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.

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; Crampé et al. 2007; Faille et al. 2010; Brought 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; Crampé 1999) and may be independently developed from a genetic predisposition (van Beest et al. 2013).
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 (Alex alces [Linnaeus, 1758]; Welch et al. 2000), elk (Cervus canadensis [Erxleben, 1777]; Millsap 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]; Vors et al. 2000; Vors 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 (Björneräs 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 benefiting 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; Wiseman et al. 2006; Colson et al. 2016). Hence, knowledge of these areas may inform forest management strategies aimed at benefiting moose populations. 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 km²) and the eastern region of Wildlife Management Unit 49 (WMU49; 1280 km²) (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.), Carriere, 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).

We obtained GPS data collected over 3 h for 1 year 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 (+SE) age of GPS-collared moose included in our analysis from APP and WMU49 was 4.0 ± 0.4 (range: 1–7) and 3.9 ± 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 geographical 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 female moose in APP to WMU49. 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 ecological 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.


Published by Canadian Science Publishing
(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. \[ \text{Distance} \sim \text{maternal age} + \text{study area} \]

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. \[ \text{Distance} \sim \text{biological season} + \text{study area} \]

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 \( 0.10 \leq p \leq 0.05 \).

**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...
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 (\(l_{[864]} = 4.69, p = 0.0001\)), but not maternal age (\(l_{[656]} = -0.58, p = 0.56\)), 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 (\(l_{[656]} = -0.32, p = 0.75\)), post-calving (\(l_{[656]} = 1.31, p = 0.19\)), or breeding (\(l_{[656]} = -0.42, p = 0.68\)) seasons from the calving season. However, inter-annual location differences were significantly farther apart during the winter season (\(l_{[656]} = -8.09, p < 0.0001\)) compared with the calving season (Fig. 2a). For moose that had a calf in only 1 of 2 consecutive years, interannual location distances were not statistically different during the pre-calving (\(l_{[656]} = -0.01, p = 0.99\)) or breeding (\(l_{[656]} = 0.79, p = 0.43\)) seasons from the calving season. But for these moose, the differences in the distances of inter-annual locations were significantly greater during the post-calving (\(l_{[656]} = -2.14, p = 0.033\)) and winter (\(l_{[656]} = -4.41, p < 0.0001\)) seasons compared with the calving season (Fig. 2b). 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 (471 ± 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; Millsbaugh 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 (Renkobi 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.

| 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 x 10^-4 | 2.6 x 10^-5 | 1529 | 16.93 | <0.0001 |
| Age | 3.2 x 10^-5 | 5.5 x 10^-6 | 1529 | -0.58 | 0.56 |
| Study area | 1.0 x 10^-4 | 2.2 x 10^-5 | 27 | -4.69 | 0.0001 |
| **Distance ~ biological season + study area** | | | | | |
| Intercept | 7.0 x 10^-4 | 7.9 x 10^-5 | 864 | 8.78 | <0.0001 |
| Pre-calving | -1.7 x 10^-5 | 5.5 x 10^-6 | 864 | -0.32 | 0.75 |
| Post-calving | 7.8 x 10^-5 | 5.9 x 10^-5 | 864 | 1.31 | 0.19 |
| Breeding | -2.1 x 10^-5 | 5.1 x 10^-5 | 864 | -0.20 | 0.86 |
| Winter | -4.3 x 10^-4 | 5.3 x 10^-5 | 864 | -0.80 | <0.0001 |
| Study area | 8.1 x 10^-5 | 9.6 x 10^-5 | 16 | 0.84 | 0.41 |
| **Distance ~ biological season + study area** | | | | | |
| Intercept | 6.2 x 10^-4 | 7.5 x 10^-5 | 656 | 8.21 | <0.0001 |
| Pre-calving | -1.5 x 10^-4 | 7.2 x 10^-5 | 656 | -2.14 | 0.033 |
| Post-calving | 8.4 x 10^-7 | 7.1 x 10^-5 | 656 | -0.01 | 0.99 |
| Breeding | 6.0 x 10^-5 | 7.6 x 10^-5 | 656 | 0.79 | 0.43 |
| Winter | -2.8 x 10^-4 | 6.3 x 10^-5 | 656 | -4.41 | <0.0001 |
| Study area | 6.8 x 10^-5 | 6.2 x 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.
were at least 1.5 years old during the operating in both study areas. All moose included in our analysis specifying that prior knowledge of sites providing access to male con- also exhibited site familiarity during the breeding season, suggest- ing 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. 2019), explaining why fidelity was similar for females between years from mid- 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 area 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

This study was part of a larger assessment of moose viability funded primarily by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant and an equipment grant from the Canadian Foundation for Innovation (CFI), both granted to D. Murray (Trent University). Primary funding for the work described here was provided by the Ontario Ministry of Natural Resources and Forestry, through Ontario Parks and the Wildlife Research and Monitoring Section. A. Silver and M. Gibson assisted greatly with logistical arrangements related to calf captures. We further thank the many students, volunteers, and technicians who participated in field searches for moose calves. We also thank R. Found and two anonymous reviewers who provided useful suggestions on an earlier draft of the manuscript.

References


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 (McLoughlin 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- 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).

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.

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; Bjerntaas 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.

During first autumn of our study period females showed modestly weak fidelity during calving and post-calving periods, but this fidelity was higher 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- 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).


