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Revisiting the Role of Aquatic Plants in Beaver Habitat Selection

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ABSTRACT—Beaver *(Castor canadensis)* can help to restore wetlands and mitigate the effects of climate change on hydrological regimes in some areas. Therefore, ongoing resource management efforts seek to promote the presence and persistence of beaver populations. The long-term success of such endeavors requires an understanding of what conditions are conducive to sustaining beaver populations, often in landscapes with degraded forest resources. Available information about beaver habitat suitability is largely based on short-term studies in stream habitats that do not consider aquatic plant suitability, even though aquatic plants may comprise over half of beavers' annual diets. In the present study, we assess whether the availability of woody plants, conditions conducive to the availability of aquatic vascular plants (macrophytes), and/or other features of basin morphology are associated with the persistence and density of beaver occupancy in 23 lakes over a 50-y period. We incorporate field-based study that includes all species of macrophytes, to extend previous work that focused specifically on water lily species *(Nymphaea* spp., *Nuphar* spp.*)*. Lake perimeter (a function of sinuosity and surface area) and total macrophyte cover were associated with the persistence and density of beaver occupancy in lakes. Each factor independently explained ~70% (R^2_{adj}) of the variation in the persistence of beaver occupancy. Percent cover of floating-leaved macrophytes was a leading predictor of beaver colony density in lakes, independently explaining 72% (R^2_{adj}) of the variation. *Brasenia schreberi* appeared particularly valuable to sustaining beaver in smaller lakes. Several lakes with abundant *Brasenia* supported high colony densities and long-term colony occupancy. Where feasible, beaver restoration efforts may increase the probability of success by facilitating beaver access to lakes that host key rhizomatous macrophyte species.

INTRODUCTION

Beaver *(Castor canadensis, C. fiber)* have long been a compelling research subject due to their extensive ecological impacts. In contemporary times understanding long-term beaver habitat selection remains important because beaver can promote ecological restoration and help mitigate the effects of climate change on water resources (Albert and Trimble, 2000; Emme and Jellison, 2004; Pollock *et al.*, 2004; Maringer and Slotta-Bachmayr, 2006; Face-Collins and Johnston, 2007; Burchsted *et al.*, 2010; Buckley *et al.*, 2011; Carpenedo, 2011; Wild, 2011; Baldwin, 2013). In addition beaver flooding of private lands continues to be problematic, requiring management decisions that are scientifically informed (Albert and Trimble, 2000; Emme and Jellison, 2004; Pollock *et al.*, 2004; Maringer and Slotta-Bachmayr, 2006; Face-Collins and Johnston, 2007; Burchsted *et al.*, 2010; Buckley *et al.*, 2011; Carpenedo, 2011; Wild, 2011; Baldwin, 2013).

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Beaver habitat selection has been extensively investigated through studies that compare beaver occupancy or density with habitat characteristics, yet several limitations remain (Appendix A, Table A1). One limitation is the duration of study. Studies of beaver habitat selection over 1 to 2 y are abundant but longer-term studies are few (*for exceptions, see* Howard and Larson, 1985; Broschart *et al.*, 1989; Fryxell, 2001). Another limitation is the type of aquatic habitat considered. Most related research has focused on stream habitats, whereas fewer studies have considered factors affecting beaver selection of different lake habitats (*for exceptions, see* Slough and Sadleir, 1977; Fryxell, 2001). Finally, empirical research demonstrates lack of consensus regarding the importance of deciduous woody vegetation to beaver habitat selection. The most broadly used beaver habitat suitability index (HSI) for North America (Allen *et al.*, 1983) considers woody vegetation a key limiting factor, and some studies have found woody vegetation variables are important to beaver occupancy or density (*e.g.*, Slough and Sadleir, 1977; McComb *et al.*, 1990; Fustec *et al.*, 2003; František *et al.*, 2010). However, in other research, woody vegetation had a weak or negligible relationship with beaver occupancy or density (*e.g.*, Howard and Larson, 1985; Beier and Barrett, 1987; Robel *et al.*, 1993; Hartman, 1996; Barnes and Mallik, 1997; Suzuki and McComb, 1998; Cox and Nelson, 2009).

Some discrepancy is to be expected between beaver habitat selection in different locations or times, particularly regarding generalist herbivores such as beaver that can adjust food choices based on availability (Northcott, 1971; Histøl, 1989). Resource availability is heterogeneous over space and time such that in different locations or time periods, varying factors may limit an animal's potential to occupy a site (Hunter and Price, 1992). Nonetheless, resource managers may benefit from further clarification of factors that address unexplained variation of beaver occupancy and density given the importance of beaver habitat selection to a range of wetlands management efforts.

Aquatic plants (macrophytes) may be important to beaver habitat selection but have scarcely been assessed in previous empirical studies (Appendix A, Table A1). Exceptions include two studies that solely considered water lily species (*Nuphar* spp. or *Nymphaea spp.).* Water lilies were important to *C. canadensis* density in lakes and streams of Ontario over time (Fryxell, 2001) but not to *C. fiber* occupancy of Swedish streams in a single year (Hartman, 1996). Macrophytes can be consumed with minimal predation risk (Fryxell and Doucet, 1993) and may offer some nutritional benefits to beaver over terrestrial plants, including better digestibility, higher crude protein, and higher sodium and iron (Fraser *et al.*, 1984; Tischler, 2004). One modeling effort found that energetics did not explain beavers' observed preference for white water lily (*Nymphaea odorata*) over terrestrial species, but authors only considered lily leaves and stems without accounting for beaver consumption of water lily rhizomes (Doucet and Fryxell, 1993).

Recent stable isotope studies have estimated that macrophytes compose ~60–80% of *C. canadensis* winter and autumn diets (Milligan and Humphries, 2010) and ~56% of beaver annual diets (Severud *et al.*, 2013). The contribution of macrophytes to winter diets is particularly notable because contribution to winter food cache was a primary reason some woody species were assumed to be the limiting vegetation factor in beaver habitat suitability (Allen *et al.*, 1983). Yet beaver have incorporated macrophyte rhizomes in winter food caches and may consume persisting aquatic plant organs under the ice (Shelton, 1966; Ray *et al.*, 2001). In Minnesota beaver assimilated approximately equal amounts of woody and aquatic vegetation during winter (Severud *et al.*, 2013). In Quebec aquatic plants were predominant in the winter diet of beaver living in lakes but not of beaver living in streams (Milligan and Humphries, 2010).

