

Seasonal shifts in habitat selection of a large herbivore and the influence of human activity

Philip D. McLoughlin^{a,*}, Eric Vander Wal^a, Stacey J. Lowe^{b,1}, Brent R. Patterson^{b,c},
Dennis L. Murray^b

^aDepartment of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada

^bTrent University, 2140 East Bank Drive, Peterborough, ON K9J 7B8, Canada

^cOntario Ministry of Natural Resources, Wildlife Research and Development Section, 2140 East Bank Drive, Peterborough, ON K9J 7B8, Canada

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Abstract

Failure to recognize factors contributing to variation in habitat models like resource selection functions (RSFs) can affect their application for projecting probabilities of occurrence, and thereby limit their relevance for conservation and management. We compared seasonal RSFs (2006–2008) for 16 adult female moose (*Alces alces*) with home ranges located in western Algonquin Provincial Park (APP), Ontario, Canada, to those of 14 adult females located in provincial Wildlife Management Unit (WMU) 49, 40 km west of the protected area. Wildlife and habitat management practices differed between regions: hunting was higher in WMU 49 compared to APP, and APP preserved large tracts of old growth forest rarely found in WMU 49. Seasonal RSFs projected expected similarities in moose resource use between regions (e.g., responses to wetlands and stands of eastern hemlock, *Tsuga canadensis* [in winter]); however, we also observed differences consistent with the hypothesis that animals, through effects of hunting, would shift habitat use seasonally and in response to roads. We further observed evidence of functional responses in habitat selection due to underlying differences in forestry practices (e.g., responses to stands of old-growth hemlock forest). Given the close proximity and shared biogeographic region between study areas, we believe that observed spatial dynamics in RSFs were ultimately reflective of divergent management strategies between areas and ensuing differences in predation and hunting mortality risk, and functional habitat.

Zusammenfassung

Fehler bei der Erkennung von Faktoren, die einen Beitrag zu Habitatmodellen wie Ressourcen-Wahl-Funktionen (RSFs) liefern, können die Anwendbarkeit der Modelle zur Vorhersage von Aufenthaltswahrscheinlichkeiten beeinflussen und dadurch die Relevanz für den Schutz und das Management verringern. Wir verglichen saisonale RSFs (2006–2008) bei 16 adulten weiblichen Elchen (*Alces alces*) deren Streifgebiete im westlichen Algonquin Provinzpark (APP), Ontario, Kanada, lagen, mit denen von 14 adulten Weibchen aus einem provinziellen Wildmanagement Gebiet (WMU) 49, 40 km westlich des geschützten Gebietes. Die Praxis des Wild- und Habitatmanagements unterschied sich zwischen den Gebieten: die Bejagung war im WMU 49 im Vergleich zum APP stärker und der APP schützte große Gebiete von Altwaldbeständen, die selten im WMU 49 gefunden werden. Die saisonalen RSFs sagten die erwarteten Ähnlichkeiten in der Ressourcennutzung der Elche zwischen den Regionen voraus (z. B. Reaktionen auf Feuchtgebiet und Bestände von östlicher Hemlocktanne, *Tsuga canadensis*, im Winter). Wir beobachteten

*Corresponding author. Tel.: +1 306 966 4451; fax: +1 306 966 4461.

E-mail address: philip.mcloughlin@usask.ca (P.D. McLoughlin).

¹ Present address. US Fish and Wildlife Service, Togiak National Wildlife

Refuge, Dillingham, AK 99576, USA.

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aber auch Unterschiede, die mit der Hypothese übereinstimmen, dass durch den Jagdeffekt Tiere die Habitatnutzung saisonal und als Reaktion auf Straßen verlagern. Wir beobachteten darüber hinaus Hinweise auf funktionale Reaktionen in der Habitatselektion aufgrund von zugrundeliegenden Unterschieden in der forstlichen Praxis (z. B. Reaktionen auf alte Bestände von Hemlocktannenwald). Unter Berücksichtigung der großen Nähe und der gemeinsamen biogeografischen Region der beiden Untersuchungsgebiete, glauben wir, dass die beobachtete räumliche Dynamik in den RSFs direkt die unterschiedlichen Managementstrategien zwischen den Gebieten widerspiegelt und Unterschiede in der Prädation, im Mortalitätsrisiko durch Jagd und im funktionellen Habitat zur Folge hat.

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Introduction

Observing dynamics in models of resource selection – obtaining substantially different functions at different times and/or places for the same species – informs us that the underlying ecological processes of resource selection can vary. We might expect models of resource selection, like the resource selection function (RSF; Manly, McDonald, Thomas, McDonald, & Erickson 2002), to differ across space and time in response to variation in inter- and intra-specific competition, predation risk, exposure to disease, anthropogenic impacts, and resource availability (McLoughlin, Morris, Fortin, Vander Wal, & Contasti 2010). When a RSF is not robust, its application for conservation and management (e.g., extrapolating distribution; Boyce & McDonald 1999) may be limited, unless factors contributing to model variation are recognized and accommodated.

Understanding responses in a RSF for a species to different biotic and abiotic modifiers of habitat is best approached through before-and-after experiments (e.g., Mao et al. 2005). Practically, however, comparing regions with contrasting regimes of wildlife and habitat management is more feasible over shorter time periods. Differences may highlight important variables underlying dynamics in a RSF.

