There's no place like home — site fidelity by female moose (Alces alces) in central Ontario, Canada

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There's no place like home — site fidelity by female moose (*Alces alces*) in central Ontario, Canada

A.A.D. McLaren and B.R. Patterson

Abstract: Site fidelity is thought to provide increased fitness through familiarity with the distribution of forage, protective cover, breeding and offspring rearing sites, and predators. For moose (*Alces alces* (Linnaeus, 1758)), previous research has documented fidelity at varying spatial scales. Our objective was to build on this knowledge and assess fidelity by adult female moose in two areas of central Ontario, Canada (Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49)). We used global positioning system data to generate mean weekly locations for collared moose, then measured the distance between paired weekly locations among consecutive years to evaluate site fidelity. We tested for effects of study area, biological season, moose age, and reproductive status using generalized linear mixed models. Moose demonstrated stronger site fidelity in WMU49, an area with more anthropogenic disturbance, than the protected area, APP. Fidelity was weakest in the winter, but was similar among other seasons and was independent of maternal age and the presence of a calf. Our study highlights the need to consider the scale of site fidelity relative to habitat management. Actions aimed at supporting moose populations might benefit more by protecting habitat classes selected by moose rather than specific sites used by individuals.

Key words: moose, *Alces alces*, calf, calving site, disturbance, movement, parturition, philopatry, spatial fidelity, ungulate.

Résumé : La fidélité au site rehausserait l'aptitude en assurant une bonne connaissance de la répartition des sites d'alimentation, de couvert protecteur, de reproduction et d'élevage de la progéniture, ainsi que des sites fréquentés par les prédateurs. Des travaux passés ont documenté la fidélité au site à différentes échelles spatiales de l'orignal (*Alces alces* (Linnaeus, 1758)), et l'objectif de la présente étude consistait à élargir ces connaissances en évaluant la fidélité au site d'orignaux femelles adultes dans deux régions du centre de l'Ontario (Canada), soit le parc provincial Algonquin (PPA) et le secteur de gestion de la faune 49 (SGF49). Nous avons utilisé des données du système de localisation GPS pour générer les emplacements hebdomadaires moyens d'orignaux munis de colliers et avons ensuite mesuré la distance entre paires d'emplacements hebdomadaires pour des années consécutives afin d'évaluer la fidélité au site. Nous avons vérifié la présence d'effets de la région d'étude, de la saison biologique et de l'âge et de l'état reproducteur de l'orignal en utilisant des modèles mixtes linéaires généralisés. Les orignaux présentaient une plus grande fidélité au site dans le SGF49, une région plus perturbée par l'activité humaine, que dans l'aire de protection, le PPA. C'est à l'hiver que la fidélité était la plus faible, alors qu'elle était semblable entre les autres saisons, en plus d'être indépendante de l'âge de la mère et de la présence d'un veau. L'étude souligne la nécessité de tenir compte de l'échelle de la fidélité au site par rapport à celle de la gestion de l'habitat. La protection de catégories d'habitat sélectionnées par les originaux plutôt que de sites précis utilisés par des individus pourrait accroître l'efficacité des mesures visant à appuyer les populations d'orignaux. [Traduit par la Rédaction]

Mots-clés : orignal, *Alces alces*, veau, site de vêlage, perturbation, déplacement, parturition, philopatrie, fidélité spatiale, ongulé.

Introduction

Understanding animal space use and movement often relies on knowledge of habitat selection, but may inherently fail to recognize the role of spatial familiarity (Piper 2011). Such familiarity is commonly referred to as site fidelity or the tendency to return to previously used locations (Switzer 1993). Fidelity can be reinforced through movement, learning, and memory, interrelated mechanisms that provide familiarity with the distribution of forage, protective cover, breeding and offspring rearing sites, and predators (Fryxell et al. 2008; Wolf et al. 2009; Faille et al. 2010; Piper 2011; van Beest et al. 2013; Merkle et al. 2014). The benefits of retaining this spatial information are thought to outweigh the time, energy, and predation risk associated with navigating an unfamiliar area (Greenwood 1980; Switzer 1993).

As such, fidelity can increase an individual's survival and fitness (Spencer 2012; Forrester et al. 2015; Bose et al. 2017), but may be poorly understood or studied.

For ungulates, particularly females, fidelity has been found at both broad (e.g., seasonal ranges; Garrott et al. 1987; Fancy and Whitten 1991; Crampe et al. 2007; Faille et al. 2010; Brough et al. 2017; Sevigny et al. 2018) and fine (e.g., reproduction, bedding, or mineral lick sites; Wiles and Weeks 1986; Nelson and Mech 1999; Welch et al. 2000; McGraw et al. 2011; Popp et al. 2011; Olson et al. 2016) spatial and temporal scales. However, such fidelity in female ungulates is not exclusively developed over time through an individual's lone experience (Tremblay et al. 2007; Colson et al. 2016; Bose et al. 2017; but see Gunn and Miller 1986; Switzer 1993); it may be inherently linked to philopatry (Cederlund and Sand 1992; Loison et al. 1999; Nelson and Mech 1999; Crampe

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et al. 2007; Bose et al. 2017), suggesting an individual's spatial knowledge is at least partially learned from its mother.

