		Nuphar variegatum						20,21

Table 11. *cont'd*.

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Quebec	*Sparganium angustifolium*						21
		Typha spp.						20
	Minnesota[c]	*Carex lacustra*[c]			0.02	8.63		25
		Carex stricta[c]			0.02	9.96		25
		Chara vulgaris[c]			0.18	7.92		25
		Eleocharis smallii[c]			0.76	5.78		25
		Myrophyllum exalbescens			0.77	12.28		25,30
		Nuphar variegatum[c]			0.51	15.70		25
		Nymphaea odorata[c]			0.17	19.88		25

Table 11. *cont'd*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Minnesota	*Potamogeton amplifolius*[c]			0.17	14.36		25
		Potamogeton richardsonii[c]			0.14	11.20		25
		Sagittaria cuneata[c]			0.39	21.81		25
		Sagittaria rigida[c]			0.24	14.78		25
		Sparganium eurycarpum[c]			0.10	7.60		25
		Sparganium fluctuans[c]			0.40	13.19		25
		Typha spp.			0.12	6.92		25,30
		Vallisneria americana[c]			0.52	15.15		25

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Great Lakes-St. Lawrence	Minnesota	*Zizania aquatica*[c]			0.25	9.88		25
Northeast – Maritimes	Newfoundland	*Carex rostrate*						9,10
		Equisetum fluviatile						10
		Menyanthes spp.						9
		Nuphar sp.						9,10
		Nymphaea odorata						10
		Pontedaria cordata						9,10
		Potamogeton gramineus						10

Table 11. *cont'd.*

Region	Location	Taxa	Consumption Rank among aquatics[a]	Consumption rank among all summer foods	Sodium Content (% Dry Weight)	Crude Protein Content (% Dry Weight)	Energy Content (Cal./g)	References[d]
Northeast-Maritimes	Newfoundland	*Scirpus cespitosus*						9,10

[a]Species listed are those reported to be consumed by moose in different geographic areas. Consumption ranks reflect ordered quantitative data where available. Species for which quantitative data (e.g., relative biomass consumed, preference indices) were not available were not included in the ranking procedure.

[b]Values have been converted to % digestible protein on a dry matter basis.

[c]Values from Minnesota were not based on study of moose consumption. Species/genera listed may not be consumed by moose in this location but were reported eaten by moose in nearby Ontario.

[d] 1 = Aho and Jordan (1979), 2= Belovsky and Jordan (1978), 3= Berube (2000), 4 = Botkin et al. (1973), 5 = Boudreau and Bisson (1983), 6 = Cobus (1972), 7 = Crete and Jordan (1981), 8=Denniston (1956), 9 = Dodds (1955), 10 = Dodds (1960), 11 = DeVos (1958), 12 = Dungan and Wright (2005), 13 = Dungan et al. (2010), 14 = Eastman and Ritcey (1987), 15 = Fraser and Hristienko (1983), 16 = Fraser et al. (1980), Fraser et al. (1982), 18 = Fraser et al. (1984), 19 = Goddard (1970), 20 = Joyal (1987), 21 = Joyal and Scherrer (1978), 22= Kielland (2001), 23 = Knowlton (1960), 24 = Leresche and Davis (1973), 25 = Linn et al. (1973), 26 = MacCracken et al. (1993), 27 = McCabe and McCabe (1928), 28 = McMillan (1953), 29 = Peterson (1953), 30 = Phillips et al. (1973), 31 = Quarnemark and Sheldon (2004), 32 = Renecker and Hudson (1985), 33 = Ritcey and Verbeek (1969), 34 = Tischler (2004), 35 = Van Ballenberghe et al. (1989)

Wyoming and Newfoundland, though not identifying as many consumed taxa as on Isle Royale or in Ontario, tended toward a pattern of broader, higher consumption ranks. An apparently consistent and sometimes very large increase in preference ranks occurred when all summer food species were included in the ranking scheme in all geographic regions where this information was available. The geographic areas with the greatest number of reported aquatic taxa consumed by moose (Ontario and Isle Royale) were also the areas where it was most difficult to generate consumption ranks for aquatic plant species relative to all summer food items. Ontario boasted the greatest number of studies on moose aquatic feeding (9) and the greatest number of aquatic food items consumed by moose in a single study (19) but no studies from this area positioned the moose's aquatic foraging behavior within the larger context of moose summer diet composition.

Sodium content ranged from 0.02% dry matter (*Carex* spp. in Alaska and *Carex stricta* in Minnesota) to 1.35% dry matter (*Utricularia* in Ontario; Table 11). *Myriophyllum* sp., *Nuphar* spp., and *Potamogeton* spp. also exhibited relatively high sodium levels in the Great Lakes – St. Lawrence region (on average, 0.74%, 0.65%, and 0.50%, respectively). On average, sodium contents of plants consumed by moose were higher in the Great Lakes – St. Lawrence region than the Alaska – North region (0.43% versus 0.07%). Within the Great Lakes – St. Lawrence region the highest mean sodium contents in plants consumed by moose were observed in Ontario (0.556%), followed by Isle Royale (0.37%) and Minnesota (0.30%). Data regarding digestible protein content (% dry matter) were only available from Alaska for four species (*Potentilla palustris* = 2.80%, *Carex* spp. = 4.90%, *Equisetum* spp. = 7.70%, and *Menyanthes trifoliata* = 9.20%; Table 11). Crude protein contents (% dry matter) ranged from 5.78% (*Eleocharis smallii* in Minnesota) to 22.90% (*Nuphar* spp. on Isle Royale) in the Great Lakes – St. Lawrence region. Relatively high mean protein contents were also reported for *Nymphaea* spp. (19.88%), *Sagittaria* spp. (17.13%), *Potamogeton* spp. (15.72%) and *Myriophyllum* spp. (13.99%) in the Great Lakes – St. Lawrence region. The average crude protein content of aquatic plants in the Great Lakes – St. Lawrence region was 13.81% (n=45). On average, crude protein contents of plants consumed by moose in the Great Lakes – St. Lawrence region were highest in Ontario (15.62%) followed by Isle Royale (12.97%) and Minnesota (12.19%). Caloric values (Cal./g dry matter) of aquatic plants consumed by moose were only available from Ontario and ranged from 2961 Cal./g (*Chara* and/or *Nitella* spp.) to 4581 Cal./g (*Potamogeton praelongus;* Table 11). Relatively high caloric contents were also reported in Ontario for *Nuphar* spp. (4507 Cal./g), *Scirpus* spp. (4423 Cal./g), *Typha latifolia* (4400 Cal./g) and *Potamogeton* spp. (4415 Cal./g, n= 10 spp.). On average, aquatic plants consumed by moose in Ontario contained 4235 Cal./g. Aquatic plant species consumed by moose are not uniform with respect to their potential nutritional value nor does it seem that mean sodium and protein contents are similar in different regions of North America, with moose in the Alaska – North region apparently consuming less nutritious aquatic forage than moose in the Great Lakes – St. Lawrence region.

2.4 Discussion

My review of the literature pertaining to aquatic habitat use by North American moose revealed several important patterns related to geographic, seasonal and diel variation in use and consumption of aquatic plants. Proportional use of aquatic habitat was markedly lower in the Alaska-North region compared to elsewhere in North America but was similar among the remaining regions (Mountain-West, Great Lakes-St. Lawrence and Northeast-Maritimes). Observational data from the Northeast-Maritimes region suggested the greatest proportional use of aquatic habitat by moose in this region relative to all others, but this could be an artifact of a single outlying study (Dodds 1955).

Seasonal variation in aquatic habitat use by moose was greatest from mid-June to July. Outside of this peak period moose showed slightly greater intensity of use later in the summer (August to early-September) compared to earlier in the summer (April to May; but see Van Dyke et al. 1995). Data pertaining to diel variation in aquatic habitat use by moose suggested a crepuscular pattern with a primary daily peak in use from 2000-2259 and a secondary daily peak from 0500-0759.

The proportion of aquatic food items in the diet was low in all regions, suggesting that moose predominately consumed terrestrial forage during summer (but see Tischler 2004). Moose preference for aquatic forage items declined when all summer food items (including terrestrial forage) were included in the rankings relative to when only aquatic forage items were considered. Aquatic foods with higher preference ranks (e.g., *Myriophyllum* spp., *Potamogeton* spp.) often had greater sodium content than aquatic foods with lower preference ranks (e.g., *Eleocharis* spp) but this pattern was not consistent. For example, *Typha latifolia* had a high preference rank in the Great Lakes-St. Lawrence and was consumed in the Mountain-West region but was low in sodium. Sodium content of aquatic plants consumed in the Alaska-North region appeared to be lower than sodium content in aquatic plants consumed by moose in the Great Lakes-St. Lawrence region. Crude protein content did not appear to consistently influence preference for aquatic forage items by moose, with several species with comparatively high levels of protein showing low preference ranks (e.g., *Potamogeton natans*). Several species with high preference ranks, however, also contained high crude protein levels (e.g., *Myriophyllum* spp., *Potamogeton foliosus*, *Nuphar* spp.). Data on caloric content of aquatic food items consumed by moose was limited to the Great Lakes-St. Lawrence region but generally did not show a consistent influence on preference by moose. *Potamogeton* spp. consumed by moose, for example, generally had similar energy contents but differed widely in their apparent preference by moose. Similarly, species with the highest preference ranks (e.g., *Utricularia* spp. and *Myriophyllum* spp.) actually exhibited some of the lowest caloric values, though it is not clear to what extent numerical differences in energy content of aquatic plants translate into ecologically meaningful differences in plant quality for moose. In general, moose preferences for aquatic vegetation do not follow consistent patterns related to sodium, protein or caloric content but moose living in the Great Lakes-St. Lawrence region tended to consume more aquatic forage items high in sodium relative to other regions (e.g., Alaska-North).

I did not find sufficient evidence to accept the hypothesis that moose use aquatic areas in order to minimize the direct risk of predation by wolves (Table 12). Wolf density in North America was greatest in the Great Lakes-St. Lawrence region followed by the Alaska-North region and lowest in the Northeast-Maritimes region. Proportional use of aquatic habitat by moose, however, was lowest in the Alaska-North region and relatively high in the Northeast-Maritimes region. The combination of low aquatic habitat use in areas with dense wolf populations (e.g., Alaska, particularly the Kenai Peninsula and south-central Alaska) and high aquatic habitat use (or at least moderate relative to other regions) in areas largely lacking canid predators (Newfoundland, Maine) suggested that North American moose are not influenced by wolf density in their use of aquatic habitat in summer. Similarly, moose showed seasonal peaks (mid-June-July) in activity well in advance of presumed peak direct predation risk. Daily patterns in aquatic habitat use by moose appeared to coincide partly with peak summer wolf activity (and thus greatest presumed direct predation risk). This must be interpreted with caution, however, since wolves typically leave the den in the evening to hunt and return sometime near morning which would mean that moose should show a nocturnal pattern of aquatic habitat use as opposed

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Table 12. Qualitative evaluation of evidence for five hypotheses explaining aquatic habitat use by North American moose presented according to the predictions outlined by the hypothetico-deductive model appearing in Table 1.

