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Seasonal Variation in Site Fidelity of Moose (Alces alces)

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“ (what the researcher) is actively and constantly aware of is his ignorance, not his knowledge; the insufficiency of his concepts, of the terms and phrases in which he tries to excogitate his problems: not their final and exhaustive sufficiency. He is, therefore, usually only a good teacher for the few who wish to use their mind as a workshop, rather than a warehouse.”

R.A. Fisher, 1935

Abstract

Species across many taxa display site fidelity, the tendency to return to previous used areas, particularly during important periods of life, such as at mating and reproduction. In general, it is expected that familiarity to an area is beneficial, and the ability to return to the same area for specific life history events should therefore have a fitness benefit. Efficient wildlife management relies on good knowledge about the tendency of the target species to display site fidelity. Here, I investigated to what extent moose show seasonal variation in site fidelity and to what extent site fidelity was related to sex, reproductive status and the tendency to conduct seasonal migration. I expected site fidelity to vary according to the costs and benefits of sex and reproductive status, and that site fidelity in spring and autumn was low due to large annual variation in important environmental conditions (green-up and snow fall). Absolute site fidelity was measured as the distance between the location on a given date and the location on the same date the following year, where a short distance indicates high site fidelity. I also calculated a relative measure of site fidelity as the absolute site fidelity after accounting for individual space use. The results revealed that site fidelity was highest in summer and lowest in autumn. Resident moose displayed higher site fidelity than migratory and females more than males, whereas no differences were found between reproductive statuses of females. During the rutting/hunting period, males showed considerably lower site fidelity than females, while there was no difference between females of different reproductive status. These results suggest that the accuracy of predicting an individual's location from one year to the next varies with sex and movement strategy and is particularly low for migratory male moose in autumn. The results may have several implications for management. For instance a more precise population estimates can be obtained by performing censuses during the period of the year with high site fidelity, i.e. late summer or mid-winter. Furthermore, as the migratory part of the population may show large annual variations in local densities it is essential that knowledge exists about the general movement patterns in the population. Combined, these aspects call for a large-scale management of Norwegian moose populations.

Sammendrag

Mange arter viser stedtrofasthet, de vender tilbake til tidligere brukte områder, spesielt i viktige perioder for livshistorien, f.eks. reproduksjon. Generelt er det forventet at stedtrofasthet er fordelsaktig, og at muligheten til å kunne vende tilbake til kjente områder i viktige perioder har en positiv effekt på fitnessen. Effektiv viltforvaltning er avhengig av god kunnskap om hvor stor grad en art er stedtrofast. Jeg undersøker i hvilken grad stedtrofasthet varierte med kjønn, reproduksjonsstatus og om individet gjennomføre årlige migrasjoner. Jeg forventet at stedtrofasthet ville variere ut fra kostnader og fordeler hos kjønn, reproduksjonsstatus, og at stedtrofastheten ville være lavere på høsten og våren grunnet høy årlig variasjon i viktige miljøfaktorer (f.eks. vegetasjonsvekst og snøsmelting). Absolutt stedtrofasthet ble målt som avstanden mellom en lokasjon på en gitt dato og lokasjonen på samme dato et år senere, hvor en kort avstand indikerer høy grad av stedtrofasthet. I beregnet også et relativt mål av stedtrofasthet hvor jeg tok høyde for individiduelle variasjoner i rombruk. Resultatene viste at stedtrofastheten var høyest på sommeren og lavest på høsten. Stasjonær elg hadde høyere stedtrofasthet enn trekkende elg, elgokser høyere enn kyr, og ingen forskjell mellom reproduktiv status hos elgkyr. I brunsten/jakten viste elgokser betraktelig lavere grad av stedtrofasthet enn elgkyr, mens det var ingen forskjell på reproduktiv status hos elgkyr. Resultatene viser at nøyaktigheten av å forutsi et individs lokasjon fra et år til det neste variere ut fra indvididets kjønn og bevegelsesstrategi, og trekkende hanner har spesielt lav stedtrofasthet på høsten. Dette har flere konsekvenser for forvaltningen. For eksempel vil mer presise estimat av bestandsstørrelser kunne bli innhentet på i perioder med høy grad av stedtrofasthet, f.eks. sommer eller midtvinters. Videre vil andelen av trekkende elg i en bestand vise store årlige variasjoner i lokale bestandstettheter, noe som forvaltningen må ta høyde for. Som konklusjon fører disse resultatene til at forvaltningen av elg i Norge må være på en stor skala.

Contents

Introduction

Animal movement - the process by which individual organisms are displaced over time (Turchin 1998) - is essential for the distribution and abundance of individuals in time and space. The ability for humans to predict the distribution of animals has always been important, as animal populations constitute both valuable resources and may pose threats to human welfare. For instance, sustainable harvesting of migratory populations, such as fish stocks, and several ungulate and bird species, require knowledge of the timing of movement into harvesting areas (Keefer et al 2004). Recently, managers have become aware of the importance of the spatial scale of wildlife management (e.g. Linnell et al 2001; Linnell 2005). This has resulted in an increased focus on borderless management (Linnell and Boitani 2011), particularly of populations with large-scale movements. However, the spatial scale of individual movement often varies between and within populations (Herfindal et al 2005; Bunnefeld et al 2011), and finding the appropriate scale for management of wildlife populations can be difficult. Individual variation is often state-dependent, movement patterns, for instance due to sex (van Beest et al 2013), reproductive status (Rettie and Messier 2001) or movement strategy (Berger 2004). Such variation in movement behaviour may therefore pose a challenge to wildlife managers, because management actions should potentially differ between age- and sex-classes in order to obtain sustainable and predictable population dynamics (Langvatn and Loison 1999)

