Title: Seasonal release from competition explains partial migration in European moose

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Supplementary Material

Model for partial migration

To investigate the relationship between seasonal variation in habitat suitability and the proportion of migrations, we used the model presented by Van Moorter et al. (2020). This model builds upon the population model from Fryxell and Holt (2013), we refer to Van Moorter et al. in which the dynamics of population size follow a Ricker model (Ricker 1954, which is a discrete-time model); with scaled densities (i.e. $N = N'/K'$, where N' is the unscaled population size in spring just prior to the reproduction season, and K' is the population size at which on average each individual replaces itself during summer). Following Fryxell and Holt (2013), we assumed recruitment (r) during summer to be density-dependent and mortality during winter (μ) to be density-independent as supported by many empirical studies of ungulates (Saether 1997, Gaillard et al. 2000).

Using the Ricker formula to represent episodes of summer reproduction, the multiplicative growth rate equals $\exp(r[1-N'/K'])=\exp(r[1-N])$, where e^r is the maximum per capita recruitment during summer. Assuming density-independent winter survival probability $e^{-\mu}$, the number of animals after one year at the end of winter is calculated as follows:

$N(t+1) = N(t) \exp(r[1 - N(t)] - \mu)$ Eq. S1

Following Fryxell and Holt (2013), we linked two seasonal ranges through the movement of migratory animals, which move with migration probability, m, and cost, c, after the winter season from range L to H and back after summer. We define range L as the range with the lowest winter mortality (i.e. $\mu_L \leq \mu_H$). Therefore, we assumed only migration during spring from L to H; we did not consider individuals moving in the opposite direction, the so called `perverse' migrants (sensu Fryxell and Holt, 2013). Importantly, we focus our analysis on migration from the shared lowland range in winter towards a highland range used only in summer, i.e. the highland range can either not sustain residents year-round or highland residents are outcompeted by migrants who benefit from lower mortality on the lowland range (see for more details Van Moorter et al. 2020).

Following the population model in Equation S1, the number of animals at the end of winter in the lowland range, N, after 1 year is the sum of residents in L and migrants:

$$N(t + 1) = (1 - m)N(t) \exp(r_L [1 - (1 - m)N(t)] - \mu_L) +$$

$$mN(t) \exp(r_H [1 - \frac{K'_L}{K'_H} mN(t)] - \mu_L - c) \qquad \text{Eq. S2}$$

where m is the migration probability, and c is the demographic cost of migration. For simplicity, we assumed that the migration cost was incurred after summer. Density-dependent recruitment (r) takes place during summer, which is for migrants in range H (i.e. r_H) and for lowland residents in range L (i.e. r_L), whereas the density-independent winter mortality (μ) occurs when migrants and lowland range residents share their common lowland range L.

As more animals migrate (i.e. increasing migration probability, m) from range L, the density of animals in L decreases and the summer fitness of residents in L increases, whereas the density of animals in H increases and the summer fitness of migrants in L decreases. We assumed an ideal-free

migration strategy (Mariani et al., 2016; Van Moorter et al. 2020), where the ideal-free migration probability ($\hat{m}$) equalizes the summer fitness for lowland residents and migrants, calculated from Equation S2:

$$\exp(r_L\,[\,1\,-(1-m)N(t)]) = \exp(r_H\,[\,1\,-\frac{K'_L}{K'_H}\,mN(t)]\,-c)$$

Since this equation is linear in m, the ideal-free migration probability ($\hat{m}$) is calculated as follows:

$$\hat{m} = \frac{1-\frac{r_L}{r_H}[\,1-N]-\frac{c}{r_H}}{[\frac{r_L}{r_H}+\frac{K'_L}{K'_H}]N} \qquad\qquad \text{Eq. S3 = Eq. 1 in main text}$$