Hypothesis	Predictions				Conclusion
	Geographic variation	Seasonal variation	Diel variation	Forage preferences	
Minimization of direct predation risk	Aquatic use did not correspond to geographic variation in wolf density	Aquatic use did not correspond to seasonal patterns in direct predation risk	Aquatic use only partially corresponded to daily patterns in direct predation risk	Some preferences for aquatic forage items that were not anticipated	Hypothesis not accepted
Biting insect avoidance	Could not be evaluated	Aquatic use corresponded to seasonal patterns in biting insect activity	Aquatic use corresponded to daily patterns in biting insect activity	Some preferences for aquatic forage items that were not anticipated	Hypothesis plausible
Heat stress amelioration	Aquatic use did not correspond to geographic variation in warm temperatures	Aquatic use did not correspond to seasonal temperature peaks	Aquatic use did not correspond to daily temperature peaks	Some preferences for aquatic forage items that were not anticipated	Hypothesis not accepted
Nutrition (sodium acquisition)	Aquatic use for the purpose of feeding appeared high in Great Lakes-St. Lawrence region but not necessarily low in coastal regions as had been anticipated	Seasonal patterns in aquatic use did not correspond to presumed sodium need but interpretation complicated by seasonal variation in plant availability	Apparent crepuscular pattern in aquatic use that was not anticipated	Terrestrial forage preferred over aquatic forage as anticipated. Many aquatic items commonly consumed were high in sodium but moose showed apparent preferences for low sodium items	Hypothesis plausible

Table 12. *cont'd.*

Hypothesis	Predictions				Conclusion
	Geographic variation	Seasonal variation	Diel variation	Forage preferences	
Nutrition (foraging efficiency)	Absence of a pronounced geographic pattern in aquatic use as anticipated but many studies from the Great Lakes-St. Lawrence region reported aquatic feeding by moose	Apparent seasonal variation in aquatic habitat use that had not been anticipated but this may have been due to confounding effects of plant availability and/or palatability	Apparent crepuscular pattern in aquatic use could be related to strategy for minimizing heat gain while maximizing daily energy intake	Aquatic forage not preferred over terrestrial forage as had been anticipated. Preferred aquatic items were not consistently high in protein or caloric content	Hypothesis plausible

to a crepuscular pattern if they are predominately using aquatic areas to minimize direct risk of predation. Overall, predation risk minimization is not the most likely mechanism driving aquatic habitat use by North American moose. In fact, there may be greater reason for moose to avoid aquatic areas since there is considerable evidence that wolves actually use the shorelines of aquatic areas such as lakes and rivers as travelling avenues while hunting (Paradiso and Nowak 1982; Bump et al. 2009). Addison et al. (1990) indicated that cow moose might select calving sites that, though in relatively close proximity to water, were actually as far away as possible from shorelines. Similarly, though Wilton and Garner (1991) suggested that water was an important predator deterrent and thus was important for calving site selection, their data indicated that elevation might play a more dominant role in determining calving site quality. Moose may actually be more, not less, vulnerable to predation when in aquatic habitat because they have a difficult time extricating themselves from mucky, aquatic substrates relative to solid, terrestrial substrates (McMillan 1954; Belovsky 1978; Timmermann and Racey 1989).

There was insufficient evidence to accept the heat stress amelioration hypothesis (Table 12). If moose were using aquatic areas primarily as thermal relief sites then the greatest proportional use of aquatic areas would occur in the hottest regions of North America. Although proportional use was lowest in the coolest region (Alaska-North) it did not seem higher in the two warmest regions (Mountain-West and Northeast-Maritimes) relative to the Great Lakes-St. Lawrence region. This interpretation, however, may be complicated by the arbitrary boundaries I set for these regions. As a result I cannot rule out the possibility that aquatic areas might still be important thermal relief sites at southern range limits (Kelsall and Telfer 1974). The seasonal peak in aquatic habitat use by moose (mid-June to July) does not coincide with the hottest portions of the summer. In all geographic regions in North America temperatures are highest in

July and August and thus moose were predicted to show peak use at this time. Though it appeared that moose had a greater tendency to use aquatic areas in August than in May, the pattern was not consistent among all studies reviewed and moose seemed to use aquatic areas in early fall as well as summer. Thus, I suggest that this seasonal variation in aquatic use is not related solely to increased temperature. Moose also did not show daily peaks in use of aquatic areas during the hottest portion of the day (1400-1659), but instead showed a relatively crepuscular pattern in aquatic habitat use with a strong peak occurring in the evening at 2000-2259.

I was unable to reject the insect avoidance hypothesis (Table 12). A lack of information in the literature precluded development of a prediction pertaining to geographic variation in proportional use of aquatic habitat by moose under an insect avoidance strategy, possibly owing to the ubiquity of culicids, simuliids and tabanids throughout North America. The seasonal peak in aquatic habitat use by moose described in my review seems to conform well to peak biting insect season, particularly for the culicids. Biting insects are relatively rare prior to mid-June, at which point they are commonly found until early August (with some exceptions). Thus, it appeared plausible that moose might increase their use of aquatic habitat in response to increasing seasonal activity of biting insects. Similarly, the approximately crepuscular pattern of aquatic habitat use reported here conforms well to the approximately crepuscular pattern exhibited by the culicids and simuliids in North America (Haufe 1952; Wolfe and Peterson 1960; Happold 1965; Toupin et al. 1996; Boyer et al. 2013). Culicids in particular appeared to show the strongest peak in the hours nearest dusk which is exactly when moose showed the greatest tendency to use aquatic habitat relative to all other hours of the day. Moose tended to use aquatic habitat least during the middle of the day and after nightfall, times when harassment from biting insects is likely to be least intense. The finding that moose might use aquatic areas to avoid harassment by biting flies appears to be supported by the work of Flook (1959) who observed this behavior and noted an absence of aquatic feeding. Renecker and Hudson (1989) noted that biting insect harassment increased energy expenditures of moose living in Alberta. Renecker and Hudson (1990) suggested the possibility that aquatic areas might be used for insect relief in their study area and I suggest that this explanation may be more plausible than their alternative suggestion that this behavior was attributable to heat stress amelioration. Furthermore, it appears that moose require suitably deep water in order to avoid biting insects (Ritcey and Verbeek 1969) and thus water depth may affect the quality of aquatic areas for moose. The presence of aquatic areas for moose to avoid biting insects may be an important consideration when examining overall habitat quality for North American moose.

I was unable to reject the nutritional hypotheses for aquatic habitat use by moose, though it was clear that the available evidence was not fully consistent with either the sodium limitation hypothesis or the foraging efficiency hypothesis (Table 12). In a geographic sense, moose should be least inclined to use aquatic areas where access to ocean-derived salt is high (i.e., in the coastal regions Alaska-North and Northeast-Maritimes). Though proportional use of aquatic habitat was low in Alaska-North it was similar in the Northeast-Maritimes relative to the remaining regions. Certainly the number of studies mentioning aquatic feeding in the Great Lakes-St. Lawrence region (the most likely to be sodium limited) was high (e.g., Fraser et al. 1980; 1982; 1984; deVos 1958; Belovsky and Jordan 1978) but it is possible that the high incidence of aquatic feeding in this region may simply be reflective of the larger number of studies devoted to aquatic feeding by moose in this region relative to other regions.

In the case of the foraging efficiency hypothesis, the possibility that aquatic habitat use is relatively consistent among several geographic regions would be suggestive of a strategy to maximize foraging efficiency throughout North America. It is problematic to this interpretation, however, that the best evidence for foraging efficiency as opposed to sodium hunger driving aquatic habitat use was derived from the Alaska-North region (MacCracken et al. 1993); the region where moose showed the lowest proportional use of aquatic habitat. The seasonal peak of aquatic habitat use observed in mid-June-early July does not seem to correspond well to either hypothesis. If the drive to use aquatic areas were to overcome a sodium deficit in early summer then moose should use aquatic areas most during the early summer months (May-June). This interpretation may be complicated by the possibility that in some regions of North America aquatic plants are not yet available in these early months (Cronk and Fennessy 2001). Perhaps a foraging efficiency mechanism is plausible given the observed seasonal peak in aquatic use by moose during the portion of the summer when aquatic plants are both palatable and highly available (Fraser et al. 1984). The pronounced crepuscular pattern in aquatic habitat use does not lend itself to the sodium limitation hypothesis since it would be highly unlikely that mineral contents of aquatic plants would differ over the course of the daily cycle (Hutchinson 1975). Conversely, a crepuscular aquatic feeding pattern might be related to a tradeoff between minimizing heat gain while maximizing energy intake (Belovsky and Jordan 1978; Renecker and Hudson 1990).

Moose consumed lower amounts of aquatic relative to terrestrial forage items, though moose on Isle Royale consumed greater proportions of aquatics than moose in Alaska or Colorado (Leresche and Davis 1973; Dungan and Wright 2005; Tischler 2004). This lends more support to the sodium limitation hypothesis than the foraging efficiency hypothesis since moose feeding only to acquire sodium might be able to meet this need by feeding on only a few sodium-rich aquatic plants. This interpretation is complicated by a lack of consistent preferences for sodium rich plants by moose engaged in aquatic feeding. Though it seemed clear that moose in the Great Lakes-St. Lawrence region showed the greatest tendency to consume sodium rich aquatic plants compared to other regions (i.e., Alaska-North), many aquatic plants preferred by moose were quite low in sodium. This would imply that perhaps moose are simply attempting to maximize diet quality under the foraging efficiency hypothesis, but moose did not show consistent preferences for aquatic plants with the highest protein or caloric content. Therefore, I suggest that aquatic feeding observed by moose throughout North America can be explained by some combination of the sodium limitation and foraging efficiency hypothesis, but not by either hypothesis acting in isolation. Similarly, aquatic feeding on Isle Royale was likely part of a larger strategy to maximize diet quality and acquire essential sodium in a nutrient-poor boreal ecosystem (Tischler 2004). I did not find evidence to suggest that sodium limitation is important to moose outside of the Great Lakes-St. Lawrence region. It appears plausible that aquatic habitat use by moose in North America is related to multiple nutritional factors that are not consistent among geographic regions and that biting insects may play a role in this behaviour. Multiple mechanisms appear to explain aquatic habitat use by North American moose and this may be indicative of different selective pressures acting upon different moose sub-populations leading to behavioral plasticity with respect to aquatic habitat use across this species' range.

If nutritional factors influence the use of aquatic areas by moose then identification of aquatic feeding sites may be an important aspect of moose habitat management (Allen et al. 1987; Adair et al. 1991; OMNR 2010). Moose may select areas for aquatic feeding according to the relative availability of aquatic plants (Fraser et al. 1980; 1984; Brusnyk and Gilbert 1983) and may attempt to meet nutritional needs rapidly by foraging in areas of dense aquatic plant growth (MacCracken et al. 1993). Fraser et al. (1980) found that the presence of the five most abundant aquatic plant species allowed for consistent differentiation between feeding and non-feeding sites within a lake in northwestern Ontario. The authors reported that variation in water depth commonly led to zonation of the aquatic plant community and later suggested that shallow water (< 50 cm) favoured the growth of submersed species that were most consistently preferred by moose (Fraser et al. 1984). Aquatic feeding sites most heavily used by moose tended to not only have shallow water, but also inorganic sediments associated with recent flooding (Fraser et al. 1980; 1984). Fraser et al. (1980) suggested that moose may target recently flooded areas for aquatic feeding because these conditions might favour rapid colonization of preferred species. Plants growing in inorganic sediments, such as those associated with newly flooded forest floor, also appeared to contain greater amounts of chemical constituents (e.g., phosphorous, calcium) that might influence palatability for moose (Fraser et al. 1984). Conversely, Adair et al. (1991), working in northeastern Minnesota, identified lakes with greater proportions of organic matter and beaver ponds as containing the greatest abundance of aquatic plants for moose. The authors contended that larger lakes with rocky bottoms typically experienced greater wave action that smaller, submersed plant species, thought to be preferred by moose, could not typically withstand. The finding that beaver ponds contained the greatest amount of species commonly consumed by moose (according to Fraser et al. 1984) provided support for the previous contention that newly flooded habitats are highly suitable for moose aquatic feeding. Adair et al. (1991) also suggested that beaver ponds might possess greater variance in their ability to provide aquatic vegetation for moose relative to lakes, since colonization by aquatic plants might be delayed initially and availability might decline in very old ponds. Further research on potential variation in aquatic plant availability between lakes and beaver ponds of various depths and ages may usefully inform an understanding of moose aquatic habitat use, particularly in the Great Lakes-St. Lawrence region where both sodium and foraging efficiency hypotheses may explain moose use of aquatic habitats.