Moose (*Alces alces*) occur across much of the forested regions of Ontario, Canada. In southeast Ontario, moose are protected from sport hunting within a large reserve, Algonquin Provincial Park. The 7653 km² park is managed principally for preservation and recreation, with some allowances for aboriginal subsistence harvesting and forestry (mainly selective and shelterwood timber harvesting). Compared to adjacent areas, park status has resulted in substantial differences in habitat (Maxie et al. 2010), likely due to contrasting logging and fire histories rather than broad climatic differences. For example, Algonquin Provincial Park contains some 40% of all forests over 140 years old found in the entire Ontario portion of the Great Lakes-St. Lawrence Forest Region, while the reserve itself occupies only 4% of the area (OMNR 2002; Henry & Quinby 2006). The park also represents the largest area in the world where the eastern wolf (*Canis lycaon*), a predator of moose, is protected. Regions outside the park are managed for multiple purposes, including more intensive logging operations and hunting.

Here we develop seasonal RSF models for adult female moose with home ranges located inside the western boundary of Algonquin Provincial Park (APP), and compare them with a sample of adult females located 40 km west of the park's boundary in Wildlife Management Unit 49 (WMU 49). For simplicity, we restrict our comparisons to a single scale of habitat selection ('within-home' range habitat selection). Given differences in regimes of wildlife and habitat management (below and Table 1; also see Maxie et al. 2010), we predict that for each season across the study area resource selection patterns for moose, as measured by rank ordering of relative probabilities of use for resources and strength of selection, will vary. We hypothesize that because moose receive greater protection from human hunting inside versus outside the park, animals will be less likely to avoid access features like roads within Algonquin Provincial Park. We further expected to see functional responses to changes in habitat availability (Mysterud & Ims 1998), e.g., as a result of differences in forest harvesting practices. We discuss why different RSF models (at the same scale) must be fitted to moose inside and outside APP to accurately predict occurrence of the species.

Material and methods

Study area

Our study area (Fig. 1) was located in southeast Ontario, Canada, divided as: (1) western Algonquin Provincial Park, hereafter referred to as APP (45° 38' N, 78° 39' W), and (2)

Table 1. Summary of differences in habitat (exact proportions of available vegetation associations) within composite home range boundaries of moose (Fig. 1) between western Algonquin Provincial Park (APP) and WMU 49 west of APP, central Ontario, Canada.

Habitat proportion	APP	WMU 49
Wetland	0.089	0.143
Mixedwood	0.141	0.243
Hemlock	0.069	0.006
Conifer	0.142	0.184
Deciduous	0.558	0.424

