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A.A.D. McLaren
Trent University

J. F. Benson
University of Nebraska - Lincoln, jbenson22@unl.edu

B.R. Patterson
Trent University

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ARTICLE

Multiscale habitat selection by cow moose (*Alces alces*) at calving sites in central Ontario

A.A.D. McLaren, J.F. Benson, and B.R. Patterson

Abstract: There is limited knowledge of moose (*Alces alces* (L., 1758)) calving site selection at the southern limit of their range. Varying results from previous research on calving habitat selection make it challenging to extrapolate to other populations. We used a combination of global positioning system (GPS) data from collared cow moose and GPS locations of expelled vaginal implant transmitters and neonatal calf captures to identify calving sites in two areas of central Ontario, Canada (Algonquin Provincial Park and Wildlife Management Unit 49 (WMU49)), that differed in terms of moose and timber harvest management. We investigated selection and avoidance of habitat types, roads, topography (slope and elevation), and forest stands of varying successional age during the calving season at three spatiotemporal scales — annual home range, seasonal range, calving site — using a combination of distance-based and classification-based variables. In both study areas, calving sites were on gentler slopes and closer to conifer stands than expected at the fine scale. Cows in WMU49 strongly selected rock–grass sites across all scales. This study also demonstrates the feasibility of using GPS collars to infer parturition and location of calving sites. We recommend ground-based microhabitat data be collected to better understand habitat selection of moose during calving.

Key words: moose, *Alces alces*, parturition, habitat selection, Euclidean distance analysis, ungulate, telemetry.

Résumé : Les connaissances sur la sélection des sites de mise bas par les orignaux (*Alces alces* (L., 1758)) à la limite méridionale de leur aire de répartition sont limitées. Les résultats variables de travaux antérieurs sur la sélection d'habitats de mise bas compliquent leur extrapolation à d'autres populations. Nous avons utilisé une combinaison de données de système de localisation GPS de femelles dotées de colliers et les emplacements GPS d'implants vaginaux émetteurs expulsés et de captures de veaux néonataux pour cerner des sites de mise bas dans deux régions du centre de l'Ontario (Canada), le parc provincial Algonquin et l'unité de gestion de la faune n° 49 (UGF49), qui diffèrent l'une de l'autre sur le plan de la gestion de la récolte des orignaux et du bois. Nous nous sommes penchés sur la sélection et l'évitement de types d'habitats, de routes, de la topographie (pente et élévation) et de peuplements forestiers à différents stades de succession durant la période de mise bas, à trois échelles spatiotemporelles, dont celles du domaine vital annuel, de l'aire de répartition saisonnière et du site de mise bas, en combinant la distance et des variables basées sur la classification. Dans les deux régions, les sites de mise bas se trouvaient sur des pentes plus faibles et plus proches de peuplements de conifères que ce qui était attendu à échelle fine. Les femelles dans l'UGF49 présentaient une forte préférence pour les sites caractérisés par des roches et de l'herbe à toutes les échelles. L'étude démontre aussi l'utilité des colliers GPS pour repérer la parturition et l'emplacement de sites de mise bas. Nous recommandons de recueillir des données de terrain sur les microhabitats pour une meilleure compréhension de la sélection d'habitats par les orignaux durant la période de mise bas. [Traduit par la Rédaction]

Mots-clés : orignal, *Alces alces*, parturition, sélection d'habitats, analyse de la distance euclidienne, ongulé, télémétrie.

Introduction

Following parturition, maternal ungulates and their young remain at birth sites from several days (Stringham 1974; Langley and Pletscher 1994; Barten et al. 2001; Poole et al. 2007) to 1 month (Bowyer et al. 1999). Neonate ungulates are vulnerable to predation during this period due to their limited strength and mobility. Thus, highest mortality on newborn ungulates typically occurs during the first few weeks from birth (Ballard et al. 1981; Wilton 1983; Kunkel and Mech 1994; Smith and Anderson 1996; Pinard et al. 2012; Patterson et al. 2013), making the selection of birth sites of critical importance for parturient females. For moose (*Alces alces* (L., 1758)), the limited mobility of calves after birth

(Leptich and Gilbert 1986; Cederlund et al. 1987; Testa et al. 2000; Poole et al. 2007; Wattles and DeStefano 2013) requires lactating females to balance nutritional requirements with minimizing predation risk to themselves and newborn calves (Lima and Dill 1990; Kie 1999) using resources available in the immediate surroundings of the birth site. Previous studies on calving site selection by moose have provided inconsistent results, with studies demonstrating both selection and avoidance of forage availability and concealment cover, in addition to other factors such as slope, elevation, and distance to water (Addison et al. 1990; Wilton and Garner 1991; Langley and Pletscher 1994; Chekchak et al. 1998; Bowyer et al. 1999; Scarpitti et al. 2007). Given these inconsistent results, a generalized understanding of habitat-selection patterns by moose during calving remains elusive.

A.A.D. McLaren* and B.R. Patterson. Ontario Ministry of Natural Resources and Forestry, Wildlife Research and Monitoring Section, Trent University, DNA Building, 2140 East Bank Drive, Peterborough, ON K9L 1Z8, Canada.
J.F. Benson.† Environmental and Life Sciences Graduate Program, Trent University, DNA Building, 2140 East Bank Drive, Peterborough, ON K9J 7B8, Canada.

Corresponding author: Ashley A.D. McLaren (email: ashley.mclaren@ontario.ca).
*Present address: Department of Environment and Natural Resources, Government of the Northwest Territories, P.O. Box 900, Fort Smith, NT X0E 0P0, Canada.
†Present address: University of Nebraska–Lincoln, School of Natural Resources, Lincoln, NE 68583, USA.

