

Appendix 1. Simulating path-dependant seasonal herd movements

The movement model assumes a Markov process driven by an externally imposed sequence of states of nature. Let q^s represent a row vector of length k whose elements describe the number of animals observed during season s in each of k habitat zones defining the range of the herd. Let P_a^s represent the transition matrix for movement of animals from season $s-1$ to season s if state of nature a^s is observed in season s . P_a^s is a square matrix whose elements, p_{aij}^s , represent the probability that an animal observed in zone i in season $s-1$ will move to zone j in season s if state of nature a^s occurs ($\sum_j p_{aij}^s = 1$). The expected number of animals in season s , given the observed distribution q^s and state of nature a^s is

$$q^s = q^{s-1} P_a^s. \quad (\text{A1.1})$$

Deriving the transition probabilities

To derive the seasonal transition matrices, P_a^s and P_b^s , we started by calculating from each caribou's movement record the proportion of time, r_{ai}^{st} that the animal spent in zone j in season s of year t and if it had been observed in zone i during the previous period ($t,s-1$) for all years and seasons for which the state of nature a was observed. Since a single animal could have been observed in multiple zones in a given season, r_{aij}^{st} represents the percentage of the total days of season s that a caribou which had been observed in zone i during the previous period spent in zone j in year t season s . (Note that if $s=1$, the previous period is the final season of year $t-1$ rather than $(t,s-1)$.) The calculated r_{ij}^{st} typically would differ among collared animals in a given year and season, as well as for the same animal observed across different years with the same seasonal state of nature. Therefore, to estimate the herd expected transition probability p_{aij}^s , we calculated the weighted average of the r_{ij}^{st} over the observed animal-seasons, using as weights the proportions to the time an animal was observed to have spent in zone i the previous season. That is, if $d_{ain}^{s-1,t}$ represents the proportion of total days of season s that animal n spent in zone i during the previous period when the seasonal state of nature was a , the transition probability is

$$p_{aij}^s = \sum_t \sum_n d_{ain}^{s-1,t} r_{aij}^{st} / \sum_t \sum_n d_{ain}^{s-1,t}. \quad (\text{A1.2})$$

For example, suppose a collared animal had spent 60 percent of the days of season 1 in 1999 in zone 1, and 40 percent of the days of season 2 in 1999 in zone 2. Suppose the same animal also had spent 40 percent of the days of season 1 in 2002 in zone 1, and 80 percent of season 2 that year in zone 2, when the same state of nature occurred as in season 2 of 1999. Suppose another animal had spent 20 percent of the days in season 1 of 2002 in zone 1, and had spent 20 percent of the days in season 2 in zone 2 that year. The three r_{a12}^{st} would be 0.4, 0.8, and 0.2, while their respective weights, d_{a1n}^{1t} , would be 0.6, 0.4, and 0.2. The weighted average p_{a12}^2 given by equation (A.2) would be $(0.24+0.32+0.04)/(0.6+0.4+0.2) = 0.6/1.2 = 0.5$.

Simulating the model

Equations (A1.1) and (A1.2) define the expected distribution of animals over time. Simulating seasonal path-dependent herd-scale movements requires modeling two types of uncertainty: (1)

uncertainty associated with the state of nature representing seasonal weather along with its ecological consequences, and (2) uncertainty associated with the movement of animals given the season and state of nature. To explain the simulation protocol, we start with the example of a single animal observed in an initial time period (0), corresponding to season $s-1$ in a simulation year. Let x^0 represent a row vector of length k describing the position of the animal among the k zones in that initial period. The animal will be observed in one of the k zones -- for example, zone i -- that is, $x^0_i = 1$; $x^0_j = 0, j \neq i$. The model starts a new time step by randomly drawing one of two states of nature for time t with a 50 percent probability. Suppose the state of nature (seasonal weather) in period 1 is revealed to be condition c . The probability that the animal will be observed in each of the k zones in period 1 is given by the vector p^1 such that

$$p^1 = x^0 P^s_c. \quad (\text{A1.3})$$

To accomplish the move to a new zone with probabilities specified by equation (A1.3), the model now draws another random number, u , from a uniform distribution between zero and one. Consider the cumulative probability matrix P^{*s}_c defined from P^s_c such that each element p^{*s}_{cij} of matrix P^{*s}_c equals the row sum from 1 to j of p^s_{cij} . That is,

$$\begin{aligned} p^{*s}_{cij} &= p^s_{cij}, (j = 1); \\ p^{*s}_{cij} &= p^s_{cij} + p^{*s}_{ci,j-1}, (1 < j \leq k). \end{aligned} \quad (\text{A1.4})$$