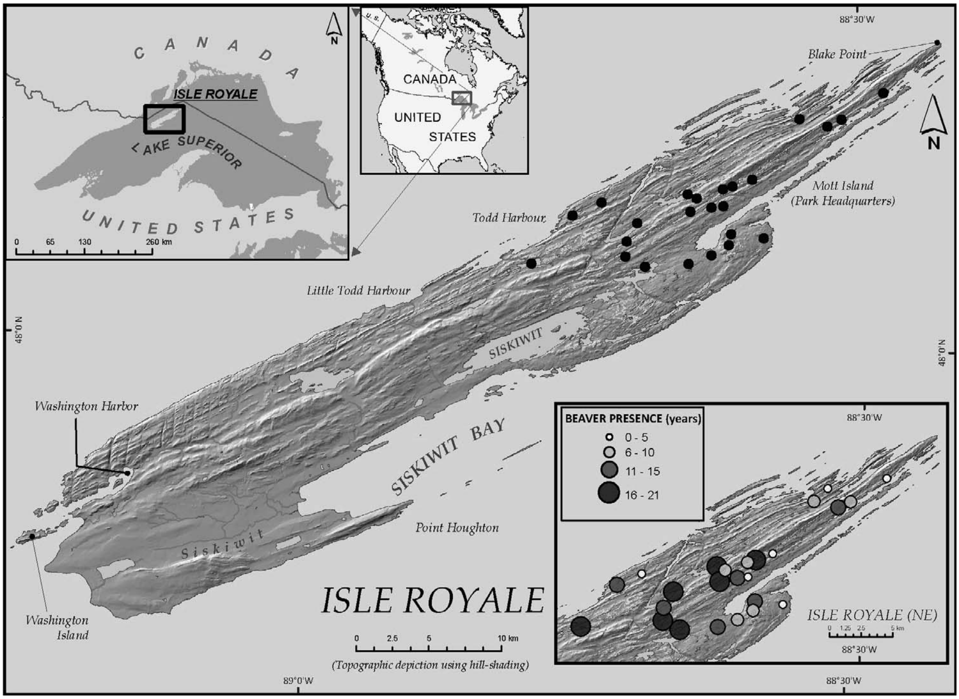

FIG. 1.—Study sites on Isle Royale, Lake Superior, U.S.A. Dots indicate the location of lakes included in the present study. In the bottom right panel, dot size indicates the beaver colony persistence, determined as the number of years in which beavers occupied the lake out of 23 assessment years between 1962–2012

In the present study, we assess factors associated with long-term habitat selection by *C. canadensis* at a landscape scale on Isle Royale National Park, Lake Superior, U.S.A. Specifically, we address the questions: (1) What habitat factors best explain the persistence and density of beaver colonies in 23 inland lakes over 50 y; and (2) Across the entire island, are active colonies more variable over time in lake or stream habitats? Our focus on lake habitats complements the extensive body of previous work on beaver occupancy and density in stream habitats. We consider 23 observation years over a 50-y period, providing a longer temporal scale of analysis than previous research. We also extend previous studies by conducting field-based study of aquatic vegetation that includes all species of aquatic plants, rather than only water lily species.

METHODS

We conducted this research on the main island of Isle Royale National Park, Lake Superior, U.S.A. (Rock Harbor: 88°29′9″W, 48°8′48″N, Fig. 1). Isle Royale has been designated as a national wilderness area since 1976. The main island is ~530 km^2, is almost completely forested and has 43 named inland lakes. Isle Royale lies in the transition zone between northern hardwood and boreal forests, hosting tree species typical of both regions (Peterson, 1977). Larger mammals that consume aquatic plants and currently reside on the island include beaver *(Castor canadensis)* and moose *(Alces americanus),* both of which were established at the beginning of the 20th century (Shelton and Peterson, 1983). Muskrat *(Ondatra zibethicus)* also occur on the island but are uncommon (https://www.nps.gov/isro/learn/nature/mammals.htm). Signs of muskrat were not observed in any of the 23 lakes during aquatic plant surveys of the present study.

COLONY PERSISTENCE AND DENSITY

We studied two response variables associated with *C. canadensis* habitat selection: (1) colony persistence, defined as the total number of years in which a lake had at least one active beaver colony over 23 observation years; and (2) colony density, defined as the mean number of colonies / km^2 lake over 23 observation years spanning 1962–2012. Data on colony persistence and density were derived from aerial surveys of the Isle Royale beaver population conducted for 23 of the 50 y from 1962 to 2012. Surveys took place at least every other year from 1978 to 2012 and were conducted annually in the 5 y from 2006–2010 (Romanski and Peterson, 2012). All beaver surveys were implemented over a period of 3–5 d in mid to late October after deciduous leaf-fall and before snow cover. Most colonies were determined active based on presence of a lodge with fresh mud and food cache. For a small portion of sites, other signs were considered where their geographic location indicated a unique colony, including food cache only, freshly cut woody vegetation, and fresh mud on a lodge (Hay, 1958; Payne, 1981; Brown and Parsons 1982; Swenson *et al.*, 1983; Romanski and Peterson, 2012). Researchers conducting the aerial surveys acquired a geographic reference for each active beaver colony. We discerned the number of beaver colonies on each study lake per year of observation by plotting active colony locations against digital topographic maps and ortho-rectified aerial photos in ArcGIS 10.1 (ESRI, 2012). All lakes in the present study met criteria of the U.S. Geological Survey (USGS) for lacustrine habitat (Cowardin *et al.*, 1979) and had at least one beaver colony present for at least two of the 23 observation years.

VARIABLES PREDICTING COLONY PERSISTENCE AND DENSITY

We selected predictor variables based on previous studies' findings of factors that are important to beaver occupancy and/or density and are relevant to lake habitats (Dieter and McCabe, 1989; McComb *et al.*, 1990; Fryxell, 2001; Fustec *et al.*, 2003; František *et al.*, 2010). These variables are of two general categories: those related to basin morphology and those related to availability of food resources (macrophytes and woody vegetation, Table 1). Percent macrophyte cover was analyzed to provide a richer context, but basin morphology variables associated with macrophyte habitat are more reliable indicators of long-term macrophyte availability due to the potential for inter-annual variation in macrophyte communities. To delineate watershed area, lake perimeter, and lake area, we used preexisting GIS layers of watersheds for larger lakes (Hyslop, 2010). We delineated the watersheds of smaller lakes with a LiDAR-derived digital terrain model. Lakeshore sinuosity was calculated as the ratio of the actual lake perimeter to the circumference of a circle of the same area, with a perfect circle being the least sinuous.

To delineate the littoral zone, we first identified the maximum depth of macrophyte growth by conducting snorkel surveys in five to 30 sectors of each lake, depending upon lake size (at least one for every 15 ha up to a maximum of 30, sensu Jeppesen *et al.*, 2000). We then collected GPS coordinates of the littoral zone edge along every 10 m of shoreline for lakes $<$450 ha, and along every 20 m of shoreline for lakes $>$450 ha, using a depth finder to

TABLE 1.—Variables assessed as potential predictors of the persistence and density of beaver occupancy in 23 lakes of Isle Royale National Park, Lake Superior, U.S.A. from 1962–2012

Candidate predictor variables	
Basin morphology	Watershed area
	Lake area
	Littoral zone area
	Lake perimeter
	Lakeshore sinuosity
Resource availability	Percent cover broad leaf deciduous within 60 m of shore
	Percent cover trees within 60 m of shore
	Percent cover all macrophyte species[a]
	Percent cover floating-leaf macrophytes
	Percent cover water lilies
	Total cover all macrophyte species[b]
	Total cover floating-leaf macrophyte species
	Total cover water lily species

[a] Percent cover of macrophytes = mean percent cover of the noted macrophyte type in all quadrats for a given lake

[b] Total cover is the area of 100% macrophyte cover, calculated as $= \frac{\sum_1^n Qx}{n} A_{lit}$, where Q_x represents the percent cover of macrophyte type x per quadrat, n is the number of quadrats for the entire lake, and A_{lit} is the area of the lake's littoral zone

identify the distance perpendicular to shoreline where the maximum macrophyte depth occurred. We subsequently plotted all coordinates to establish a littoral zone boundary for each lake. We refined these delineations by plotting and assessing them against orthophotography from the months of greatest macrophyte biomass on Isle Royale (late July–early August) and, where available, previous bathymetric analyses (https://irma.nps.gov). Littoral zone area was calculated using littoral zone delineations for the inner littoral zone boundary and orthophotography for the outer boundary.