Various factors may influence site fidelity of ungulates within their home range, including anthropogenic landscape disturbance, weather conditions, particularly winter weather, and reproductive status. For example, anthropogenic development, logging, and associated roads have been shown to alter movement and space use of moose (*Alces alces* (Linnaeus, 1758); Welch et al. 2000), elk (*Cervus canadensis* (Erxleben, 1777); Millspaugh et al. 2004; Webb et al. 2011), mule deer (*Odocoileus hemionus* (Rafinesque, 1817); Northrup et al. 2016), and woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788); Rettie and Messier 2000; Vors et al. 2007; Faille et al. 2010) generally through site avoidance. Consequently, spatial fidelity may be less common among individuals experiencing landscape disturbance within their home range. Furthermore, winter severity can influence the areas used by ungulates as they preferentially seek areas of low snow cover to minimize energetic costs of travel (Parker et al. 1984; Miquelle et al. 1992). Areas that meet these conditions may vary across years depending on snow accumulation, thereby altering patterns of fidelity. In addition to environmental factors, biological considerations, such as the reproductive status of a female, can influence seasonal patterns of habitat use (Bjørneraas et al. 2012), suggesting that across years for the same individual, the areas used by the female may vary according to whether she has a young at heel (Main 2008; Viejou et al. 2018; Melin et al. 2019).

For moose, previous research has demonstrated that both migratory (Cederlund et al. 1987; Sweanor and Sandegren 1989; Borowik et al. 2020) and non-migratory (Cederlund and Sand 1992; McGraw et al. 2011) populations display site fidelity across various spatial scales. Most relevant to moose management, however, may be an understanding of areas used at a spatial scale that is relevant to overall population fitness, such as areas used by females for birthing and raising of calves. Areas selected for calf rearing can influence reproductive success (Main 2008; Piper 2011) due to the vulnerability of newborn calves to predation immediately following birth (Ballard et al. 1981; Wilton 1983; Patterson et al. 2013; Severud et al. 2019a). Returning to calving and post-calving areas where calf survival was high may increase reproductive success in subsequent years (Testa et al. 2000; Wiseman et al. 2006; Colson et al. 2016). Hence, knowledge of these areas may inform forest management strategies aimed at benefitting moose populations.

It is unknown whether moose in the Great Lakes – St. Lawrence Forest of Ontario, Canada, exhibit spatial fidelity during calving or even more broadly across other seasons. Results from an analysis on moose habitat selection during calving in the region (McLaren et al. 2017) found a median distance between consecutive calving sites of adult female moose of 1.6 km, with one female returning to calve in a location that was 94 m from her previous calving site, similar to other studies showing that some moose will return to the same area during successive reproductive events (Testa et al. 2000; Tremblay et al. 2007). Yet, defining fidelity based on distance thresholds from a previously used calving area may be problematic, because it introduces subjectivity when setting upper distance threshold limits. Furthermore, it remains unknown whether such apparent site fidelity is restricted only to parturient females during the calving season.

Our objective was to test for site fidelity among seasons by adult female moose, varying in age and reproductive status, using a comparative approach by examining differences in distances between site locations across years in two regions of central Ontario. We predicted that (1) fidelity within home ranges would be independent of age; (2) there would be stronger fidelity in the study area with less anthropogenic disturbance (hunting and logging); (3) fidelity would be strongest during the non-winter seasons; and (4) moose having calves in consecutive years would show stronger fidelity from spring through summer than other times of the year, whereas this relationship would not hold for moose with calves in only 1 of 2 consecutive years.

We caution the misinterpretation of site fidelity as habitat selection per se, because individuals may still be selecting the same habitat types even when using sites separated by large geographic distances (i.e., weak site fidelity may not equate to weak seasonal habitat selection).

Materials and methods

Global positioning system (GPS) collars (Lotek 3300 GPS collars, Lotek Wireless Inc., Newmarket, Ontario, Canada) were fitted to adult female moose in two study areas in central Ontario from 2006 to 2009 as part of a broader study (for details see Lowe et al. 2010; Murray et al. 2012). The study areas were approximately 50 km apart and included the western portion of Algonquin Provincial Park (APP; 1587 km^2) and the eastern region of Wildlife Management Unit 49 (WMU49; 1280 km^2) (Fig. 1). Western APP contained protected lands with restricted or selective logging and no moose hunting, whereas WMU49 contained both public and private lands and was subject to logging, including clearcutting, and moose hunting (bull, cow, and calf licences available). As a result of forestry practices, mature forest was common throughout APP (Quinn 2005) and was dominated by sugar maple (*Acer saccharum* Marsh.), poplar (genus *Populus* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), eastern hemlock (*Tsuga canadensis* (L.) Carrière), spruce (genus *Picea* A. Dietr.), and fir (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; Patterson et al. 2016). Main predators in both study areas included wolves (genus *Canis* Linnaeus, 1758), coyotes (*Canis latrans* Say, 1823), and American black bears (*Ursus americanus* Pallas, 1780), with a higher abundance of coyotes and black bears in WMU49 than in APP (McLaren et al. 2017).

Location data collected every 2 h for 2.5 years from adult female moose in APP (*n* = 16) and WMU49 (*n* = 13) resulted in 259 377 valid GPS fixes. We included only females with at least two complete consecutive years of location data (i.e., having no weekly gaps) in our analysis. The mean ($\pm$SE) age of GPS-collared moose included in our analysis from APP and WMU49 was 4.0 $\pm$ 0.4 (range: 1–7) and 3.9 $\pm$ 0.7 (range: 1–9) years, respectively, and was determined by cementum annuli examination using an extracted incisor (Matson's Laboratory, Manhattan, Montana, USA). To prepare our data for analysis, we first computed mean weekly locations for each moose (from date of collaring), calculated as the geographic centre of weekly locations using the Mean Center tool in ArcGIS version 10.3.1 (ESRI, Inc. 2015). We then used the Point Distance tool to calculate the inter-annual distance between paired weeks of data, represented as the distance between the geographic mean location for a moose for a given week in 1 year and the geographic mean location for the same week in the subsequent year, following Schaefer et al. (2000). Given the low variability of mean daily movement of moose within weeks in our study areas (McLaren et al. 2017), we deemed a comparative approach using a weekly scale appropriate for our analysis. For each moose, we then compared its overall mean inter-annual distance with a calculated maximum within-year weekly movement distance using paired *t* tests with Bonferroni correction to evaluate support for moose fidelity within our study areas (see Brough et al. 2017). If mean inter-annual distances were shorter than the maximum within-year weekly distances, then we inferred this as evidence of fidelity. We used the maximum within-year weekly movement distance as a reference to quantify the distances moose in our sample were capable of travelling.