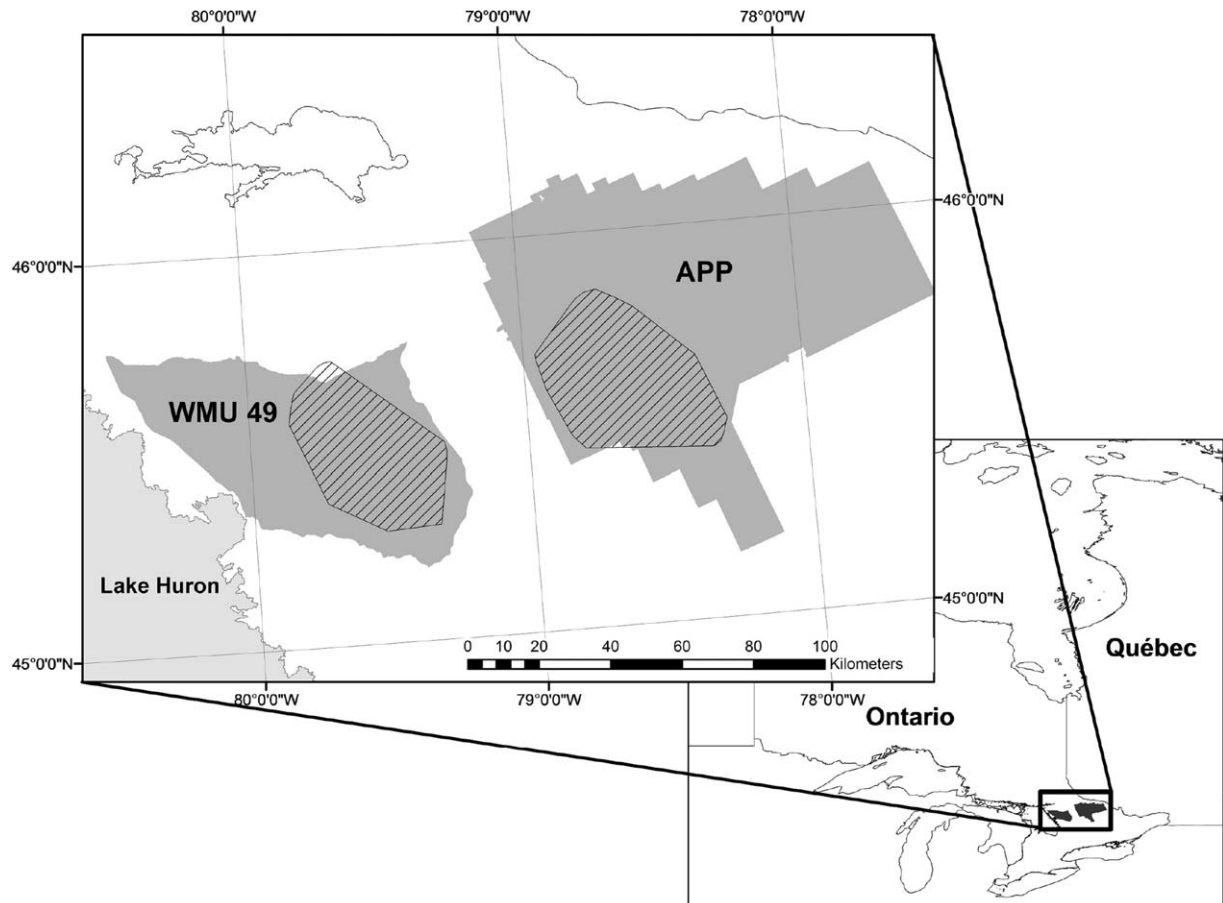


Fig. 1. Study areas within Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49 in southern Ontario, Canada, 2006–2008. Hatched convex polygons indicate the maximum extent of moose movements recorded during study; grey polygons denote boundaries of APP and WMU 49.

provincial Wildlife Management Unit (WMU) 49 (45° 30' N, 79° 32' W). Climate in the region is temperate continental, with warm summers and cool winters. The majority of precipitation falls as snow in winter. Both APP and WMU 49 span a transition zone between the Great Lakes–St. Lawrence Forest Region (Rowe 1972) and the boreal forest at the southern margin of the Canadian Shield. The study sites differed in elevation, with APP (320–580 m) being generally higher than WMU 49 (73–549 m). Both areas are a mosaic of eastern hardwood and coniferous forests interspersed by wetlands, although WMU 49 has more developed/agricultural land and greater forest fragmentation (see Table 1 and Lowe 2009 for a description of dominant plant species in the region), and Fig. 2 for information on road densities. It is possible that moose densities differed between the study areas; however, empirical data on differences in moose densities was equivocal. Bisset, McLaren, Edmonds and Sawyer (2000) surveyed both APP and WMU 49 for moose in the late 1990s and observed densities of 0.38 animals/km² in APP compared to 0.24 animals/km² in WMU 49. The latest available estimates of moose densities were 0.43 moose/km² in APP in 2009 and 0.29 moose/km² in WMU 49 in 2005, although a 2006 survey for moose in APP suggested only 0.30 moose/km² in the

park (Ontario Ministry of Natural Resources, unpublished data).

Animals

In January–February 2006, 2007, and 2008 we used a net gun operated from a helicopter (Bighorn Helicopters Inc., Cranbrook, British Columbia, Canada) to capture moose in APP and WMU 49 for the purpose of deploying and/or recovering Global Positioning System (GPS) tracking collars (Lotek 3300 GPS collars, Lotek Wireless Inc., Newmarket, Ontario, Canada). Our sampling effort targeted only adult females (ages 2+, aged from tooth cementum as 3.8 ± 2.0 years [$\bar{x} \pm 1$ SD]). Our analysis is restricted to a sample of 16 and 14 females in APP and WMU 49, respectively, that received collar deployments in 2006. We equipped moose with GPS collars programmed to record location every 2 h.

Spatial analyses

Locations of moose from GPS collars were imported into a Geographical Information System (ArcGIS 9.3; ESRI,