This ideal-free migration probability is determined by three main components: migration cost (scaled by the recruitment on the highland range), relative habitat suitability of highland versus lowland range both in terms of the relative intrinsic growth ($\frac{r_H}{r_L}$) and the relative carrying capacity ($\frac{K'_H}{K'_L}$), and population density or saturation with respect to the lowland range (N). Consequently, increasing the cost of migration leads to a reduction in the migration probability. However, as the cost of migration seems negligible for moose (Rolandsen et al. 2017), we will assume zero migration cost in this paper. Whereas, increasing the benefits of migration from access to suitable habitat (increasing $\frac{r_H}{r_L}$ or $\frac{K'_H}{K'_L}$) increases migration probability (Figure 1). If the intrinsic growth rate differs between migrants and residents, then the migration rate will be density-dependent (Figure 1). If the intrinsic growth rate of migrants is higher than those of residents (e.g. due to higher quality forage following the forage maturation hypothesis; Fryxell and Sinclair 1988, Hebblewhite et al. 2008), all individuals of the population would be migrating at low densities. As the highland range becomes more crowded due to increasing population density, some individuals will shift to a resident strategy. The opposite will occur if the migrants experience a lower intrinsic growth on the highland ranges (red line in Figure 1), then individuals will only start migrating once the population density on the lowland range is sufficiently high.

Supplementary Figures

Figure S1

Moose migration in Fennoscandia

For each moose in our study the centroid of the summer (in green) and winter (in blue) locations are connected with a red line.