Animals which return to a previously visited location are said to show site fidelity (Switzer 1993). Site fidelity is expected to be beneficial for a number of factors, the most important being decreased costs of exploring new areas, establishment and familiarization with environmental conditions (Piper 2011). The consequence can be increased individual survival (Wolf et al 2009) and recruitment (Hoover 2003), which may also increase population viability (Schmidt 2004). As a consequence, species across many taxa tend to return to previously used areas, i.e. they display site fidelity. For instance, the migratory prothonotary warblers (*Protonotaria citrea*) display higher site fidelity to areas with previously high reproductive success compared to areas where reproduction failed (Hoover 2003), whereas broadnose sevengill sharks (*Notorynchus cepedianus*) were found to return to previously used feeding grounds during summer, more than 900 km from their wintering areas Barnett et al (2011). On a smaller spatial and temporal scale, two species of lizards (*Anolis gundlachi* and *Anolis cristatellus*) showed diurnal patterns in site fidelity by returning to the same locations for sleeping during night (Clark and Gillingham 1990). However, displaying high site fidelity may also involve a cost, for instance by causing the individual to overlook areas of higher quality. The slow recovery of southern right whales (*Eubalaena australis*) may be due to that individuals utilizing feeding grounds with diminishing food availability, and high site fidelity towards previous feeding grounds hindered the utilization of available and higher-quality areas (Valenzuela et al 2009).

Although the adaptive significance for displaying site fidelity is evident for many species (see above), many environments are rather predictable at the appropriate spatial and temporal scale, which may affect animal movement pattern. Seasonal fluctuation in environmental conditions are generally predictable, and is claimed as one of the most important drivers for the occurrence of migratory movement patterns (Milner-Gulland et al 2011). This has been proposed as a driver for the migratory behaviour of golden takin (*Budorcas taxicolor bedfordi*), which seems to follow the phenological development of plants, resulting in utilizing the same areas at the same time each year due to the high spatial autocorrelation in the timing of plant phenology (Zeng et al 2010). Thus, site fidelity may not be a result of animals showing preference for previously visited and familiar areas, but because high spatio-temporal covariation in environmental conditions leads to movement into the same areas at the same time in consecutive years.

In Scandinavia, the moose (*Alces alces*) is considered the most important wildlife resource (Lavsund et al 2003; Solberg et al 2012) and due to intense management of moose and forests the moose population size has increased manifold since the 1970s (Solberg et al 2012). Moose hunting generates considerable values annually, both in terms of income and recreational opportunities for the local landowners (Storaas et al 2001). Much research is therefore conducted to improve the management of moose populations. One important action is to collect relevant data used for deciding the annual hunting quotas. Quotas are presently based primarily on indexes of change in population size, which are based on observations and harvested data collected by hunter during the hunting season (September through October) (Solberg et al 2010).

For managers, it is important to know to what extent moose show site fidelity, and to what extent this varies between groups of individuals and seasons. Given the large-scale movement patterns of moose in large parts of Norway (Rolandsen 2012), it is of particularly importance to know at what spatial scale abundance data should be sampled to precisely capture the population dynamics. For instance, if the timing of the large-scale seasonal movements in moose varies annually, density indices based on data collected at the municipal level in autumn may contain considerable variation which is not related to variation in population size. The same may be true if there are state-specific patterns in the extent individuals return to similar areas, as indices of population structure may then fail to capture the dynamics of the age and sex-structure in the population.

However, high-abundance moose populations also come with a cost, such as the observed increase in moose-vehicle collisions with increasing moose densities (Rolandsen et al 2011), and browsing damages on regenerating forest stands (Wam and Hofstad 2007). Often, the timing and location of costs do not overlap with the benefits, for instance browsing damages do not occur on the same properties which receive the income from hunting. Such socioeconomic costs have increased the focus on the spatial scale of management (Skonhoft 2005) and the importance of understanding how moose movement is predictable in time and space. It is also important to know if factors posing costs (i.e. traffic accidents, forest damage) are predictable in time and space in order to efficiently implement actions to reduce costs. This could involve warning signs at roads when moose crossing frequency is high, and culling of individuals that cause forest damage.

In this study, I aim to describe the level of site fidelity of moose in a population in central Norway. I do this by investigating individual variation in site fidelity, measured as the displacement between locations at the same dates, but between two consecutive years. This allows me to describe site fidelity throughout the year, and to test the prediction (P1) that site fidelity is higher during periods that are more predictable (Switzer 1993). In my study area, summer and winter represent the seasons with highly predictable resource distribution, whereas during spring and autumn weather change causes rapid changes in spatial distribution of resources. The large annual variation in the timing of these changes (Karlsen et al 2009) is likely to cause lower site fidelity during spring and autumn if site fidelity is caused by environmental tracking, but to a smaller extent if site fidelity is caused by preference for familiar area at a specific time during the year. Although my main focus will be on the entire year, I will also do more detailed analyses during rutting/hunting period, as this is the period of moose monitoring, as well as the period when mating causes gene flow through the population.

In moose, males use larger areas than females (Herfindal et al 2009; van Beest et al 2011; Bjørneraas et al 2011), which can be explained by the higher food demand of males due to their larger body mass (Harestad and Bunnel 1979). I expect this larger space use by males to result in lower site fidelity (prediction P2.1), all else being equal between males and females. However, females may benefit from a more risk-averse behaviour, as they for the greater part of the year are constrained by the higher predation risk of their offspring at foot and trade high-quality foraging for cover (Bjørneraas et al 2012). Females without offspring are less constrained with respect to mortality risk, and can be expected to have a male-like movement pattern (Bjørneraas et al 2012). Assuming that the annual variation in distribution of shelter is more stable than food abundance and quality, females with offspring should therefore display higher site fidelity than males and females without offspring (prediction P2.2).