Percent cover of deciduous trees and percent cover of all trees at 30 m and 60 m from shoreline were determined from the USGS-National Park Service (NPS) vegetation mapping program (TNC, 1999). We chose distances from shoreline based on previous research findings that on Isle Royale beaver forage an average of 37 m from shore and may generally be restricted to a maximum safe harvesting distance of 30–60 m in the presence of predators (Shelton, 1966). Other studies have found beaver usually limit foraging to 20–30 m from shore (Hall, 1960; Jenkins, 1980) or to within 60 m from shore (Donkor and Fryxell, 1999), although maximum foraging distances of up to 200 m have been reported (Bradt, 1938). We applied a 60-m buffer in all analyses of woody vegetation and subsequently conducted a sensitivity analysis to assess for the effect of reducing the buffer to 30 m.

We used ArcGIS 10.1 to establish buffers of 30 m and 60 m around each lake. Each resulting buffer area included multiple sub-plots of unique vegetation communities, as delineated through vegetation mapping (TNC, 1999). A weighted mean percent tree cover for the entire buffer zone was calculated as $\bar{x} = \sum_{i=1}^{n} AiPi \ / \ \sum_{i=1}^{n} Ai$ where Ai = the area of each subplot, and P_i = median percent tree cover in the subplot. To estimate percent cover broad of leaf deciduous trees for each buffer zone, we multiplied P_i by the median percent deciduous trees in each plot's cover type. We assessed sensitivity to the use of medians by randomly generating 100 data sets of values within the minimum–maximum range of each variable and assessing whether any of these data sets significantly altered modeling results.

We used snorkel surveys to estimate macrophyte percent cover and total cover for the 2012 data used in all regression analyses. We assessed macrophytes within five to 30 sectors depending upon lake size (as above, at least one for every 15 ha up to a maximum of 30, sensu Jeppesen *et al.*, 2000). Within each sector, we estimated percent cover by species within 0.25 m^2 quadrats in each of four depth ranges (0–33 cm, 34–66 cm, 67–100 cm, >100 cm). Percent cover of macrophytes was subsequently calculated as the average percent cover for all quadrats for: (a) all macrophyte species, (b) floating-leaved species only, and (c) water lily species only (*Nuphar spp.* and *Nymphaea spp.*). Floating-leaved species were defined as all planmergent species, which have a "conspicuous portion of plant body on water surface" according to Schuyler's (1984) classification of aquatic macrophytes. Total macrophyte cover was calculated as: total cover $= [(\sum_1^n Qx \ / \ n) \ A_{\mathrm{lit}}]$, where Q_x represents the percent cover of macrophytes of type *x* per quadrat, *n* is the number of quadrats for the entire lake, and A_{lit} is the area of the lake's littoral zone. We explored which macrophyte species are most abundant in lakes that sustained high beaver colony density by identifying all macrophyte species with ≥5% cover in lakes with the highest beaver densities.

In 2011 we measured macrophyte abundance in 11 of the study lakes (48% of the 2012 total) as a baseline for estimating inter-annual variation. In 2011 we used rakes to estimate percent cover of submerged vegetation (Deppe and Lathrop, 1992; Ray *et al.*, 2001). We compared each year's relative percent cover by species (the percentage of total macrophyte cover that each species represented in a given lake each year) to account for measurement sensitivity to the different methods used in 2011 and 2012.

COLONY PERSISTENCE IN LAKE VS. STREAM HABITATS

We assessed the persistence of active beaver colonies in lakes versus other available aquatic habitats by calculating the coefficient of variation for the annual number of beaver colonies in (a) inland lake habitats, and (b) stream or wetland habitats for each of the 23 observation years between 1962–2012. We delineated beaver colonies by aquatic habitat type by plotting locations against topographic maps and ortho-rectified photos in ArcGIS 10.1, as noted under "colony persistence and density" above. We classified all colonies within 20 m of an inland lakeshore as "lake" and all other inland colonies as "stream or wetland." Detection probability based on flying style (height of plane and frequency of overlapping circles flown during surveys) was incorporated into the final data set (Romanski, 2010). As for the 23 lakes included in the data set under "colony persistence and density," an inland lake was defined as any standing water body meeting the definition of "lacustrine system" in the USGS system for wetlands classification (Cowardin *et al.*, 1979).

STATISTICAL ANALYSIS

We used general linear regression to analyze the relationship between predictor and response variables. We first assessed the shape of the relationship between the response variable and each potential predictor because animals generally respond to environmental gradients in a nonlinear fashion (Heglund, 2002). All candidate predictor variables and the response variable colony density were log transformed to improve a linear relationship and to meet regression assumptions. All predictor variables mentioned hereafter refer to their log transformed version.

Once we identified the appropriate transformations and modeling methods we constructed and tested separate linear regression models for all possible combinations of predictor variables and their quadratic terms up to a maximum of two variables per model.

This maximum was applied given the sample size (n = 23) and the criterion of at least 10 observations per predictor variable in multiple regression (Harrell *et al.*, 1996; Babyak, 2004; Sauerbrei *et al.*, 2007). Analysis of colony density as a response variable excluded lake area and its correlates (watershed area, littoral zone area, lake perimeter, total cover of floating leaved macrophytes, total cover of all macrophyte species) as potential predictor variables due to the likelihood of multicollinearity. We tested regression assumptions as follows: the assumptions of a linear relationship and homoscedasticity of errors were tested through examination of residual vs. predicted plots; the assumption of no autocorrelation among residuals was examined with the Durbin–Waston test ($\alpha = 0.05$); and the assumption of normality of error distribution was tested with the Shapiro–Wilk test ($\alpha = 0.05$). We tested for outliers using the Jackknife distance ($\alpha = 0.05$). Variance Inflation Factor (VIF) was assessed for all two-predictor models to determine whether VIF >10 for any model, which would warrant remediation to address multicollinearity (Kleinbaum *et al.*, 2013 p. 368).

To identify the best fitting models we calculated values of Akaike information criterion corrected for small sample bias (AIC_c). We determined Δ_i as the difference between a given model's AIC score and the lowest AIC score of all models (Burnham and Anderson, 2004). AIC_c weight (w_i) represents the probability that a model best represents the given data and set of candidate predictor variables (Anderson and Burnham, 2002). We calculated w_i as $w_i = \exp(-\Delta_i)/2) \ / \ \sum_{r=1}^{R} \exp(-r)/2)$ using all models with $\Delta_i < 10$ (Burnham and Anderson, 2004; Wagenmakers and Farrell, 2004). A 95% confidence set of models was identified, consisting of all models with a cumulative w_i of 0.95 (Anderson and Burnham, 2002). To assess the relative strength of individual predictors, we also constructed and tested all possible single-predictor models using the methods and criteria described above.