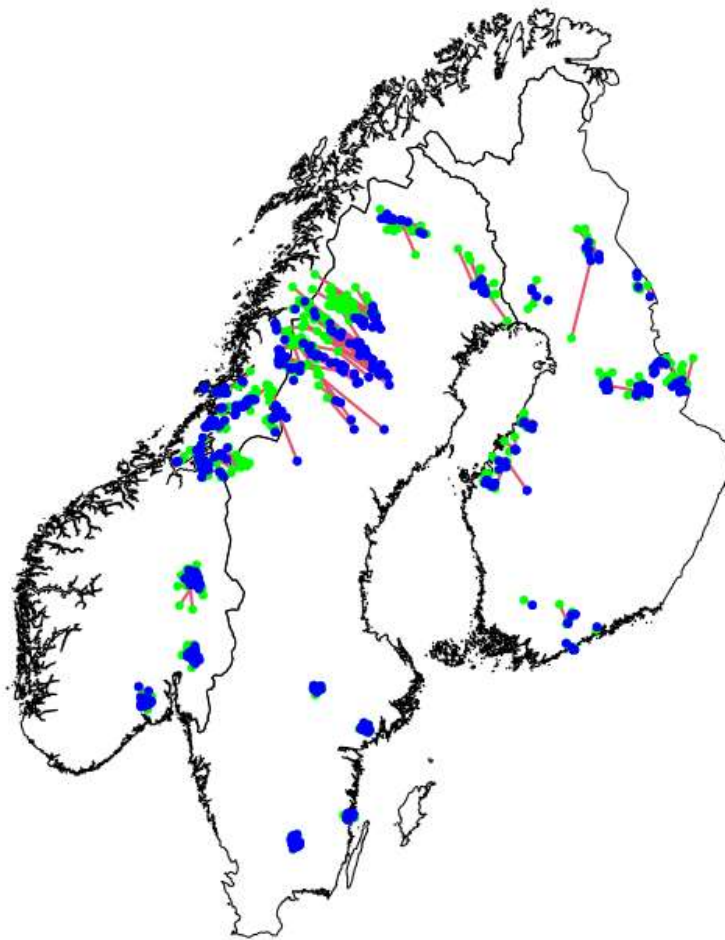
Moose migration in Fennoscandia

Figure S2

Boxplot with the individual-based k-fold cross validation

The Spearman rank correlation for each individual moose between the observed and predicted occupancy from a model fitted without the focal individual for the summer and winter resource selection probability function.
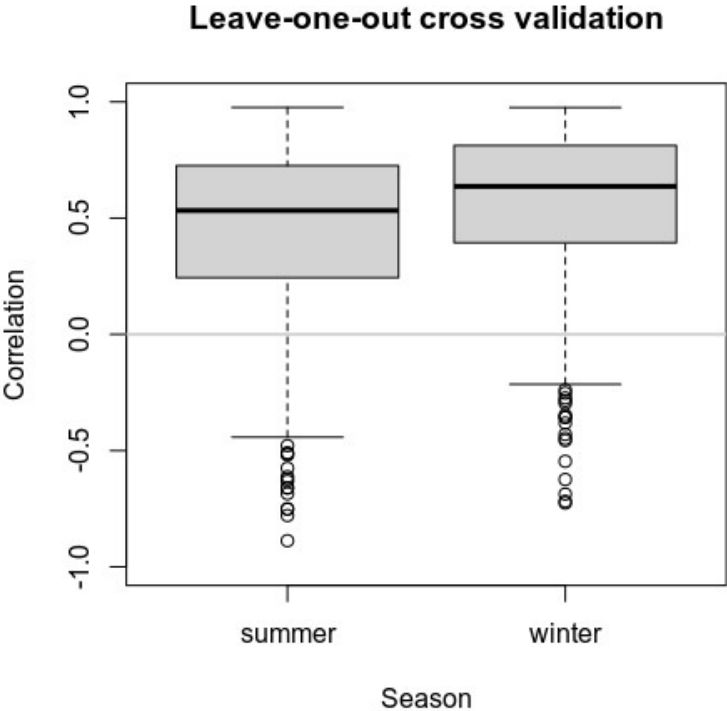
Figure S3

Residuals from the relationship between harvest and habitat suitability in Fennoscandia

