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Ecologically based definition of seasons clarifies predator–prey interactions

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Species interactions within food webs are driven by multiple constraints, including those imposed by seasonal changes in the environment. Ecologically sound definitions of seasons may therefore be a prerequisite for clarifying predator–prey interactions. Most studies define biological seasons based on fixed schedules or on temporal changes in a single movement measurement. We used a novel clustering approach based on homogeneous space-use patterns of GPS-collared animals to reveal 7 biological seasons for caribou *Rangifer tarandus caribou,* and 5 for both moose *Alces alces* and grey wolves *Canis lupus* interacting in a boreal ecosystem. Subsequent evaluation of niche overlap showed that, as predicted, wolves had a stronger spatio-temporal connection with moose, its main prey, than with caribou. Movement constraints and limiting resource distributions similarly affected all species in some instances, but also caused temporal changes in the extent of niche overlap between wolves and its two prey. The risk that caribou faced was not only linked to the niche overlap with wolves, but also to the extent of wolf-moose niche overlap during the same period. Food-web properties emerged from the analysis, with temporal changes in relative niche overlap reflecting the strength of trophic interactions during the year. Our study demonstrates how the study of trophic interactions can benefit from comprehensive definitions of biological seasons.

Most organisms live in seasonal environments (Fretwell 1972). Changes in weather conditions affect primary production (Nemani et al. 2003), which can result in strong cyclic variation in resource availability for herbivores during the course of the year. These temporal fluctuations then propagate through the food chain, often creating spatial synchrony in animal populations (Vasseur and Fox 2009). Synchrony between predators and prey has been intensively studied in terms of population dynamics. A famous example is the 10-yr cycle of the Canadian lynx *Lynx canadensis* (Elton and Nicholson 1942) that reflects delayed density-dependent regulation caused by its interaction with the snowshoe hare *Lepus americanus* (Stenseth et al. 1998). Because many life-history traits are controlled by seasonality, such as reproduction and recruitment, growth, dormancy, dispersal or migration (Dayton 2008), environmental variation can have a tremendous effect on food-web dynamics.

A particular impact of environmental variation can be expected in predator–prey systems, in which each component can behaviourally adjust its response to create the predator–prey race (Sih 1984). Herbivores can be directly affected by sunlight and air temperature; for example, the mountain hare *Lepus timidus* changes its coat colour in relation to daylight length (Küderling et al. 1984), thereby influencing its interactions with predators in snowy environments. The life-history traits of predators also vary during the year. Gray wolves *Canis lupus*, for instance, restrict their movements near the den during the breeding season. This concentration of activity in a fraction of the territory gives rise to spatial refuges for their prey (Jędrzejewski et al. 2001). On the other hand, Sih's (1998) theoretical assessment of predator–prey habitat selection shows that the evolutionary game can lead to strong correspondence between land-cover types used by predators and their key prey. Consequently, environmental variation can strongly affect predator–prey dynamics and thus govern the seasonality of the system (Brassil 2006).

Current space-use analyses generally rely on the division of the year into somewhat arbitrary periods, which makes the definition of the periods critical and can lead to faulty conclusions if the periods do not match biological reality, such as contrasted periods that have been merged together. For example, a study of black bear *Ursus americanus* revealed strong inter-annual variation in the selection of northern

hardwood forest and was positive or negative, depending on the abundance of beechnut *Fagus grandifolia* (Schooley 1994). However, the analysis on data pooled for the entire period failed to highlight this variation in selection and, therefore, would have provided a biased assessment of plant–omnivore interactions. As outlined above, temporal variation in the environment can affect every species in a food chain during the course of the year, such that space-use behaviours will vary at finer temporal scales. It is thus desirable to account for seasonality, and defining seasons objectively based on temporal variation in animal behaviours (Fryxell et al. 2008) provides a powerful framework for studying many aspects of animal ecology, such as habitat use and selection, and species interactions.