Fig. 1. Location of the two moose (*Alces alces*) study areas (hatched polygons) in Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49) in central Ontario, Canada.
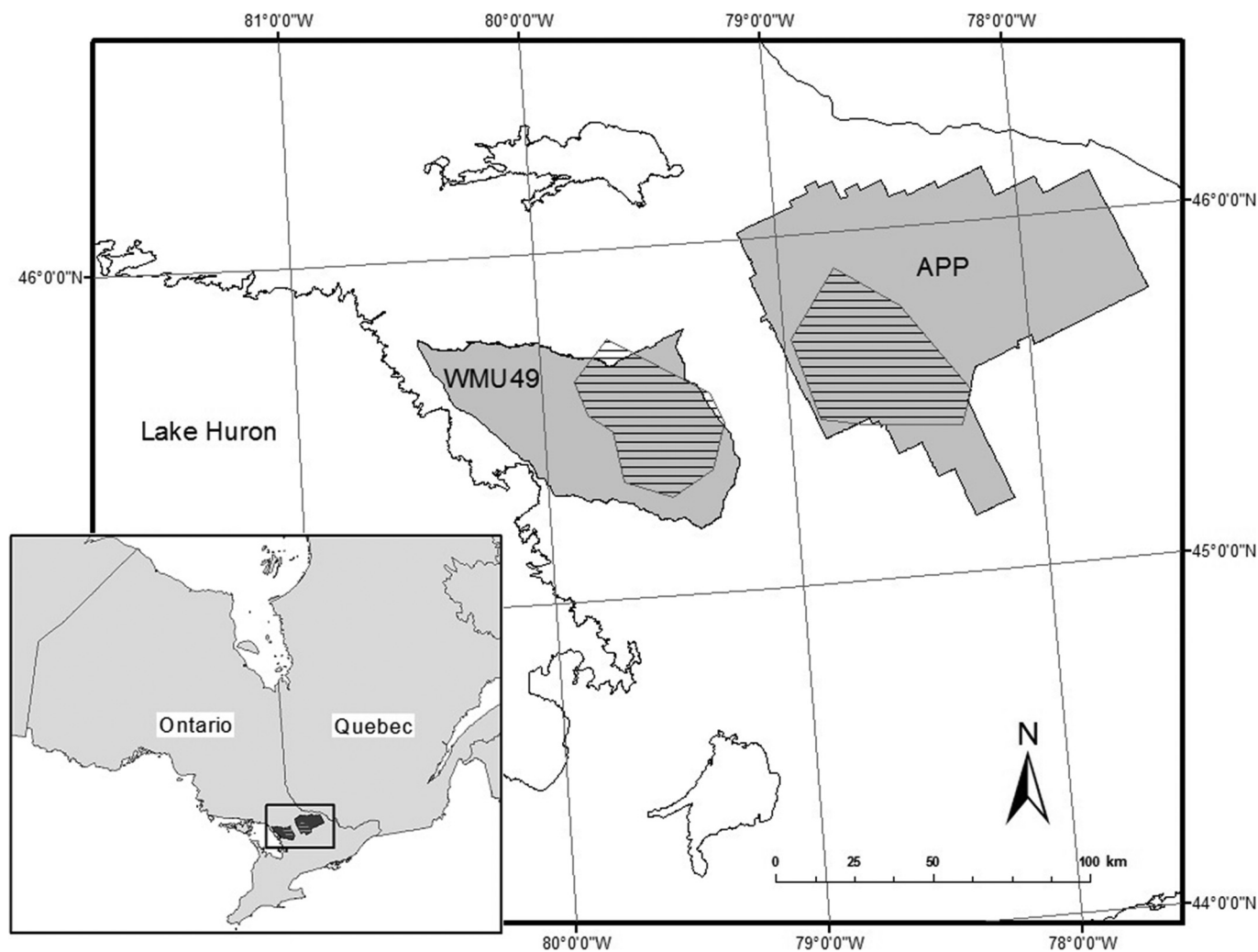
In Ontario, moose in the Great Lakes – St. Lawrence Forest exist at the southern edge of their distribution and are found in mixed conifer – deciduous forests that are frequently disturbed by land development and logging, yet limited data are available on moose calving habitat requirements in this region (see Addison et al. 1990; Wilton and Garner 1991). A better understanding of such requirements is important, as it can inform future forest management decisions with regards to providing and (or) maintaining adequate calving habitat.

Our objectives were to investigate whether specific habitat types and physical features of the landscape were selected or avoided by parturient cow moose during calving in two study areas in central Ontario subjected to different forest and wildlife management. We also sought to determine the spatiotemporal scale at which calving site selection occurs. Given that calving sites are likely to influence moose reproductive success, we hypothesized that cows would exhibit strong habitat selection in response to natural and anthropogenic landscape features. As noted above, variable results from previous work made strong directional predictions difficult. Instead, we objectively evaluated our overall hypothesis at multiple scales in a multivariate context.

Specifically, we investigated habitat selection at three scales by assessing whether calving sites were (*i*) closer to or farther away from specific habitat types relative to their availability, (*ii*) positively or negatively associated with physical landscape attributes and roads, and (*iii*) closer or farther away from forest patches of varying successional age than expected by chance.