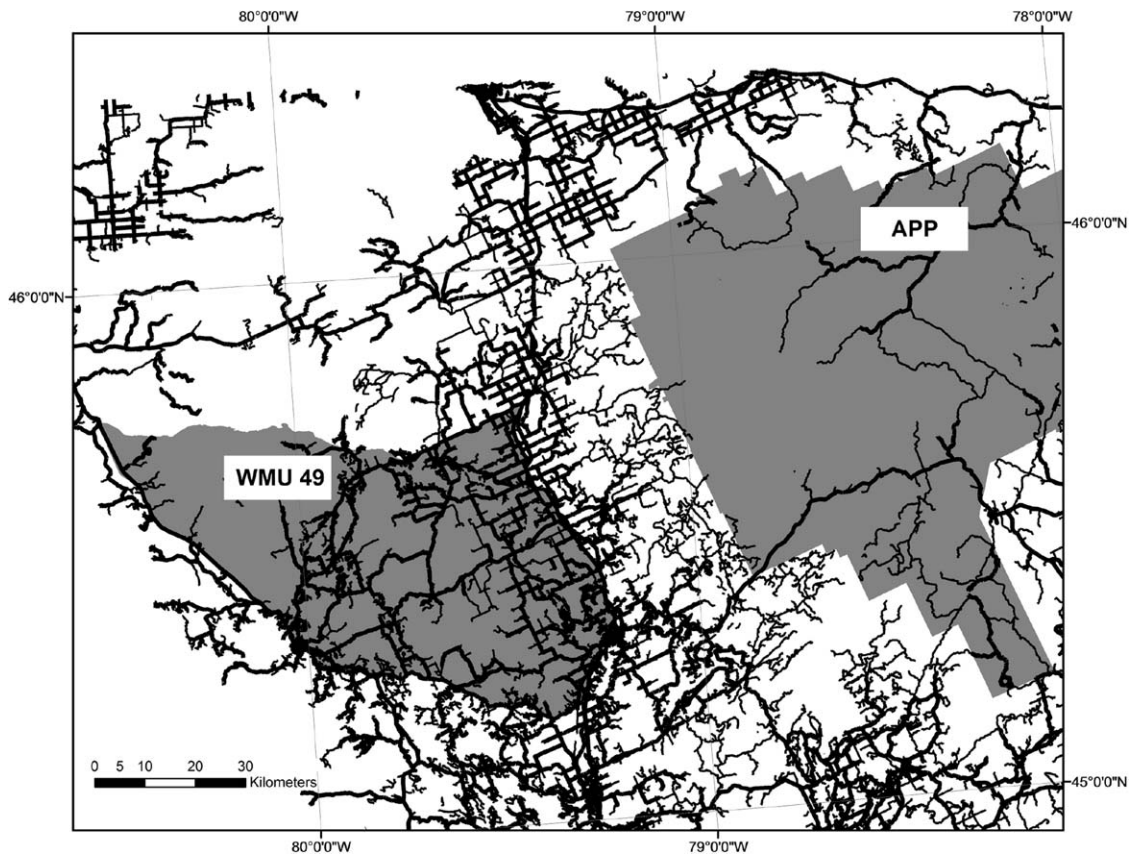


Fig. 2. Differences in densities of primary and secondary road features in Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49, southern Ontario, Canada, 2006–2008. Primary and secondary roads are differentiated by decreasing line thickness, respectively.

Redlands, California, USA). We delineated multiannual home ranges as 95% fixed kernel ranges using the Home Range Tools for ArcGIS of Rodgers, Carr, Smith, and Kie (2005). After delineating home ranges, we determined quantities of available habitat (vegetation associations) to moose within individual home ranges, and vegetation associations in which each GPS location was observed to occur.

Following the Ontario Forest Resource Inventory (FRI) classification system of the Ontario Ministry of Natural Resources, we used ArcGIS to rasterize 5 main vegetation associations (habitat variables, grain 30 m^2) to which we believed moose would likely respond: (1) deciduous stands including those originating from a recent perturbation ('deciduous'); (2) older growth coniferous stands with eastern hemlock, *Tsuga canadensis* ('hemlock'); (3) coniferous stands without hemlock ('conifer'); (4) mixed deciduous and coniferous stands ('mixedwood'); and (5) wetlands supporting emergent vegetation, including marshes, beaver ponds, bogs, and fens ('wetlands'). For analyses of resource selection, we excluded open water, developed areas, and non-regenerated or non-forested areas; however, we identified in the GIS access roads (primary, secondary, and tertiary roads, in relative order of size and frequency of use) as a potential modifying covariate of other habitat variables (incorporated in the analysis as a continuous variable, 'distance from roads').

Statistics

We stratified our analysis by study area (APP vs. WMU 49) and season based on biological events relevant to adult females (83% of our sampled moose were pregnant): parturition and lactation (summer: 16 May–31 July), rut (autumn: 1 August–30 November), early winter pregnancy (winter: 1 December–28 February), and late winter pregnancy (spring: 1 March–15 May). We estimated RSFs following mixed-effects logistic regression for samples of used and available map pixels of habitat within the home range of each moose (design III data [Manly et al. 2002]; third-order selection [Johnson 1980]), with random intercepts for each individual to account for differences in sample size (Gillies et al. 2006). Models with random intercepts were fitted using the library lme4 (Bates 2007) implemented in R Version 2.10.0 (R Development Core Team 2009). The binary response variable in the model was used vs. available points (pixels). Used pixels corresponded to locations for the GPS-collared individuals (stratified by season). Available pixels were random pixels sampled within individual home ranges, which corresponded to the total number of points used to define an individual's home range (approximately $4 \times$ the number of used pixels per season). Prior to analysis we standardized the continuous variable 'distance from roads' to mean 1.0 (by dividing each observation in meters for points of use

and availability by their mean combination of 869 m). Models included fixed effects of habitat variables and distance from roads, as well as their interactions. We acknowledge that habitat \times road interactions may be influenced by type of road (e.g., Elfström, Swenson, & Ball 2008); however, to minimize the number of terms in our RSF models and allow for model convergence we did not stratify models based on type of road included for an interaction term.

We selected final models of candidate sets based on lowest Akaike's Information Criterion (AIC; Burnham & Anderson 2002). For the selected model of each study area, we estimated relative probability of use (P_{use}) and tabulated how this value interacted with distance from roads by holding all predictors constant except for the habitat variable of interest (scored 1, all others scored 0) and varying distance from roads. Note that due to differences in availability of habitat resources between APP and WMU 49, actual differences in predicted effect sizes of P_{use} between areas was not used for comparisons; rather, we focused on relative differences in rankings of coefficients and P_{use} between times and areas.

Results

We tracked 16 adult female moose with home ranges in APP, obtaining a mean number of locations of 8267 ± 1606 per animal ($\bar{x} \pm 1$ SD) and 2067 ± 236 points per animal in each season. Fourteen adult females were tracked in WMU 49, with 8331 ± 1668 locations obtained per moose and 2083 ± 219 points per animal in each season. Home range size using the 95% fixed kernel method averaged 40.5 ± 5.1 km² for females in APP ($\bar{x} \pm 1$ SE); in WMU 49 home range size was 27.4 ± 3.5 km². Differences in available proportions of vegetation associations within composite home range boundaries of study animals in APP and WMU 49 are presented in Table 1.

For all RSF models considered, including moose identification number as a random effect in the logistic regression model was a clear improvement of model fit (Δ AIC was >359 units from any fixed-effects only model considered). The same argument held for including interactive effects of habitat \times distance to road effects (of all mixed-effects RSF models considered, minimum Δ AIC from additive-effects only and models with interactions was 39). Coefficients and significance of final mixed-model RSF models, stratified by season, are presented for APP and WMU 49 (Table 2). For comparison, we also present results for the pooled-study area model (Appendix A: Table 1).