Approaches currently used to define biological seasons include expert-based definitions established from knowledge of the species' ecology. For example, Houle et al. (2010) defined three seasons in their study of space use by grey wolves based on wolf ecology: denning, rendezvous, and nomadic seasons. This approach results in seasons with high generality, applicable in most cases, but not necessarily reflecting the specificity of the ecosystem under study because factors triggering seasonal changes (e.g. temperature, snow cover, day length) often vary over space. To circumvent this problem, quantitative approaches have also been developed based on movement analysis. Ferguson and Elkie (2004) fitted a polynomial regression to changes in movement rate to define five seasons for the woodland caribou *Rangifer tarandus caribou.* Likewise, Courbin et al. (2009) used sudden temporal changes in the distance moved from a starting location to delineate six biological seasons for woodland caribou. It is not simply because an animal does not display temporal changes in a particular behaviour (e.g. movement) that seasonal patterns would not become evident from other behaviours. Indeed, cyclic variation in environmental conditions may influence more than just movement rates. As needs, costs and constraints vary over the course of the year, animals should display behavioural plasticity reflecting these temporal changes in resource (and more generally habitat) use as well. More comprehensive quantitative approaches to the study of temporal variation in behaviour decisions, notably in resource, such as resource use, should give a clearer appreciation of behavioural adjustments occurring during the course of the year, thereby providing a more complete, and presumably more revealing, understanding of trade-offs shaping food webs.

Here, we developed a framework using cluster analysis (Tibshirani et al. 2001, Van Moorter et al. 2010) to define homogeneous space-use behaviours, based on both the use of habitat attributes (i.e. land-cover type, elevation) and movement characteristics (i.e. speed, turning angles). We demonstrate how the approach can distinguish biological seasons and clarify temporal trends of niche overlap between interacting species.

We applied this approach to identify seasons for forest-dwelling woodland caribou and the moose *Alces alces,* together with their primary predator, the grey wolf. Forest-dwelling woodland caribou are threatened in Canada (Committee on the Status of Endangered Wildlife in Canada, COSEWIC 2002). In the caribou-moose-wolf system, even if wolves are responsible for most adult mortality in caribou, moose remain the primary prey of wolves (Bergerud and Elliot 1986), which makes wolf interaction with moose stronger than with caribou. Regenerating conifer forests that originate from logging increase habitat quality for moose by providing high browse availability (Collins and Schwartz 1998, Courtois et al. 1998, Potvin et al. 2005), which can result in a numerical response by wolves (Bergerud 1974, Seip 1992). The increase in wolf density, in turn, intensifies predation pressure on caribou, initiating a situation of apparent competition between moose and caribou (James et al. 2004, Wittmer et al. 2007). We investigated whether or not similar constraints (e.g. snow in winter, cover, human disturbance) translated into synchronous space-use patterns by the different species of this predator–prey system. We predicted a close link between the strength of trophic interactions and ecological similarity in seasonality between interacting species; this prediction implies that, in our case, the biological seasons of wolves should be more similar to those of moose than to caribou.

Material and methods

Data collection

Our study area (18 500 km^2) was located in the boreal forest of the Cote-Nord region, Quebec, Canada, (50–52°N, 68–71°W; Fig. 1), and in the core of the continuous distribution of forest-dwelling woodland caribou. The forest is characterised by a matrix of mature conifers that is dominated by black spruce *Picea mariana*, balsam fir *Abies balsamea*, and jack pine *Pinus banksiana*, while trembling aspen *Populus tremuloides*, and paper birch *Betula papyrifera* are common deciduous tree species. Terrestrial fruticose lichens are generally abundant (Morneau and Payette 1989) and the fire cycle lasts 270 yr (Bouchard et al. 2008). Logging is progressing northwards, with 4% of the land consisting of regenerating cutblocks. In the study area, caribou pregnancy rate is nearly 100%, indicating that females are unlikely limited by food, which is further supported by a carrying capacity of the area, based on lichen production, 3 to 4 times the caribou density (Courtois et al. 2007).