The residuals from the linear regression between the average annual harvest and the total summer suitability for each mapping unit in Fennoscandia ($\log(harvest) = \beta_0 + \beta_1 \log(RSPF_{summer}) + \varepsilon$). The largest deviation from the prediction occurs in the Norwegian west coast, which has extremely low numbers of moose compared with the amount of available habitat. This area is generally not considered part of the moose range in Fennoscandia, however, the mechanisms for this are not well understood. It could be a combination of historical overharvest combined with difficulties in recolonization due to topography and local competition with red deer. If we removed those municipalities from the analysis, we obtained an even stronger relationship between the amount of suitable habitat and moose harvest (see Figure S5). Note that none of the other results, related to moose migration, are affected by the in- or exclusion of the Norwegian west coast, as for obvious reasons we studied migration only in areas where moose are present.
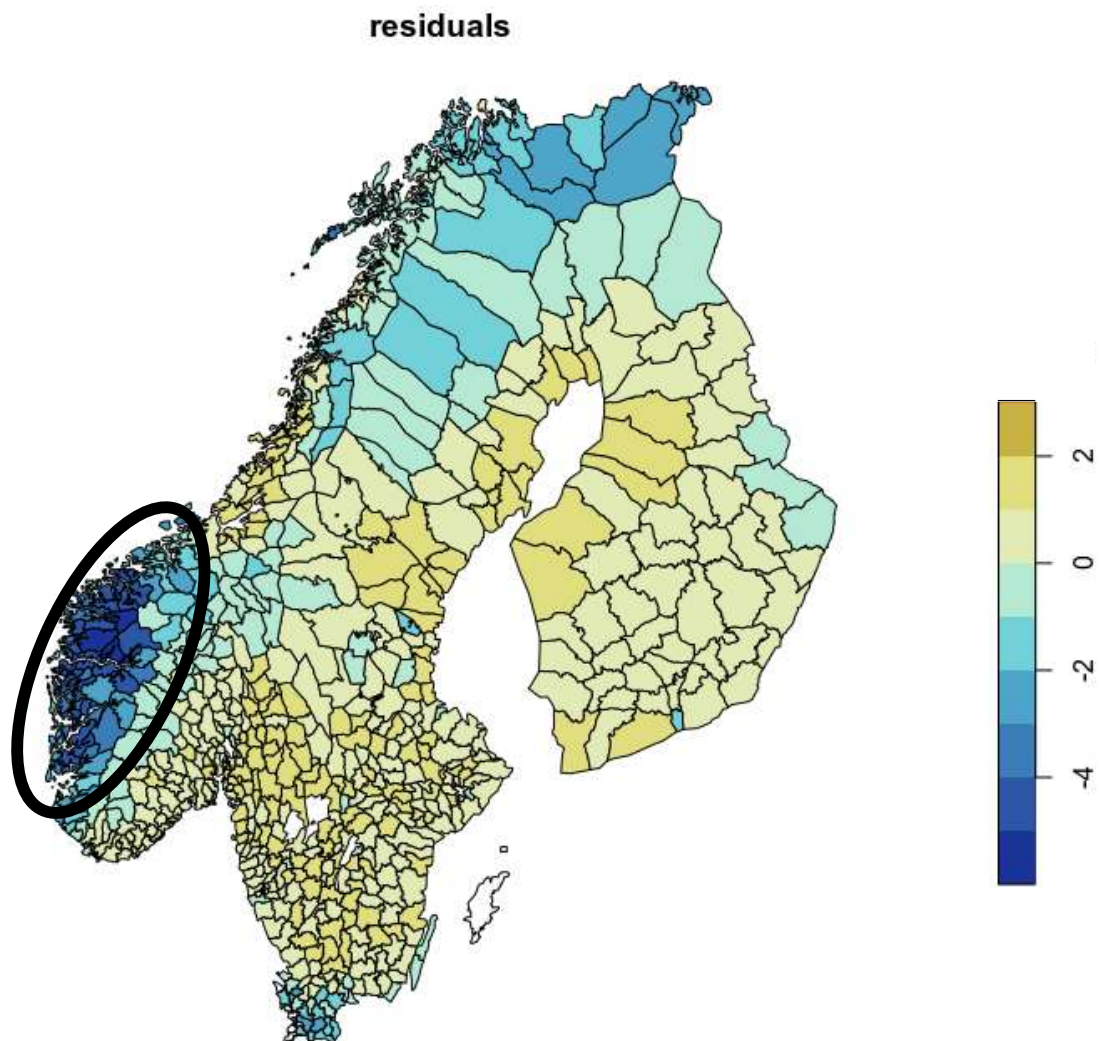