Considering the general response of moose to habitat variables (e.g., P_{use} at standardized road distance 1.0), moose in APP and WMU 49 shared a number of responses (Tables 3 and 4). For example, in summer and autumn, relative P_{use} for hemlock forest was lowest of all vegetation associations in both areas, and wetlands were more important in summer and autumn than in other months (in both

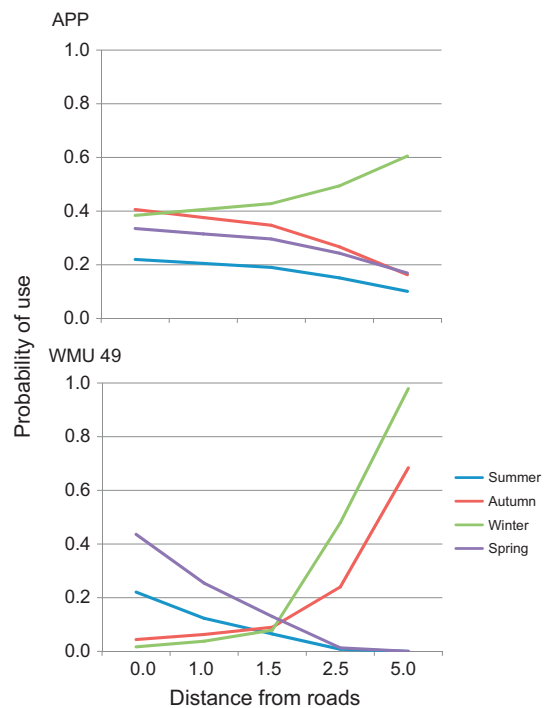


Fig. 3. Probability of use of available hemlock forest as a function of standardized distance from roads and season (see text) for moose in Algonquin Provincial Park (APP) and Wildlife Management Unit (WMU) 49 in southern Ontario, Canada, 2006–2008.

areas in winter and spring P_{use} for wetlands ranked lowest). The avoidance of hemlock was seasonal, however: in winter, hemlock stands located far from roads were characterized by our highest observed values of P_{use} in both APP and WMU 49 (Fig. 3). Moose in both areas also showed higher rankings for deciduous and mixedwood forests. Despite these similarities in RSF models, we also observed several differences. For example, moose in APP consistently ranked mixedwood forest as their highest preferred vegetation association in all seasons at the mean distance to roads; however, mixedwood forest was usually a mid-ranked habitat in WMU 49. Relative rankings of P_{use} were highly influenced by the modifying covariate 'distance from roads', except in only a few cases (e.g., spring use of mixed-wood forest in APP [Tables 2 and 3]).

Resource selection patterns of moose in APP contrasted with those of WMU 49 in almost all seasons with respect to how moose were responding to roads (Tables 3 and 4). In general, moose avoided habitat closer to roads more in WMU 49 than in APP. In summer, highest relative P_{use} for moose in APP was for mixedwood forest closer to roads; however, in WMU 49 mixedwood forest was highly ranked only when located far from roads. The sharpest contrast in resource selection patterns between moose of each area was during autumn, where there was strong evidence that P_{use} of moose was enhanced by increasing distance from roads in all vegetation associations in WMU 49; yet in APP moose were generally not responding or responded positively to

Table 2. Summary of mixed-effects logistic regression models for predicting seasonal habitat selection for 16 adult female moose in western Algonquin Provincial Park and 14 adult female moose in WMU 49 (west of Algonquin Provincial Park), central Ontario, Canada, 2006–2008.