The suitability of aquatic feeding sites for moose may also be determined in part by the seasonal availability or quality of aquatic vegetation (Fraser et al. 1982; Brusnyk and Gilbert 1983). Fraser et al. (1982) found that sodium content of vegetation showed a slight decline in late summer (late-July onward) when moose ceased using aquatic areas for feeding. These authors, however, felt that the midsummer peak in aquatic feeding that they observed in lakes (late-June to early-July, in agreement with other studies in the present review) was most likely associated with increased growth of preferred species with high sodium contents at this time rather than seasonal changes in the other chemical constituents of aquatic plants. Brusnyk and Gilbert (1983), also working in lake habitats, found that peak availability of aquatic plants (measured as total percent cover) occurred from 30 July – August 15; after the midsummer peak in aquatic habitat use by moose. In general, peak biomass of aquatic plants often occurs late in summer (Hutchinson 1975; Cronk and Fennesy 2001) after moose use of aquatic areas has declined. MacCracken et al. (1993) suggested that following initial selection of aquatic areas with dense plant growth, that moose switch to a time-minimization rather than energy-maximization strategy and feed non-selectively on available aquatic plants. Taken together, the above evidence might suggest that moose select aquatic areas based on the relative availability of a few important plant species (e.g., those with the greatest sodium contents) and time their use of these areas to coincide with the greatest seasonal abundance of these preferred species. MacCracken et al. (1993) noted that few studies have attempted to quantify aquatic plant availability over the course of the growing season and it remains unclear if seasonal patterns of abundance of aquatic plant species preferred by moose might differ in habitats other than lakes (e.g., beaver ponds).

Future directions for research on aquatic habitat use by moose in the Great Lakes-St. Lawrence region should include assessment of aquatic plant availability throughout the summer in lakes and beaver ponds that vary with respect to limnological characteristics (e.g., depth, wave action; disturbance history). Research on aquatic plant availability under various conditions could help identify critical summer habitat components for moose living in the Great Lakes-St. Lawrence region and help discriminate the relative importance of sodium limitation versus the foraging efficiency hypothesis.

3.0 RICHNESS AND BIOMASS OF AQUATIC VEGETATION IN LAKES AND BEAVER PONDS

3.1 Introduction

Different aquatic patch types are often viewed as being similarly suitable in analyses of moose habitat needs and use (Allen et al. 1987; Lenarz et al. 2011) but it is not clear whether all aquatic habitat is similar with respect to richness and biomass of aquatic forage. For example, Adair et al. (1991) demonstrated that shallow lakes with mucky bottoms and beaver ponds provided more aquatic moose forage than other wetland types. Both lake bays and beaver ponds typically have been identified as potential moose aquatic feeding areas but increased wave action and reduced nutrient availability in lakes may decrease the abundance and diversity of aquatic plants relative to calmer, more nutrient-rich habitats provided by beaver ponds (Wetzel 1983; Bornette and Puijalon 2011). Therefore, beaver ponds may contain a greater number of preferred moose forage species and greater yields (biomass m^{-2}) of submersed and floating-leaved plants than lake bays. Furthermore, water depth in lakes may result in zonation of plant communities based on the ability of different species to thrive in deep water environments (Hutchinson 1975; Bornette and Puijalon 2010). This influence of water depth on plant community composition should be considered when assessing richness and biomass of aquatic forage potentially available to moose. Increased turbidity, resulting from frequent sediment disturbance, can further reduce growth rates of aquatic plants by inhibiting or compromising photosynthesis (Bornette and Puijalon 2011). Movement of beavers in these aquatic areas could create these turbid conditions when movement through aquatic patches is frequent, and thus, it would be valuable to assess whether the presence of beaver activity has a negative impact on the richness and biomass of aquatic forage for moose. Beyond these indirect effects on forage production, beaver also consume aquatic vegetation (Milligan and Humphries 2010; Severud et al. 2013), and thus, could directly compete with moose for aquatic forage.

As the spatio-temporal mosaic of beaver ponds on the North American landscape is extensive and likely influenced by climate change (Johnston and Naiman 1990; Jarema et al. 2009), more detailed information on richness and biomass of submersed and floating-leaved plants in this wetland type may lend itself to improved management of aquatic moose habitat in the future. Beaver pond age may influence richness and biomass of aquatic forage in aquatic areas that may be used by moose (Adair et al. 1991; Ray et al. 2001). Submersed and floating-leaved plant richness and abundance was greater in beaver ponds of intermediate (11-40 years) age compared to either newly formed (< 11 years) and older (> 40 years) beaver ponds (Ray et al. 2001). These increases in intermediate-aged ponds were attributed to the provision of niche space for both early successional aquatic species (e.g., coontail - *Ceratophyllum demersum*) and late successional species (e.g., water shield - *Brasenia schreberi*). Large (i.e., > 1 ha) surface area for colonization by vegetative propagules may also increase species richness and yield in beaver ponds (Ray et al. 2001). Open water sites near beaver ponds may serve as sources of dispersing vegetative propagules that colonize beaver ponds (Ray et al. 2001). Some measure of landscape connectivity between beaver ponds and open water sites should be considered when assessing richness and biomass of aquatic forage potentially used by moose.

Ray et al. (2001) went on to suggest the possible existence of alternative stable states of late successional beaver pond communities, one with a dense floating-leaved canopy and the other dominated by submersed species. The author suggested that beaver herbivory on floating-leaved plants (e.g., *Nuphar variegatum*) was responsible for the creation of a late successional community dominated by submersed species. These alternative states could also be due to periodic flooding events resulting from re-colonization by beaver (Fryxell 2001, Vincent 2010). It would thus be useful to test for effects of beaver colonization on the richness and biomass of floating-leaved and submersed aquatic vegetation in areas potentially used by moose in beaver ponds.

The first objective of the current study was to contrast species richness and biomass of aquatic forage between open water lake bays and beaver ponds. A secondary component of this objective was to determine what effect, if any, beaver presence in an aquatic area might have on richness and biomass of aquatic forage. Based on previous studies outlined above, species richness and biomass (g m^{-2} open water) should be significantly higher in beaver ponds compared to lake bays (Adair et al. 1991), and beaver presence should have a significant negative effect on both species richness and biomass of submersed and floating-leaved vegetation through the combined effect of herbivory and frequent sediment disturbance (turbidity).

A second objective of the current study was to examine potential effects of variation in age and surface area of beaver ponds on richness and biomass of aquatic forage. In this case, ponds of intermediate age (21-38 years in this study, relative to young ponds 6-14 years and old ponds >50 years) should have significantly higher species richness and biomass of both submersed and floating-leaved aquatic species due to higher available niche space for both early and late successional species (Ray et al. 2001). In addition, large ponds (i.e., surface areas >1 ha) should have significantly higher species richness and biomass levels of floating-leaved aquatic vegetation compared to smaller ponds (< 1 ha), as ponds with larger surface areas would have a greater probability of being randomly colonized by dispersing propagules of aquatic plants (Ray et al. 2001).

The final objective of the current study was to determine what effect, if any, seasonal timing had on richness and biomass of aquatic forage. For this objective, species richness and biomass of submersed and floating-leaved vegetation were compared between two sampling periods spanning initial growth of aquatic vegetation and presumed peak biomass of aquatic vegetation (June-early July and late July-August, respectively; Cronk and Fennessy 2001). Here I predicted that significantly greater amounts of aquatic forage for moose (species richness and biomass of submersed and floating-leaved vegetation) would be present in late July-August compared to the June-early July period as most aquatic plant species do not reach peak biomass until mid to late summer.

3.2 Methods

3.2.1 *Study Area*

This study was conducted in Voyageurs National Park (VNP; 882 km^2), Minnesota, USA, located on the Kabetogama Peninsula (330 km^2) and surrounding mainland (210 km^2) in north-central Minnesota (48°34' N, 93°23' W). The VNP has a complex topography (maximum relief of 90 m), and includes four large lakes (Kabetogama, Namakan, Rainy, Sand Point; a total of 342 km^2) and numerous inland lakes of varying size (13-305 ha). Based on a vegetation survey of VNP (Kurmis et al. 1986), tree species composition is a combination of southern boreal and northern hardwood species, including jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), white pine (*Pinus strobus*), red maple (*Acer rubrum*) and green ash (*Fraxinus pennsylvanica*).

Beaver in VNP have created an extensive network of ponds, marshes and meadows (n = 835 in 1986; 13% of land mass) varying with respect to size and the forest type in which they are situated (Naiman et al. 1988). All beaver ponds present since 1927 have been aged using an aerial photo-sequence taken over a time series (1927,1940, 1948, 1961, 1972, 1981, 1986, 1990, 1997, 2003, and 2005) and these pond ages have been incorporated into a GIS layer (Johnston and Naiman 1990a; Host and Meysembourg 2009). Adult moose (n=12) within and adjacent to VNP were fitted with GPS collars transmitting via the Argos satellite system as of January 2011 (Windels 2014), which allowed me to select aquatic patches that were presumably directly available to moose.

3.2.2 Aquatic patch selection

I identified a number of candidate beaver ponds on the Kabetogama peninsula in VNP under the conditions that ponds were within 800 m of Kabetogama or Namakan Lake shorelines or hiking trails and were within areas available to moose (i.e., based on known moose locations from GPS collar fixes; summer 2011). From this pool of candidate sites, I randomly selected 18 ponds, stratifying the sample by pond size (< 1 ha or 1-6 ha) and pond age (young: 6-14 years; intermediate: 21-38 years, or old: exceeding 50 years). I also selected six mesotrophic lake bays on the Kabetogama Peninsula under the same restrictions described above.

3.2.3 Aquatic vegetation surveys

I employed a modified rake technique (Ray et al. 2001; Kenow et al. 2007) to assess the quantity and species composition of submergent and floating-leaved vegetation within aquatic patches of VNP. Plant surveys took place during two discrete sampling periods to compare periods of initial plant growth and presumed peak biomass (June 8-July 11 and July 12-August

3). Only beaver ponds were sampled during the second period due to logistical constraints. Prior to sampling, 20 random sample points were generated within each patch and the coordinates of each point were entered into a handheld GPS unit.

A field crew used an inflatable raft to sample each aquatic patch. Any sign of recent beaver activity within the patch (e.g., peeled sticks, fresh mud on lodges or dams, fresh cut stems, direct observation of beaver) was recorded. Aquatic patches where recent beaver activity was observed were deemed 'beaver present' patches and aquatic patches where no recent beaver activity was observed were deemed 'beaver absent' patches. The crew navigated to within 2 m of each sampling point using the handheld GPS and anchored the raft to define the sampling point. Water depth (cm) was measured using a graduated measuring stick and was considered to be the depth at which it just penetrated the flocculent material on the bottom. Depth of organic matter was also measured for at least four random points per beaver pond using a soil corer.

A double-sided rake (35 cm wide with 5 cm long tines) was lowered into the water at each sampling point, dragged 1 m along the substrate towards the boat and lifted vertically from the water column, spinning the rake as it was lifted to prevent loss of submersed and floating leaved plants (Ray et al. 2001). I assigned scores 0 - 5 to each rake drag based on total percent coverage of the rake tines for each plant species present (0% = 0, 1%-20% = 1, 21%-40% = 2, 41%-60% = 3, 61%=80% = 4, 81%-100% = 5). If rake drags were impeded by submersed logs, the sampling point was repeatedly moved 1 m in a pre-determined arbitrary direction until a successful drag was performed. I assumed that all submersed and floating leaved plants were collected during each successful drag.