Materials and methods

We used data collected from 35 global positioning system (GPS) collared (Lotek 3300 GPS collars; Lotek Wireless Inc., Newmarket, Ontario, Canada) cows in two study areas in central Ontario from 2006 to 2009 (for details see Lowe et al. 2010; Murray et al. 2012) to locate calving sites. The study areas included the western portion of Algonquin Provincial Park (APP; 1587.3 km²; *n* = 18 moose) and the eastern region of Wildlife Management Unit 49 (WMU49; 1280.4 km²; *n* = 17 moose) (Fig. 1). Through years of our study, moose densities were estimated at 29–43 moose/100 km² (B. Steinberg and E. Francis 2006[1]; B. Steinberg 2009[2]) in APP and 30–32 moose/100 km² (MNRF 2013) in WMU49. The two study areas were approximately 50 km apart; no collared moose moved between study areas. West-

ern APP contained protected lands with restricted or selective logging, whereas WMU49 contained both public and private lands and was subject to logging, including clearcutting. As a result of forestry practices, mature forest was common throughout APP (Quinn 2005) and was dominated by sugar maple (*Acer saccharum* Marsh.), poplar (species of the genus *Populus* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* (L.) Carrière), spruce (species of the genus *Picea* A. Dietr.), and fir (species of the genus *Abies* Mill.). Forest cover in WMU49 was comparable, but early successional forest was more common (Benson et al. 2017), with lower abundance of hemlock and more habitat fragmentation due to agricultural lands and development (Lowe et al. 2010). Densities of canids (species of the genus *Canis* L., 1758) in APP were 2.3–3.0 canids/100 km² (Patterson et al. 2004). Eastern wolves (*Canis lycaon* Schreber, 1775; in Ontario, also referred to as Algonquin wolves) and gray wolves (*Canis lupus* L., 1758) accounted for 80% of resident canids in APP, but were less common in WMU49, where 64% of resident canids were eastern coyotes (*Canis latrans* Say, 1823) and 29% were wolf–coyote hybrids (Benson et al. 2012). Black bear (*Ursus americanus* Pallas, 1780) densities were estimated at 37 bears/100 km² (95% CI 21–66) and 32 bears/100 km² (95% CI 15–57) for WMU49 and APP, respectively (MNRF, unpublished data). Hunting was prohibited in the western portion of APP, but was permitted in WMU49, including the harvest of moose (cow, bull, and calf licenses available).

We programmed collars to record a GPS location every 2 h for 2.5 years. In addition to GPS collaring, vaginal implant transmitters (VITs) were deployed in cows from 2007 to 2009 to assist in locating and radio-collaring a random sample of moose calves as part of a companion study (see Patterson et al. 2013). For calves found using VITs (n = 42), we used the locations of the expelled VITs to represent calving locations in our analysis. In other cases (n = 34), we used the location where calves were captured and radio-collared. We were confident that these locations accurately represented birth sites, because most ground searches for newborn calves were conducted within 36 h of VITs being expelled (median = 19 h, range = 9.5–58 h; Patterson et al. 2013) and we often observed calving beds (see Addison et al. 1990; Scarpitti et al. 2007) at or near the capture locations. Calving beds were conspicuous, with leaves and loose vegetation scrapped away and the remaining vegetation flattened. Additionally, these sites generally contained numerous shed moose guard hairs.

For cows without VITs or those that were not located for purposes of calf capture and collaring, we used GPS-collar data to infer reproductive status and calving location (n = 44) based on detection of a sedentary movement pattern between May and June (i.e., calving season). Other researchers have documented a reduction in activity by collared maternal cow moose during the calving season (e.g., Testa et al. 2000; Severud et al. 2015; Melin et al. 2016), owing to a cow's tendency to remain close to her newborn calf after birth. Accordingly, we calculated mean daily movements by cow moose and defined the putative calving period as consecutive days from 1 May to 15 June when total daily movement was <1 km (i.e., period of localization). This period ensured that we examined a broad interval around the mean date of calving for our study sites (APP: 13 May; WMU49: 14 May; pooled: 13 May; determined from dates that VITs were expelled or when calves were collared; Patterson et al. 2016) to detect parturition activity from location data. When we detected restricted movement indicative of calving, we calculated the mean centre of GPS locations of consecutive days with movement <1 km and assumed that this represented the calving site. We assessed the accuracy of this approach using cases (n = 12) where a collared cow had location data in the same year her VIT was expelled (if implanted) or her calf was located and collared. For each moose, we determined the accuracy of the predicted date of calving and location using the actual date of VIT expulsion or calf collaring and the distance from where the VIT or calf was found to the mean centre calcu-

Table 1. Habitat variables used in Euclidean distance analysis of calving site selection by moose (*Alces alces*) in Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49), Ontario, Canada, with percentage land cover for each habitat type calculated within actual study-area boundaries.

Habitat variable	Description	% Land cover	
		APP	WMU49
CON	Conifers	10.2	13.4
HWD	Hardwoods Tolerant hardwood Mid-tolerant hardwood Yellow birch, *Betula alleghaniensis* Northern red oak, *Quercus rubra* L.	65.0	41.7
MIX	Mixed woods Upland mixed wood Lowland mixed wood White birch, *Betula papyrifera* Marshall Poplar, *Populus* spp.	13.1	14.0
WAT	Water	19.7	7.7
WETL	Wetlands Brush and alder Open muskeg Treed muskeg	8.6	9.1
RCK–GRS	Rock Grass meadows	0.1	7.5

lated from the GPS-collar data, respectively. Because of extensive GPS-collar failure in 2009, we could not infer reproductive status from GPS-location data and, therefore, relied solely on VIT expulsion or capture locations of calves, when available, for cow moose during that year (n = 20).