Many fennoscandian moose populations are partially migratory (Ball et al 2001; Rolandsen 2012), meaning that some individuals perform long-term range-shifts between summer and winter areas, whereas other stay resident in the same area throughout the year (Chapman et al 2011). This introduces an additional source of variation in individual movement patterns which can affect the level of site fidelity in a population. I therefore also test if the seasonal pattern in site fidelity varies among migratory and resident moose. Migratory routes and timing of migration of moose may be affected both by parental imprinting and yearly variation in snow and vegetation distribution (Sweanor and Sandegren 1989; Andersen 1991a; Ball et al 2001; Bunnefeld et al 2011; Rolandsen 2012). Thus, migratory moose may either 1) display higher site fidelity than resident moose due to a more fixed movement behaviour, which may be optimal on a long-term average (prediction P3.1), or, 2) display lower site fidelity than resident moose as their long-distance movement to a larger extent is shaped by environmental stochasticity which varies among years (prediction P3.2).

Because the level of site fidelity may depend on the spatial scale of movement, I will test for differences in displacement between years both at the absolute scale, and at the relative scale where I account for individual scale of movement. This allows me to disentangle mechanisms related to scale of movement (e.g. males using larger areas than females, and migratory individuals moving over larger areas than resident) from mechanisms related to other factors such as degree of environmental tracking or state-dependent habitat selection.

Method

Study area and moose population

The study area is the county of Nord-Trøndelag and the two adjacent municipalities of Rissa and Bindal in Sør-Trøndelag and Nordland county, respectively (total area: 24 295 km^2, Figure 1). The study area is inhabited by approximately 11,000 moose (Rolandsen et al 2010). The landscape is dominated by fjords and valleys running from south-west to north-east direction.

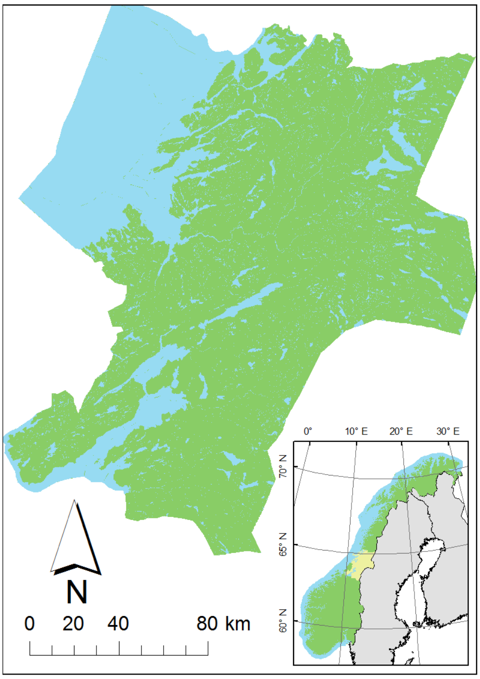

Figure 1: The study area, Nord-Trøndelag County and the municipalities of Rissa and Bindal in central Norway. Projected on WGS1984 UTM Zone 32N

Much of the study areas is forested, where the main tree species are spruce (*Picea abies*) and birch (*Betula pubescens*) (Moen 1999). Only 2% of the area is above 900 m.a.s.l. Agricultural land is mainly found in the valley floors and closer to the fjord in the south. The area is sparsely populated (5.9 per km^2), with the highest concentration in coastal towns Stjørdal, Steinkjer, Namsos and Levanger (Statistics Norway, www.ssb.no).

During the period 2006-2008 the average winter temperature (January - April) was 0°C and summer temperature (June) was 13 °C. Average snow depth was 25 cm between December and April (Rolandsen et al 2010).

The moose population in the study area is partially migratory, where approximately half of the population migrate from winter ranges, usually at lower altitudes, to summer ranges at higher altitudes (Rolandsen et al 2010). The onset of autumn migration is triggered by snow fall and normally takes place in November and the first week of December, while spring migration typically starts in the two last weeks of April or the two first in May. Migratory males move considerably further than migratory females, on average 38 km and 25 km, respectively (Rolandsen et al 2010).

The predation rates on moose are generally low in Norway (Stubsjoen et al 2000), and the same is true in my study area. During 2006 - 2010 only 6 of 247 collared moose were killed by bears (*Ursus arctos*) (Rolandsen et al 2010).

Data collection

Moose positions were collected with GPS collars, of type VECTRONIC Aerospace GmbH, in the project “Elgundersøkelsene i Nord-Trøndelag, Bindal og Rissa 2005-2010” (Rolandsen et al 2010). The GPS-collars were programmed to obtain a location every 2 hours, and the data were screened for location errors following the method of Bjørneraas et al (2010). A total of 171 individuals were marked with GPS-collars. However as the design of my study required at least two years of continuous data to obtain measures of site fidelity, the number of moose in my study was limited to 57 individuals monitored in the period 2006-2010. Due to periodically failed location fixes and different sampling regimes, not all animals had the same sampling intensity. I therefore resampled the data to eight random locations each day, assuming that the sample bias within a day would be minimal. For each individual moose, I had information about sex, reproductive status (females with calves in both years, or in only one of the two years for which site fidelity was calculated) and movement strategy (resident or migratory) (Table 1). Individuals were termed migratory if summer and winter ranges did not overlap (Rolandsen 2012), otherwise they were termed resident (stationary). Females with a single calving during the two years included two migratory individuals that calved only in the first year, and one migratory and three resident females that calved only in the second year. In the analyses I do not differentiate between females that calved in the first or second year, and assume that the effect will be independent of the reason for not having a calf.