3.2.4 Plant Biomass Sampling

In summer (June-August) 2012, 6-10 samples of each rake score of three common aquatic plant species, *(Ceratophyllum demersum*, *Brasenia schreberi, Nymphaea odorata*) were collected opportunistically from study bays and ponds. Additional biomass sampling was done in summer (July-August) 2013, targeting the less dominant species recorded in the 2012 vegetation surveys. For six species (*Potamogeton pectinatus*, *Myriophyllum verticillatum*, *Utricularia vulgaris*, *Vallisneria americana*, *Elodea canadensis*, and *Potamogeton natans*) 5-7 samples of each rake score were collected from bays and ponds within the study area. Five taxa (*Potamogeton zosteriformis*, *Chara vulgaris*, *Potamogeton* spp, *Utricularia minor*, and *Nuphar variegata*) were only encountered at rake scores of 1-3 during 2012 vegetation surveys. For these species, samples were only collected that corresponded to the rake scores for which they occurred (e.g., 10 samples of rake score 1 were collected for *Potamogeton* spp., 6 samples each of rake scores 1, 2 and 3 were collected for *Nuphar variegata*, etc.). In the field, all harvested plant material was placed in clear plastic bags, returned to the laboratory and processed the same day of collection. Plants were rinsed of all particulate matter and macroinvertebrates (e.g., gastropods), placed in paper bags and dried to constant weight at 105°C. For rarely encountered species (i.e., recorded in ≤ 3% of all rake drags), it was assumed that their biomass did not contribute meaningfully to moose diets in the study area, and they were not included in the biomass estimates. These included the floating-leaved species *Sparganium fluctuans* and the submersed species *Najas flexilis*, *Zosterella dubia*, *Sagittaria graminea,* and *Myriophyllum sibiricum*.

For each species, mean biomass values were generated for each rake score and applied to the aquatic vegetation survey data (i.e., 20 random sampling points per aquatic patch – 18 ponds;

6 lake bays). For example, the mean biomass value for *Ceratophyllum demersum* with rake score=1 was 3.22 g m^{-2} (see RESULTS) and thus each time *Ceratophyllum demersum* was present at a sample point within a pond or lake bay with rake score = 1 it was assigned a dry weight biomass value of 3.22 g m^{-2} at that point. I summed all submersed and floating-leaved biomass values at each point and calculated the total mean biomass (g m^{-2}; n=20) of submersed and floating-leaved vegetation in each aquatic patch (lake or beaver pond). Aquatic patches were used as the sampling unit in all subsequent statistical analyses.

3.2.5 Statistical analysis

Objective 1: Examining the differences in richness and biomass of aquatic forage between beaver ponds and lake bays, and evaluating the influence of beaver activity on richness and biomass of aquatic forage.

A generalized linear model (GLM) that included aquatic patch type (i.e., beaver pond versus lake bay) and beaver activity (binary variable: present versus absent, see above) as response variables in a two-factor completely randomized design (CRD) was used to make comparisons of forage production. Specifically, the six response variables were: richness*m^{-2} and biomass*m^{-2} of floating leaved aquatic vegetation (hereafter floating-leaved richness and floating-leaved biomass, respectively), richness*m^{-2} and biomass*m^{-2} of submersed aquatic vegetation (hereafter submersed richness and submersed biomass, respectively) and combined richness*m^{-2} and biomass*m^{-2} of both submersed and floating-leaved vegetation (hereafter, combined richness and combined biomass). The GLM was run using the aov function in R 2.14.1 (R Core Development Team 2008) using the following generalized form:

$$Y_{ijk} = \mu + A_i + B_j + AB_{ij} + \varepsilon_{(ij)\,k} \qquad [1]$$

$$(i=2 \quad j=2 \quad k=2)$$

where: y_{ijk} = kth value of y from the ith aquatic patch type and the jth beaver presence, A_i = effect of the ith aquatic patch type, B_j= effect of the jth beaver presence-absence, AB_{ij} = interaction effect of the jth category of beaver presence with the ith patch type, $\varepsilon_{(ij)k}$ = effect of the kth replicate on the jth beaver presence category with the ith aquatic patch type. In addition, mean aquatic patch depth was considered as a potential covariate. Pearson’s product moment correlation tests were conducted to determine if depth significantly influenced each of the response variables. Only richness of floating-leaved aquatic vegetation was correlated significantly with depth ($p=0.031$, $t_{22}=2.309$, $r=0.44$) and was thus the only response variable where depth was included as a covariate in the GLM.

Objectives 2 and 3: Examining the differences in richness and biomass of aquatic forage between beaver ponds differing in age and size class, as well as time during the summer.

For this examination, the GLM was treated as a 3 factor CRD that included pond age class (6-14 year, 21-38 years, > 50 years), size class (surface area < 1 ha, surface area > 1 ha), and sample period (early summer = June 8-July 11, mid-summer = July 12-August 3). Similar to Objective 1, the response variables were richness and biomass of floating leaved vegetation, richness and biomass of submersed vegetation, and combined richness and biomass of aquatic vegetation. The generalized form of the GLM was:

$$y_{ijkl} = \mu + A_i + B_j + C_k + AB_{ij} + AC_{ik} + BCjk + \varepsilon(ijk)l \qquad [2]$$

$$(i=3 \quad j=2 \quad k=2 \quad l=1)$$

where: y_{ijkl} = lth value of y from the ith pond age class, jth pond size class, and kth sample period, A_i = effect of the ith pond age class, B_j= effect of the jth pond size class, C_k= effect of the kth sample period, AB_{ij}=effect of the jth size class with the ith age class, AC_{ik}= effect of the kth sample period category with the ith age class, BCjk= effect of the kth sample period with the jth size class, $\varepsilon_{(ijk)l}$= effect of the lth replicate on the jth pond size with the ith age class with the kth sample period. The 3-way interaction term was considered to not be ecologically meaningful, and was therefore pooled with the experimental error term.

For this model, three additional variables were considered as potential covariates: aquatic patch depth, the number of hydrologically connected upstream ponds (i.e., potential sources of dispersing aquatic plants), and the area of open water within a 1 km^2 radius of each pond (i.e., reservoir of potential colonizing organisms). Again Pearson product moment correlations were run against all response variables, including covariates when $p<0.05$. Based on this preliminary analysis, depth was included with richness of floating-leaved vegetation ($p=0.029$, $t_{34}=2.28$, $r=0.36$) and biomass of floating-leaved vegetation ($p=0.043$, $t_{34}=2.11$, $r=0.34$), number of upstream ponds was included as a second covariate for richness of floating-leaved vegetation ($p=0.010$, $t_{34}=-2.72$, $r=-0.42$), and area of open water within 1 km^2 was added as a second covariate for biomass of floating leaved vegetation ($p<0.001$, $t_{34}=3.95$, $r=0.56$).

In all cases, data normality was assessed using the Shapiro-Wilk's test, and homogeneity of variance was evaluated using Barlett's test. In all cases the data conformed to the test for normality ($p>0.25$) and homogeneity of variance ($p>0.10$), with the exception of biomass of submersed vegetation in GLM [1] (Shapiro-Wilk's $W=0.909$, $p=0.034$; Barlett's $k^2=4.99$, $p=0.026$) and GLM [2] (Shapiro-Wilk's $W=0.926$, $p=0.019$; Barlett's $k^2=3.10$, $p=0.021$). In this case, the data were transformed (square root transformation of biomass of submersed vegetation data) prior to running the ANOVAs. Post hoc examination of significant factors in the ANOVAs were performed using the Least Significant Difference (LSD) multiple range test ($p<0.05$).

3.3 *Results*

3.3.1 Rake Score to Biomass Values

Due to the broad differences in life forms, growth and development strategies, and water contents of aquatic plants (Hutchinson 1975; Cronk and Fennessy 2001) there were substantial differences in biomass among aquatic plant species (Table 13). There tended to be higher variability in biomass of individual species with higher rake scores and some degree of a curvilinear increase in biomass between rake scores for some species (e.g., *P. pectinatus, M. verticillatum, P. natans;* Figure 1). This variability is largely a function of the broad rake score classes (20% classes of rake tines being covered) and not a true reflection of experimental error. Rake scores of 5 are particularly variable since the percent coverage of the rake could increase exponentially with no corresponding increase in rake score (e.g., rake scores of 5 with percent coverage > 200% was sometimes observed due to overlapping layers of plant material).

3.3.2 Influence of aquatic patch type and beaver presence on species richness and biomass

Patch type significantly influenced combined richness ($p=0.008$) and submersed richness ($p=0.002$), but not floating-leaved richness ($p=0.098$; Table 14). The combined richness was nearly double in beaver ponds compared to lake bays (beaver ponds: 7.0; lake bays: 3.7; Figure 2). This difference was largely a function of a higher number of submersed species in beaver

Table 13. Biomass values (g m^{-2}) for 14 aquatic plant species, belonging to 2 functional groups, submersed and floating-leaved plants, for each of 5 categorical rake scores used as part of a sampling technique modified from Kenow et al. (2007).

Species	Statistic	Rake Score				
		1	2	3	4	5
		-------------------------- g m^{-2} -------------------------------				
<u>Submerged:</u>						
Ceratophyllum demersum	Mean	3.22	16.65	35.38	45.77	86.245
	Std Err	0.676	1.712	5.35	4.297	6.41
	n	7	7	7	7	7
Potamogeton pectinatus	Mean	0.91	4.01	13.12	27.95	71.49
	Std Err	0.166	0.244	1.084	1.524	4.81
	n	6	5	6	6	6
Myriophyllum verticillatum	Mean	1.07	3.7	10.03	21.91	46.19
	Std Err	0.154	0.372	0.784	1.519	1.133
	n	6	6	6	6	6
Utricularia vulgaris	Mean	0.476	2.947	9.26	19.29	33.1
	Std Err	0.214	0.22	0.603	2.001	2.558
	n	6	7	6	6	6
Vallisneria americana	Mean	0.53	3.01	8.01	15.06	31.74
	Std Err	0.091	0.356	0.428	0.325	2.823
	n	6	6	6	6	6
Elodea canadensis	Mean	0.33	3.024	5.45	10.26	28.257
	Std Err	0.097	0.209	0.361	0.252	2.674
	n	6	6	6	6	6
Potamogeton zosteriforms	Mean	0.93	4.62	10.83		
	Std Err	0.271	0.75	1.213		
	n	6	3	6		
Chara vulgaris	Mean	0.5	2.81			
	Std Err	0.161	0.602			
	n	7	4			
Potamogeton spp .	Mean	0.22				
	Std Err	0.058				
	n	10				
Utricularia minor	Mean	0.03				
	Std Err	0				
	n	5				
<u>Floating:</u>						
Brasenia schreberi	Mean	2.68	27.31	62.5	94.32	179.74
	Std Err	0.807	1.207	3.795	6.56	18.175
	n	7	7	7	7	7
Nymphaea odorata	Mean	1.62	18.79	43.63	77.03	110.79
	Std Err	0.459	2.027	3.473	4.663	13.872
	n	7	7	6	6	10
Potamogeton natans	Mean	1.162	6.48	15.97	33.7	77.8
	Std Err	0.211	0.353	1.041	1.854	8.116
	n	6	6	6	6	6
Nuphar variegata	Mean	4.4	16.09	41.97		
	Std Err	0.682	1.175	3.083		
	n	6	6	6		