For each row of P^{*s}_c , one destination column j will contain the largest p^{*s}_{cij} for which $p^{*s}_{cij} \leq u$. Define Y^1_c as a square k by k matrix whose elements $y^1_{ij} = 1$ if j corresponds to the destination for row i with maximum $p^{*s}_{cij} \leq u$:

$$\begin{aligned} y^1_{ij} &= 1, \text{ if } p^{*s}_{cij} = \max_j p^{*s}_{cij} \mid (p^{*s}_{cij} \leq u) \\ y^1_{ij} &= 0, \text{ otherwise.} \end{aligned} \quad (\text{A1.5})$$

Finally, the model moves the animal to a position in period 1 described by the vector x^1 :

$$x^1 = x^0 Y^1_c. \quad (\text{A1.6})$$

The sequence is repeated for the next season corresponding to period 2, with a new random draw for the state of nature and a random move according to the season $s+1$ transition matrix associated with the newly revealed state of nature, and so on.

The model scales up from movement of a single animal to movement of the herd by defining a set of n clusters of animals, each of size m . Each of the m animals in a given cluster moves together among zones as if it were a single animal, according to the dynamics of equations (A1.3 through A1.6). While all the clusters use the same outcome for the seasonal state of nature in a given time step, each cluster has its own independent random draw for the vector u , used for random assignment to zones. The distribution of the herd among zones at time 1 is built up, therefore, from the sum over n of $q_n x^1_n$.

An example (Table A1.1) illustrates an example for one animal in a single time step: fall migration (August 8 – October 7). Table A1.1a shows the transition matrix, P^s , for its two possible climatic states, i.e., whether the first snowfall arrives early or late in the season, and Table A1.1b shows the associated cumulative probability matrix, P^{*s} . Since animals were never observed in zones 7, 9, 10, 11 or 12 during the previous season (mid summer) those rows are omitted from the table. Assume that the animal was in the Chandalar Basin region (Zone 4) the previous season, and that fall snow came early that year. The model generates a random number uniformly distributed between zero and one: for example, 0.427. It then goes to the zone 4 row of the ‘Early snowfall’ cumulative probability table (first row of shaded cells), to find the largest entry that does not exceed 0.427 (in this case, the third number, 0.107; the model moves the animal to zone 3). If fall snow had been *late* instead of *early*, the model would have used the late snowfall table and searched across row 4 until it found the value 0.359, which would have kept the animal in zone 4.

Table A1.1 (a) Transition table for fall migration season (Aug 8-Oct 7) for two environmental conditions: early and late snowfall. **(b)** Cumulative probability table for model lookup. Shaded rows indicate the numbers used in the example.

(a) *Normalized probability that caribou move into zone:*

	From zone	1	2	3	4	5	6	7	8	9	10	11	12	13
Early snowfall	1	0.018	0.342	0.081	0.450	0.027	0.027							0.054
	2	0.038	0.221	0.198	0.189	0.247	0.064	0.004	0.002					0.038
	3		0.027	0.329	0.116	0.335	0.181		0.011	0.001				
	4		0.015	0.092	0.409	0.326	0.091		0.060			0.007		
	5		0.020	0.146	0.083	0.453	0.184	0.001	0.103	0.003		0.007		
	6		0.030	0.065	0.065	0.476	0.349	0.001	0.015					
	8					0.500			0.500					
	13		0.224		0.139	0.004								0.633
Late snowfall	1	0.002	0.191	0.107	0.179	0.356	0.079	0.002	0.019					0.065
	2	0.005	0.170	0.129	0.225	0.343	0.089	0.004	0.025	0.001	0.001	0.001		0.007
	3		0.006	0.160	0.058	0.507	0.206	0.002	0.047	0.010	0.001	0.004		
	4		0.023	0.086	0.251	0.382	0.145	0.011	0.047	0.017	0.003	0.035		
	5		0.003	0.119	0.134	0.494	0.118	0.011	0.086	0.017	0.003	0.016		
	6		0.006	0.129	0.094	0.395	0.258	0.004	0.060	0.047		0.007		
	13					0.136	0.011							0.852
		0.007	0.399	0.730	0.940	2.613	0.906	0.034	0.284	0.092	0.007	0.062		0.924