Table 1: The number of resident and migratory individuals used to analyse site fidelity among months, and during rutting/hunting period. The reproductive status was classified according to whether females performed either one single calving in two consecutive years ("Female 1") or two calvings during the two consecutive years ("Female 2"). Total sample size is given in parentheses.

	Monthly (57)		**Rutting/hunting (49)**	
Reproductive status	Resident	Migratory	Resident	Migratory
Male	9	15	5	7
Female 1	3	3	4	3
Female 2	10	17	14	16

The rutting/hunting period was defined as the period between the 20th of September and 20th of October, with an expected peak between 30th of September and 2nd of October (Garel et al 2009; Rolandsen et al 2010).

Site fidelity measures

I used two measures of site fidelity. The absolute site fidelity was defined as the euclidian distance between the centre location in a given week, from one year to the next (AD, Eq. 1, Figure 2), (Wittmer et al 2006; Tremblay et al 2007). Each week was assigned to the month including the majority of days.

Because space use varies among individuals (van Moorter et al 2013), I also calculated a relative measure of site fidelity (RD, Eq2, Figure 2). In this measurement I accounted for individual variation in space use by subtracting the mean distance between all daily locations during the week site fidelity was measured in both years ($\overline{d_j}$,$\overline{d_k}$, for year j and k) from AD (Eq1, Figure 2). Degree of site fidelity can be considered the inverse of the between year distance, i.e. high AD or RD means low degree of absolute and relative site fidelity, respectively.

$$AD_{week} = d_{week} \tag{1}$$

$$RD_{week} = AD_{week} - \frac{\overline{d_j} + \overline{d_k}}{2} \tag{2}$$

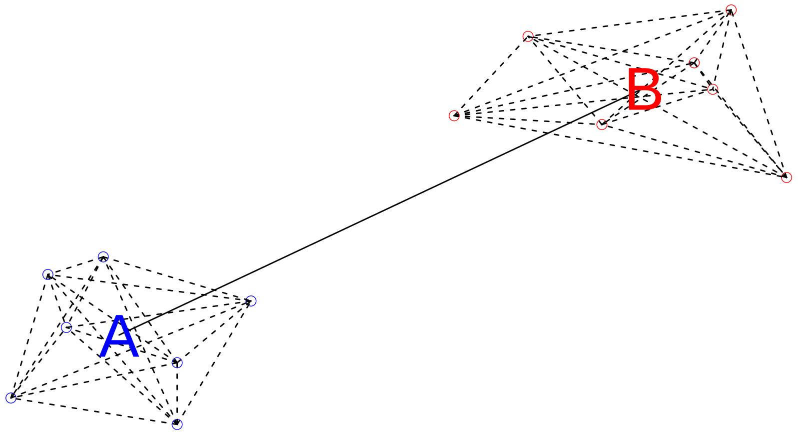

Figure 2: Illustration of how absolute site fidelity and relative site fidelity was calculated. The figure shows a paired seven-day period in two consecutive years, where A and B are the centre locations. The solid line is the between-year distance, while the dashed lines represent the within-week distances. Absolute distance (AD) is the length of the solid line, whereas the relative distance (RD) is the difference between the length of the solid line and the mean length of the dashed lines.

If the between-year displacement is lower than the average within-week displacement, the RD will be negative and the individual shows high relative site fidelity. In contrast, if the distance between centre locations of the same week in two consecutive years is higher than the average daily movement, the RD will be positive, meaning that the individual show low relative site fidelity. Seven-day periods were chosen for both the monthly and rutting/hunting analyses.

Statistical analyses

Due to repeated data on individuals, I used linear mixed models with moose identity as a random factor in all analyses. An initial inspection of the absolute site fidelity showed that residuals were strongly skewed. I therefore ln-transformed the absolute site fidelity measure to normalise the residuals. No transformation was necessary for the relative site fidelity measure. Temporal autocorrelation of the residuals of the fitted models was explored, and considered to be of negligible magnitude.

For site fidelity during the year and for rutting/hunting period, I run parallel analyses on AD and RD with similar modelling procedures. To select the most parsimonious model I ranked all candidate models according to the Akaike Information Criterion (AIC) with correction for small sample size (AICc; Burnham and Anderson 2002). AIC is an estimate of the distance between the candidate models and the unknown process generating the data, and the model with the lowest AICc is assumed to be the best model explaining the variation in the data. However, if ΔAICc between two models was <2 they were assumed equal in describing the empirical data. I also calculated AICc weights for each model set. AICc weights give an estimate of the strength of evidence for a model and can be interpreted as the probability of a model being the best, given a set of alternative models and the data (Burnham and Anderson 2002). To further examine the strength of one model in favour of another I calculated evidence ratios, AIC-weight$_{r}atio$ = AIC-weight$_{m}odel1$ / AIC-weight$_{m}odel2$ (Burnham and Anderson 2002). AICc values were computed based on Maximum Likelihood (ML) estimates of the log-likelihood for a model, while parameter estimates were calculated using Restricted Maximum Likelihood (REML) (Zuur 2009).

To further evaluate the uncertainty of the parameter estimates, I resampled the estimates from the posterior parameter distribution of the highest ranked model. Using 10 000 Markov Chain Monte Carlo samples, I constructed 95 % confidence intervals of each variable from the posterior distribution (as recommended for large/unbalanced datasets by Baayen et al 2008; Bolker et al 2009).

The within-year variation in site fidelity was modelled with month, sex and reproductive status and movement strategy included as categorical fixed explanatory variables. To simplify modelling, sex and reproductive status were combined to one categorical variable (SRS) with three levels: male, females with one single calving in two consecutive years and females with two calvings in two consecutive years. I also included an interaction between movement strategy and month, as the distinct behaviour of migratory moose during spring and autumn might affect site fidelity. In addition, as males and females may differ in behaviour during rutting/hunting period, and have seasonally dependent energy allocation, I included the two-way interaction between sex and month in the global model.