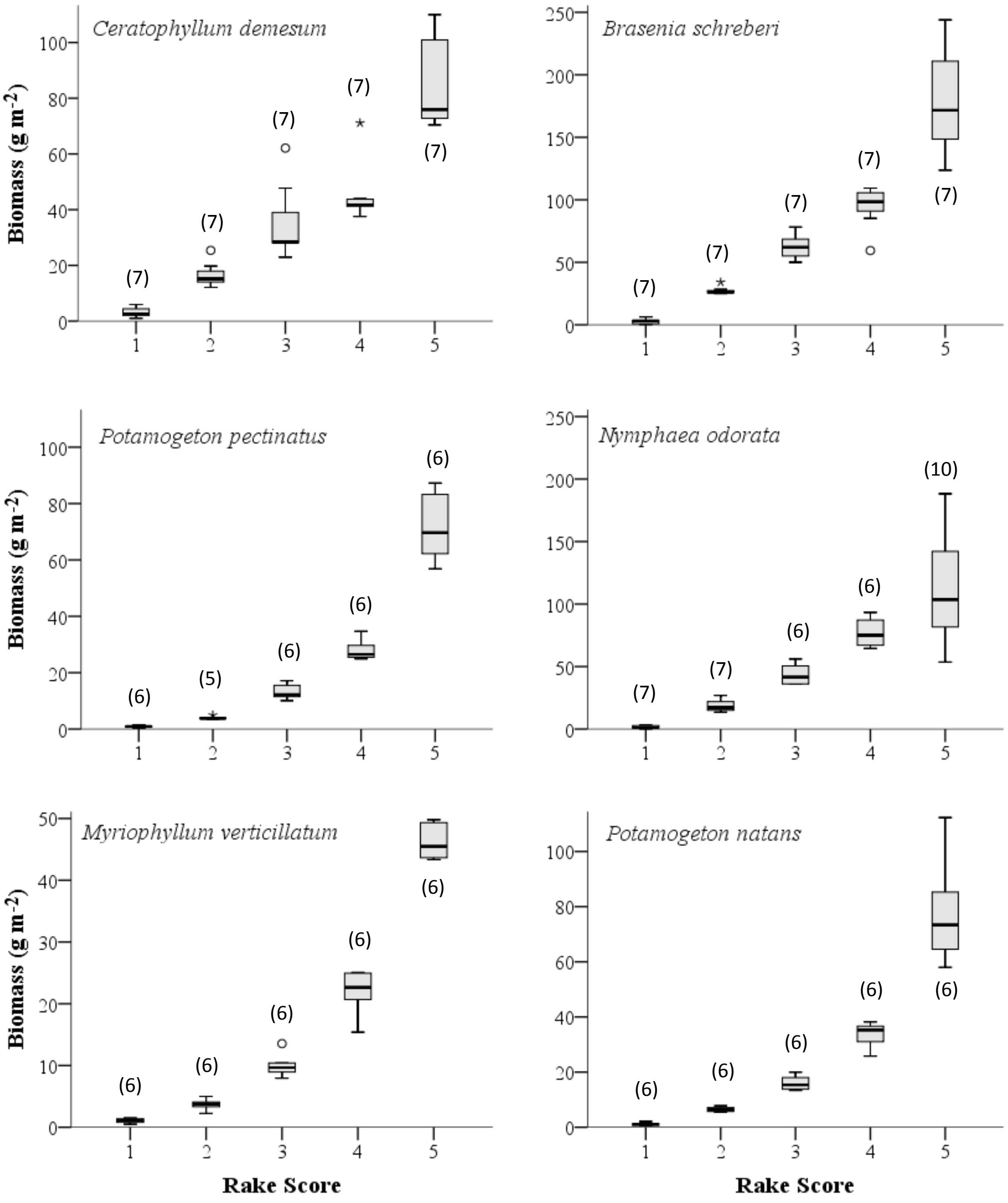


Figure 1. Box plots (sample sizes in parentheses) depicting the variability associated with the biomass estimates for various rake score classes of 6 aquatic plant species encountered during summer 2012 aquatic vegetation surveys in Voyageurs National Park.

Table 14. ANOVA results summarizing the influence of aquatic patch type (beaver pond versus lake bay) and beaver presence (present versus absent) on aquatic plant species richness (# of species m^{-2}). Bolded p values are <0.05.

Source	df	MS	F-ratio	P value
Richness(allspecies):				
Patch Type (PT)	1	49.53	8.80	**0.008**
Beaver Presence (BP)	1	2.25	0.40	0.534
PT * BP	1	0.78	0.14	0.713
Error	20	5.63		
Richness(submerged)[1]:				
PT	1	2.58	11.30	**0.002**
BP	1	0.01	0.01	0.933
PT * BP	1	0.45	1.96	0.169
Error	20	0.23		
Richness(floating):				
Depth (covariate)	1	3.44	3.68	0.070
PT	1	2.83	3.03	0.098
BP	1	5.04	5.39	**0.032**
PT * BP	1	0.29	0.31	0.582
Error	19	0.93		

[1] data were square root transformed prior to ANOVA to meet normality and homogeneity of variance assumptions.

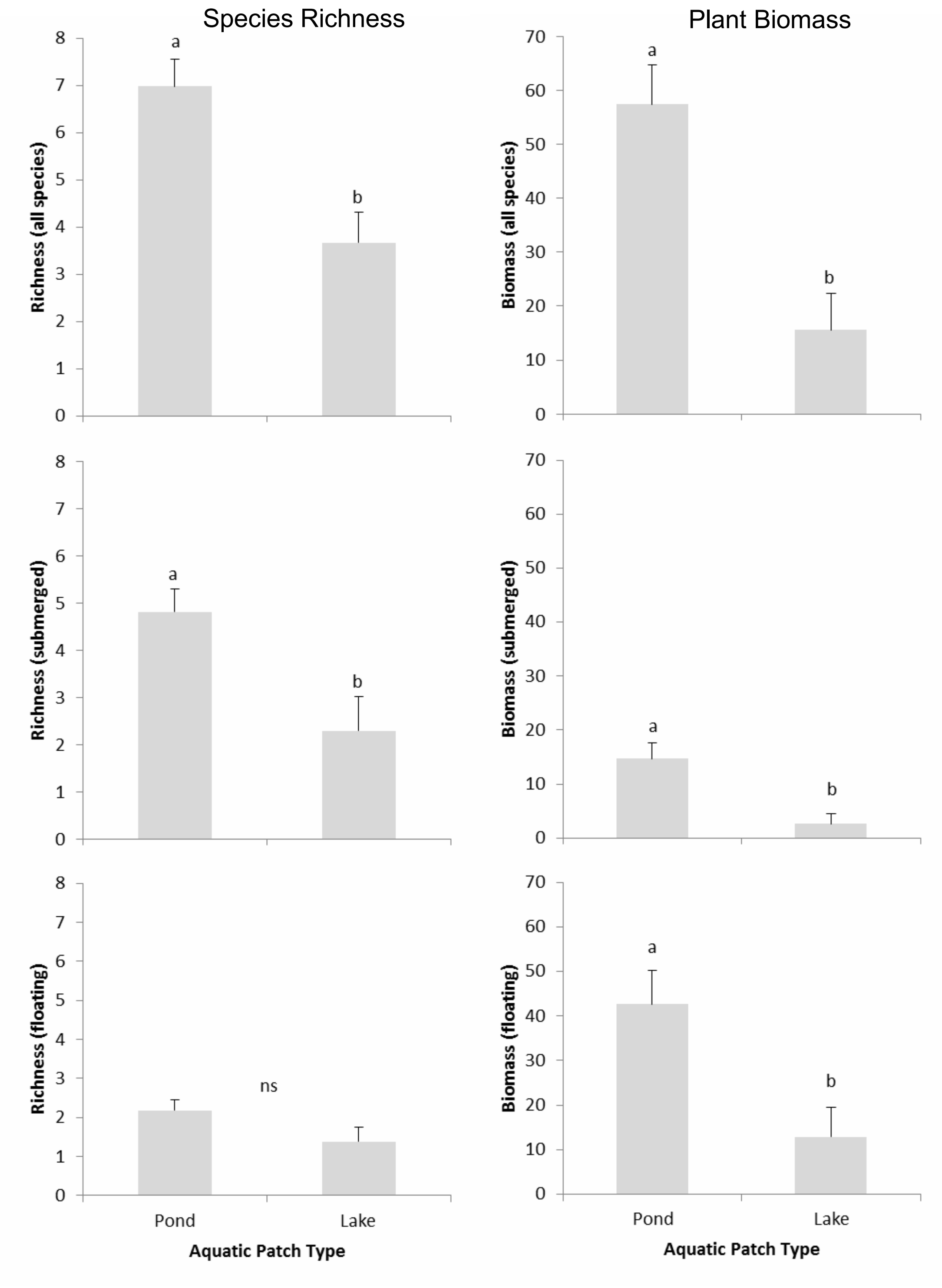


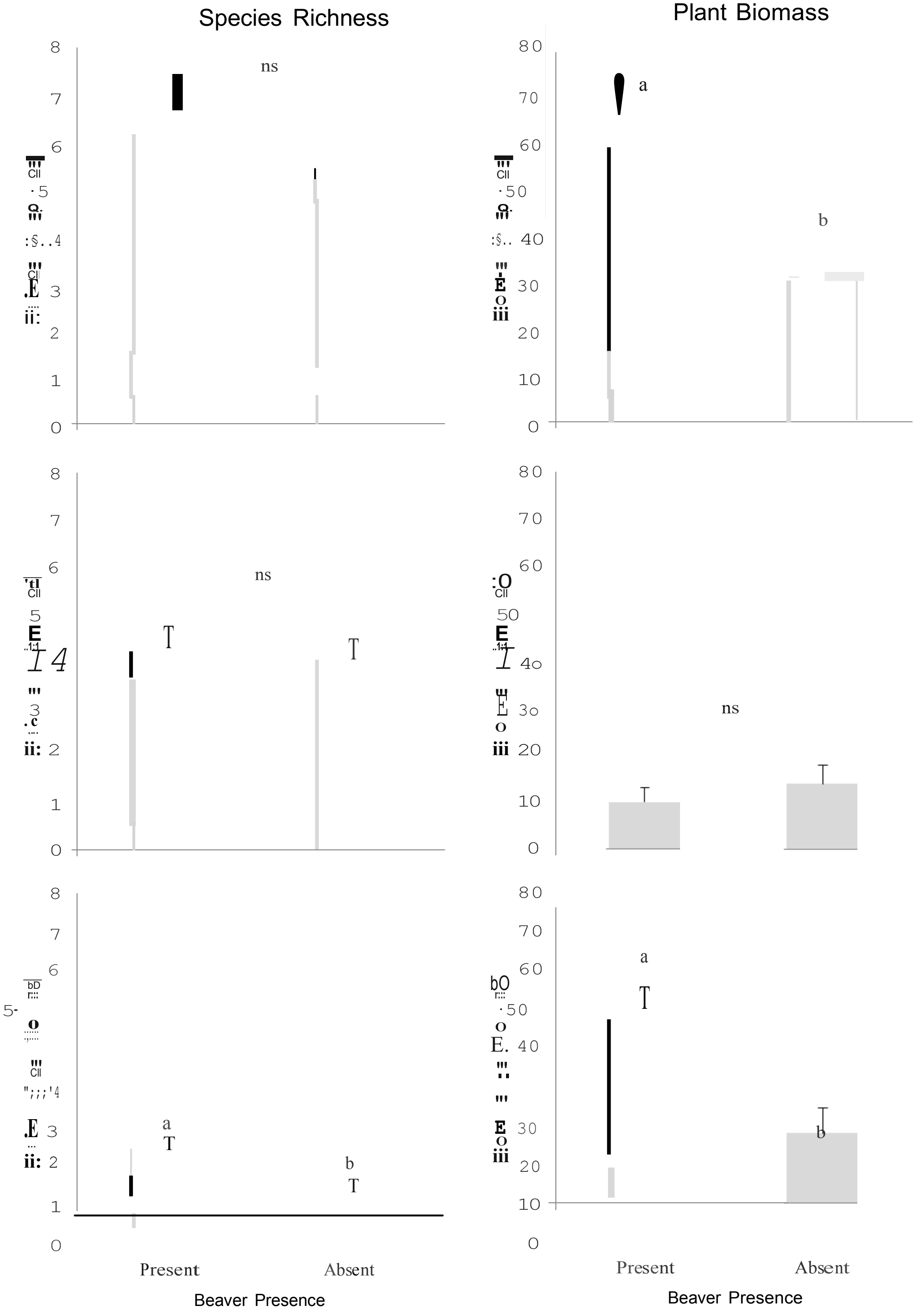
Figure 2. The influence of aquatic patch type (beaver pond versus lake bay; n=18 and n=6, respectively) on species richness (left panel) and plant biomass (right panel). Vertical bars represent standard errors. Different lower case letters signify significant differences ($p<0.05$), based on a post-hoc Least Significant Difference (LSD) multiple range test.

ponds (beaver ponds: 4.8; lake bays: 2.3). Beaver presence did not, however, influence combined richness ($p=0.534$) or submersed richness ($p=0.933$) but did have a positive influence on floating-leaved richness (present: 2.5; absent: 1.4; Figure 3). The patch type x beaver presence interaction was not significant for any of the three richness response variables ($p\geq0.17$; Table 14).