All candidate predictor variables and the response variable colony density were log transformed to improve a linear relationship and to meet regression assumptions. All predictor variables mentioned hereafter refer to their log transformed version. Percent cover was allowed to exceed 100% (Fargione *et al.*, 2003; Fukami *et al.*, 2005). Because three study lakes did not have lily species *(Nuphar* spp., *Nymphaea* spp.*)*, we applied a generalized procedure for log transformation to percent cover of water lilies and total cover of water lilies that: (1) maintains the order of magnitudes and (2) results in zero if the initial value was zero (McCune *et al.*, 2002, p. 69). Following these transformations of predictor variables, all models in the 95% confidence set met all regression assumptions, with a VIF <1.6 and no outliers as defined by the Jackknife distance (α 0.05).

All statistical analyses were conducted using SAS and JMP Pro (JMP®, Version 11.0. SAS Institute Inc., Cary, NC, 1989–2007).

RESULTS

COLONY PERSISTENCE

The total number of active beaver colonies counted on Isle Royale between 1962 and 2012 ranged from a low of 73 in 1980 to a high of 329 in 2012. Lake perimeter independently explained 71% (R^2_{adj}) of the variation in colony persistence, comprised the only single-predictor model to fall within this confidence set, and had a 69% probability of being included in the best model ($\sum w_i$). The overall highest ranking model ($w_i = 0.47$), explaining ~79% of the variation in colony persistence, included percent cover of floating-leaved macrophytes and lake perimeter (R^2_{adj}, Table 2, Fig. 2). Two models in the 95% confidence set included percent cover of all trees, which showed a slight negative relationship with *colony persistence*. Variables related to macrophytes (specifically, total and percent cover of all

TABLE 2.—Predictors[a] of the highest-ranking general linear models of beaver persistence in 23 lakes of Isle Royale National Park, Lake Superior, U.S.A. from 1962–2012 (95% confidence set)[b]

Predictor variables[c,d]		R^2_{Adj}	AICc	Δ AICc	w_i
% cover fl. lf. mac. +	Lake perimeter +	0.79	120.7	0.0	0.47
Total cover fl. lf. mac. +	Lakeshore sinuosity +	0.77	122.7	2.1	0.17
Total cover fl. lf. mac. +	Lake perimeter +	0.77	123.6	2.9	0.11
% cover all mac. +	Lake perimeter +	0.75	124.8	4.1	0.06
% cover fl.lf. mac. +	Lake area +	0.75	125.3	4.6	0.05
% cover trees −	Lake perimeter +	0.74	126.4	5.7	0.03
	Lake perimeter +[e]	0.71	126.8	6.1	0.02
Total cover fl. lf. mac. +	Lake area +	0.73	127.0	6.3	0.02
Total cover all mac. +	% cover trees −	0.72	127.9	7.2	0.01
Total cover all mac. +	Lake perimeter +	0.71	128.1	7.5	0.01

[a] All predictor variables were log transformed

[b] Selection criteria = Akaike information criterion corrected for small sample bias (AICc)

[c] "+" indicates positive relationship, "–" indicates inverse relationship

[d] Abbreviations: "fl. lf. mac" = macrophyte species with floating leaves; "all mac" = all macrophyte species; "% cover" = mean percent cover of the noted macrophyte type in all quadrats for a given lake; "total cover" = $\frac{\sum_1^n Qx}{n} A_{lit}$, where Q_x represents the percent cover of macrophyte type x per quadrat, n is the number of quadrats for the entire lake, and A_{lit} is the area of the lake's littoral zone

[e] In an analysis of single predictor models, Plake had an Akaike weight of 0.85, indicating an 85% probability of being the best single predictor model to represent these data given the candidate set of models. The other single predictor model within the 95% confidence set: was MTall +, with R2 = 0.70, R2adj = 0.68

species, total and percent cover of floating leaved species) collectively occurred in 80% of the top-ranking models. Total or percent cover of water lilies did not appear in the confidence set. Total macrophyte cover was the second strongest single predictor of colony persistence (R^2_{adj} = 0.68) and the only other candidate in the 95% confidence set of single-predictor models (Table 2).

COLONY DENSITY

All models within the 95% confidence set for colony density included percent cover floating leaved macrophytes as a predictor, each explaining at least 70% of the variation in colony density (Table 3). The best model explained 77% (R^2_{adj}) of the variation in colony density with the variables percent cover of floating-leaved macrophytes and lakeshore sinuosity. Percent cover of floating-leaved macrophytes independently explained 73% of the variation in colony density (Fig. 4) and had an AICc score over 10 points higher than any other single predictor model, making it stand alone in the 95% confidence set of single-predictor models (Table 3). Lakeshore sinuosity comprised the second best single predictor model, explaining 47% (R^2_{adj}) of the variation in colony density. In analyses of factors affecting both colony persistence and *colony density*, sensitivity analyses for terrestrial vegetation predictors revealed no significant differences in model fit or parameter estimates resulting from the use of 30-m vs. 60-m buffers or from varying percent tree cover within the reported range of values.

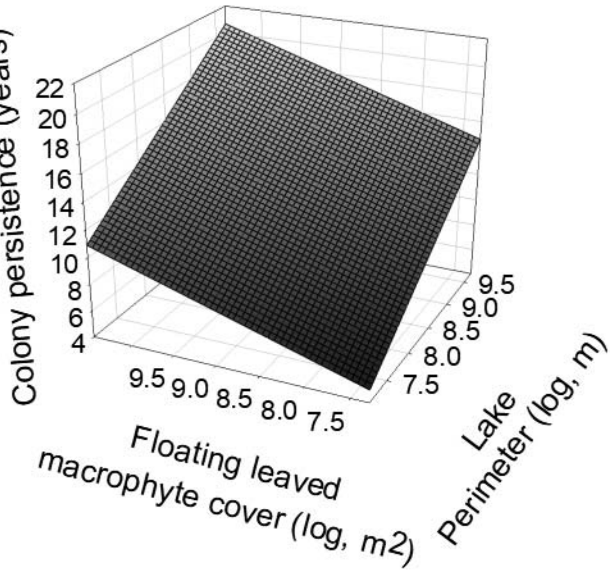

FIG. 2.—A rendition of the highest-ranking model of *colony persistence* for 23 lakes on Isle Royale National Park, Lake Superior, U.S.A. The specific model, explaining 79% (R^2_{adj}) of the variation, is: *Colony persistence* = 3.770 (log (*lake perimeter*)) + 1.887 (log (*floating-leaved macrophytes*)) − 35.676. *Colony persistence* indicates the number of years in which beavers occupied a lake out of 23 assessment years between 1962–2012. This figure was generated based on data from four lakes selected at random. Raw data are provided in Appendix A (Table A2)

TABLE 3.—Predictors[a] of the highest-ranking models of colony density[b] in 23 lakes of Isle Royale National Park, Lake Superior, U.S.A. from 1962–2012 (95% confidence set)[c]