Caribou and wolves were captured with a net gun fired from a helicopter, while moose were captured using a combination anaesthetic of carfentanil and xylazine. Naltrexone was injected intravenously as an antidote to carfentanil just prior to release (Delvaux et al. 1999). All animals were fitted with GPS collars (Lotek Engineering, Newmarket, ON) or ARGOS/GPS collars (Telonics, Mesa, AZ). Particular attention was paid to capturing individuals from the three species randomly spread over the study area. From March 2005 to April 2010, 29 adult female caribou (≥ 2.5-yr old) were monitored by taking one location every hour (19 individuals) or every 2 to 8 h (10 individuals). Sixteen adult female moose (≥ 2.5-yr old) were also monitored once every hour from March 2005 to September 2007. Finally, nine adult wolves (≥ 1.5-yr old) from four packs were monitored from March 2005 to April 2010 by taking one location every 2 h two days a week and every 4 h for the remainder of the week.

Other prey species of wolves that are present in the area included beaver *Castor canadensis* and snowshoe hare *Lepus*

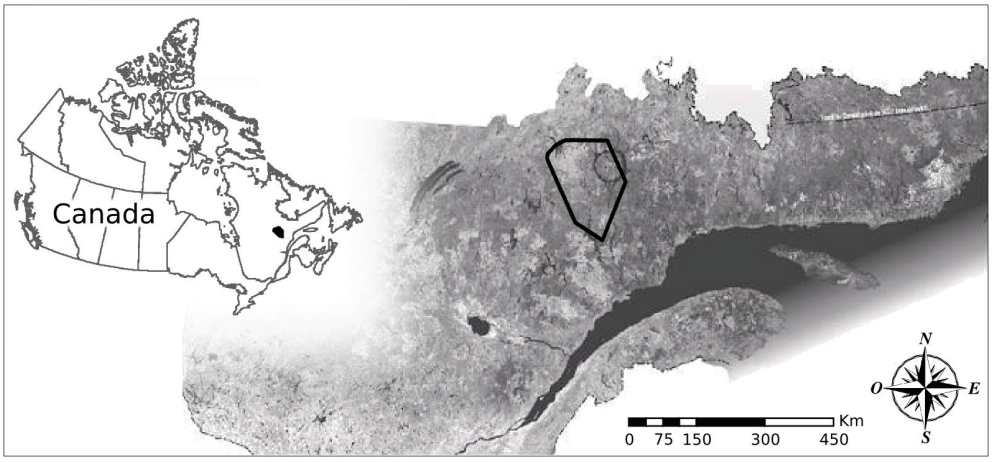

Figure 1. The study area (50–52°N, 68–71°W) located in the Côte-Nord region of Québec, Canada.

americanus, which are often associated with young forests where browse is abundant (Lariviere et al. 2000, Potvin et al. 2005). Black bear *Ursus americanus* was also present at low densities in the area (Courtois et al. 2007, Courbin et al. 2009).

Statistical analyses

Determining temporal trends

We calculated movement speed (i.e. the Euclidean distance between the current location and the next location, divided by the time interval) and turning angle (i.e. the direction from the current location to the next location measured relative to the direction of the current location from the previous location, Turchin 1998) between every successive individual location. Land-cover types were identified using Landsat Thematic Mapper images taken in 2000 with a 25-m resolution grid (Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre). Satellite images were composed of 48 land-cover classes from which we extracted three classes that were relevant to the three focal species: closed-canopy mature conifer forest, mature conifer forest with lichen, and deciduous forest, which covered approximately 30% of the total study area. We then added recent ($\leq$ 5 yr) and regenerating (5–20 yr) cuts, together with the road network, based on information provided annually by local forestry companies, and we estimated road density within a 1-km buffer radius to account for possible edge effects associated with these linear features. Finally, elevation was estimated using a 25-m resolution digital elevation model at the scale of 1:20 000.