We grouped the inter-annual distances data set into five biological periods representative of an annual cycle of an adult female moose (pre-calving: 1 April – 7 May; calving: 8 May – 5 June; post-calving: 6 June – 31 August; breeding: 1 September – 31 October; winter: 1 November – 31 March). The calving period was based on the first and last days of calving noted for collared moose in our study areas

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. Figure was created using ArcGIS version 10.3.1 and assembled from the following data shapefiles: Provincial Park Administrative Zone, Wildlife Management Units, Ontario Hydro Network (OHN) 200K Waterbody, and Canada Boundary. Study area boundaries were created using a bounding polygon around collared moose home ranges. Map data provided by the Ontario Ministry of Natural Resources and Forestry under the Open Government Licence – Ontario (https://www.ontario.ca/page/open-government-licence-ontario).
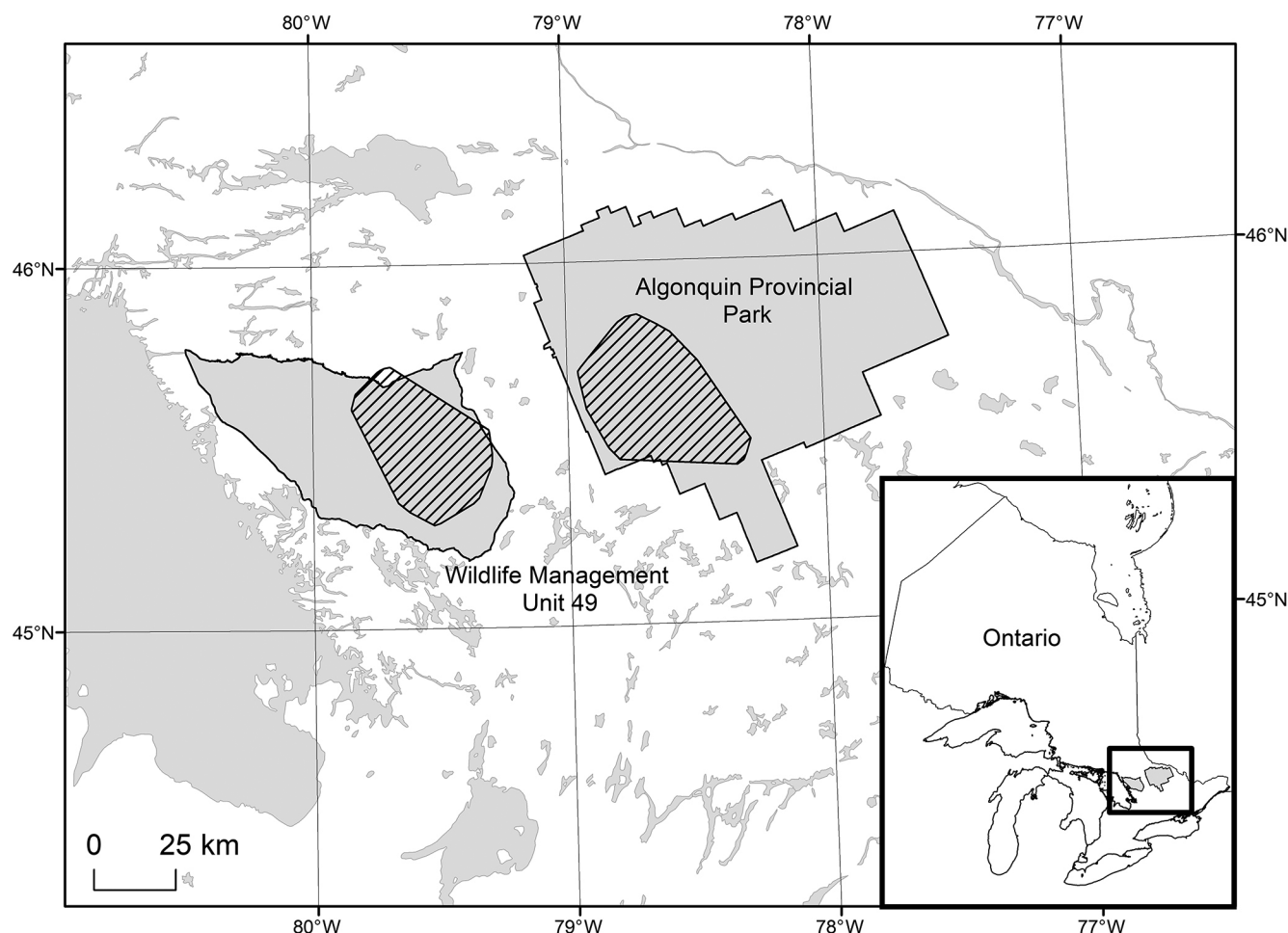
(Patterson et al. 2016) and the remaining periods were modified from McLoughlin et al. (2011). In particular, we shortened the breeding period by 1 month, because moose in our study areas are not believed to breed beyond October, which is consistent with the literature (e.g., Van Ballenberghe and Miquelle 1993; Sigouin et al. 1997).

Furthermore, we categorized all moose into a reproductive status group: (A) calf born in 2 consecutive years or (B) calf born in only 1 of 2 consecutive years. Annual reproductive output was either confirmed through expulsion of a vaginal implant transmitter (VIT) and (or) calf collaring (see Patterson et al. 2013) or determined based on movement activity and sedentary behaviour during the calving period (see McLaren et al. 2017).