Previous research on calving site selection in moose has evaluated preference for various habitat and physical variables such as cover type, distance to nearest water, distance to roads, as well as slope and elevation (Edwards 1983; Wilton and Garner 1991; Langley and Pletscher 1994; Lemke 1998; Bowyer et al. 1999; Poole et al. 2007). To test our predictions, we assessed similar variables in our analysis including six habitat types — conifers (CON), hardwoods (HWD), mixed woods (MIX), water (WAT), wetlands (WETL), and open rocky areas and grass meadows (RCK–GRS) (Table 1) — from the corrected forest resource inventory (FRI) geographic information system (GIS) layers (see Maxie et al. 2010). The FRI habitat maps of our study areas were digitized from aerial photos taken in 1989 at a scale of 1:20000 and then reclassified by Maxie et al. (2010) to improve agreement of the forest classifications with data collected during ground-based vegetation surveys to 77% in APP and 63% in WMU49. We did not include eastern hemlock in our analysis. Maxie et al. (2010) found that forest stands classified as hemlock in the FRI of our study areas corresponded with field observations only 50% of the time and were often mistaken for hardwood and (or) mixed forests, making it challenging to combine this habitat type with any of our other habitat types. Furthermore, we excluded areas identified as buffered roads and developed agriculture due to their redundancy and correlation with our road variables. For analyses with data from APP, we excluded RCK–GRS given its relatively sparse occurrence across all ranges of moose in that study area (0.1%).

In addition to habitat type, we included slope and elevation in our analysis using data from digital elevation maps of 10 m resolution (Provincial Digital Elevation Model version 2.0.0: MNRF 2006). We also tested for an effect of roads on calving site selection and included three categories of roads in our analysis (primary, secondary, tertiary: Table 2; MNRF road segment layer: MNRF 2012, unpublished data; additional tertiary roads for APP obtained

Table 2. Description and density (km roads/km²) of three road types used in Euclidean distance analysis of calving site selection by moose (*Alces alces*) in Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49), Ontario, Canada.

Road class	Description		Density (km roads/km²)	
	APP[a]	WMU49[b]	APP	WMU49
Primary	13.7 m wide	Freeway Highway Arterial Paved roads	0.05	0.09
Secondary	9.1 m wide	Local Collector Ramp	0.07	0.45
Tertiary	9.1 and 6.7 m wide	Alleyway or laneway Resource or recreation Service Winter	0.42	0.27

[a]Algonquin Provincial Park Management Plan (Ontario Parks 1998).
[b]Reclassified from Ministry of Natural Resources and Forestry road segment layer (MNRF 2012, unpublished data).

from Algonquin Provincial Park road layer: MNRF 2009, unpublished data). APP consisted of protected lands and, therefore, had fewer roads than the more developed WMU49 (Lowe et al. 2010).

Lastly, we tested for selection of areas that had been disturbed, either through forest harvest activities or natural occurrences. Logged forest patches or areas affected by natural forest disturbance, such as fire or extensive blow down, often have an abundance of understory re-growth in the early successional stages. These areas can provide quality forage and concealment cover from predators (Jackson et al. 1991; Dussault et al. 2005; Mao et al. 2005; Bowman et al. 2010; Mabille et al. 2012), making them potentially desirable calving locations because of high nutritional demands during lactation and restricted movement by maternal cows and their newborn calves after birth (Stringham 1974; Leptich and Gilbert 1986; Jackson et al. 1991; Bowyer et al. 1999). Logging occurred in both study areas, with operations in APP being restricted to selective harvest more so than logging operations in WMU49. Both areas were subjected to natural disturbances. Therefore, using forest harvest and disturbance data (FRI GIS layer, updated to 2008) for our two study areas, we created four categories representing different successional stages: <10 years, 10–25 years, 26–40 years, >40 years post disturbance. The percentages of forest cover in APP in these stages were 8.3%, 17.1%, 5.0%, and 69.6%, respectively, and in WMU49 in these stages were 14.5%, 17.3%, 11.0%, and 57.2%, respectively. We refer to our variables as habitat (six habitat types), physical (slope, elevation, three road types), and forest disturbance (four classes) variables in subsequent sections.

We investigated habitat selection by assessing calving site selection at three spatiotemporal scales. Specifically, we used GPS-location data to generate annual, seasonal, and calving ranges for each cow for each year using ArcGIS 9 (ArcMap version 9.3.1; ESRI, Inc. 2009). At the broadest scale, we estimated an annual home range as the 100% minimum convex polygon (MCP) surrounding all locations collected during a complete calendar year (4150 ± 67.2 locations) using Hawth's Analysis Tools for ArcGIS version 3.26 (Beyer 2006). A 100% MCP was also estimated for each moose using only the location data collected from 13 April to 13 June (715 ± 22.8 locations), defined as the seasonal range. This time period represented 1 month before and after the peak in calving activity across both study areas (13 May). The calving range represented the finest scale range for our calving site selection analysis. We generated calving ranges by buffering all calving sites in both study areas by 550 m, resulting in a common calving range size of 0.95 km². The

buffer distance represented an approximate daily total movement distance for cows during their period of localization (546.0 ± 20.8 m), allowing us to assess short-term decisions of selection based on habitat and physical features from the area immediately surrounding each calving site (Vore and Schmidt 2001; Brook 2010; Barbknecht et al. 2011; Kaze et al. 2016). Unlike the annual and seasonal ranges that required GPS-location data from the collared cows, we generated calving ranges for all calving sites identified during the study ($n = 120$) in the fine-scale analysis.