Predictor variables[d]	R^2_{Adj}	AICc	ΔAICc	w_i
% cover fl. lf. mac. + lakeshore sinuosity +	0.77	34.8	0.0	0.52
% cover fl. lf. mac. + [e]	0.72	37.0	2.2	0.17
% cover fl. lf. mac. + % cover broad leaf deciduous −[f]	0.74	37.0	2.2	0.17
% cover fl. lf. mac. + % cover trees −	0.71	40.1	5.3	0.04

[a] All predictor variables were log transformed

[b] Colony density was calculated as the mean number of active beaver colonies/km^2 lake over 23 years of observation between 1962 and 2012, and was log transformed

[c] Selection criteria = *Akaike information criterion corrected for small sample bias* (AICc)

[d] "fl. lf. mac" = macrophyte species with floating leaves

[e] This was the only single predictor model within the 95% confidence set of single predictor models for *density* $_{aquatic}$, with an AIC score over 10 points higher than any other single predictor model

[f] One outlier prevented this original model from meeting the assumption of normally distributed residuals. Following the removal of this outlier, the model met all regression assumptions. Fit statistics were not significantly different between the versions with and without the outlier. The more conservative fit values (before outlier removal) are reported here

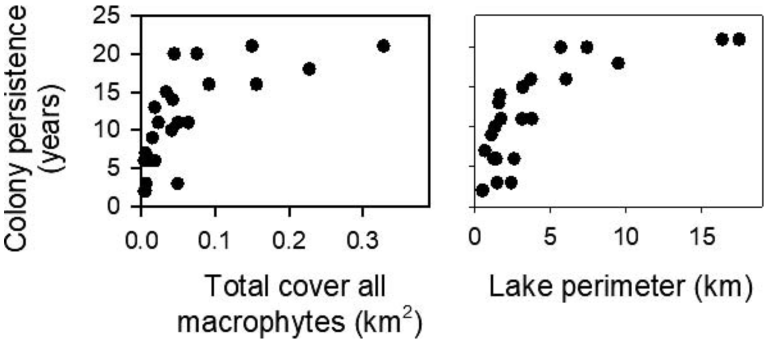

FIG. 3.—Direct relationship of beaver colony persistence with lake perimeter and total macrophyte cover for 23 lakes on Isle Royale National Park, Lake Superior, U.S.A. Data in these graphs were not transformed before plotting, in order to illustrate the direct relationship between variables. Colony persistence indicates the total number of years in which beaver inhabited a lake out of 23 observation years between 1962–2012. Total macrophyte cover is the area of 100% macrophyte cover, calculated as $= \frac{\sum_1^n Qx}{n} A_{lit}$, where Q_x represents the percent cover of macrophyte type x per quadrat, n is the number of quadrats for the entire lake, and A_{lit} is the area of the lake's littoral zone (*see* "Methods")

MACROPHYTE COMMUNITIES

Water lilies *(Nymphaea odorata, Nymphaea tetragona, Nuphar variegata)* comprised an average 9% (±2% SE) of the total macrophyte cover within a given lake (Appendix A, Fig. A2), and 25% (±5% SE) of all floating leaved species. Other floating leaved species included *Brasenia schreberi, Potamogeton amplifolius, P. epihydrus, P. gramineus, P. illinoensis,* and *Sagittaria latifolia.* Together, all floating-leaved macrophyte species represented an average 42% (± 5% SE) of a lake's total macrophyte cover. Between 2011 and 2012 surveys the estimated proportion of total macrophyte community represented by a given species varied by an average 4.5% (±0.5% SE).

No one macrophyte species was consistently common (>5% cover) in all lakes with the highest colony densities. However, four of eight total lakes with the highest beaver colony

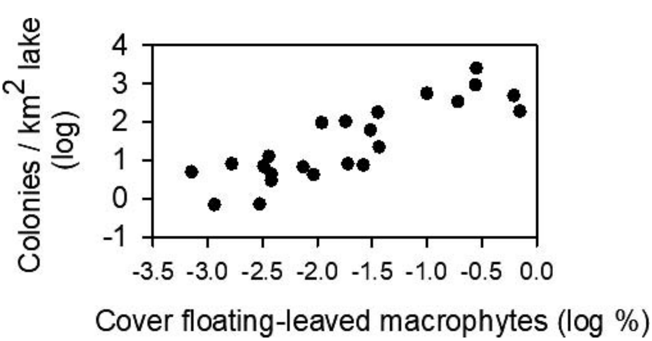

FIG. 4.—Percent cover of floating leaved macrophytes (log-transformed) explained 71% of the variation in colony density (log-transformed) for 23 lakes on Isle Royale National Park, Lake Superior, U.S.A. Colony density represents the mean number of colonies per km^2 lake observed over 23 survey years between 1962–2012

density between 2006 and 2012 ($\geq$20 colonies/km^2) had >50% cover *Brasenia schreberi* in 2012. One of these lakes had the highest number of colonies between 2006–2012 (three to four colonies each year) and showed minimal signs of tree cutting or shoreline activity based on a perimeter check in 2009 (Romanski and Peterson, 2012). Among small lakes in this study (<0.25m^2), all three with the longest colony persistence had >50% cover *B. schreberi* in 2012. Other common macrophyte species (>5% cover) in lakes with high beaver density included *Potamogeton amplifolius, Nymphaea odorata, Utricularia vulgaris,* or *Nuphar variegata* (Appendix A, Fig. A3).

COLONY PERSISTENCE IN LAKE VS. STREAM HABITATS

The co- efficient of variation for the number of beaver colonies on lake habitats across Isle Royale (530 km^2) between 1962 and 2012 was 0.25. For beaver colonies on stream or wetland habitats the coefficient of variation over the same period was 0.48. The total number of active colonies in lake sites was on average 46% ($\pm$4% SE) of the total active colonies in streams or wetlands.

DISCUSSION

With efforts ongoing to restore and support the health of beaver populations (*e.g.*, Albert and Trimble, 2000; Baker, 2003; Pollock *et al.*, 2004; Maringer and Slotta-Bachmayr, 2006; Burchsted *et al.*, 2010; Buckley *et al.*, 2011; Carpenedo, 2011; Baldwin, 2013), insights into conditions that promote long-term colony occupancy and density remain valuable. In particular little information is available regarding (1) factors affecting beaver habitat selection of lakes in comparison to the wealth of research on beaver habitat selection of streams and (2) the potential value of macrophytes other than water lilies to beaver habitat selection (Appendix A).

Our findings suggest that in a natural landscape with predators and minimal human interference, *C. canadensis* occupied lakes more persistently than streams and wetlands over time. The number of beaver colonies in streams or wetlands was ~twice as variable as and ~twice as numerous as the number of beaver colonies in lake habitats between 1962–2012 across Isle Royale.