To test predictions 1 and 2, we modelled inter-annual location distances of moose as a function of maternal age and study area (eq. 1). Data used in our analyses spanned multiple years, and therefore, we adjusted maternal age of each moose accordingly.

(1)   Distance ~ maternal age + study area

For predictions 3 and 4, we analyzed data separately for each reproductive group (A and B) to test for an effect of reproductive status on inter-annual distances across all moose biological seasons (eq. 2; analyzed for each reproductive group).

(2)   Distance ~ biological season + study area

We analyzed our data using inverse-weighted generalized linear mixed models (GLMMs) with individual moose as the random effect and APP study area and calving season as the reference categories. Normal Q–Q plots suggested our data were right skewed, so we fit our three GLMMs using the penalized quasi-likelihood method (Breslow 2004) with a gamma distribution. All statistical analyses were performed in R version 3.5.1 (R Core Team 2018) using the MASS package. Data are presented as mean ± SE unless otherwise stated. We considered all tests to be statistically significant when $p \leq 0.05$ and marginally statistically significant if $0.10 \leq p \geq 0.05$.

Ethics approval

All methods of capture and handling were approved by the animal care committees of Trent University and the Ontario Ministry of Natural Resources and Forestry (permit numbers 07-66, 08-66, 09-66). Additionally, we were authorized by Ontario Parks to conduct this research in APP.

Results

Mean inter-annual distances of moose were significantly shorter than maximum within-year weekly distances in APP ($t_{[15]} = -5.20$, $p = 0.002$) and WMU49 ($t_{[12]} = -7.23$, $p = 0.0001$). Specifically, there

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Table 1. Results of generalized linear mixed models (GLMM) testing for site fidelity of adult female moose (*Alces alces*) in two study areas of central Ontario, Canada — Algonquin Provincial Park (APP) and Wildlife Management Unit 49 (WMU49).

Model parameters	Estimate	SE	df	t	p
Distance ~ maternal age + study area					
Intercept	4.4×10^{-4}	2.6×10^{-5}	1529	16.93	**<0.0001**
Age	-3.2×10^{-6}	5.5×10^{-6}	1529	−0.58	0.56
Study area	1.0×10^{-4}	2.2×10^{-5}	27	4.69	**0.0001**
Distance ~ biological season + study area (reproductive group A)					
Intercept	7.0×10^{-4}	7.9×10^{-5}	864	8.78	**<0.0001**
Pre-calving	-1.7×10^{-5}	5.5×10^{-5}	864	−0.32	0.75
Post-calving	7.8×10^{-5}	5.9×10^{-5}	864	1.31	0.19
Breeding	-2.1×10^{-5}	5.1×10^{-5}	864	−0.42	0.68
Winter	-4.3×10^{-4}	5.3×10^{-5}	864	−8.09	**<0.0001**
Study area	8.1×10^{-5}	9.6×10^{-5}	16	0.84	0.41
Distance ~ biological season + study area (reproductive group B)					
Intercept	6.2×10^{-4}	7.5×10^{-5}	656	8.21	**<0.0001**
Pre-calving	-1.5×10^{-4}	7.2×10^{-5}	656	−2.14	**0.033**
Post-calving	-8.4×10^{-7}	7.1×10^{-5}	656	−0.01	0.99
Breeding	6.0×10^{-5}	7.6×10^{-5}	656	0.79	0.43
Winter	-2.8×10^{-4}	6.3×10^{-5}	656	−4.41	**<0.0001**
Study area	6.8×10^{-5}	6.2×10^{-5}	11	1.10	0.29

Note: Reproductive group A is female with calf born in 2 consecutive years and reproductive group B is female with calf born in 1 of 2 consecutive years. APP study area and calving season are used as reference categories. Individual moose was used as the random effect in all models. The *p* values in boldface type indicate statistical significance.

was approximately a 2.3-fold difference between inter-annual and within-year distances for moose in both APP (2.3 ± 0.2 vs. 5.4 ± 0.6 km) and WMU49 (1.9 ± 0.1 vs. 4.3 ± 0.4 km). Results of GLMMs (Table 1) showed that study area ($t_{[27]}$ = 4.69, *p* = 0.0001), but not maternal age ($t_{[1529]}$ = −0.58, *p* = 0.56), was a significant predictor of overall inter-annual location differences for adult female moose, with inter-annual distances being shorter in WMU49 (1.9 ± 0.1 km) compared with APP (2.3 ± 0.2 km). For moose having calves in consecutive years, inter-annual location distances were not statistically different during the pre-calving ($t_{[864]}$ = −0.32, *p* = 0.75), post-calving ($t_{[864]}$ = 1.31, *p* = 0.19), or breeding ($t_{[864]}$ = −0.42, *p* = 0.68) seasons from the calving season. However, inter-annual location differences were significantly farther apart during the winter season ($t_{[864]}$ = −8.09, *p* < 0.0001) compared with the calving season (Fig. 2*a*). For moose that had a calf in only 1 of 2 consecutive years, inter-annual location differences were not statistically different during the post-calving ($t_{[656]}$ = −0.01, *p* = 0.99) or breeding ($t_{[656]}$ = 0.79, *p* = 0.43) seasons from the calving season. But for these moose, the differences in the distances of inter-annual locations were significantly greater during the pre-calving ($t_{[656]}$ = −2.14, *p* = 0.033) and winter ($t_{[656]}$ = −4.41, *p* < 0.0001) seasons compared with the calving season (Fig. 2*b*). Study area did not have a significant effect on inter-annual location differences when data were analyzed by reproductive status (*p* > 0.20 for both reproductive models).

Discussion

We used a comparative analysis to assess moose site fidelity in central Ontario. We deemed this approach appropriate given that differences in moose home-range sizes between study areas (47.1 ± 4.3 and 36.8 ± 2.5 km² in APP and WMU49, respectively; McLaren et al. 2017) made it challenging to define fidelity by absolute distance thresholds alone, and our approach is commonly used in ungulate fidelity studies (e.g., Garrott et al. 1987; Popp et al. 2011; Brough et al. 2017).