Individual variation in site fidelity during rutting/hunting was analysed at a weekly level with data between 20th September and 20th October. Week number, SRS and movement strategy were included as categorical variables. In addition to the main effects, I included all the three two-way interactions. The interaction between SRS and week was included to assess whether the differences between males and the reproductive statuses of females changed as the rutting/hunting period progressed next, the interaction between movement strategy and week allowed me to test if site fidelity of migratory moose decreased as the rut progressed. The interaction between SRS and movement strategy was included to test whether the effect of SRS depended on movement strategy. Finally, I also included the full three-way interaction, which allowed me to assess if the differences between SRS were affected by movement strategy as the rut progressed.

All statistical analyses were done in R for windows version 2.15.0 (R Development Core Team 2012), where the mixed models (family=Gaussian) were run within the package lme4 (Bates et al 2012).

Results

The level of site fidelity varied much among categories of moose. The absolute distance between years (AD) of migratory moose was on average 7681 m (SD = 10714), whereas resident moose had an average AD of 2969 m (SD = 3679). Females had an AD of 4882 m (SD = 8506), whereas males' AD was 7806 m (SD = 9874). Females with one or two calvings during a two year period had AD of 5851 m (SD = 8330) and 4704 m (SD = 8530), respectively.

Relative distance between years (RD) showed similar patterns to AD among categories. The RD was on average 5768 m (SD = 10415) for migratory and 1819 m (SD = 3563), for resident moose. Males had higher values of RD than females, 5757 m (SD = 9561) and 3490 m (SD = 8239), respectively. Females with a single calving during a two year period showed higher RD than females with two calvings during a two consecutive years, 4225 m (SD = 7790) and 3351 m (SD = 8315), respectively.

Monthly variation in site fidelity

The highest ranked model regarding monthly variation in AD included the sex and reproductive status (SRS), movement strategy and month, as well as the two-way interactions SRS × month and movement strategy × month (AICc=6813.14, 2a). No alternative models had a ΔAICc<2. The highest ranked model for RD had the same explanatory variables and interactions as the one for AD (AICc = 46818.68, 3b). No alternative models for RD received considerable support (all ΔAICc>2, 2b).

The highest ranked models suggested that site fidelity measure at the absolute scale (AD) varied during the year (Figure 3). In general, moose showed highest site fidelity during summer and lowest during autumn, supporting my prediction that moose are more faithful to an area during seasons with more predictable resource distribution (P1). However, when accounting for individual space use (RD) the monthly differences in site fidelity were mainly absent in resident moose (Figure 3d), which may suggest that seasonal variation in absolute displacement in resident moose is related to higher movement rates this season. Regarding sex-differences in site fidelity (P2.1), females tended to be closer to the previous year's location than males both at the absolute and relative measure of site fidelity (females had lower values of AD and RD compared to males, Figure 4a,b,d,e), supporting the prediction that females in general are more faithful to their area of use (Prediction 2.1). However, as monthly values of AD and RD did not differ between females with calving in one or both years (Figure 4c,d), I found no support for my prediction that the reproductive status of females affected site fidelity (Prediction 2.2). Furthermore, I found only partially support for migratory moose being less faithful to their areas than resident moose, as difference in AD and RD were only evident in spring and autumn (Figure 5a,b). The difference in site fidelity between resident and migratory moose was significant (95% CI of difference did not overlap zero) in more months when measured as AD (8 months) than RD (5 months, Figure 5). The monthly variation in site fidelity among resident moose showed less clear seasonal patterns than for migratory moose (Figure 3), particularly when measured as RD. That the seasonal pattern in site fidelity among migratory moose were mainly similar when measures as AD or RD (Figure 3a,c), suggests that the monthly variation in site fidelity is not caused by variation in scale of movement, but rather caused by seasonal variation in environmental conditions that affect when and where to go.

Table 2: The five highest ranked models, according to AICc, explaining monthly variation in absolute site fidelity (a) and relative site fidelity (b) of moose in central Norway. The explanatory variables included sex and reproductive status (SRS), movement strategy (M) and month as well as all two-way interactions. A × indicates an interaction, and always include the main effects.

	Rank	Model	ΔAICc	AIC-weight
a)	1	Month × SRS + Month × M	0.00	0.78
	2	SRS + Month × M	2.95	0.18
	3	Month × M + SRS × M	5.78	0.04
	4	Month × M	10.94	<0.01
	5	M + Month × SRS	26.99	<0.01
b)	1	Month × SRS + Month × M	0.00	>0.99
	2	M + Month × SRS	16.08	<0.01
	3	SRS + Month × M	17.00	<0.01
	4	Month × M	18.43	<0.01
	5	Month × SRS + SRS × M	20.08	<0.01