Patch type strongly influenced combined biomass ($p=0.004$), as well as both submersed ($p=0.003$) and floating-leaved ($p=0.031$) biomass (Table 15). The average biomass estimate for beaver ponds was four times greater than in lake bays at nearly 60 g m^{-2} compared to just over 15 g m^{-2} (Figure 2). Similar to richness, beaver presence had a positive influence ($p=0.029$) on floating-leaved biomass (present: 49.8 g m^{-2}; absent: 18.0 g m^{-2}; Figure 3) but not submersed biomass.

3.3.3 Influence of beaver pond age, size, and sampling period on species richness and biomass

Sampling period (early- versus mid-summer) did not significantly influence ($p>0.50$) floating-leaved, submersed or combined richness and biomass in beaver ponds (Tables 16 and 17). Both pond age and size did significantly influence combined richness and submersed richness, with only pond size influencing floating-leaved richness (Table 16). In terms of pond age effects on species richness, the old ponds (>50 yrs) did not have as many species as either of the younger age classes (6-14 yrs: 7.62; 21-38 yrs: 7.21; >50 yrs: 5.40), an effect for both submerged and floating species, although only significantly different for the submersed species (Figure 4). The larger ponds (>1 ha), also had higher species richness values compared to the smaller ponds (<1 ha) for both the submersed (5.2 compared to 4.0) and floating species (2.5 compared to 1.8; Figure 5).



!Figure 3. The influence ofbeaver presence (presence versus absence; n=12 for each) on species richness (left panel) and plant biomass (right panel). Vertical bars represent standard errors. Different lower case letters signify significant differences ($p<0.05$), based on a post-hoc Least Significant Difference (LSD) multiple range test.

Table 15. ANOVA results summarizing the influence of aquatic patch type (beaver pond versus lake bay) and beaver presence (present versus absent) on aquatic plant biomass (g m^{-2}). Bolded p values are < 0.05.

Source	df	MS	F-ratio	P value
Biomass(allspecies):				
Patch Type (PT)	1	7874.88	10.55	**0.004**
Beaver Presence (BP)	1	2316.98	3.10	0.093
PT * BP	1	41.10	0.06	0.817
Error	20	746.57		
Biomass(submerged)[1]:				
PT	1	27.96	10.34	**0.003**
BP	1	2.24	0.83	0.369
PT * BP	1	0.01	0.00	0.961
Error	20	2.70		
Biomass(floating):				
PT	1	3983.25	5.36	**0.031**
BP	1	4130.91	5.56	**0.029**
PT * BP	1	146.06	0.20	0.662
Error	20	742.75		

[1] data were square root transformed prior to ANOVA to meet normality and homogeneity of variance assumptions.

Table 16. ANOVA results summarizing the influence of beaver pond age, size class, and sampling period on aquatic plant species richness (# species m^{-2}). Bolded p values are < 0.05.

Source	df	MS	F-ratio	P value
Richness (all species):				
Age (A)	2	16.68	4.53	**0.021**
Size (S)	1	32.65	8.87	**0.006**
Sample Period (SP)	1	2.04	0.55	0.463
A * S	2	1.84	0.50	0.612
A * SP	2	1.35	0.37	0.696
S * SP	1	0.00	0.00	1.000
Error	26	3.68		
Richness (submerged)[1] :				
A	2	0.53	3.33	**0.050**
S	1	0.86	5.37	**0.029**
SP	1	0.05	0.33	0.571
A * S	2	0.89	2.77	0.081
A * SP	2	0.08	0.25	0.782
S * SP	1	0.00	0.00	0.992
Error	26	0.16		
Richness (floating):				
Depth (covariate)	1	1.86	2.53	0.125
Upland Ponds (covariate)	1	1.40	1.91	0.180
A	2	1.20	1.63	0.217
S	1	4.29	5.82	**0.024**
SP	1	0.10	0.13	0.722
A * S	2	3.91	5.30	**0.012**
A * SP	2	0.17	0.24	0.792
S * SP	1	0.01	0.01	0.934
Error	24	0.74		

[1] data were square root transformed prior to ANOVA to meet normality and homogeneity of variance assumptions.

Table 17. ANOVA results summarizing the influence of beaver pond age, size class, and sampling period on aquatic plant biomass (g m^{-2}). Bolded p values are < 0.05.

Source	df	MS	F-ratio	P value
Biomass (all species):				
Age (A)	2	513.99	0.69	0.510
Size (S)	1	10831.29	14.56	**0.001**
Sample Period (SP)	1	214.90	0.29	0.596
A * S	2	509.42	0.68	0.513
A * SP	2	6.70	0.01	0.991
S * SP	1	0.12	0.00	0.990
Error	26	743.84		
Biomass (submerged)[1] :				
A	2	6.22	2.82	0.078
S	1	12.44	5.64	**0.025**
SP	1	0.47	0.21	0.649
A * S	2	7.73	3.51	**0.045**
A * SP	2	0.24	0.11	0.897
S * SP	1	0.09	0.04	0.843
Error	26	2.20		
Biomass (floating):				
Depth (covariate)	1	693.51	0.88	0.358
A	2	157.56	0.20	0.821
S	1	6130.73	7.75	**0.010**
SP	1	409.24	0.52	0.479
A * S	2	1760.06	2.23	0.129
A * SP	2	8.61	0.01	0.989
S * SP	1	2.71	0.00	0.954
Error	25	790.91		

[1] data were square root transformed prior to ANOVA to meet normality and homogeneity of variance assumptions.

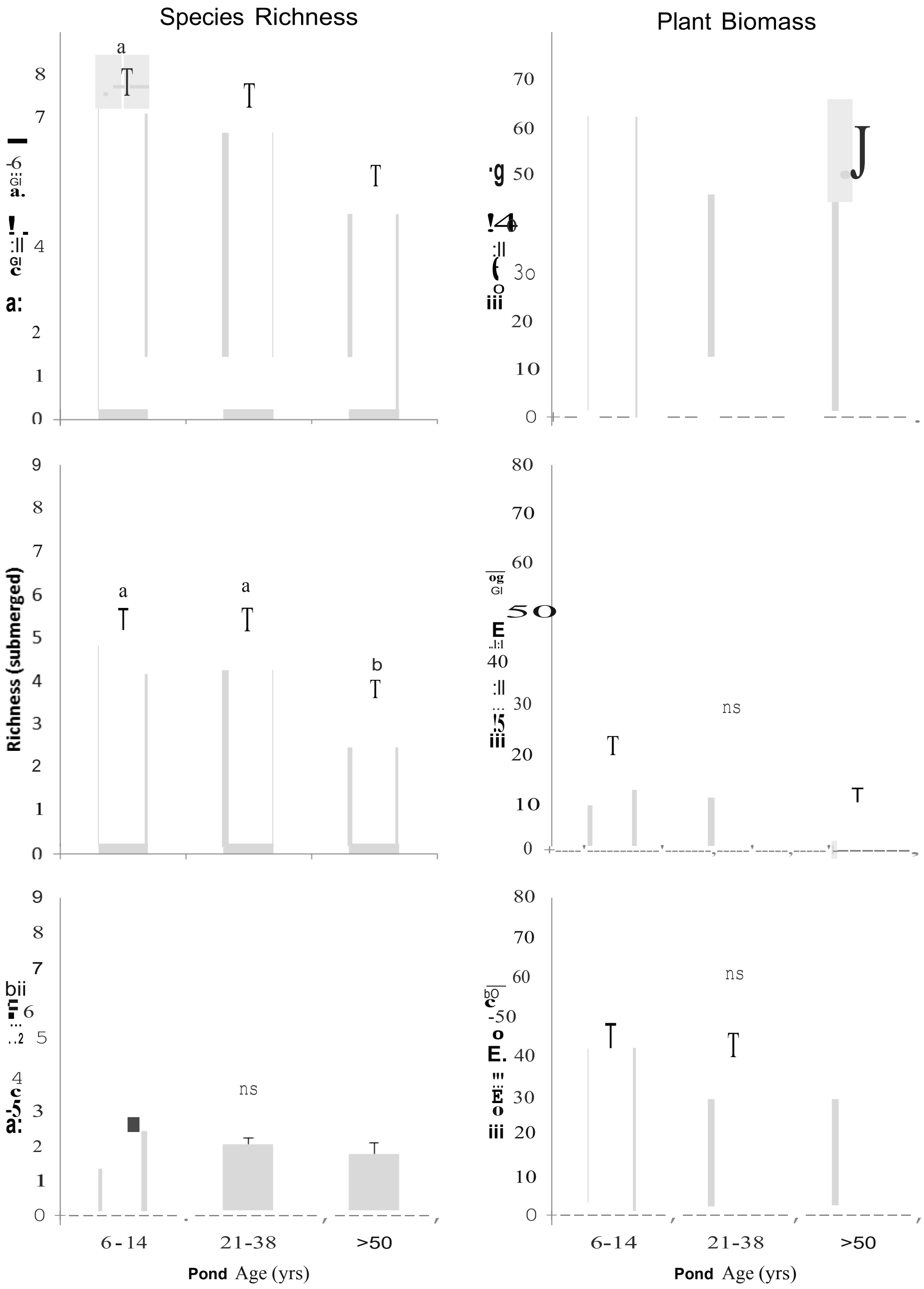


Figure 4. The influence of pond age (6-14 years, 21-38 years, > 50 years; n=6 for each) on species richness (left panel) and plant biomass (right panel). Vertical bars represent standard errors. Different lower case letters signify significant differences ($p<0.05$), based on a post-hoc Least Significant Difference (LSD) multiple range test.