Results indicate colony persistence has a significant relationship with lake perimeter (R^2_{adj} = 0.71) and total macrophyte cover (R^2_{adj} = 0.68, Fig. 3). Total macrophyte cover may be important because beaver are energy efficient swimmers (Allers and Culik, 1997) and can readily access aquatic food throughout the lake with minimal predation risk (Fryxell and Doucet, 1993). Lake perimeter increases with lakeshore sinuosity and with surface area and may therefore serve as a higher-order factor incorporating these features, which were both included in top-ranking models of colony persistence (Table 2). The bays and inlets created by sinuous shorelines provide beaver needed protection from wind and ice (Shelton, 1966; Allen *et al.*, 1983) and improve habitat conditions for macrophytes by reducing exposure to turbulence (Spence, 1967; Lacoul and Freedman, 2006). Lake area, which equates to the amount of available macrophyte habitat, is often the best predictor of macrophyte richness in lakes (Weiher and Boylen, 1994; Toivonen and Huttunen, 1995) and was also important in previous analysis of factors affecting beaver occupancy of lakes in a single year (Slough and Sadleir, 1977). The shape of the relationship between colony persistence and predictor variables suggests colony persistence may plateau when lake perimeter or total macrophyte cover increase above a given value (*e.g.*, >0.1 km^2 total macrophyte cover or >15 km lake perimeter, Fig. 3). The nonlinear relationships we found are consistent with the prediction of niche theory that species responses to environmental variables are generally curvilinear (Heglund, 2002).

Percent cover of floating-leaved macrophytes appeared in the confidence set for both colony persistence and colony density and was the strongest single predictor of colony density (Fig. 4). Of the floating-leaved species, *Brasenia schreberi* may be particularly important for beaver on Isle Royale given its predominance in lakes with particularly high colony densities.

Woody vegetation cover is also subject to potential inter-annual variation, but our sensitivity analyses revealed no differences in model fit when percent tree cover was varied within the reported range of values. Further, terrestrial data were collected near the median year of this study, which helps to reduce but not negate the sensitivity of results to long-term changes in woody vegetation cover.

MACROPHYTES AS WINTER BEAVER FORAGE

A central reason for perceived differences between various habitat studies is their focus on specific resources without discerning the underlying mechanisms that actually affect occupancy, survival, and fecundity (Morrison and Hall, 2002). Our findings and recent dietary analyses (Milligan and Humphries, 2010; Severud *et al.*, 2013) suggest a meaningful assessment of *C. canadensis* winter forage limitation should also understand and include the potential role of macrophytes.

White and yellow water lilies *(Nuphar* spp. and *Nymphaea* spp.*)* have been the primary focus of previous beaver habitat research involving macrophytes (Hartman, 1996; Fryxell, 2001). Total or percent cover of water lilies did not appear in our confidence set for colony persistence or colony density, suggesting that other macrophyte species may also play a substantive role in sustaining beaver in winter. The thick, enduring rhizomes of *Nymphaea spp.* and *Nuphar* spp. are key to their value as winter forage (Longley and Moyle, 1963; Jenkins, 1981). Most submerged macrophytes form clones connected by rhizomes (Wolfer *et al.*, 2006), and beaver rhizome consumption is not limited to *Nymphaea spp.* and *Nuphar spp.* For example, European beaver (*Castor fiber*) consumed the rhizome but avoided the leaf blade of *Menyanthes trifoliata* in a feeding experiment (Law *et al.*, 2014). Seasonally, macrophyte rhizomes often provide the greatest nutritional value in winter and spring when plants are storing nutrients in rhizomes in preparation for spring leaf growth (Harrison and Mann, 1975; Haraguchi, 2004).

The biomass and lifespan of rhizomes varies with species, age, and habitat, and is often proportional with above ground biomass (Westlake, 1966; Ozimek *et al.*, 1976). For *Elodea canadensis*, underground parts have been estimated at 2.6% of the total plant biomass, whereas underground parts were ~50% of the biomass of *Littorella uniflora* and *Potamogeton lucens* (Westlake, 1966; Ozimek *et al.*, 1976). The rhizomes of many emergent macrophyte taxa can persist for 2 to 3 y and can represent 30–90% of the plant's total biomass (Westlake, 1966). Rhizomes of *Brasenia schreberi*, which dominated lakes $0.25<km^2$ where beaver persisted longest (Appendix A, Fig. A1), only have a life expectancy of ~1.5 y (Kunii, 1991). However, *B. schreberi* rhizomes extensively branch and can cover most of the littoral zone surface where the species dominates, resulting in prolific biomass at any given point in time (Kunii, 1991).

Overall, the availability and quality of winter macrophyte forage is likely to vary greatly across the range of *C. canadnesis* and *C. fiber.* Future research should examine the appropriateness of using water lilies as the sole macrophyte variable in assessment of beaver habitat suitability (Allen *et al.*, 1983; Hartman, 1996; Fryxell, 2001). In particular future work could help to refine the evolving picture of macrophytes' importance to beaver habitat suitability by discerning the availability, quality, and species composition of macrophytes available to beaver in winter across a range of locations where beaver and macrophytes occur.

RESOURCE RENEWABILITY

A concern in assessing the suitability of a habitat patch for long-term occupancy is the rate at which essential resources are depleted and renewed. High renewal rates of some aquatic macrophyte species may help them to support high beaver colony densities over time. In the present study area, some macrophyte communities appear to sufficiently renew from herbivory to provide biomass toward sustaining beaver over many years in locations where terrestrial forage has been depleted. In terrestrial habitats beaver browsing can shift woody species composition toward nonpreferred or inedible taxa, particularly in the boreal region and other areas with limited soil nutrients (Barnes and Dibble, 1988; Johnston and Naiman, 1990; Rosell *et al.*, 2005). In freshwater environments comparatively little has been known regarding the long-term effects of native mammalian herbivores on macrophyte communities (Lodge *et al.*, 1998). One exception is a study of macrophyte community changes following beaver introduction. Over 10 y of *Castor fiber* occupancy in a nutrient-rich pond in Scotland, the macrophyte community demonstrated increases in total cover, species richness, and diversity, with increased cover of species that were either preferred but grazing-tolerant or unpalatable (Law *et al.*, 2014). Law et al. (2014) caution that long-term effects of herbivory on macrophyte biomass may not be directly inferred from studies of inter-annual effects. Exclosure studies over 1 to 2 y have suggested beaver can reduce biomass of some species over this timeframe (Bergman and Bump, 2015; Parker *et al.*, 2007; Law *et al.*, 2014), but this effect is variable with abiotic conditions and macrophyte community composition (Bergman and Bump, 2015).

Macrophytes that reproduce through vegetative propagation, such as *Nuphar* spp., *Nymphaea* spp., *Brasenia schreberi*, and *Myriophyllum spp.* probably have greater resistance to herbivory and other forms of harvesting (Barrat-Segretain and Amoros, 1996; Combroux *et al.*, 2001; Cherry and Gough, 2009). In the present study, three lakes had $>50\%$ cover *B. schreberi* after ≥ 13 y of beaver presence. Overall, factors likely to affect macrophyte renewability likely include the nutrient status of the water body, life strategies of the macrophyte species present, whether the herbivore is endemic or invasive, the relative benefit of available macrophyte species to the herbivore's nutritional and energetic needs, and the time period over which herbivore effects are assessed (Smirnov and Tretyakov, 1998, Law *et al.*, 2014, Law *et al.*, 2014, Bergman and Bump, 2015).