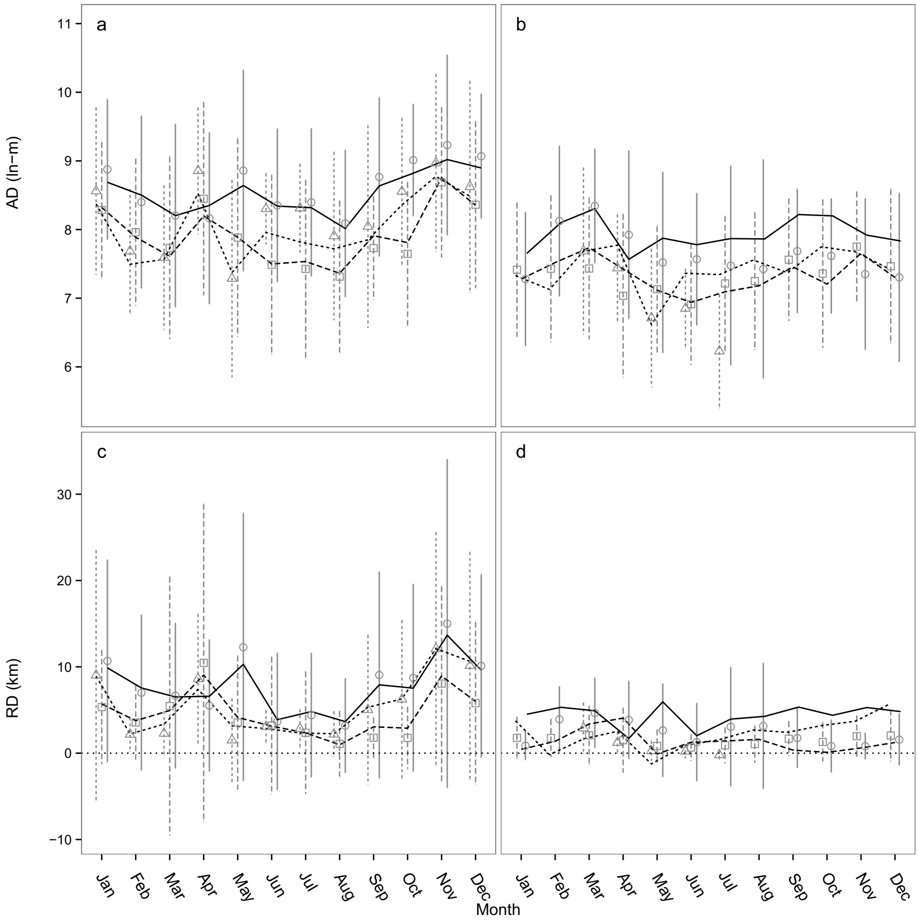

Figure 3: Monthly variation in absolute (a, b) and relative (c, d) site fidelity of a migratory (a, c) and resident (b, d) moose in central Norway. Grey colour indicates measured mean ± SD), while black colour indicates estimated mean site fidelity. Males = solid line/circle, Female 1 = dotted line/triangle, Female 2 = dashed line/square. A high value of AD or RD corresponds to low site fidelity.

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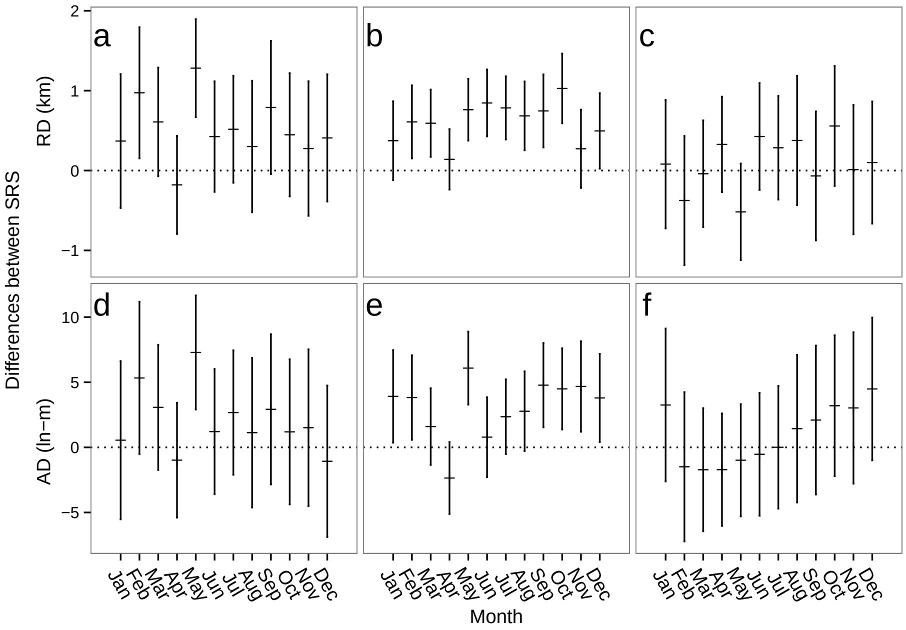

Figure 4: Estimated differences in AD (d-f) and RD (a-c) between females with a single or two calvings (c, f), males and females with two calvings (b, e), and males and females with a single calving (a, d) in two consecutive years , with bars indicating 95 % CI. Positive values indicate that individuals in the latter group display higher site fidelity than the former.

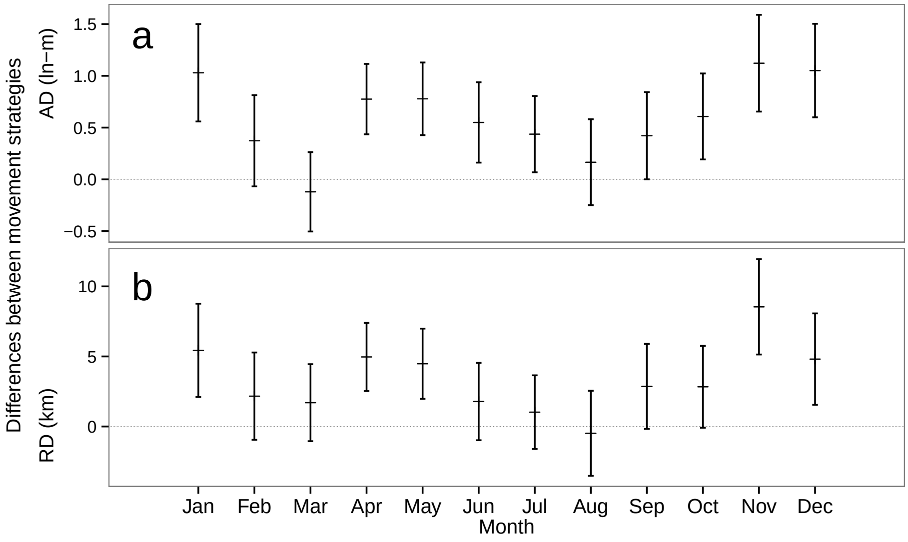

Figure 5: Estimated differences in AD (a) and RD (b) between migratory and resident moose in central Norway, with bars indicating 95 % CI. A positive value of AD/RD indicate lower site fidelity of migratory moose compared to resident moose.