Despite the range in ages of female moose in our study (1–9 years old), we did not find an effect of age on site fidelity, supporting our prediction and results of other studies (Wiseman et al. 2006; Tremblay et al. 2007; Forrester et al. 2015; Northrup et al. 2016; Bose et al. 2017). Affinity to an area is achieved through repetition (Gunn and Miller 1986; Spencer 2012), but it seems that

earning and memory were fully developed by the time most moose entered our study, potentially influenced by cues from their mothers from a young age as a result of natal philopatry (Tremblay et al. 2007; Colson et al. 2016).

Contrary to our prediction, site fidelity was stronger in the more disturbed area (WMU49) despite the area being subject to anthropogenic disturbance through development, agriculture, and hunting, with a high proportion (50%) of accessible public land (Patterson et al. 2013). However, study area effects were eliminated when data were separated by reproductive group, possibly reflecting a reduction in statistical power. Though some ungulates may respond to increasing development and logging within their home ranges through site avoidance and reduced movements (Rettie and Messier 2000; Millspaugh et al. 2004; Vors et al. 2007; Faille et al. 2010; Webb et al. 2011; Northrup et al. 2016), we speculate that disturbance within the home ranges of moose that we studied may not have been at a magnitude or frequency required to detect our predicted response (Beyer et al. 2013). Alternatively, the temporal scale of our analysis may have been insufficient to allow for a detectable response. Moose may have also responded to disturbance at higher orders of selection than we examined here. If either are true, then it is plausible that moose in WMU49 used known preferred areas within their home range out of necessity compared with moose in APP that may have more intact habitat available to them. Furthermore, our inferences are limited to the variables that we included in our models, but there could be other factors that we did not examine that influenced fidelity patterns between our study areas (e.g., differences in moose predation risk; Murray et al. 2012).

As predicted, female moose in our study areas had the lowest site fidelity during the winter season. This agrees with results of other ungulate fidelity studies (Benkobi et al. 2005; Faille et al. 2010) and is thought to be driven by temporal variability in winter severity and forage availability (van Beest et al. 2010; Bjørneraas et al. 2011; Popp et al. 2011; Joly et al. 2015; Northrup et al. 2016). Mean snow depth measured at various stations in our study areas showed variability in snow accumulation across winters during our study, with a general trend of increasing mean snow depth in winters 2006–2007 to 2008–2009 (e.g., 2006–2007: 20.7 cm; 2008–2009: 52.5 cm; western APP; MNRF, unpublished data). Snow accumulation can affect movement and the type of forest stand selected by ungulates

Fig. 2. Difference in distance (km) of mean weekly locations of GPS-collared adult female moose (*Alces alces*) between consecutive years in Algonquin Provincial Park (*n* = 16) and Wildlife Management Unit 49 (*n* = 13) by biological period (winter (W), pre-calving (Pre-C), calving (C), post-calving (Post-C), breeding (B)). Results are presented by reproductive status group: (*a*) moose with calf born in 2 consecutive years and (*b*) moose with calf born in 1 of 2 consecutive years.
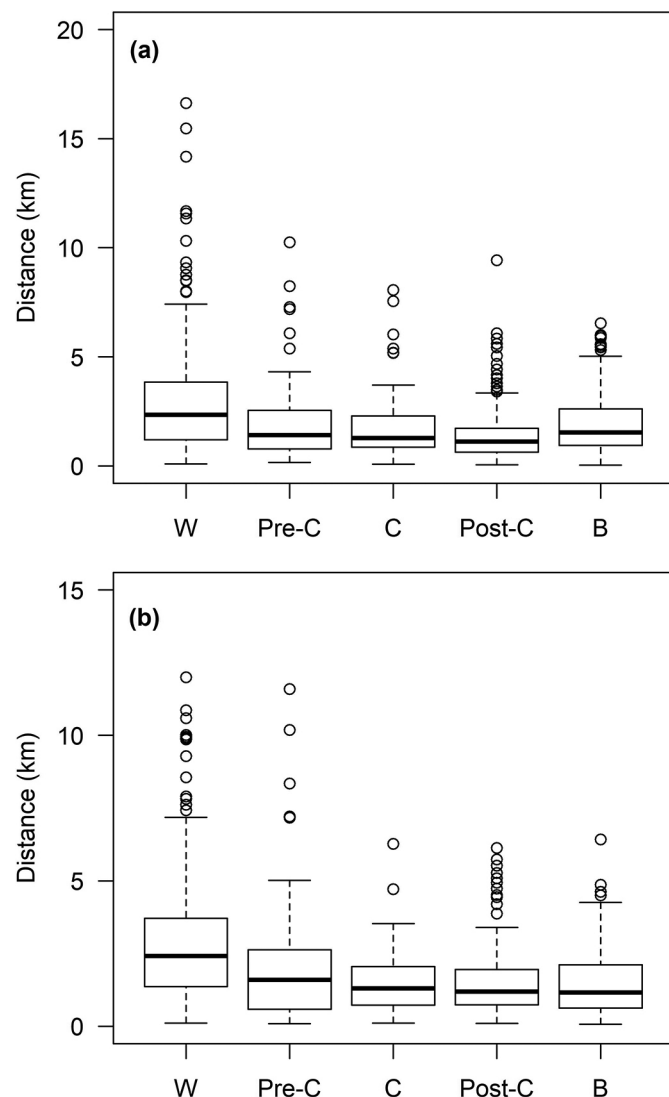
during winter (Miquelle et al. 1992; Lowe et al. 2010; Bjørneraas et al. 2011), as can the timing and duration of snow cover (Sweanor and Sandegren 1989; Benkobi et al. 2005), possibly contributing to moose in our study areas showing the lowest spatial fidelity during winter.