Algonquin Provincial Park					WMU 49				
Variable	Beta	SE	z-value	P	Variable	Beta	SE	z-value	P
Summer									
Intercept	−1.527	0.531	−2.9	0.004	Intercept	−2.349	0.084	−28.1	<0.0001
Wetland	0.525	0.059	9.0	<0.0001	Wetland	0.601	0.050	12.1	<0.0001
Mixedwood	0.966	0.055	17.7	<0.0001	Mixedwood	0.187	0.048	3.9	0.0001
Hemlock	0.263	0.062	4.2	<0.0001	Hemlock	1.090	0.265	4.1	<0.0001
Conifer	0.243	0.055	4.4	<0.0001	Conifer	0.927	0.046	20.4	<0.0001
Deciduous	0.546	0.048	11.4	<0.0001	Deciduous	0.101	0.045	2.3	0.023
Distance from roads	−0.195	0.044	−4.4	<0.0001	Distance from roads	0.462	0.021	22.3	<0.0001
Wetland × Roads	0.093	0.053	1.8	0.076	Wetland × Roads	−0.161	0.025	−6.3	<0.0001
Mixedwood × Roads	−0.143	0.048	−3.0	0.003	Mixedwood × Roads	−0.071	0.025	−2.8	<0.0001
Hemlock × Roads	0.011	0.071	0.2	0.88	Hemlock × Roads	−1.876	0.319	−5.9	<0.0001
Conifer × Roads	0.326	0.049	6.6	<0.0001	Conifer × Roads	−0.306	0.026	−12.0	<0.0001
Deciduous × Roads	0.203	0.045	4.5	<0.0001	Deciduous × Roads	−0.025	0.031	−0.8	0.422
Autumn									
Intercept	−2.070	0.540	−3.8	0.0001	Intercept	−2.622	0.094	−27.8	<0.0001
Wetland	1.535	0.065	23.7	<0.0001	Wetland	0.696	0.052	13.4	<0.0001
Mixedwood	1.847	0.062	29.7	<0.0001	Mixedwood	0.790	0.047	16.9	<0.0001
Hemlock	1.691	0.065	26.0	<0.0001	Hemlock	−0.458	0.320	−1.4	0.153
Conifer	1.498	0.062	24.1	<0.0001	Conifer	1.505	0.045	33.4	<0.0001
Deciduous	1.528	0.059	26.1	<0.0001	Deciduous	0.924	0.044	21.1	<0.0001
Distance from roads	−0.159	0.055	−2.9	0.004	Distance from roads	0.647	0.02	31.8	<0.0001
Wetland × Roads	0.076	0.059	1.3	0.202	Wetland × Roads	−0.243	0.025	−9.6	<0.0001
Mixedwood × Roads	0.176	0.056	3.1	0.002	Mixedwood × Roads	−0.107	0.023	−4.6	<0.0001
Hemlock × Roads	−0.093	0.068	−1.4	0.177	Hemlock × Roads	0.123	0.271	0.5	0.649
Conifer × Roads	0.149	0.058	2.6	0.01	Conifer × Roads	−0.327	0.023	−14.0	<0.0001
Deciduous × Roads	0.15.0	0.055	2.7	0.007	Deciduous × Roads	−0.121	0.027	−4.5	<0.0001
Winter									
Intercept	−2.345	0.558	−4.2	<0.0001	Intercept	−2.406	0.088	−27.3	<0.0001
Wetland	0.911	0.076	12.0	<0.0001	Wetland	−0.684	0.080	−8.5	<0.0001
Mixedwood	1.998	0.069	29.1	<0.0001	Mixedwood	0.990	0.050	19.9	<0.0001
Hemlock	1.874	0.07	26.7	<0.0001	Hemlock	−1.624	0.403	−4.0	<0.0001
Conifer	1.679	0.068	24.5	<0.0001	Conifer	0.396	0.055	7.2	<0.0001
Deciduous	1.318	0.065	20.1	<0.0001	Deciduous	1.463	0.047	31.2	<0.0001
Distance from roads	−0.136	0.062	−2.2	0.03	Distance from roads	−0.071	0.027	−2.7	0.008
Wetland × Roads	0.198	0.070	2.8	0.005	Wetland × Roads	0.067	0.042	1.6	0.109
Mixedwood × Roads	0.232	0.064	3.6	0.0003	Mixedwood × Roads	0.125	0.030	4.2	<0.0001
Hemlock × Roads	0.316	0.070	4.5	<0.0001	Hemlock × Roads	1.649	0.281	5.9	<0.0001
Conifer × Roads	0.252	0.065	3.9	0.0001	Conifer × Roads	0.165	0.031	5.3	<0.0001
Deciduous × Roads	0.309	0.063	4.9	<0.0001	Deciduous × Roads	0.244	0.032	7.6	<0.0001
Spring									
Intercept	−2.654	0.542	−4.9	<0.0001	Intercept	−2.089	0.062	−33.7	<0.0001
Wetland	0.746	0.086	8.7	<0.0001	Wetland	−0.551	0.066	−8.3	<0.0001
Mixedwood	1.852	0.077	24.2	<0.0001	Mixedwood	0.532	0.048	11.2	<0.0001
Hemlock	1.968	0.079	25.0	<0.0001	Hemlock	1.832	0.198	9.2	<0.0001
Conifer	1.594	0.076	21.0	<0.0001	Conifer	0.191	0.050	3.8	0.0002
Deciduous	1.738	0.072	24.0	<0.0001	Deciduous	1.028	0.043	23.7	<0.0001

Table 2 (Continued)

Algonquin Provincial Park					WMU 49				
Variable	Beta	SE	z-value	P	Variable	Beta	SE	z-value	P
Distance from roads	0.044	0.061	0.7	0.471	Distance from roads	−0.081	0.025	−3.3	0.001
Wetland × Roads	0.212	0.069	3.1	0.002	Wetland × Roads	0.139	0.035	4.0	<0.0001
Mixedwood × Roads	0.056	0.063	0.9	0.374	Mixedwood × Roads	−0.065	0.029	−2.2	0.026
Hemlock × Roads	−0.225	0.075	−3.0	0.003	Hemlock × Roads	−1.56	0.242	−6.5	<0.0001
Conifer × Roads	0.186	0.064	2.9	0.004	Conifer × Roads	0.304	0.029	10.4	<0.0001
Deciduous × Roads	−0.178	0.062	−2.9	0.004	Deciduous × Roads	0.031	0.031	1.0	0.321

decreasing proximity to roads (e.g., hemlock forest; Fig. 3). In winter, P_{use} of all vegetation types for both APP and WMU 49 (save wetlands in WMU 49) was enhanced by an increase in distance away from roads. Effects of roads on P_{use} were also similar between study areas in spring. We did not observe any appreciable differences in ability to detect habitat selection inside versus outside APP.

Differing responses to habitat interactions with roads between APP and WMU 49 would have been missed if we had

considered only the study-area pooled analysis (Appendix A: Table 2), e.g., contrasting responses inside and outside of APP in autumn (Tables 3 and 4, and Appendix A: Table 2). In the pooled model, probability of use of habitat improved as distance to roads increased in all vegetation associations from summer through winter, save hemlock (summer and autumn) and wetlands in winter. In spring, the pooled model matched the similar responses of moose observed in both study areas.