residuals

Figure S4

Relationship between harvest and habitat suitability in Fennoscandia

The logarithm of the average annual harvest plotted against the total summer suitability for each reporting unit in Fennoscandia. As noted above, an important deviation from the prediction occurs in Western Norway (see Figure S4). After removal of this area the linear regression ($\log(harvest) = \beta_0 + \beta_1 \log(RSPF_{summer}) + \varepsilon$) explains 66% of the variance in harvest (compared to a variance explained of 50% reported in the main text, and $\beta_1 = 0.86$).
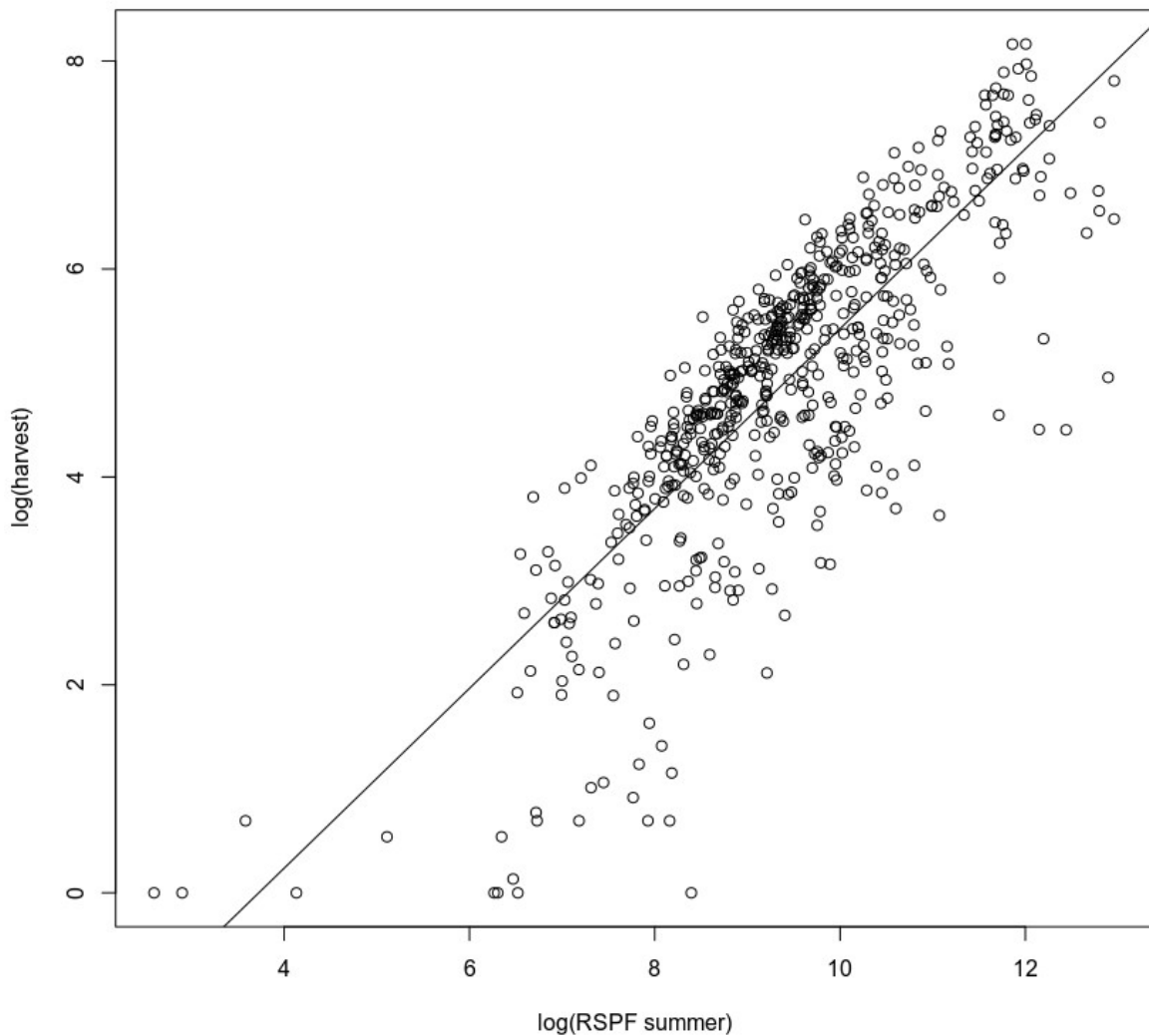
Figure S5