Site fidelity during rutting/hunting

The AICc-based model selection regarding AD during rutting/hunting showed that the highest ranked model included SRS and movement strategy, as well as their interaction (Table 3a). No alternative models for AD received considerable support (all ΔAICc>2, Table 3a). Regarding RD during rutting/hunting showed that four candidate models had ΔAICc<2 (Table 3b). The highest ranked model included week and SRS (Table 3b). This model had an evidence ratio of 1.41, and the variables included were also present in the majority of the highest ranked models (Table 3b). Consequently, I found the highest ranked model to be the most likely of the candidate models for explaining absolute site fidelity during the rutting/hunting period.

According to the highest ranked model for AD, migratory females were more faithful to their area during rutting/hunting period than migratory males (Figure 6a), and migratory females with two calvings in two consecutive years were somewhat more faithful than migratory females with a single calving. There were only minor differences between SRS-groups among resident moose (Figure 6a). The highest ranked model regarding variation in RD during rutting/hunting suggested that site fidelity decreased during the four first weeks of the period, and then increased the last week (Figure 6b). Moreover, males had considerably higher RD (lower displacement) than females, but there were only minor differences among females depending on their reproductive status (Figure 6b).

Table 3: The five highest ranked models, according to AICc, explaining variation in AD (a) and RD (b) during rut among moose in central Norway. The explanatory variables included sex and reproductive status (SRS), movement strategy (M) and week (W) as well as all two-way interactions. A × indicates an interaction, and always include the main effects.

	Rank	Formula	AICc	ΔAICc	AICc-weights
a)	1	M × SRS	647.59	0.00	0.66
	2	M + SRS	650.92	3.33	0.13
	3	SRS + W + M + SRS × M	651.25	3.66	0.11
	4	SRS	652.28	4.68	0.06
	5	SRS + W + M	654.24	6.65	0.02
b)	1	Week + SRS	4788.12	0.00	0.24
	2	SRS	4788.83	0.72	0.17
	3	SRS + Week + M	4788.95	0.83	0.16
	4	M + SRS	4789.58	1.46	0.12
	5	SRS + Week + M + SRS × M	4790.31	2.19	0.08

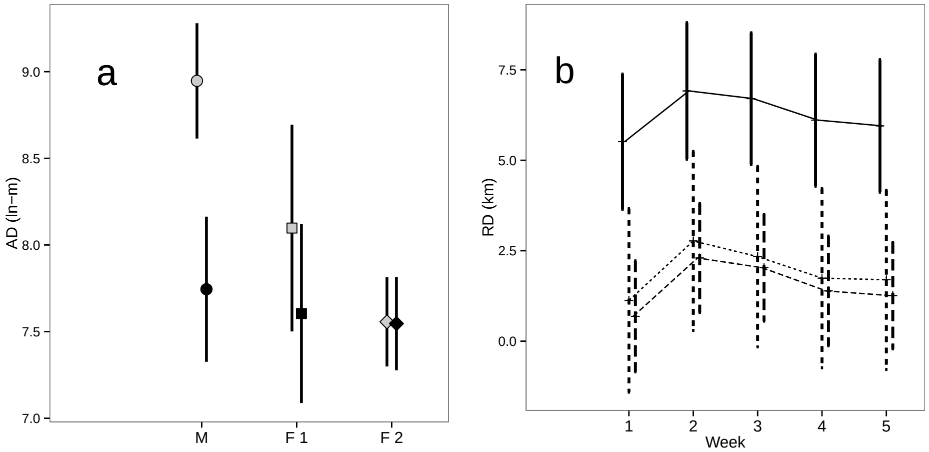

Figure 6: Variation in moose AD (a) and RD (b) during rut in central Norway. a) Weekly estimated mean AD for migratory (grey) and resident (black) males (circle), females with single calving (square) and females with two calvings (diamond) in two consecutive years, b) weekly estimated mean RD for males (solid), females with single calving (dotted) and females with two calvings (dashed) in two consecutive years. A high value of AD or RD corresponds to low site fidelity.

Discussion

By using an extensive dataset on GPS-marked moose, I described within-year variation in site fidelity, and tested whether this pattern differed depending on individual characteristics such as sex, reproductive status and movement strategy. I found that the faithfulness to an area was highest during summer (P3, Figure 3), and lowest during spring and autumn. In addition, a large part of the variation in site fidelity could be explained by individual movement strategy and reproductive status. My results suggest that the ability to predict to what extent individuals return to the same area at the same time in two different years depends on 1) the focal month and 2) the segment (sex, reproductive status, movement strategy) of the population of interest. This has consequences for the precision of population indices based on seasonal counts, and consequently for many tools which are used to manage Norwegian moose populations. Below I discuss my results in relation to moose biology and animal movement ecology, and end with some considerations regarding improvement of Norwegian moose management.