We investigated calving site selection using Euclidean distance analysis (EDA) (Conner and Plowman 2001; Conner et al. 2003) by comparing distance from calving site locations to each habitat type, disturbance class, and road type with distances from systematic points distributed across each cow's three ranges to these same features (Benson 2013). We generated six Euclidean distance rasters for WMU49, one for each habitat type, and five for APP in ArcGIS using a 25 m pixel size to match the resolution of the habitat map and approximate accuracy of GPS-collar locations. We also created four distance rasters of 25 m pixel size for each of the four disturbance classes and three distance rasters of 5 m pixel size for each of the three road types. We used a smaller pixel size for the road rasters to account for the minimum road width in our study areas. All the rasters calculated the distance from the centre of each pixel in each study area to the edge of the closest representative patch of habitat, disturbance class, or road type of interest (i.e., distance from systematic points). For every year with collar data for each parturient cow moose, we intersected the annual and seasonal ranges with the relevant study-area distance rasters for each habitat type, disturbance class, and road class to get the mean expected distances to these features for each range. This was repeated using the buffered calving ranges. Thus, we used distances calculated from every pixel (at the resolution of the GIS data) across each range ensuring that our mean expected distances were robust to sampling error (Benson 2013). Observed distances to each habitat type, disturbance class, and road type were calculated using calving locations determined from the GPS location of VIT expulsion or calf collaring or inferred from the collar data of parturient cows. We then calculated distance ratios of mean observed/mean expected for use in EDA to test for habitat selection within moose annual home ranges, similar to Johnson's (1980) third order of selection, as well as to test for habitat selection at our two finer scales. For each calving location, we used a classification-based approach to create ratios of mean observed/mean expected for slope and elevation by comparing the mean slope and elevation at the calving site to the overall means across annual, seasonal, and calving ranges. We used the term "selection" to indicate (*i*) that used locations (calving sites) were significantly closer to distance-based variables (habitat types, disturbed forest patches, roads) than were available locations, or (*ii*) that values of classification-based variables (elevation and slope) were significantly greater at used locations relative to available locations.

We analyzed ratios from each scale separately by study area using a multivariate analysis of variance (MANOVA) to test the hypothesis that the distance to various habitat and physical features did not differ from what would be expected by chance. We analyzed the forest disturbance variables in a separate MANOVA for each study area due to a lack of independence between disturbance and habitat classes. We could not test for an effect of forest disturbance in either study area at the calving-range scale or an effect of roads in APP at the calving-range scale due to a lack of representation of these variables at this fine scale. Additionally, because we used calving site as the experimental unit across years, our analyses included calving sites from multiple years for some cows ($n = 24$ cows). Although individual cows did not reuse calving sites across years during our study, the lack of independence between multiple calving sites of the same cows could potentially introduce pseudoreplication in our analysis. Therefore,

Fig. 2. Mean daily movement (km) from GPS-collared parturient ($n = 35$) and nonparturient ($n = 18$) cow moose (*Alces alces*) for annual cycles from 2006 to 2008 in central Ontario, Canada. Parturient cows showed a decline in movement during the calving period (1 May – 15 June; vertical dotted lines). Bars represent ±SE.
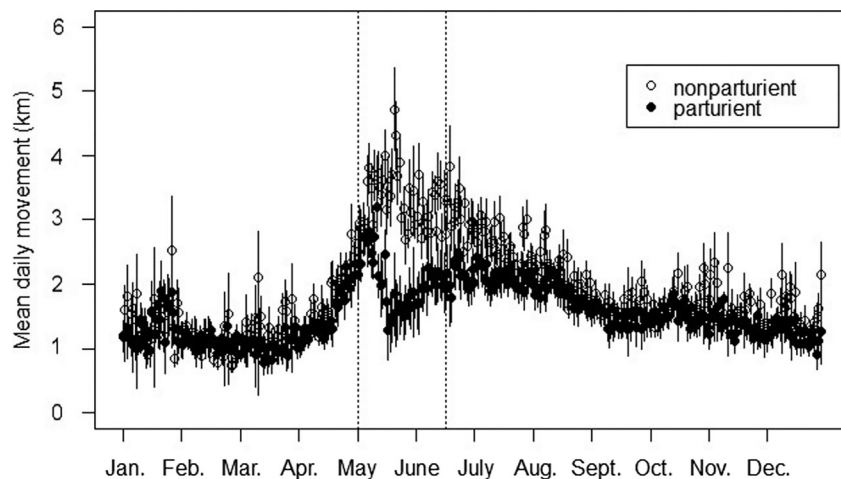
in cases where the calving sites of individual cows across successive years were closer than the overall mean distance between calving sites in consecutive years (~2 km), we averaged the distance ratios across years, reducing our maximum available sample size of calving sites from $n = 120$ to $n = 103$. We used all years of data for cows with calving sites >2 km apart, because we believed these sites were independent of one another. If any of the MANOVAs were significant, indicating the mean of the distance ratios differed from a vector of ones, we used univariate t tests on the observed/expected ratios for each variable to determine which were different from one (Conner and Plowman 2001). We performed all statistical analyses using R version 3.2.3. Data are presented as mean ± SE, unless otherwise stated. We considered all tests to be statistically significant when $p < 0.05$ and marginally statistically significant if $0.10 > p > 0.05$.

Results

Of the 56 parturition events documented for cows with location data during our study, 51 (91.2%) of these included an extensive 1 day movement (7.2 ± 0.5 km) by the cow on the day preceding her period of localization. The mean length of localized activity was 5.8 ± 0.4 days. Nonparturient cows did not show consecutive days of localization in movement anytime during May and June. The difference in daily movements between parturient and nonparturient moose was evident from May to mid-June (Fig. 2), corresponding to the calving period in our study areas.

Ten of the 12 moose having simultaneous GPS-location data and known reproductive status based on VIT expulsion or calf collaring would have been accurately classified as parturient based solely on detection of localized movement in their GPS data. Daily movement of these 10 cows during their identified localization periods was 550.5 ± 52.1 m and such restricted movements were sustained for 6.4 ± 1.1 days. The two exceptions involved cases where presence of a calf was later confirmed, but its mother showed no movements <1 km during the calving season, including the day the calf was radio-collared. Of the 10 cases of localization, 8 cases accurately predicted the exact timing of calving (i.e., the VIT was expelled or calf was collared during the dates of localization suggested from the cow's collar location data). There were two cases where calves were collared 2 days before the dates of calving predicted from the location data. The mean distance between the predicted calving sites of the 12 cows (based on the mean centre of localization calculated from location data) and the actual calving sites (based on the GPS location of the expelled VIT or calf collaring) was 247.9 ± 125.9 m.