(b) *Cumulative probability $\geq x$ that caribou move into zone:*

	From zone	1	2	3	4	5	6	7	8	9	10	11	12	13
Early snowfall	1	0.018	0.360	0.441	0.892	0.919	0.946	0.946	0.946	0.946	0.946	0.946	0.946	1.000
	2	0.038	0.259	0.457	0.646	0.893	0.956	0.960	0.962	0.962	0.962	0.962	0.962	1.000
	3	0.000	0.027	0.356	0.472	0.807	0.988	0.988	0.999	1.000	1.000	1.000	1.000	1.000
	4	0.000	0.015	0.107	0.516	0.842	0.933	0.933	0.993	0.993	0.993	1.000	1.000	1.000
	5	0.000	0.020	0.166	0.249	0.701	0.886	0.887	0.990	0.993	0.993	1.000	1.000	1.000
	6	0.000	0.030	0.094	0.159	0.634	0.984	0.985	1.000	1.000	1.000	1.000	1.000	1.000
	8	0.000	0.000	0.000	0.000	0.500	0.500	0.500	1.000	1.000	1.000	1.000	1.000	1.000
	13	0.000	0.224	0.224	0.363	0.367	0.367	0.367	0.367	0.367	0.367	0.367	0.367	1.000
Late snowfall	1	0.002	0.193	0.300	0.479	0.835	0.914	0.916	0.935	0.935	0.935	0.935	0.935	1.000
	2	0.005	0.175	0.305	0.530	0.873	0.962	0.966	0.991	0.992	0.993	0.993	0.993	1.000
	3	0.000	0.006	0.166	0.224	0.731	0.937	0.939	0.986	0.995	0.996	1.000	1.000	1.000
	4	0.000	0.023	0.109	0.359	0.741	0.887	0.898	0.945	0.962	0.965	1.000	1.000	1.000
	5	0.000	0.003	0.122	0.256	0.750	0.867	0.878	0.964	0.981	0.984	1.000	1.000	1.000
	6	0.000	0.006	0.135	0.229	0.624	0.882	0.886	0.947	0.993	0.993	1.000	1.000	1.000
	13	0.000	0.000	0.000	0.000	0.136	0.148	0.148	0.148	0.148	0.148	0.148	0.148	1.000

The transition tables determine movement of animals into the 13 large zones. To place each of the m animals in a cluster into the 39 smaller hunting subzones, the model uses the results of the kernel analysis described in McNeil et al. (2005). That analysis calculated utilization density grids for the 16 seasonal condition combinations (8 seasons x 2 conditions per season) from the same satellite collar dataset (McNeil et al. 2005: Table 2). We derived a conditional subzone transition matrix, H^s_{aj} , for the relevant season and climate driver from these McNeil et al. (2005) density grids. The elements of H^s_{aj} , h^s_{ajz} , express the probability that an animal will be found in subzone z , given assignment to the larger zone j . We calculated the conditional subzone cumulative probability table, H^{*s}_{aj} , with elements h^{*s}_{ajz} , as given by equation (A1.7):

$$\begin{aligned} h^{*s}_{cjz} &= h^s_{cjz}, (z = 1); \\ h^{*s}_{cjz} &= h^s_{cjz} + h^{*s}_{cj,z-1}, (1 < z \leq g_j). \end{aligned} \tag{A1.7}$$

Once a cluster of animals moves to zone j according to equations (A1.3-A1.6), the model draws a separate random number for each of the m members of the cluster, looking this number up in the relevant H^{*s}_{aj} table of subzone cumulative probabilities to assign each animal in the cluster to one of zone j 's g_j subzones. The potential to simulate two hierarchical levels of random movement provides flexibility for modeling spatial heterogeneity of herd dynamics.

Running the model and evaluating model results against empirical observations

We ran 1,000 Monte Carlo simulations, each with 28 animals spanning a 19-year simulation period: June 1985 - May 2003, using historical seasonal environmental states (Figure A1.1). Observed calving distributions from June 1985 using (Griffith et al. 2002) initialized the model. Each model run moved 7 clusters of 4 animals apiece into one of the 13 large zones with seven random draws per season. Four additional random draws per season for each of the 7 groups assigned the 4 caribou within each cluster individually to subzones.

Figure A1.1. Environmental conditions by season and year used for historical simulation.

Model year ^a	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01	02	03
Calving		■	■	■	■			■					■			■	■		
Post-calving				■	■				■	■	■		■		■	■	■		
Summer (A and B)	■			■	■	■			■	■	■	■	■	■				■	
Fall (A and B)	■	■			■		■						■	■	■		■	■	■
Winter				■	■	■	■	■	■							■	■	■	■
Spring	■	■	■					■				■	■		■	■	■	■	

^a The eight seasons of a model year run from calving in calendar year t through spring of calendar year $t+1$ (i.e., Calving in the first column represents June 1985, while Spring represents April/May 1986). Summer and Fall are each subdivided into two model seasons (see Table 3 for details). Sample sizes (number of animals collared) for each seasonal condition ranged from 41 to 93.