MANAGEMENT IMPLICATIONS

Findings of this study may be of practical interest for those involved with managing beaver habitat. Of relevance to those conducting landscape-scale habitat assessments, key variables that we found to affect long-term beaver occupancy and density in lakes (lake perimeter and floating-leaved macrophyte cover) could be estimated via remotely sensed data without extensive field surveys. Of relevance to beaver restoration efforts, beaver persistence on the landscape may be promoted by creating conditions for beaver to colonize lakes where possible, rather than being restricted to streams and wetlands. On Isle Royale the number of beaver colonies in lake habitats was about half as variable as the number in stream or wetland habitats between 1962–2012. Lakes that host macrophyte species with long-lived or prolific edible rhizomes may be of particular value to beaver. Some macrophyte taxa appear to be more resilient to beaver herbivory than many woody species and in sufficient quantities could help to sustain beaver. Our findings suggest these taxa are probably not limited to water lilies and include the species *Brasenia schreberi*. However, it is unclear whether the same macrophyte taxa are equally resilient to sustained high population densities of other mammalian herbivores whose feeding habits differ from those of beaver, such as moose. Over time, creating the conditions for beaver colonization of lakes could realize multiple ecological benefits at the landscape scale.

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APPENDIX A

TABLE A1.—Published studies on habitat factors that affect beaver occupancy or density[a]

Yrs[b]	Aquatic habitat	Mac[c]	Habitat (explanatory) variables studied. Those included in the best model or with the highest explanatory power are indicated in bold.	Source
Occupancy				
1	Stream	No	Stream width, stream depth, stream gradient, bank slope, bare soil (%), elevation, riparian zone width, litter cover (%), abundance of: Aspen, Alder, Cottonwood, Willow, Lodgepole pine, Jeffrey pine, Fire, Dogwood, Grasses/ forbs	1
1	Stream	No	Slope of river bank, percent understory cover 2 m high at 10 m from water, percent understory cover 2 m high at 15 m from water, percent understory cover 1 m high at 10 m & 15 m from water, percent canopy cover, river depth, river width	2
1	Stream	No	Vegetation classes: Tamarix, Pluchea, Prosopis-Acacia, Baccharis-Salix, shrub, sparse, nonvegetation, wetland	3
2	Stream	No	Percent canopy cover of: all tree species 10–15 m tall, Salicaceae spp. trees 10–15 m tall, Salicaceae spp. shrubs 5–12 m tall, sandbank presence/absence; percent canopy cover of: all tree species 5–10 m tall, Salicaceae spp. 5–10 m tall, all shrub species 5–12 m tall, herbs; bank slope, riprap presence/absence	4
1	Stream	Yes	Stream tortuosity, understory vegetation of grasses and forbs, water depth, stream width, occurrence of rapids, angle of bank slope, bank soil type, percent deciduous species in riparian zone (5 m), percent deciduous in forest stands, understory vegetation of bushes, saplings, presence/ absence of water lilies[d]	5
1	Stream	No	Bank slope, stream gradient, percent hardwood cover, stream width, stream depth, floodplain width, bank type, distance to nearest road, building or bridge, drainage area, percent shrub cover, percent cover all trees, grazing pressure	6
2	Stream	No	Stream width, stream gradient, valley floor width, grass/ sedge cover, percent cover red alder, percent cover shrub, stream depth, bank slope, percent cover of: tree canopy, overstory tree, mid-story tree, bare ground, forbs, ferns, Douglas-fir, salmonberry, elderberry, vine maple, stinking current, California hazel, thimble berry, huckleberry	7
1	Stream	No	River width, bank slope, percent deciduous, <20% shrub and/or hardwood cover, water depth 1 m from bank, bank substrate, river flow speed, water depth 2 m from bank	8

TABLE A1.—Continued

Yrs[b]	Aquatic habitat	Mac[c]	Habitat (explanatory) variables studied. Those included in the best model or with the highest explanatory power are indicated in bold.	Source
1	Stream	No	Percentage of roadside area devoid of woody vegetation, stream width, stream gradient, stream depth, stream substrate suitability as material to construct dams, distance from the culvert to the nearest food tree source, presence or absence of topographic constriction along streams	9
1	Stream	No	Upstream watershed area, stream gradient, stream cross-sectional area, woody stem diameter classes 1.5–4.4 cm, density of woody plants, shoreline slope, woody stem diameter classes <1.5 and >4.5 cm	10
1	Stream	No	Riverine willow scrub, willow-poplar forests, ash-alder alluvial forests, hardwood forests, spruce plantations, meadows, ruderal vegetation, fields, river gravel banks, reed and tall sedge beds, oak-hornbeam forests, urbanized areas	11
Density				
6[e]	All [f]	No	Shallow marsh, seasonally flooded meadow. Percent cover of vegetation, hydrology classification according to Cowardin *et al.* (1979)	12
1	Stream	No	Percent riparian trees <15 cm dbh, width of the riparian zone, river gradient, road density, average water fluctuation, percent canopy closure, percent shrub cover, shrub height, woody species composition within 200 m of the stream; bank texture and slope, tree species composition and dbh, number of important food plants, proximity of crop fields, presence of permanent water[g]	13
11	Lake	Yes	Biomass/m^2 of 10 preferred deciduous woody species, biomass/m^2 of white water lilies *(Nymphaea odorata)*	14
1 /38[h]	Lake and stream	No	Multiple variables related to climate, nature and extent of waterways, shorelines, vegetation cover, soil composition, slope, beaver harvest intensity, and predator abundance	15
1	Stream	No	Habitat type: aspen forest, farmland, urban, grassland; extent of human management of beaver	16
1	Stream	No	Stream width, depth, and gradient; average annual water fluctuations; percent tree canopy closure; percent of trees in 2.5–15.2 cm dbh, percent shrub crown cover; average height of shrub cover; species composition of trees and shrubs	17
1	Lake and stream[i]	No	Streams: combined miles of nonproductive brush and swamp shoreline, length of stream section of equal gradient and width, gradient, flow rate, width; miles of shoreline covered by at least 10% gross volume of *Populus tremuloides* Lakes: miles of shoreline covered by at least 10% gross volume of *P. tremuloides*, combined miles of nonproductive brush and swamp shoreline, area, perimeter, water level stability, ratio of lake area: perimeter, miles of shoreline covered by at least 10% gross volume of *P. balsamifera*	18

TABLE A1.—Continued

Yrs[b]	Aquatic habitat	Mac[c]	Habitat (explanatory) variables studied. Those included in the best model or with the highest explanatory power are indicated in bold.	Source
Colony site longevity				
28	Stream	No	Percent hardwood vegetation within 100 m and 200 m, watershed size, stream width, stream gradient, soil drainage capacity, percent softwood vegetation within 100 m and 200 m of the site center, percent hardwood/softwood mixed vegetation within 100 m and 200 m of the site center, percent shrub/wetland vegetation within 100 m and 200 m of the site center, percent cover abandoned fields within 100 m and 200 m of the site center	19

Sources: (1) Beier and Barrett (1987); (2) Dieter and McCabe (1989); (3) Breck *et al.* (2012); (4) Fustec *et al.* (2003); (5) Hartman (1996); (6) McComb *et al.* (1990); (7) Suzuki and McComb (1998); (8) Pinto *et al.* (2009); (9) Curtis and Jensen (2004); (10) Barnes and Mallik (1997); (11) František and Kostkan (2009); (12) Broschart *et al.* (1989); (13) Cox and Nelson (2009); (14) Fryxell (2001); (15) Jarema *et al.* (2009); (16) Loates and Hvenegaard (2008); (17) Robel *et al.* (1993); (18) Slough and Sadleir (1977); (19) Howard and Larson (1985)