Sizes of the annual home range and seasonal range calculated as 100% MCPs for moose in APP averaged 47.1 ± 4.3 and 20.2 ± 1.9 km², respectively. Sizes of the annual and seasonal ranges in WMU49 averaged 36.8 ± 2.5 and 18.8 ± 2.3 km², respectively. Calving sites in APP were located in conifer forests ($n = 11$), hardwood forests ($n = 18$), mixed forests ($n = 13$), water ($n = 11$), wetlands ($n = 1$), and unclassified habitat ($n = 6$). Calving sites in WMU49 were located in conifer forests ($n = 14$), hardwood forests ($n = 17$), mixed forests ($n = 7$), wetlands ($n = 6$), rock–grass meadows ($n = 10$), and unclassified habitat ($n = 1$). Four calving sites in APP and one calving site in WMU49 were in stands classified in the FRI as eastern hemlock, but due to the error associated with this habitat layer, we could not be confident of the forest-stand type in which these sites were located.

Overall tests for nonrandom habitat selection in APP were not significant across the annual and seasonal moose ranges for habitat and physical features (annual: Wilks' $\lambda = 0.62$, $F_{[10,13]} = 0.79$, $p = 0.641$, $n = 23$; seasonal: Wilks' $\lambda = 0.83$, $F_{[10,13]} = 0.27$, $p = 0.978$, $n = 23$), but were highly significant at the calving-range scale (Wilks' $\lambda = 0.69$, $F_{[7,51]} = 3.24$, $p = 0.006$, $n = 58$). Cows in APP marginally selected conifer forests and gentle slopes, while avoiding water (Table 3) within their calving ranges. The results also suggested statistically significant selection for high elevation calving sites, but the mean observed/expected ratio was very close to 1.0, indicating a small effect size that we did not consider to be biologically significant.

Cow moose in WMU49 exhibited non-random habitat use at all spatiotemporal scales (annual: Wilks' $\lambda = 0.22$, $F_{[11,10]} = 3.13$, $p = 0.041$, $n = 21$; seasonal: Wilks' $\lambda = 0.14$, $F_{[11,10]} = 5.70$, $p = 0.005$, $n = 21$; calving: Wilks' $\lambda = 0.45$, $F_{[11,34]} = 3.72$, $p = 0.002$, $n = 45$). Across annual, seasonal, and calving ranges, cows consistently selected open rocky areas and grass meadows for calving and avoided steep slopes (Table 4). Additionally, cows strongly selected conifer forests at the finest spatiotemporal scale. Cows showed no selection for or avoidance of the remaining habitat and physical features we considered.

We did not find a significant effect of forest disturbance on calving site selection by moose in APP (annual: Wilks' $\lambda = 0.95$, $F_{[4,19]} = 0.26$, $p = 0.902$, $n = 23$; seasonal: Wilks' $\lambda = 0.96$, $F_{[4,19]} = 0.19$, $p = 0.942$, $n = 23$) or WMU49 (annual: Wilks' $\lambda = 0.80$, $F_{[4,17]} = 1.09$, $p = 0.392$, $n = 21$; seasonal: Wilks' $\lambda = 0.86$, $F_{[4,17]} = 0.72$, $p = 0.592$, $n = 21$). These results indicate that overall use of forest patches of varying successional age did not differ significantly from what would be expected by random chance at the annual and seasonal home-range scales for both study areas.

Table 3. Results of univariate *t* tests for fine-scale habitat selection of adult cow moose (*Alces alces*) (*n* = 58) during calving in Algonquin Provincial Park, Ontario, Canada.

Variable	Observed value (mean ± SE)[a]	Ratio[b]	*t*	*p*	Conclusion
CON	556.9±68.6	0.85	−1.93	0.058[c]	Select
HWD	321.6±50.5	2.18	0.82	0.417	NS
MIX	793.7±109.9	0.95	−0.45	0.654	NS
WAT	161.5±35.3	2.08	2.75	**0.008**	Avoid
WETL	662.6±62.8	1.27	0.90	0.373	NS
Slope	4.5±0.5	1.36	1.97	0.054[c]	Select
Elevation	426.64±3.7	1.01	2.04	**0.046**	Select[d]

Note: CON, conifer; HWD, hardwoods; MIX, mixed woods; WAT, water; WETL, wetlands; NS, not significant. The *p* values in boldface type indicate statistical significance.

[a]Mean observed distance to each habitat and road type is measured in metres (m), whereas mean observed slope is measured in degrees (°) and mean observed elevation is measured in metres (m).

[b]Mean distance ratios for observed/expected distance to habitat and physical features. For all distance-based variables (excludes slope and elevation) ratios <1 indicate selection and ratios >1 indicate avoidance.

[c]Marginally significant.

[d]Small effect size indicating limited biological significance.

Discussion

Cow moose exhibited nonrandom habitat use during calving across all spatiotemporal scales in WMU49, as well as the finest scale in APP. In terms of the broad, macrohabitat types and topographical features we considered, our data suggest calving sites are not limiting in APP. Moose in APP initiated long-distance movements during the early stages of labour, possibly making fine-scale habitat selection decisions along the way, before stopping immediately prior to calving (within 1 day) to select an appropriate site in which to give birth. Such selection of habitat features available at finer scales surrounding calving sites is similar to findings by Bowyer et al. (1999). In contrast, moose in WMU49 selected habitat similarly at calving sites from what was available in their annual, seasonal, and calving ranges.