Interestingly, female moose in both study areas demonstrated fidelity during the breeding season. In WMU49, the breeding season also overlapped with moose hunting season, so moose may have been familiar with areas that offered refugia from hunters (McLoughlin et al. 2011), providing benefits similar to having knowledge of predator distribution (Greenwood 1980; Forrester et al. 2015). However, female moose in APP, a non-hunted area, also exhibited site fidelity during the breeding season, suggesting that prior knowledge of sites providing access to male conspecifics during breeding season was an additional mechanism operating in both study areas. All moose included in our analysis were at least 1.5 years old during the first autumn of our study and therefore of reproductive age.

Although female moose in both study areas showed site fidelity from spring through summer, contrary to our prediction, it was not limited only to moose having calves in consecutive years. However, females that were reproductive in only 1 of 2 consecutive years showed modestly weak fidelity to previously used sites in early spring (the pre-calving season), suggesting that when parturient, females chose familiar calving areas, which may have consisted of specific habitat characteristics for protection of their impending calves (McLaren et al. 2017; Severud et al. 2019b), whereas when they were non-parturient, females may have selected sites based on forage availability, leading to tortuous, less directed movements (Fryxell et al. 2008) and use of different areas than when parturient (Viejou et al. 2018). Beyond early spring, we hypothesize that female moose likely selected areas of high forage (McLoughlin et al. 2011; Melin et al. 2019), independent of having a calf at heel (McGraw et al. 2011; Severud et al. 2019b), explaining why fidelity was similar for females between years from mid- or late spring to autumn, regardless of reproductive status. Further investigation may be warranted to determine the effect of forage on patterns of site fidelity of moose in our study areas (see van Beest et al. 2010).

Our results add to the knowledge of moose site fidelity within home ranges. By using a comparative approach among seasons, we were able to demonstrate site fidelity by female moose throughout most of their biological year, findings that may have been overlooked if our analysis was limited only to the reproductive season. Knowledge of site fidelity during calving and post-calving periods can have important implications for conservation, particularly when females show strong site fidelity during those periods (Popp et al. 2011). However, the median distance between confirmed calving sites in consecutive years for female moose in our study areas was 1.6 km. Because the scale of fidelity (e.g., 1–2 km) may not match the scale of management (e.g., forest stand), it may be difficult to incorporate knowledge of moose site fidelity into habitat management practices in our study areas. Rather, management actions aimed at supporting moose populations might benefit more by protecting habitat classes selected by moose (e.g., McLoughlin et al. 2011) rather than specific sites used within home ranges.

Acknowledgements

References

Ballard, W.B., Spraker, T.H., and Taylor, K.P. 1981. Causes of neonatal moose calf mortality in south central Alaska. J. Wildl. Manage. **45**(2): 335–342. doi:10.2307/3807916.

Benkobi, L., Rumble, M.A., Stubblefield, C.H., Gamo, R.S., and Millspaugh, J.J. 2005. Seasonal migration and home ranges of female elk in the black hills of South Dakota and Wyoming. Prairie Nat. **37**(3): 151–166.

Benson, J.F., Loveless, K.M., Rutledge, L.Y., and Patterson, B.R. 2017. Ungulate predation and ecological roles of wolves and coyotes in eastern North America. Ecol. Appl. **27**(3): 718–733. doi:10.1002/eap.1499. PMID: 28064464.

Beyer, H.L., Ung, R., Murray, D.L., and Fortin, M.J. 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. J. Appl. Ecol. **50**(2): 286–294. doi:10.1111/1365-2664.12042.

Bjørneraas, K., Solberg, E.J., Herfindal, I., Van Moorter, B., Rolandsen, C.M., Tremblay, J.-P., et al. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildl. Biol. **17**(1): 44–54. doi:10.2981/10-073.

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.-E., Van Moorter, B., and Rolandsen, C.M. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia, **168**(1): 231–243. doi:10.1007/s00442-011-2072-3. PMID:21766188.

Borowik, T., Ratkiewicz, M., Maślanko, W., Duda, N., and Kowalczyk, R. 2020. The level of habitat patchiness influences movement strategy of moose in Eastern Poland. PLoS ONE, **15**(3): e0230521. doi:10.1371/journal.pone.0230521. PMID:32191742.

Bose, S., Forrester, T.D., Brazeal, J.L., Sacks, B.N., Casady, D.S., and Wittmer, H.U. 2017. Implications of fidelity and philopatry for the population structure of female black-tailed deer. Behav. Ecol. **28**(4): 983–990. doi:10.1093/beheco/arx047.

Breslow, N. 2004. Whither PQL? *In* Proceedings of the Second Seattle Symposium in Biostatistics. Analysis of Correlated Data. Lecture Notes in Statistics. Vol. 179. *Edited by* D.Y. Lin and P.J. Heagerty. Springer, New York. pp. 1–22.

Brough, A.M., DeRose, R.J., Conner, M.M., and Long, J.N. 2017. Summer–fall home-range fidelity of female elk in northwestern Colorado: implications for aspen management. For. Ecol. Manage. **389**: 220–227. doi:10.1016/j.foreco.2016.11.034.

Cederlund, G., Sandegren, F., and Larsson, K. 1987. Summer movements of female moose and dispersal of their offspring. J. Wildl. Manage. **51**(2): 342–352. doi:10.2307/3801014.

Cederlund, G.N., and Sand, H.K.G. 1992. Dispersal of subadult moose (*Alces alces*) in a nonmigratory population. Can. J. Zool. **70**(7): 1309–1314. doi:10.1139/z92-183.