Symbol legend:

■	Late snowmelt or snowfall, shallow snow	□	Early snowmelt or snowfall, shallow snow
■	Fast vegetation green-up	□	Slow vegetation green-up
■	High insect abundance	□	Low insect abundance

We took the output of the 1,000 runs, and computed the 5th percentile, 50th percentile, 95th percentile number of caribou in each of the 39 hunting subzones for each year-season, and also summed the total number of animals over all 1,000 runs. This sum represented a dynamic simulation of the distribution of 28,000 animals. Since the Porcupine Caribou Herd during this period averaged around 140,000 animals, multiplying by 5 provides an estimate of the actual expected total number of animals by subzone. Although the approach outlined above differs from that of computing density kernels, the simulated caribou abundance by subzone mimics what would be obtained from computing a conditional density kernel for each season, given the environmental state and the caribou distribution the previous season.

Presence/absence cross-tabulations with observed satellite collar location data

To confirm that the model had been correctly parameterized and coded, we compared model simulation output with the original satellite location point data from which it was derived. Using GIS overlays, we compared the satellite collar data (19,509 individual location points) to the model output joined to subzone polygons. Next, we compared observed caribou locations (the satellite data) with predicted distributions (the model) for each season and year by subzone. This produced a dataset of 5,616 data points – 39 subzones by 8 seasons per year by 18 years – at different statistical thresholds: 5 percent, 50 percent, and 95 percent. (Although collar data spanned 19 years, no collars transmitted location data in 1996.)

We cross-tabulated the number of instances (i.e., the number of seasons by subzone and year) that model predictions and satellite locations agreed or disagreed. In this ‘cross-tab’ analysis there were four possible outcomes: (a) model predicted animals in the same subzone where caribou were observed (true positive: +/+); (b) model predicts no animals where no animals were observed (true negative: -/-); (c) model predicts no animals where animals were observed (false negative: -/+); (d) model predicts animals where no animals were observed (false positive: +/-).

The cross-tabulations between the satellite locations and model output showed that the model generated results that were consistent with the original satellite collar locations. Table A1.2 summarizes the results of the cross-tab analysis. The top panel of the cross-tab analysis compares the satellite data with output from the 95th percentile model run (100=most animals in a subzone that year and season, 0=least). There were 2,856 cases (51 percent of 5,616 total subzone-season-years) in which the model predicted that caribou were absent (i.e., no caribou clusters in that subzone). In 73 (2.6%) of these were cases, at least one satellite location was recorded, while the remaining 2,783 cases (97.4%) had no satellite collars present. Hence, using a conservative model threshold for predicting caribou absence, there was a high correlation with the satellite data: the model rarely predicted caribou absence when satellite data showed presence.

Of the 1,164 cases in which at least one collared caribou was observed in a subzone-season-year, Table A1.2 showed that the model assigned caribou to the correct subzone in 1,091 cases (93.6%), and failed to assign caribou in 73 cases (6.4%). The 5th percentile threshold describes where the model almost always predicted caribou presence in a given subzone, season, and year. In the 5th percentile results, the model predicted that caribou were very likely to be present in only 1.4 (81) percent of subzone-season-year cases. In most of these cases (52, or 64.2%),

collared animals were also present in the observed dataset (Table A1.2). We concluded that both the 95th percentile and fifth percentile results from the model were fully consistent with the empirical observations from which they were derived.

Table A1.2. Cross-tabulation of simulated caribou distribution by observed satellite locations: 5616 subzone-seasons (39 subzones, 8 seasons per year, 18 years), percentiles indicate rank of simulation runs (0=least predicted caribou in the subzone that season and year, 100=most)

Percentile run	Simulated caribou distribution		Observed collared animals		
	Model category	Comparison	No caribou (-)	At least one (+)	TOTAL
95 th	No caribou (-)	Subzone-seasons	2783	73	2856
		% of model category	97.4	2.6	100
		% of total	49.6	1.3	50.9
	At least one (+)	Subzone-seasons	1669	1091	2760
		% of model category	60.5	39.5	100
		% of total	29.7	19.4	49.1
50 th	No caribou (-)	Subzone-seasons	4020	586	4606
		% of model category	87.3	12.7	100
		% of total	71.6	10.4	82.0
	At least one (+)	Subzone-seasons	432	578	1010
		% of model category	42.8	57.2	100
		% of total	7.7	10.3	18.0
5 th	No caribou (-)	Subzone-seasons	4423	1112	5535
		% of model category	79.9	20.1	100
		% of total	78.8	19.8	98.6
	At least one (+)	Subzone-seasons	29	52	81
		% of model category	35.8	64.2	100
		% of total	0.5	0.9	1.4

These tests provided confidence that the model did not have internal coding or parameterization errors that would obviously invalidate it. The tests were insufficient by themselves to evaluate the model, however, since the tests and model were derived from the same original data.

Literature Cited

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