Table 3. Comparison of effect size for habitat variables and interactions with distance to roads included in mixed-effects logistic regression models defining resource selection functions for moose in western Algonquin Provincial Park, central Ontario, Canada, 2006–2008. Effects are interpreted from predicting proportional probability of occurrence based on RSF models presented in Table 2 holding all x -variables constant except for the habitat variable of interest (scored 1, all others scored 0) and ‘distance from roads’ (standardized to mean of 1.0). ‘Trend’ summarizes the either positive (+) or negative (−) impact on P_{use} of a habitat variable as distance to a roadway increases from a point of use. Non-significant trends i.e., interactions, Table 2 at $P > 0.05$ are presented in parentheses.

APP	P_{use} at standardized road distance ^a					Trend
	0.0	0.5	1.0	2.5	5.0	
Summer						
Wetland	0.269	0.259	0.249	0.222	0.181	(−)
Mixedwood	0.363	0.325	0.289	0.197	0.095	−
Hemlock	0.220	0.205	0.190	0.151	0.101	(−)
Conifer	0.217	0.228	0.240	0.278	0.348	+
Deciduous	0.273	0.273	0.274	0.276	0.280	+
Autumn						
Wetland	0.369	0.360	0.350	0.323	0.279	(−)
Mixedwood	0.444	0.446	0.449	0.455	0.465	+
Hemlock	0.406	0.376	0.347	0.267	0.163	(−)
Conifer	0.361	0.359	0.358	0.355	0.349	−
Deciduous	0.368	0.367	0.366	0.363	0.358	−
Winter						
Wetland	0.192	0.197	0.202	0.218	0.245	+
Mixedwood	0.414	0.426	0.438	0.473	0.533	+
Hemlock	0.384	0.406	0.428	0.494	0.605	+
Conifer	0.339	0.352	0.366	0.407	0.478	+
Deciduous	0.264	0.281	0.299	0.356	0.460	+
Spring						
Wetland	0.129	0.144	0.161	0.219	0.348	+
Mixedwood	0.309	0.320	0.331	0.365	0.425	(+)
Hemlock	0.335	0.315	0.296	0.243	0.169	−
Conifer	0.257	0.280	0.304	0.381	0.523	+
Deciduous	0.286	0.272	0.259	0.223	0.170	−

^aStandardized road distance scores (both study areas pooled) of 0.0 through 5.0 correspond to distances in meters of 0.0, 434.3, 868.6, 2171.4, and 4342.9, respectively.

Table 4. Comparison of effect size for habitat variables and interactions with distance to roads included in mixed-effects logistic regression models defining resource selection functions for moose in WMU 49, central Ontario, Canada, 2006–2008. Effects are interpreted from predicting proportional probability of occurrence based on RSF models presented in Table 2 holding all x -variables constant except for the habitat variable of interest (scored 1, all others scored 0) and ‘distance from roads’ (standardized to mean of 1.0). ‘Trend’ summarizes the either positive (+) or negative (–) impact on P_{use} of a habitat variable as distance to a roadway increases from a point of use. Non-significant trends i.e., interactions, Table 2 at $P > 0.05$ are presented in parentheses.

WMU 49	P_{use} at standardized road distance ^a					Trend
	0.0	0.5	1.0	2.5	5.0	
Summer						
Wetland	0.148	0.168	0.190	0.269	0.439	+
Mixedwood	0.103	0.123	0.145	0.234	0.448	+
Hemlock	0.221	0.123	0.065	0.008	0.000	–
Conifer	0.194	0.207	0.220	0.262	0.344	+
Deciduous	0.096	0.116	0.141	0.239	0.484	(+)
Autumn						
Wetland	0.127	0.151	0.179	0.286	0.523	+
Mixedwood	0.138	0.173	0.215	0.382	0.704	+
Hemlock	0.044	0.063	0.090	0.240	0.684	(+)
Conifer	0.247	0.277	0.311	0.421	0.618	+
Deciduous	0.155	0.192	0.236	0.405	0.717	+
Winter						
Wetland	0.044	0.043	0.043	0.043	0.043	(–)
Mixedwood	0.195	0.200	0.204	0.217	0.241	+
Hemlock	0.017	0.038	0.079	0.479	0.979	+
Conifer	0.118	0.123	0.128	0.145	0.177	+
Deciduous	0.280	0.298	0.316	0.375	0.480	+
Spring						
Wetland	0.067	0.068	0.070	0.076	0.087	+
Mixedwood	0.174	0.164	0.154	0.128	0.092	–
Hemlock	0.436	0.254	0.130	0.013	0.000	–
Conifer	0.130	0.143	0.158	0.207	0.314	+
Deciduous	0.257	0.252	0.248	0.234	0.212	(–)

^a Standardized road distance scores (both study areas pooled) of 0.0 through 5.0 correspond to distances in meters of 0.0, 434.3, 868.6, 2171.4, and 4342.9, respectively.

Discussion

Our results highlight substantial differences in resource selection patterns of a large herbivore. We observed our most striking differences in moose behaviour within vs. outside APP during autumn, which corresponded with timing of the regular hunting season for moose in WMU 49. Hunting pressure is much higher outside the park vs. within, where only limited moose harvesting by aboriginal subsistence hunters is allowed. Moose clearly avoided using vegetation associations (including both rare and common habitat types) close to roads in WMU 49, but this was not the case in APP. We suspect that moose outside the park were actively avoiding habitat closer to road features in autumn in response to hunting activity. Experimental protection from hunting through access management has been shown to immediately increase the occupancy of moose in an area (Crichton, Barker, & Schindler 2004). The results also suggest that there were strong trends of avoiding roads in WMU 49 through most of the year, not just in autumn (compared to APP where road avoidance was only very strong across vegetation associations in winter).