Colson, K.E., White, K.S., and Hundertmark, K.J. 2016. Parturition site selection in moose (*Alces alces*): evidence for social structure. J. Mammal. **97**(3): 788–797. doi:10.1093/jmammal/gyw006.

Crampe, J.-P., Bon, R., Gerard, J.-F., Serrano, E., Caens, P., Florence, E., and Gonzalez, G. 2007. Site fidelity, migratory behaviour, and spatial organization of female isards (*Rupicapra pyrenaica*) in the Pyrenees National Park, France. Can. J. Zool. **85**(1): 16–25. doi:10.1139/z06-185.

ESRI, Inc. 2015. ArcMap. Version 10.3.1. Environmental Systems Research Institute, Inc. (ESRI), Redlands, Calif.

Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H., and Dussault, C. 2010. Range fidelity: The missing link between caribou decline and habitat alteration? Biol. Conserv. **143**(11): 2840–2850. doi:10.1016/j.biocon.2010.08.001.

Fancy, S.G., and Whitten, K.R. 1991. Selection of calving sites by Porcupine herd caribou. Can. J. Zool. **69**(7): 1736–1743. doi:10.1139/z91-242.

Forrester, T.D., Casady, D.S., and Wittmer, H.U. 2015. Home sweet home: fitness consequences of site familiarity in female black-tailed deer. Behav. Ecol. Sociobiol. **69**(4): 603–612. doi:10.1007/s00265-014-1871-z.

Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., et al. 2008. Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc. Natl. Acad. Sci. U.S.A. **105**(49): 19114–19119. doi:10.1073/pnas.0801737105. PMID:19060190.

Garrott, R.A., White, G.C., Bartmann, R.M., Carpenter, L.H., and Alldredge, A.W. 1987. Movements of female mule deer in northwest Colorado. J. Wildl. Manage. **51**(3): 634–643. doi:10.2307/3801282.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**(4): 1140–1162. doi:10.1016/S0003-3472(80)80103-5.

Gunn, A., and Miller, F.L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. Rangifer, **6**(2): 151–158. doi:10.7557/2.6.2.640.

Joly, K., Craig, T., Sorum, M.S., McMillan, J.S., and Spindler, M.A. 2015. Variation in fine-scale movements of moose in the upper Koyukuk River drainage, northcentral Alaska. Alces, **51**: 97–105.

Loison, A., Jullien, J.-M., and Menaut, P. 1999. Subpopulation structure and dispersal in two populations of chamois. J. Mammal. **80**(2): 620–632. doi:10.2307/1383306.

Lowe, S.J., Patterson, B.R., and Schaefer, J.A. 2010. Lack of behavioral responses of moose (*Alces alces*) to high ambient temperatures near the southern periphery of their range. Can. J. Zool. **88**(10): 1032–1041. doi:10.1139/Z10-071.

Main, M.B. 2008. Reconciling competing ecological explanations for sexual segregation in ungulates. Ecology, **89**(3): 693–704. doi:10.1890/07-0645.1. PMID:18459333.

McGraw, A.M., Moen, R., and Schrage, M. 2011. Characteristics of post-parturition areas of moose in northeast Minnesota. Alces, **47**: 113–124.

McLaren, A.A.D., Benson, J.F., and Patterson, B.R. 2017. Multiscale habitat selection by cow moose (*Alces alces*) at calving sites in central Ontario. Can. J. Zool. **95**(10): 891–899. doi:10.1139/cjz-2016-0290.

McLoughlin, P.D., Vander Wal, E., Lowe, S.J., Patterson, B.R., and Murray, D.L. 2011. Seasonal shifts in habitat selection of a large herbivore and the influence of human activity. Basic Appl. Ecol. **12**(8): 654–663. doi:10.1016/j.baae.2011.09.001.

Melin, M., Matala, J., Pusenius, J., and Packalen, T. 2019. Calving and post-calving habitat use of female moose in two contrasting landscapes. Wildl. Biol. **2019**(1): 1–12. doi:10.2981/wlb.00569.

Merkle, J.A., Fortin, D., and Morales, J.M. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. Ecol. Lett. **17**(8): 924–931. doi:10.1111/ele.12294. PMID:24811575.

Millspaugh, J.J., Brundige, G.C., Gitzen, R.A., and Raedeke, K.J. 2004. Herd organization of cow elk in Custer State Park, South Dakota. Wildl. Soc. Bull. **32**(2): 506–514. doi:10.2193/0091-7648(2004)32[506:HOOCEI]2.0.CO;2.

Miquelle, D.G., Peek, J.M., and Van Ballenberghe, V. 1992. Sexual segregation in Alaskan moose. Wildl. Monogr. **122**: 3–57.

Murray, D.L., Hussey, K.F., Finnegan, L.A., Lowe, S.J., Price, G.N., Benson, J., et al. 2012. Assessment of the status and viability of a population of moose (*Alces alces*) at its southern range limit in Ontario. Can. J. Zool. **90**(3): 422–434. doi:10.1139/z2012-002.

Nelson, M.E., and Mech, L.D. 1999. Twenty-year home-range dynamics of a white-tailed deer matriline. Can. J. Zool. **77**(7): 1128–1135. doi:10.1139/z99-085.

Northrup, J.M., Anderson, C.R, Jr., and Wittemyer, G. 2016. Environmental dynamics and anthropogenic development alter philopatry and space-use in a North American cervid. Diversity Distrib. **22**(5): 547–557. doi:10.1111/ddi.12417.

Olson, B.T., Windels, S.K., Moen, R.A., and McCann, N.P. 2016. Moose modify bed sites in response to high temperatures. Alces, **52**: 153–160.

Parker, K.L., Robbins, C.T., and Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. **48**: 474–488. doi:10.2307/3801180.

Patterson, B.R., Benson, J.F., Middel, K.R., Mills, K.J., Silver, A., and Obbard, M.E. 2013. Moose calf mortality in central Ontario, Canada. J. Wildl. Manage. **77**(4): 832–841. doi:10.1002/jwmg.516.