In WMU49, moose selected calving sites closer to open rocky areas and grass meadows. Our results support observations by our field crews of calving beds on rocky outcrops, a finding similar to other moose studies (Langley and Pletscher 1994). Other ungulates have also been observed calving in areas that were mostly rock (Bergerud et al. 1984). There may be anti-predator benefits of these areas for calving. For example, open habitat and rocky outcrops may provide earlier detection of predators due to increased visibility and might allow moose better maneuverability to defend calves from predators. Without trees around the calving site, it may be more difficult for predators to avoid defensive charges from maternal cows and to successfully separate them from their calves. In addition, such open areas may provide more wind, thereby helping to reduce harassment by biting insects on cows and calves (Renecker and Hudson 1990; Walsh et al. 1992). Calving season in central Ontario overlaps with black fly (species of the genus *Simulium* Latreille, 1802) season and the emergence of mosquitoes (family Culicidae) and selecting for calving sites that provide some relief from these insects may be desirable, especially because of the sedentary nature of cow–calf pairs following parturition.

Moose in WMU49 showed an avoidance of steep slopes for calving, but calving sites in this study area were on slopes of approximately the same degree as those in APP (Tables 3 and 4). Therefore, despite the different responses to slope from a use-availability perspective, moose in both study areas generally calved on gentle slopes. Use of gentle slopes (up to 17°) by maternal cow moose in our study areas is consistent with fine-scale movement results from moose in Quebec during spring (Leblond et al. 2010). While gentle slopes may provide forage opportunities dur-

Table 4. Results of univariate *t* tests for habitat selection of adult cow moose (*Alces alces*) during calving in Wildlife Management Unit 49, Ontario, Canada, at annual, seasonal, and calving-range scales.

Variable	Observed value (mean ± SE)[a]	Ratio[b]	*t*	*p*	Conclusion
Annual (*n* = 21)					
CON	519.6±112.9	1.02	0.11	0.914	NS
HWD	647.4±204.9	1.23	1.01	0.326	NS
MIX	518.0±119.4	1.33	1.16	0.258	NS
WAT	398.5±48.5	0.95	−0.47	0.644	NS
WETL	172.9±32.8	0.80	−1.15	0.265	NS
RCK–GRS	387.5±75.2	0.73	−2.15	**0.044**	Select
PRD	5343.5±782.1	1.04	0.50	0.620	NS
SRD	1389.5±235.6	0.92	−0.86	0.400	NS
TRD	1402.8±214.7	1.03	0.31	0.760	NS
Slope	2.2±0.4	0.57	−4.46	**<0.001**	Avoid
Elevation	317.4±3.9	0.99	−0.96	0.349	NS
Seasonal (*n* = 21)					
CON	519.6±112.9	1.03	0.15	0.886	NS
HWD	647.4±204.9	1.37	1.45	0.164	NS
MIX	518.0±119.4	1.21	0.74	0.466	NS
WAT	398.5±48.5	0.96	−0.39	0.701	NS
WETL	172.9±32.8	0.84	−0.83	0.414	NS
RCK–GRS	387.5±75.2	0.67	−2.83	**0.010**	Select
PRD	5343.5±782.1	1.10	1.03	0.315	NS
SRD	1389.5±235.6	0.88	−1.54	0.140	NS
TRD	1402.8±214.7	1.03	0.24	0.810	NS
Slope	2.2±0.4	0.54	−4.94	**<0.001**	Avoid
Elevation	317.4±3.9	0.99	−0.59	0.561	NS
Calving (*n* = 45)					
CON	395.1±73.0	0.73	−3.35	**0.002**	Select
HWD	425.5±111.0	1.08	0.49	0.627	NS
MIX	560.9±79.0	0.90	−1.48	0.146	NS
WAT	412.3±37.7	0.99	−0.36	0.719	NS
WETL	205.0±30.7	0.90	−0.93	0.356	NS
RCK–GRS	422.5±56.9	0.78	−3.17	**0.003**	Select
PRD	4692.6±460.1	1.00	0.081	0.936	NS
SRD	1211.4±163.9	0.99	−0.50	0.618	NS
TRD	1093.4±146.9	0.96	−1.19	0.240	NS
Slope	2.4±0.4	0.72	−2.41	**0.020**	Avoid
Elevation	320.75±3.1	1.00	−0.10	0.920	NS

Note: CON, conifer; HWD, hardwoods; MIX, mixed woods; WAT, water; WETL, wetlands; RCK–GRS, rocky areas and grass meadows; PRD, primary road; SRD, secondary road; TRD, tertiary road; NS, not significant. The *p* values in boldface type indicate statistical significance.

[a]Mean observed distance to each habitat and road type is measured in metres (m), whereas mean observed slope is measured in degrees (°) and mean observed elevation is measured in metres (m).

[b]Mean distance ratios for observed/expected distance to habitat and physical features. For all distance-based variables (excludes slope and elevation) ratios <1 indicate selection and ratios >1 indicate avoidance.

ing leaf-out (Leblond et al. 2010), these areas may also offer good moisture drainage resulting in drier calving sites. Well-drained sites are advantageous for thermoregulation in calves, because they lack insulating fat layers making them more susceptible to thermal stress (Linnell et al. 1995; MacCracken et al. 1997).

At the finest scale, moose in APP and WMU49 selected conifer stands for calving. This is consistent with results from other studies of habitat use by maternal cow moose (Dussault et al. 2005; McGraw et al. 2011), where it has been suggested that conifer forests provide cover from predators. Without field-collected data on density of understory growth in conifer stands in APP and WMU49, we cannot explicitly comment on the provision of adequate concealment cover from predators. Rather, we infer that cows used conifer forests to space away from predators. Out of the main forest-stand types in our study areas (CON, MIX, HWD), coyotes and wolf–coyote hybrids were least likely to use conifer forests from spring to late autumn, compared with mixed and

hardwood forests (Benson et al. 2015a), suggesting that conifer forests provided the lowest risk of encounter with those predators during calving.