Moose population distribution during summer in Fennoscandia

The population distribution of moose (in harvested individuals per km^2) derived from the harvest data and the predicted summer RSPF.
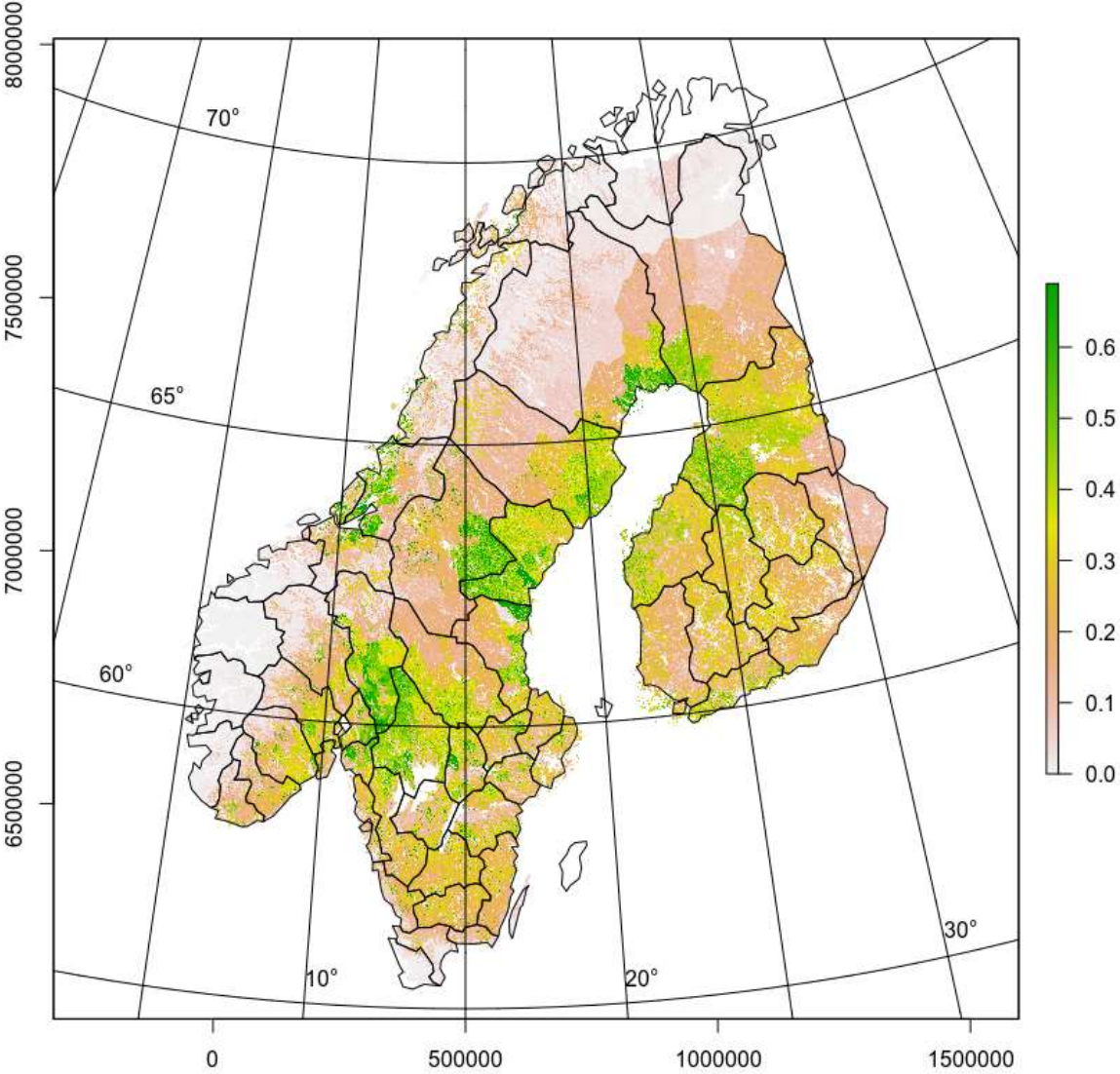
Figure S6