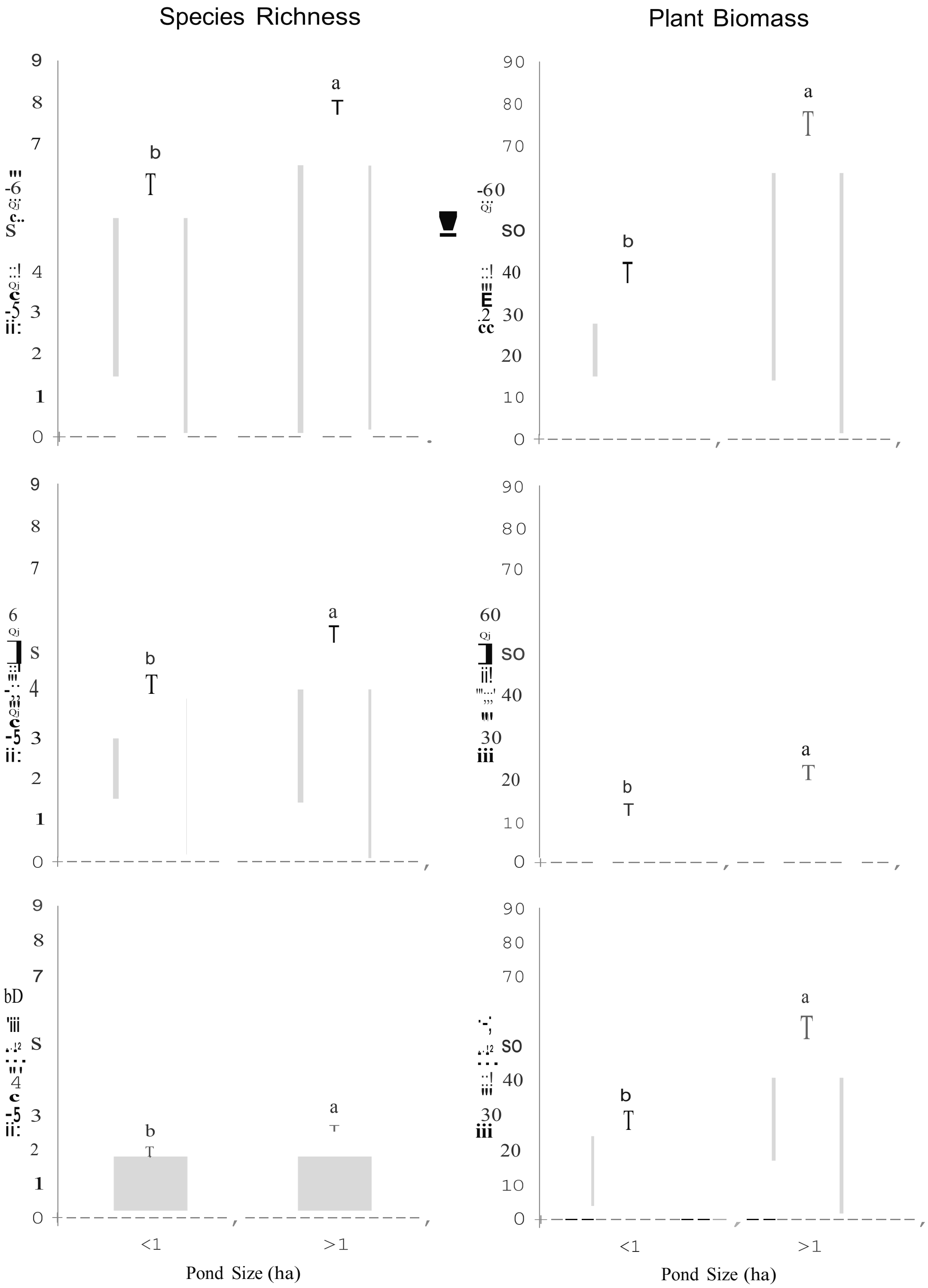


Figure 5. The influence of pond size (< 1 ha and > 1 ha; n=9 for each) on species richness (left panel) and plant biomass (right panel). Vertical bars represent standard errors. Different lower case letters signify significant differences ($p<0.05$), based on a post-hoc Least Significant Difference (LSD) multiple range test.

The effect of pond age on biomass was not nearly as pronounced as it was for richness, with only a slight, non-significant decline with increasing age (Table 17, Figure 4). In contrast, the larger ponds consistently had higher biomass values. For example, total aquatic plant biomass was nearly double in the larger ponds compared to the smaller ponds (>1 ha: 72.3 g m^{-2} versus <1 ha: 37.6 g m^{-2}). This pattern was consistent for both the submersed and floating-leaved species (Figure 5).

There was a significant or near significant pond age x pond size interaction for both richness and biomass (Figure 6). For submersed species, there was a non-significant (p=0.118) decline in richness with increasing age in the smaller (<1 ha) ponds, but a significantly higher (p=0.043) richness in the intermediate-aged (21-38 yrs), larger (>1 ha) ponds. The opposite pattern was true, however, for floating-leaved species, with richness values highest in the young (6-14 yrs) ponds and lowest in the intermediate (21-38 yrs) ponds. Submersed biomass was significantly higher (p=0.019) in the young, small ponds (22.1 g m^{-2}) compared to the older ponds (intermediate: 5.9 g m^{-2}; old: 6.0 g m^{-2}), but highest (27.6 g m^{-2}, compared to 17.8 and 14.5 g m^{-2} for the young and old ponds, respectively) in the intermediate-aged, larger ponds. In contrast, floating-leaved biomass tended to be high (36.2 g m^{-2}) in the intermediate, small ponds compared to the other age classes of small ponds (young: 20.8 g m^{-2}; old: 21.8 g m^{-2}). Floating-leaved biomass was lowest (34.6 g m^{-2}) in the intermediate, large ponds compared to either the young (64.1 g m^{-2}) or old (58.3 g m^{-2}) large ponds.

3.4 Discussion

The greater richness and biomass of submersed aquatic plants and the greater biomass of floating aquatic plants in beaver ponds relative to lake bays has provided further clarification

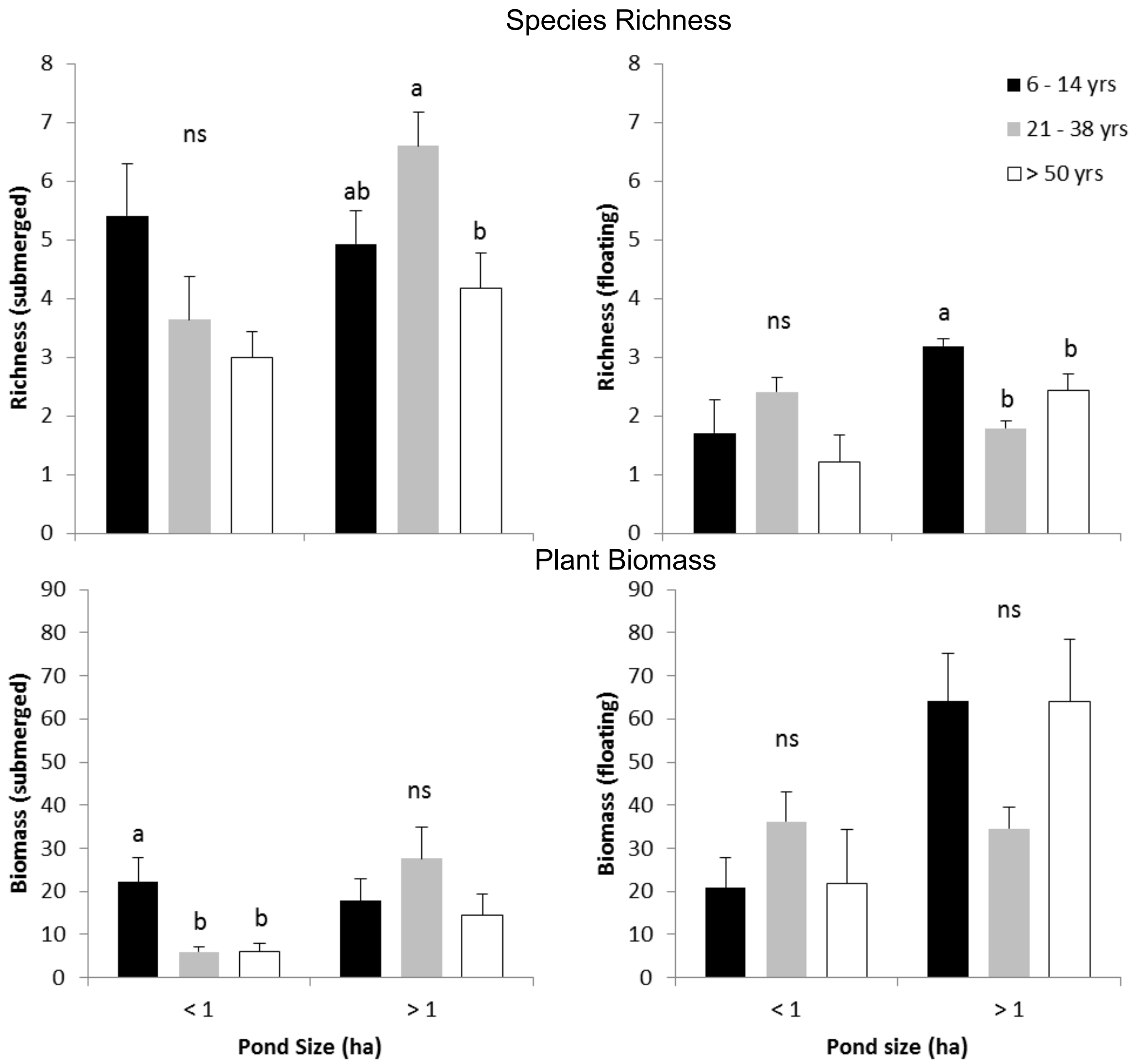


Figure 6. Differential effects of pond age on species richness (upper panel) and biomass availability (lower panel) depending on pond size (n=3 for each of 6 possible age-size combinations). Vertical bars represent standard errors. Different lower case letters signify significant differences ($p<0.05$), based on a post-hoc Least Significant Difference (LSD) multiple range test.

regarding the effect of aquatic patch type on the amount of aquatic forage in aquatic areas potentially used by moose in northern Minnesota (Adair et al. 1991). Lake bays with mucky bottoms and beaver ponds were reported previously to provide more aquatic forage than lakes with rocky bottoms or fast flowing streams, but to my knowledge this is the first study with an emphasis on moose habitat quality to reveal increased richness and biomass of submersed and floating-leaved aquatic plants in beaver ponds relative to lakes. It is possible that both wind and wave action, along with substrate structure, may have played a role in the greater richness and biomass of aquatic plants in beaver ponds relative to lakes in this study (Bornette and Puijalon 2011). Since only sheltered bays with substrates comprised primarily of organic matter were sampled, it does not appear that this apparent difference in plant richness and biomass was related to substrate quality, as was the case in the reduced abundance of aquatic plants observed in large lakes with rocky bottoms by Adair et al. (1991). It is somewhat more plausible that increased wave action may have contributed since lake bays are open on at least one side to the lake and thus fetch length, representative of wind and wave action, was likely greater in lakes relative to ponds. This interpretation is in agreement with previous work on aquatic forage in areas used by moose that demonstrated within-lake variation in aquatic plant abundance was partially attributed to shoreline exposure (Fraser et al. 1980). Floating-leaved plants represented a greater proportion of combined biomass in lakes relative to ponds and this may be because floating-leaved plants possess a sturdy stalk that may help anchor these plants more effectively to the substrate than less robust submersed species (Hutchinson 1975; Fraser et al. 1980; Cronk and Fennessy 2001).

Damming of streams by beaver may promote the growth of submersed and floating-leaved aquatic plants (Fryxell 2001; Ray et al. 2001) through creation of aquatic areas with intermediate levels of flow and thus higher nutrient content available to plants (Westlake 1967; Naiman et al. 1988). Areas recently flooded by beaver may serve as colonization sites for aquatic plants (Ray et al. 2001) and it has been suggested that the presence of early colonizing submersed aquatic plant species improves aquatic habitat quality for moose (Fraser et al. 1980; 1984). The combination of a harsher abiotic environment in lakes and the creation of more favourable conditions for plant growth through damming of streams by beaver was likely responsible for the variation in aquatic plant richness and biomass with respect to aquatic habitat type observed in the present study.

A fairly consistent interactive effect of patch type and size on aquatic plant richness and biomass was observed, but the nature of the interaction appeared to differ between submersed and floating-leaved aquatic plants. Floating-plants showed greatest richness in ponds aged 6-14 years of either size (< 1 ha and > 1 ha), with slightly more floating-leaved species being found in ponds > 1 ha. Floating-leaved biomass was greatest in ponds > 1 ha. Among large ponds, floating-leaved biomass appeared markedly lower in ponds 21-38 years old. The most dominant species, both submersed and floating, within the present study area was *Brasenia schreberi*, a canopy forming floating-leaved species. *B. schreberi* was present in greater than 80% of all rake drags from ponds > 1 ha and a closed canopy was visually observed to cover large swaths of ponds > 1 ha beginning June 15, 2012. The probability that *B. schreberi* colonizes a pond may be positively influenced by the surface area of open water available to dispersing propagules (Ray et al. 2001). I suggest that the decreased richness in smaller ponds with respect to floating-leaved plants may be because there was a lower probability of colonization by *B. schreberi* in smaller ponds relative to larger ponds. Once established in larger ponds, *B. schreberi* might show improved yield relative to other floating leaved species due to allelopathic effects (Elakovich and

Wooten 1987) or improved access to light following canopy establishment (Scheffer 2003). Thus, young ponds (6-14 years), especially those <1 ha, are more diverse with respect to floating-leaved vegetation because *B. schreberi* canopies have not yet become established in the sections of open water needed by competing floating-leaved plants for survival and reproduction.