We did not find strong evidence to support the results of Wilton and Garner (1991), where elevation was found to be an important factor in moose calving site selection in APP. Although there was a statistically significant effect of elevation on habitat selection at the calving-range scale in APP, the differences we observed between elevation of calving sites and mean elevation of the surrounding calving buffers were not great (mostly <10 m). Although even slight increases in elevation could increase a cow's visibility and auditory range of the surrounding landscape, potentially allowing for more effective detection of predators (Wilton and Garner 1991; Bowyer et al. 1999), we do not believe our results warrant a strong biological support for the importance of elevation in calving site selection.

Despite close proximity of calving sites to water in APP (approximately 162 m), this distance was indicative of avoidance by parturient moose, suggesting that moose strongly avoided calving on the edge of water, but water was still highly available to them in the area surrounding their calving site. Close proximity to water has been documented for calving moose elsewhere (Leptich and Gilbert 1986; Addison et al. 1990; Chekchak et al. 1998) and serves as an important source of drinking water during the period of localization at calving sites (Addison et al. 1990). Proximity to water by calving on islands is also thought to be an antipredator strategy of maternal ungulates (Edwards 1983; Bergerud 1985; Addison et al. 1990), but in nonisland settings, proximity to water may actually increase predation risk given the strong selection of water by wolves during pup-rearing (Benson et al. 2015b), a time which coincides with moose calving season.

Only in WMU49 were we able to examine the effect of roads on calving site selection at all three spatiotemporal scales. Cow moose showed no response to primary, secondary, or tertiary roads during calving at any scale. Minimum distances of calving sites to primary, secondary, and tertiary roads in our study areas were 260, 165, and 30 m, respectively, indicating at least some moose may be selecting sites along roads. However, the response to roads is likely complex and variable by individual moose, because of the trade-off related to proximity to roads (Beyer et al. 2013), whereby access to forage may be increased (Rempel et al. 1997; Bowman et al. 2010), as well as exposure to predators (Musiani et al. 1998; James and Stuart-Smith 2000; Whittington et al. 2005; Latham et al. 2011a, 2011b; Whittington et al. 2011). In APP, low road density and use likely minimized any response to such features during calving (Beyer et al. 2013).

Disturbed landscape patches of varying successional age were not directly selected at the coarse scales in both study areas and could not be properly assessed at the smaller scale due to underrepresentation within the smaller calving ranges. With abundant understory regrowth, disturbed forest patches may be ideal areas for moose during calving due to forage availability and potential predator concealment (Puttock et al. 1996; Bowman et al. 2010), but we could not detect a response with the data available in our study areas.

Learned or innate behavioural traits may also have influenced calving site selection if parturient cows in our study areas showed fidelity to calving sites used in previous years, regardless of the habitat characteristics of those sites. Many ungulates demonstrate fidelity to calving sites (Nixon et al. 1992; Testa et al. 2000; Wittmer et al. 2006; Tremblay et al. 2007; but see Chekchak et al. 1998 and Bowyer et al. 1999) and postcalving sites (McGraw et al. 2011) and a similar behavioural pattern may exist in our study areas. Further examination of our data showed that successive calving sites of cows with multiple years of GPS-collar data ($n = 24$) were 2.10 ± 0.38 km apart with eight females returning to a location <1 km of their previous calving site. Such cows may return to these areas due to previous successful rearing of a calf (Testa et al.

2000; Welch et al. 2000) or familiarity of the location (e.g., natal philopatry; Cederlund and Sand 1992; Colson et al. 2016), and such behaviour may mask or preclude selection for habitat characteristics among parturient moose.

The analysis of location data from cow moose in our study areas showed extensive movement in the days leading up to calving. This result is consistent with other studies showing extensive pre-calving movement by ungulates (Testa et al. 2000; Vore and Schmidt 2001; Poole et al. 2007; Wattles and DeStefano 2013; Severud et al. 2015). Furthermore, the mean time moose in our study stayed near their calving site (5.8 days) was comparable with other studies (6.2 days: Langley and Pletscher 1994; 6.5 days: Poole et al. 2007; 6.1 days: Severud et al. 2015). These results suggest that location data from GPS collars can be reliably used to determine the reproductive status of ungulates, such as moose, by tracking movement patterns during the calving season. Although our sample size was small for verification with VIT expulsion and calf collaring ($n = 12$), the reproductive status of all but two cow moose could have been accurately predicted based solely on GPS-collar data without the need for invasive field methods, such as VIT implantation. This further validates the use of reproductive status dependent movement patterns to infer parturition in ungulates (Vore and Schmidt 2001; Ciuti et al. 2005; Dzialak et al. 2011; DeMars et al. 2013; Severud et al. 2015; Melin et al. 2016). Overall, our study highlights the value of modern advances in telemetry equipment for studying moose reproductive ecology and calving site selection.

Based on our results, we recommend that forest and moose management practices in central Ontario aimed at supporting moose populations should maintain heterogeneous patches of conifer forest interspersed with open grass meadows and rocky outcrops to promote protection of important calving areas. We also suggest that future studies collect ground-based microenvironment data to better understand the broad- and fine-scale habitat selection we detected for parturient cow moose. More generally, it is imperative that efforts are made to improve the accuracy of imagery upon which GIS habitat layers are developed and to combine these with detailed field-collected data to better characterize forest stands for use in habitat analyses.

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