Boxplot with the distribution of elevation at the lowland and highland range across Fennoscandia. We labelled the geographic areas that were more selected during winter than during summer as lowland ranges and those that were more selected during summer than during winter as highland ranges. We used these geographic labels instead of summer and winter ranges to avoid confusion with summer and winter in reference to seasons. Although, altitude is unlikely to be a direct driver of migration itself, it is common to observe altitudinal migration in response to ecological variables with an altitudinal gradient. For instance, in our study snow was an important variable related to migration. Not surprising and in support of our a priori labels, we did observe lower elevations in the areas more selected during winter, and higher elevations in the areas more selected during summer.
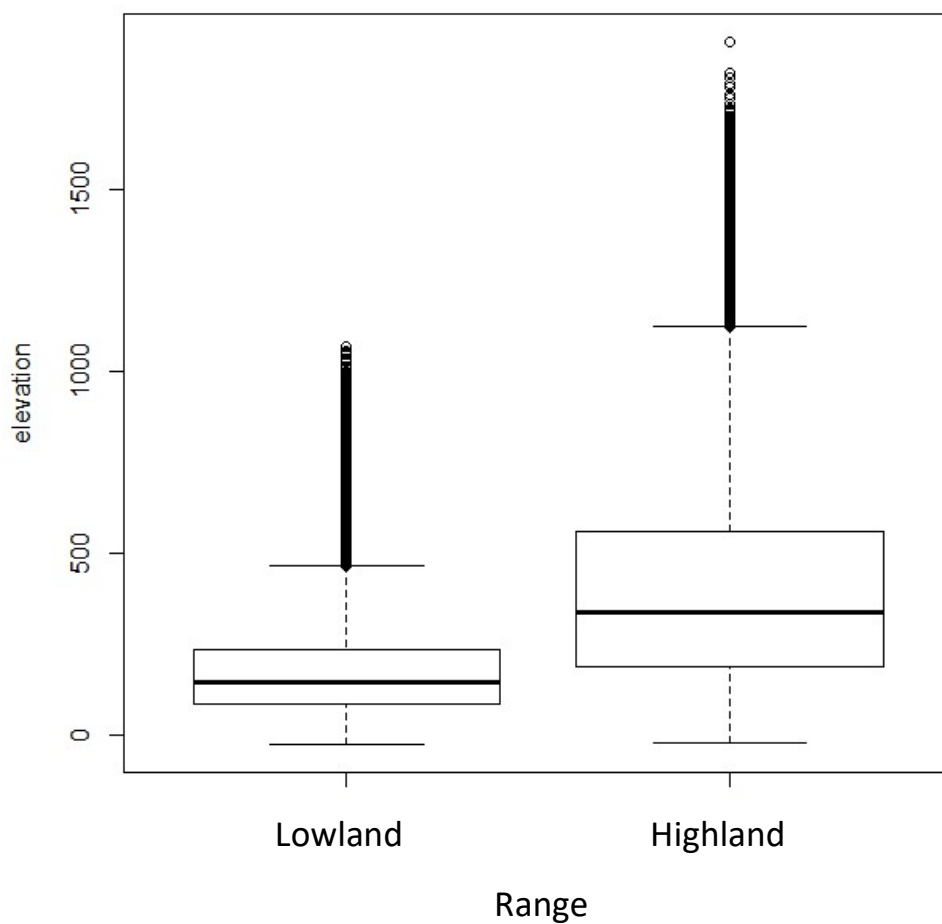
Figure S7

Descriptive details for the different clusters: number of individuals (N), number of males, number of females, number of migrants & residents (VI criterion), mean age of the moose at marking (note that age was not available for all clusters).

Name	N_{total}	N_{male}	N_{female}	$N_{migrant}$	$N_{resident}$	avg(age)
A	30	9	21	29	1	4.9
B	54	8	46	31	23	4.8
C	54	8	46	49	5	5.2
D	19	6	13	16	3	5.5
E	16	4	12	7	9	5.8
F	21	2	19	1	20	8.4
G	42	20	22	31	11	NA
H	29	7	22	15	14	NA
I	13	4	9	5	8	NA
J	13	8	5	7	6	NA
K	24	3	21	0	24	7.1
L	22	5	17	1	21	6.7
M	43	6	37	15	28	3.0
N	31	10	21	17	14	2.7
O	13	2	11	8	5	3.1
P	41	13	28	11	30	NA
Q	22	4	18	2	20	NA
R	26	0	26	13	13	7.1
S	32	0	32	15	17	8.7

Figure S8

Relationship between different migration criteria

The proportion of migrants in each cluster determined by the Volume of Intersection VI criterion on the x-axis and the distance above 10km criterion on the y-axis. Given the high agreement between both criteria results were qualitatively identical, we therefore only reported those for the VI criterion.