Different levels of predation risk might influence resource selection patterns (for ungulates see, e.g., Sinclair & Arcese 1995; Kittle, Fryxell, Desy, & Hamr 2008; Hebblewhite & Merrill 2009). For example, there is good evidence that if wolves are able to use linear features for travel, ungulates may avoid these features (e.g., woodland caribou [*Rangifer tarandus*]; James & Stuart-Smith 2000). Alternatively, ungulates may be attracted to anthropogenic features like roads to avoid predation if human presence creates refugia from predators, as observed for elk (*Cervus elaphus*) in mountain parks (Hebblewhite & Merrill 2009). Outside of winter, the latter may be more important in explaining observed differences between RSF patterns between regions of our study area, where attraction to habitat located near roads was more evident in APP than WMU 49. That said, avoidance of linear features during winter is strong in both APP and WMU 49; this may be a winter response to fast-moving predators on linear features (following the caribou-wolf model of Alberta [James & Stuart-Smith 2000]), or because avoidance of human activity may be beneficial in winter to minimize expenditure of energy.

Given lack of hunting protection to predators (wolves and black bears [*Ursus americanus*]) outside the park vs. within, it is likely that predator densities were higher in WMU 49 than in APP. McLoughlin et al. (2010) reviewed potential effects of predation on ungulate habitat selection. Evidence suggests moose can lower predation risk by selecting for increased levels of visual cover (Kunkel & Pletscher 2000; Dussault et al. 2005). If predation risk is lower in APP than WMU 49, our results support this contention: open habitat (wetlands) was significantly avoided in winter and spring outside the park, but was significantly selected during the same periods inside the park (Table 2). The extent to which predation risk influences moose resource use remains the subject of debate (e.g., Kittle et al. 2008) and is a topic deserving of further research; however, lack of precise information on predator densities in our study areas limits our discussion on this topic. Similarly, lack of data on differences in population density during our study period restricts our ability to comment on density-dependent habitat selection and its influence on our results (Fretwell & Lucas 1969; Rosenzweig 1991; McLoughlin, Boyce, Coulson, & Clutton-Brock 2006; McLoughlin et al. 2010).

Heterogeneity in habitat and thus resource availability can lead to functional responses in habitat selection (Mysterud & Ims 1998; Osko, Hiltz, Hudson, & Wasel 2004; Godvik et al. 2009), which may further account for differences in RSF models between APP and WMU 49. If animals require a particular resource, they may demonstrate a stronger preference for it when it is rare on the landscape; however, when it is common, use of that resource may not increase proportionately with availability. We suspect that a functional response is indicated for moose selection of stands of hemlock forest in our study area. Routledge and Roese (2004) noted that in the Great Lakes-St. Lawrence Forest Region near Sault Ste. Marie, Ontario, eastern hemlock had a low availability, yet it was the most intensively-browsed species (and ranked second among ten species of browse in contributing to moose diets). Within APP, moose have access to considerably more hemlock forest than outside the park (Table 1), in part because of different logging histories and ages of the forest between these areas (APP possesses older stands than does WMU 49). Relative P_{use} of hemlock in WMU 49 was almost zero close to roads during winter, but increased dramatically to become the most preferred resource (in the entire study) as distance from roads increased (Fig. 3 and Table 4). An increase in relative use of hemlock as animals were farther from roads was also evident for APP in winter, but the changes with distance were much less dramatic (Fig. 3 and Table 3). The difference may be because available hemlock forests in WMU 49 were not only rarer, but these remnant forests occurred comparatively far from roads: hemlock stands in WMU 49 were, on average, 4.4 times farther from the nearest road access than in APP.

Abiotic, weather-related modifiers of habitat quality may further account for lack of robustness in RSF models across space and time, and in northern temperate environments one

of the most important covariates of habitat selection for ungulates is snowfall (Månsson 2009; Kittle et al. 2008). The impact of snow on habitat selection of moose is likely to be complex, as avoidance of deep snow or predators could have significant energetic implications because habitat components providing the best shelter (e.g., coniferous stands) generally have reduced amounts of food (Dussault 2002; Dussault et al. 2005). In our study area, due to lake-effect snowfall, there may be marginally higher winter precipitation in WMU 49 (which is closer to Georgian Bay, Lake Superior) than APP: mean January total precipitation ranges from 121 to 160 mm in WMU 49, but ranges from 81 to 120 mm in APP (Natural Resources Canada, <http://atlas.nrcan.gc.ca>). That said, we did not detect substantial differences in rankings of shelter habitat like coniferous forest and old growth hemlock forest (Tables 3 and 4). These results are consistent with Lowe (2009), who, although showing a year-effect on adult female moose movements and home range size between high and low snow years in APP, did not detect any effect on habitat preferences.

Our results suggest different land-use practices and approaches to wildlife management may cause predicted responses of a species to habitat to vary substantially. This may occur even over relatively similar areas in terms of biota and climate. The implication is that applications of models like RSFs for conservation and management – especially extrapolating distribution (e.g., Boyce & McDonald 1999) – may be limited, unless factors contributing to model variation are recognized and accommodated.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.09.001.

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