Norwegian moose lives in highly seasonal environments (Bjørneraas 2012). Such environments often invoke repeated movement patterns (Milner-Gulland et al 2011), where movement during the more stable seasons (normally summer and winter) is more predictable than during the seasons with large changes in environmental conditions (spring and autumn). Seasonal patterns have been found in habitat utilization (Bjørneraas et al 2011) and in the scaling of movement patterns (van Moorter et al 2013). In line with these studies, I found that the level of site fidelity varied during the year, where moose had higher displacement (lower site fidelity) in spring and autumn, whereas distances between observations from two consecutive years were shorter during winter and summer (Figure 3). This does not necessarily mean that moose were not found in the same areas during spring and autumn, but that the timing of being in that area would differ from year to year. Due to annual variation in weather conditions, the timing of important environmental events, such as the end of the growing season, the first snow fall, the timing of snow melting and the start of vegetation green-up, is often highly variable in spring and autumn (Andersen 1991b; Karlsen et al 2009; Bunnefeld et al 2011).

During winter moose forage to a large extent in closed canopy forests (Bjørneraas et al 2011), probably as these areas provide a combination of high food abundance, reduced movement costs due to lower snow depths, and shelter and cover from harsh weather and predators (van Beest et al 2010; Leblond et al 2010; Bjørneraas et al 2011). During summer, the moose diet constitutes more plants from the field layer

(Wam and Hjeljord 2010), and open areas such as clear-cuts, agricultural areas and high altitude areas closer to the tree limit are important foraging areas (Bjørneraas et al 2011; Rolandsen 2012). The higher site fidelity during winter and summer suggests that moose return to similar foraging grounds each year at the same time. Alternatively, the spatial scale of movement in these periods may be low so that any displacement between years is low (van Moorter et al 2013). Independent of cause, these results suggest that indices of population sizes or change in population size are best obtained from summer or winter counts. As the whereabouts of moose is less predictable, counts from spring and autumn will be connected with larger uncertainties.

The overall seasonal pattern in absolute site fidelity described above was only to a small extent affected by accounting for individual spatial scale of movement (Figure 3c, d). However, the space use pattern is not randomly distributed among individuals. In moose, males often have larger home ranges than females (Herfindal et al 2009; Bjørneraas et al 2012), and migratory moose move over considerably larger spatial scales than resident moose (Bunnefeld et al 2011; Rolandsen 2012). In accordance with my predictions, I therefore found significant differences among groups in the absolute distance of displacement (Figure 4 and 5). For instance, males showed a higher absolute displacement than females with two calvings in all but three months of the year (Figure 4c), and also overall higher displacement than females with one calving (Figure 4e). However, as the sex-differences prevailed even after accounting for the spatial scale of movement (Figure 4d, f), mechanisms other than different spatial scale of movement may also affect the sex-specific site fidelity in moose. These may include sex differences in the utilization of the landscape (Miquelle et al 1992; Bjørneraas et al 2011), e.g. as females are more cautious than males and seem to be more restricted in the habitat types they utilize (Bjørneraas et al 2011; 2012). Males also have a greater energy demand (Miquelle et al 1992) and experience a lower predation risk than females (Miquelle et al 1992), and seem to have a habitat selection strategy which is more opportunistic with respect to variation in the distribution of resources between years. Consequently, familiarity as a risk-reducing strategy may be more important for females than males.

In addition to sex, the spatial scale of moose space use is highly dependent on whether individuals are migratory or resident (Bunnefeld et al 2011; Rolandsen 2012). However, the difference in movement rate among migratory and resident individuals varies among seasons, being largest in the migratory periods during autumn and spring (Rolandsen 2012). Consequently, I expected that any seasonal pattern in site fidelity among resident and migratory individuals, measured at the absolute scale, would be reduced when accounting for the spatial scale of movement (the relative displacement). Indeed, the difference in displacement between resident and migratory individuals was significant for larger parts of the year (9 months, Figure 5a) when measured as absolute displacement, compared to relative displacement (6 months, Figure 5b). Still, there were considerable differences in relative displacement, particularly during the migratory periods (Figure 5b). The effect of scale of movement is also present even within the limited period of rutting/hunting (20. Sept. – 20. Oct). During rutting/hunting males have substantially higher movement rate than females (Rolandsen et al 2010), which in line with the considerably lower site fidelity, suggests that males roam around in this period searching for ovulating females. The same period also corresponds to the hunting period in Norway (late September, all October), when most population monitoring occur in Norway. The large variation in absolute site fidelity between movement strategy and SRS during this period (absolute displacement from 1 - 9 km, Figure 6a) suggests that the proportion of the population which is included in counts, even at the municipality level, most likely varies among years. This is particularly true if a large part of the population is migratory due to their considerably higher displacement during rutting/hunting season.

Management implications

Norwegian moose management is based on harvesting a proportion of the population to achieve a population size and structure which correspond to the local food conditions, land-owners economic expectations (Skonhoft 2005), as well as the societal acceptance of traffic accidents (Olaussen and Skonhoft 2011) and forest damage (Wam et al 2005; Wam and Hofstad 2007). To reach the determined management goals, it is of general interest that the management tools are precise. Much effort is spent in monitoring populations each year, particularly by hunters during the hunting season (Solberg and Sæther 1999). A recent study has shown that this method captures changes in population size and structure quite well (Solberg et al 2010). However, this study came from an isolated moose population on an island of approximately 120 km^2, with limited possibilities for spatial displacement among years.

In my study, I documented large variation in site fidelity in moose from a mainland population, which may have several implications for management. First, I suggest that more precise population estimates can be obtained by performing censuses during the period of the year with high site fidelity, i.e. late summer or mid-winter. Second, the large difference in site fidelity between males and females (Figure 3, 4, 6) suggests that estimates of changes in the female segment of the population are more precise than for the male part of the population. Finally, as migratory moose show higher displacement among years, and particularly during spring and autumn (the main period for moose population monitoring), it is essential that knowledge exists about the general movement patterns in the population, in order to select the appropriate spatial scale for moose population monitoring. Combined, these aspects call for a large-scale monitoring and management of Norwegian moose populations.

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