Patterson, B.R., Mills, K.J., Middel, K.R., Benson, J.F., and Obbard, M.E. 2016. Does predation influence the seasonal and diel timing of moose calving in central Ontario, Canada? PLoS ONE, **11**(4): e0150730. doi:10.1371/journal.pone.0150730. PMID:27082234.

Piper, W.H. 2011. Making habitat selection more "familiar": a review. Behav. Ecol. Sociobiol. **65**(7): 1329–1351. doi:10.1007/s00265-011-1195-1.

Popp, J.N., Schaefer, J.A., and Mallory, F.F. 2011. Female site fidelity of the Mealy Mountain caribou herd (*Rangifer tarandus caribou*) in Labrador. Rangifer, **31**(2): 87–95. doi:10.7557/2.31.2.1993.

Quinn, N.W.S. 2005. Reconstructing changes in abundance of white-tailed deer, *Odocoileus virginianus*, moose, *Alces alces*, and beaver, *Castor canadensis*, in Algonquin Park, Ontario, 1860–2004. Can. Field-Nat. **119**(3): 330–342. doi:10.22621/cfn.v119i3.142.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Rettie, W.J., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography, **23**(4): 466–478. doi:10.1111/j.1600-0587.2000.tb00303.x.

Schaefer, J.A., Bergman, C.M., and Luttich, S.N. 2000. Site fidelity of female caribou at multiple spatial scales. Landsc. Ecol. **15**(8): 731–739. doi:10.1023/A:1008160408257.

Severud, W.J., Obermoller, T.R., DelGiudice, G.D., and Fieberg, J.R. 2019*a*. Survival and cause-specific mortality of moose calves in northeastern Minnesota. J. Wildl. Manage. **83**(5): 1131–1142. doi:10.1002/jwmg.21672.

Severud, W.J., DelGiudice, G.D., and Obermoller, T.R. 2019*b*. Association of moose parturition and post-parturition habitat with calf survival. J. Wildl. Manage. **83**(1): 175–183. doi:10.1002/jwmg.21570.

Sevigny, J., Sevigny, M., George-Wirtz, E., and Summers, A. 2018. Spatial distribution, site fidelity, and home range overlap in the North Cascades Elk Herd: implications for management. Northwest Sci. **92**(4): 251–266. doi:10.3955/046.092.0403.

Sigouin, D., Ouellet, J.-P., and Courtois, R. 1997. Geographical variation in the mating and calving periods of moose. Alces, **33**: 85–95.

Spencer, W.D. 2012. Home ranges and the value of spatial information. J. Mammal. **93**(4): 929–947. doi:10.1644/12-MAMM-S-061.1.

Sweanor, P.Y., and Sandegren, F. 1989. Winter-range philopatry of seasonally migratory moose. J. Appl. Ecol. **26**(1): 25–33. doi:10.2307/2403648.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitat. Evol. Ecol. **7**(6): 533–555. doi:10.1007/BF01237820.

Testa, J.W., Becker, E.F., and Lee, G.R. 2000. Movements of female moose in relation to birth and death of calves. Alces, **81**: 155–163. doi:10.1093/jmammal/81.1.162.

Tremblay, J.-P., Solberg, E.J., Sæther, B.-E., and Heim, M. 2007. Fidelity to calving areas in moose (*Alces alces*) in the absence of natural predators. Can. J. Zool. **85**(8): 902–908. doi:10.1139/Z07-077.

Van Ballenberghe, V., and Miquelle, D.G. 1993. Mating in moose: timing, behavior, and male access patterns. Can. J. Zool. **71**(8): 1687–1690. doi:10.1139/z93-236.

van Beest, F.M., Mysterud, A., Loe, L.E., and Milner, J.M. 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J. Anim. Ecol. **79**(4): 910–922. doi:10.1111/j.1365-2656.2010.01701.x. PMID:20443990.

van Beest, F.M., Vander Wal, E., Stronen, A.V., Paquet, P.C., and Brook, R.K. 2013. Temporal variation in site fidelity: scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. Oecologia, **173**(2): 409–420. doi:10.1007/s00442-013-2647-2. PMID:23552985.

Viejou, R., Avgar, T., Brown, G.S., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., et al. 2018. Woodland caribou habitat selection patterns in relation to

predation risk and forage abundance depend on reproductive state. Ecol. Evol. **8**(11): 5863–5872. doi:10.1002/ece3.4124. PMID:29938099.

Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R., and Patterson, B.R. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. J. Wildl. Manage. **71**(4): 1249–1256. doi:10.2193/2006-263.

Webb, S.L., Dzialak, M.R., Harju, S.M., Hayden-Wing, L.D., and Winstead, J.B. 2011. Influence of land development on home range use dynamics of female elk. Wildl. Res. **38**(2): 163–167. doi:10.1071/WR10101.

Welch, I.D., Rodgers, A.R., and McKinley, R.S. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces, **36**: 93–103.

Wiles, G.J., and Weeks, H.P., Jr. 1986. Movements and use patterns of white-tailed deer visiting natural licks. J. Wildl. Manage. **50**(3): 487–496. doi:10.2307/3801111.

Wilton, M.L. 1983. Black bear predation on young cervids — a summary. Alces, **19**: 136–147.

Wiseman, P.A., Carling, M.D., and Byers, J.A. 2006. Frequency and correlates of birth-site fidelity in pronghorns (*Antilocapra americana*). J. Mammal. **87**(2): 312–317. doi:10.1644/05-MAMM-A-180R1.1.

Wolf, M., Frair, J., Merrill, E., and Turchin, P. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. Ecography, **32**(3): 401–410. doi:10.1111/j.1600-0587.2008.05626.x.