It also appears that beaver ponds that are closer to one another show increased probability of colonization by dispersing floating-leaved plants as illustrated by a positive effect of nearby open water on floating-leaved biomass. This interpretation is in agreement with previous work on aquatic plant dispersal by wind and water birds in beaver ponds and other ephemeral bodies of water (Figuerola and Green 2002; Vanschoenwinkel et al. 2008; Arthaud et al. 2013). Thus, stands of *B. schreberi* appear to be most readily established within large (> 1 ha) beaver ponds that are colonized as a result of *B. schreberi* dispersal via wind and waterbirds from other, nearby beaver ponds. These stands of *B. schreberi*, once established, become very dense, contain few other species and represent very large amounts of floating-leaved biomass. Moose, however, do not typically feed on *B. schreberi* (Ch. 1; but see Joyal and Scherrer 1978) and thus aquatic areas where submersed species typically preferred by moose (Fraser et al. 1984; Adair et al. 1991; Ch. 1) are able to establish themselves might serve as more important feeding sites for moose.

Submersed plants showed greater richness but similar biomass in large, young ponds (6-14 years) relative to small (< 1 ha) ponds 21-38 years of age and older ponds of both sizes (> 50 years old, < 1 ha and > 1 ha). This agrees with the above interpretation for floating-leaved plants, whereby ponds that have been flooded relatively recently (6-14 years) serve as rapid colonization sites for submersed plants, many of which are typically preferred by moose, and this phenomenon leads to increased richness relative to other aquatic habitat types. That submersed biomass was not significantly greater in young ponds relative to the other habitat types listed above is not necessarily surprising when one considers that these smaller, submersed growth forms must establish themselves in gaps in the floating-leaved canopy (Ray et al. 2001) and thus a limited space for growth might set some initial limit on submersed biomass immediately following colonization. This increased space hypothesis is consistent with the finding that larger ponds contained greater submersed biomass relative to smaller ponds, irrespective of age, since ponds > 1 ha presumably contain more available area for growth and establishment relative to ponds < 1 ha. Also, the ability for submersed annual plants to proliferate into dense stands might be dependent somewhat on the establishment of a seed bank in the sediment, a process that might take many years (Bonis et al. 1995; Combroux et al. 2001), and might also explain lower submersed biomass in young ponds relative to intermediate aged ponds. It appears that following initial establishment within young ponds submersed plants are able to proliferate to the point of increasing significantly with respect to biomass. Ponds 21-38 years old and > 1 ha show the greatest submersed biomass relative to all other aquatic habitat types, and this may be partially explained by the establishment and proliferation of a submersed seed bank. That this pattern only occurred in large ponds would also suggest that zoochorous and anemochorus (waterbirds and wind) dispersal might contribute to the increased biomass (and richness) observed in ponds 21-28 years old since these mechanisms of dispersal would have a greater likelihood of resulting in colonization when surface area of available open water is greater (Ray et al. 2001; Figuerola and Green 2002; Vanschoenwinkel et al. 2008; Arthaud et al. 2013).

That beavers, after initial flooding of an area, frequently engage in abandonment-recolonization cycles (i.e., pond switching; Fryxell 2008; Vincent 2010) might also explain increased growth and biomass in ponds 21-38 years old relative to younger ponds. Pond drawdown events that may occur upon abandonment of a pond (Fryxell 2008; Johnston and

Naiman 1988) would result in exposure and subsequent oxidation of the sediment that would make nutrients, e.g. phosphorous and nitrogen, more available to plants growing annually from the established seed bank (Hutchinson 1975; Fraser et al. 1984; Cronk and Fennessy 2001). Therefore, I have suggested that beaver ponds initially become colonized by floating-leaved and submersed plants at 6-14 years but that these two functional groups follow different trajectories in terms of peak richness and biomass. Floating-leaved communities often become low diversity stands of *B. schreberi* under appropriate conditions (large pond surface area for colonization and available nearby open water for propagule input), and it is only through rapid initial establishment and proliferation in large, young ponds that submersed species (and other floating-leaved species) can stave off competitive exclusion in time and space.

The positive relationship between beaver presence and floating-leaved species richness and biomass in lakes and beaver ponds must be interpreted with caution as there are multiple plausible explanations. Fryxell (2001) reported that beaver ponds occupied for the greatest length of time were associated with greater abundance of floating-leaved vegetation and suggested that the creation of these ponds produced ideal conditions for growth of these plants. Indeed, beaver impoundments undergo succession from newly-flooded forest floor to open water wetlands, which favours increased establishment of floating-leaved plants such as water lilies, as discussed above (Johnston and Naiman 1990a). Alternatively, the association between beaver and floating-leaved plants may be due to beaver habitat selection for stands of floating-leaved plants as these plants are consumed by beaver in summer (Milligan and Humphries 2010; Severud et al. 2013; Law et al. 2014). This association may be further enhanced if beaver movement between ponds (Fryxell 2001; Vincent 2010) leads to floating-leaved plant dispersal between sites or if beaver bury floating-leaved vegetative structures (e.g., water lily rhizomes) in food caches (Milligan and

Humphries 2010). Perhaps the most parsimonious explanation for the association between beaver and floating-leaved plants is that beaver select habitats with preferred terrestrial forage (e.g., *Populus tremuloides*; Vincent 2010), irrespective of aquatic conditions. Aquatic plants growing in areas associated with hardwood trees such as *P. tremuloides* are likely to receive less acidic leaf litter input than aquatic areas associated with conifer trees (Gregory et al. 1991; Cronk and Fennessy 2001), which might favour growth of floating-leaved aquatic plants. Also, beaver foraging decreases the basal area of riparian forest (Johnston and Naiman 1990b), and thus decreased canopy cover leading to greater light penetration might also favour growth of floating-leaved aquatic plants. Lakes within the present study tended not to be associated with beaver dams as beaver living at these sites typically created lodges on sheltered shorelines as opposed to within impounded areas (Pers. obs.) Thus, I suggest that the most likely explanation for the association between beaver and floating-leaved plants observed in this study is that of habitat selection by beaver for areas containing terrestrial hardwood forage, floating-leaved aquatic forage or some combination of both forage types rather than the creation of conditions ideal for floating-leaved plant growth by beaver.

I did not observe an effect of sampling period on the richness or biomass of floating-leaved or submersed aquatic plants. The sampling periods chosen conformed closely to those utilized by Brusnyk and Gilbert (1983) who found greater availability of aquatic vegetation in late summer relative to early summer. I utilized a more intensive (i.e., greater number of random sample points across and within sites) sampling protocol over a larger spatial scale than did Brusnyk and Gilbert (1983) and thus I am relatively confident that my results represent accurately the conditions in northern Minnesota with respect to richness and biomass of aquatic plants. A potential caveat of this study, however, is that because only two functional groups were used (submersed and floating-leaved plants) I may have missed seasonal variability at the species level that might be important for moose (Fraser et al. 1982). The submersed group, however, contained all genera reported by Fraser et al. (1980; 1984) as preferred by moose and thus it is probable that this group conforms well to species that would be eaten by moose if given the opportunity. Beyond the scope of my study, however, was an analysis of chemical constituents of submersed and floating-leaved aquatic plants that might have showed seasonal variation. Fraser et al. (1982), for example, reported a decline in sodium content of preferred aquatic plant species in late summer concomitant with a decline in aquatic feeding behavior of moose. Due to logistical constraints I was unable to re-sample lake habitats and thus it is possible that seasonal variation in aquatic plant availability for moose reported elsewhere (Fraser et al. 1982; Brusnyk and Gilbert 1983) might be restricted to lakes, perhaps due to harsher abiotic conditions leading to more rapid senescence. This restriction in seasonal variation would suggest that beaver ponds may be additionally important to moose relative to lakes because of their ability to provide aquatic food throughout the summer, but given data available from the present study this remains speculative.

I also determined that water depth did not influence richness and biomass of aquatic plants in areas potentially used by moose, at least within the ranges of depths present in my study area (11 cm – 295 cm). This finding is in agreement with previous work that has suggested moose aquatic feeding is restricted to the littoral zone (< 3 m in depth; Adair et al. 1991; Lenarz et al. 2011). Further research might explore the possibility that greater water depths are important for moose for the purpose of avoiding biting insects (Ch. 1; Ritcey and Verbeek 1969).

Further work on aquatic plant biomass might include a third functional group, emergent plants, which are also consumed by moose (Aho and Jordan 1979; Fraser et al. 1984; Morris

2002) and beaver (Milligan and Humphries 2010; Severud et al. 2013). Emergent plants typically form a ring around beaver ponds and the abundance of these plants might also be influenced by pond age (Naiman et al. 1988; Johnston and Naiman 1990a). Also important for understanding nutritional quality of aquatic vegetation in areas potentially used by moose would be a seasonal examination of mineral (especially sodium), protein, and energy content. Tischler (2004) combined nutritional analysis of terrestrial and aquatic forage with isotopic analysis of moose hooves to estimate the quality and identity of moose diets on Isle Royale. Since geographic variation in aquatic moose diets seems likely (Peek 1974; Ch. 1), research surrounding seasonal variation in aquatic (submersed, floating-leaved, and emergent) and terrestrial forage quantity, quality and moose summer diet composition from a variety of North American locales would improve understanding of moose nutritional energetics under a variety of climatic conditions. Understanding how moose meet their energy and essential nutrient and mineral requirements in different areas of North America would help wildlife managers identify important habitats for moose in different geographic regions and to maintain these habitats on the landscape. I have suggested that beaver ponds in northern Minnesota may serve as important habitat for moose and thus maintenance of beaver on the landscape may help facilitate moose in meeting their nutritional needs in summer.

4.0 CONCLUSION

I have demonstrated that, though variable across North America, aquatic habitat use by moose is characteristic of their summer behaviour especially in the Great Lakes-St. Lawrence region. Moose in this region appear to use aquatic habitat for the purpose of feeding, though it is not completely clear whether sodium hunger or foraging efficiency drive this pattern. Moose may also use aquatic areas to escape biting insects but do not appear to use aquatic areas as part of general strategies to minimize predation risk or ameliorate heat stress. It is plausible that moose use aquatic habitat to ameliorate heat stress only at southern range limits but it was not possible to confirm this hypothesis here.

I have further demonstrated that, within north-central Minnesota, richness and biomass of aquatic plants in aquatic areas potentially used by moose is influenced by the presence and damming activity of beaver. The creation of beaver ponds appears to quadruple total aquatic plant biomass potentially available to moose relative to lakes. Beaver ponds have greater richness and available biomass of submersed species often preferred by moose, particularly in the case of ponds 21-38 years old possessing established seed banks. Beaver also create newly flooded ponds that serve as rapid colonization sites for both floating-leaved and submersed aquatic plants consumed by moose. The creation of large (> 1 ha) ponds by beaver provides the physical space needed for colonization and establishment of aquatic plants preferred by moose and may help maintain landscape level aquatic plant diversity. Without the presence and activity of beaver it is plausible that the highly competitive yet not necessarily palatable species *Brasenia schreberi* would dominate ponded areas of north-central Minnesota leading to an overall decrease in the diversity and quality of aquatic forage potentially available to moose.

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