[a] Studies were identified through search of *ProQuest* and *Wildlife and Ecology Studies Worldwide* databases using the keywords "beaver" and "castor" in association with search terms "habitat," "density," "occupancy," "abundance" in titles, keywords, or abstracts; and through review of bibliographies from related studies. This is a representative, rather than exhaustive, list of related studies

[b] Yrs = number of years of beaver observation incorporated in analysis

[c] Mac = "Were macrophytes included in the analysis?" (Y = yes, N = no)

[d] The species of "water lilies" studied were not specified

[e] Six years over a 46-y timespan

[f] The data of this study are based on landscape-scale analysis of all potential habitats using aerial photography

[g] This study considered both beaver density and occupancy. The variables listed represent results of factors affecting density

[h] Surveys took place over a 38-y period, but data were collapsed temporally in analysis by using, for any given geographic area, only data from the year of the most extensive beaver survey, or an average of data from multiple extensive survey years

[i] The response variable in this study was presence or absence of a beaver dam

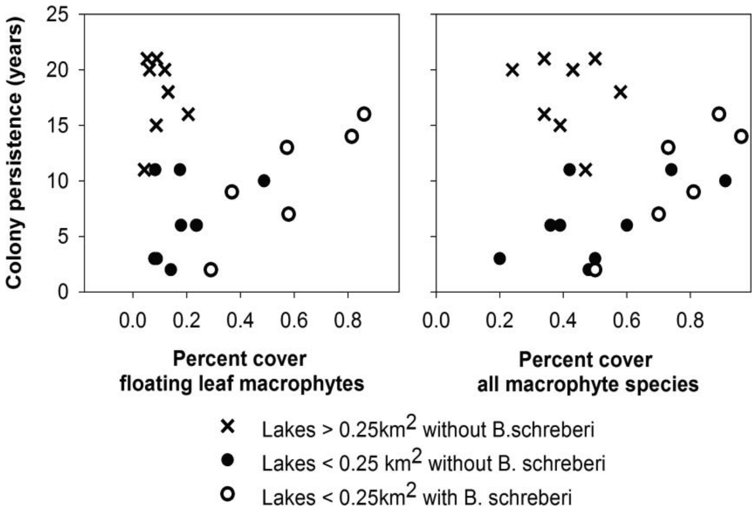

FIG. A1.—Direct relationship between colony persistence and percent cover macrophytes for 23 lakes of Isle Royale National Park, Lake Superior, U.S.A. Persistence was defined as the years of beaver occupancy, out of 23 total assessment years between 1962–2012. *Brasenia schreberi* is a species of floating-leaf macrophyte that tends to dominate macrophyte communities where it occurs. In the far right panel, a beaver is swimming amidst *B. schreberi.* Data in these graphs were not transformed before plotting, in order to illustrate the direct relationship between variables

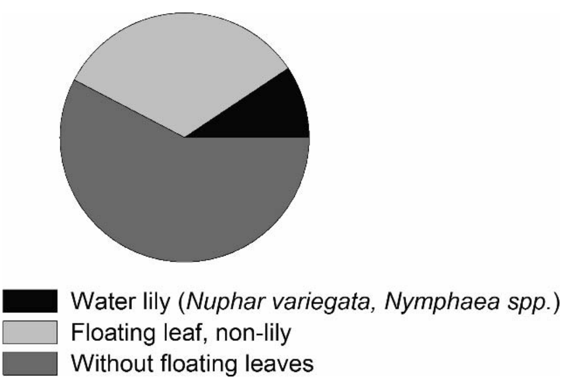

FIG. A2.—The mean proportion of cover represented by macrophyte groups included in regression analyses. Specifically, analyses considered: all macrophyte species, floating-leaved species only (including water lily, *Nuphar variegata* and *Nymphaea spp.*), and water lily species only. All floating-leaf macrophyte species represented 42% (±5% SE) of a lake's total macrophyte cover, whereas water lily species represented 9% (±2% SE) of the macrophyte cover.

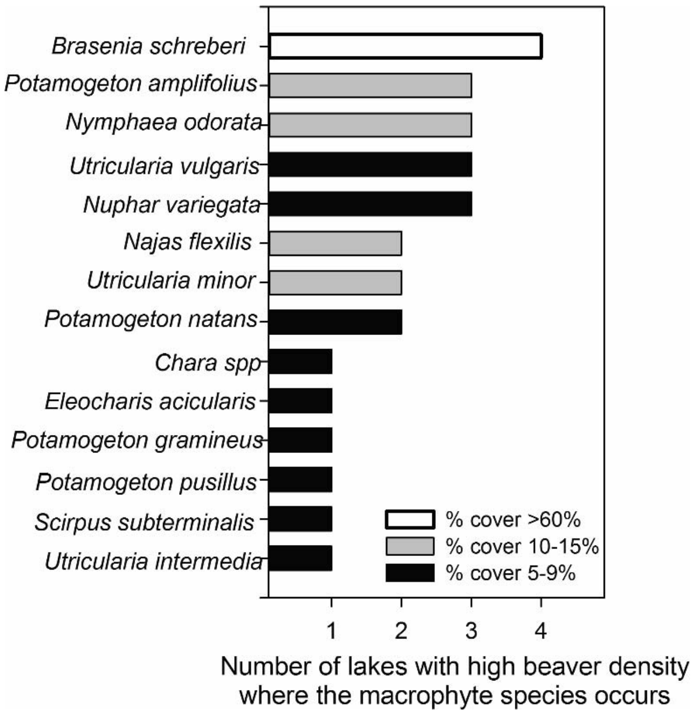

FIG. A3.—Macrophyte species with ≥5% cover in lakes supporting high beaver colony density (≥10 average colonies / km^2 lake between 2006–2012, $n = 9$), by number of lakes in which the taxa occurred.

TABLE A2.—Raw data for parameters in best fitting model of colony persistence

Lake	Colony persistence (y)	Lake perimeter (m)	% cover macrophytes (2012)
Ahmik	1	2163.60	25.9
Angleworm	20	7398.41	6.2
Beaver	11	3108.09	8.3
Benson	15	3156.34	8.7
Chickenbone	18	9478.50	13.1
Forbes	3	1461.20	8.9
Harvey	16	6028.61	20.6
Hidden	2	484.43	14.1
Le Sage	20	5684.09	11.9
Livermore	11	3765.92	4.3
McDonald	3	2406.65	8.0
Moose Creek Pond	14	1669.40	81.4
Moose Lake	9	1092.88	36.8
Newt	6	1235.63	23.5
Ojibway	16	3696.32	86.0
Patterson	6	2590.96	17.9
Richie	21	16364.45	5.3
Sargent East	21	17479.04	8.9
Standing Dead Birch	7	665.64	57.9
Sumner	11	1717.03	17.5
Wagejo	6	1417.05	23.8
Wallace	10	1318.35	48.8
Wolf Trail Pond	13	1572.52	57.3
Zen	2	534.39	19.1