We then used a 15-d moving window to characterise space use of each individual in each year. For a given day (from Julian day 1 to 365), the moving window summarises nine movement and habitat variables based on every location available between 7 d before and 7 d after that focal day. This approach smoothed the temporal trends and provided more consistent seasons rather than a succession of short and spurious seasons by removing fine-grained spatio-temporal variation, such as hourly variation, in space use. In addition, it allowed us to work with different monitoring schedules (one location every 1 to 8 h) because averaged values over the window included at least 45 locations for a given animal, which was a number large enough to be representative of space use during that time period (Supplementary material Appendix 1). Over the window, we computed: 1) the mean speed (in m h^{-1}); 2) the tortuosity, as the average absolute departure from 0° (straight-ahead movement) to 180° of turning angle; 3) the average elevation (in m); 4) the average road density (in km km^{-2}); and the proportion of locations in the moving window located in 5) closed-canopy mature conifer forest; 6) mature conifer forest with lichen; 7) deciduous forest; 8) recent cuts; and 9) regenerating cuts.

Range standardisation (i.e. $z_i = (x_i - \min(x))/(\max(x) - \min(x))$) is the recommended standardisation procedure for clustering (Steinley 2006). Each individual-year measurement was thus range standardised, and all were averaged, first by individual, and second for the whole set of individuals, to ensure that a behaviour displayed particularly prominently one year and individuals monitored during many years did not contribute more than others to the averaged trends. The resulting 365×9 data frame (i.e. 365 d over 9 variables) was finally range standardised for each variable to ensure that each variable had the same weight in clustering (Steinley 2006).

Clustering with the K-means analysis

K-means clustering (MacQueen 1967, Hartigan and Wong 1979) aims at identifying k groups of observations with similar characteristics in a set of n observations measured on p variables. Each variable included in the analysis corresponds to a dimension in a multivariate space which defines the scatterplot to be classified. The method starts by placing into this space k random points that are called seeds within the data range. The squared Euclidean distance between each observation and the seeds is then measured to associate each observation with its closest seed. The algorithm then works iteratively; new seeds are generated at the centroid (i.e. the geometric centre of all points considered) of the groups previously created, the squared Euclidean distance between each observation and the seeds is measured again, and each observation is associated with the closest new

seed until convergence is reached (i.e. the group structure is stable). The result is k groups, with each observation of one group being closer to its group centroid than to any other group centroid.

Choosing the number of clusters using the gap statistic

As K-means analysis does not provide a criterion of choice for the optimal number of clusters, we determined that number from the *DD*-weighted gap method (Yan and Ye 2007), based on the gap statistic. Let $d_{i,i'}$ be the distance between two observations ($i = 1,..., n$), and n_m the number of observations within the cluster m ($m = 1,..., k$). Within-cluster homogeneity can be estimated for k clusters from:

$$W_k = \sum_{m=1}^{k} \frac{1}{2n_m(n_m - 1)} D_m$$

where $D_m = \Sigma_{i,i' \in m}\, d_{i,i'}$ is the sum of pairwise distances. The gap statistic (Tibshirani et al. 2001) then contrasts W_k with the expected within-clusters homogeneity W_k^*, under the assumption of uniform multivariate distributions over the range of the data set. B random multivariate data sets are generated (with $b = 1,..., B$) using uniform distributions along the range of each principal component of the initial data set. The weighted gap statistic is thus computed as:

$$\text{gap}_k = E^*\{\log(W_{kb})\} - \log(W_k) = (1/B) \sum_{b=1}^{B} \log(W_{kb}^*) - \log(W_k)$$

A structure in the data set is revealed if $\text{gap}_1 < \text{gap}_2 - sd_2 \sqrt{(1+1/B)}$, where $sd_2 = [(1/B)\ \{\sum_{b=1}^{B} \log(W_{2b}^*) - (1/B) \sum_{b=1}^{B} \log(W_{2b}^*)\}^2]^{1/2}$. As the gap statistic tends to overestimate the real number of clusters, Yan and Ye (2007) proposed using a 'multilayer' clustering approach to estimate the number of clusters when $k > 1$, using $D\text{gap}_k = \text{gap}_k - \text{gap}_{k-1}$, and $DD\text{gap}_k = D\text{gap}_k - D\text{gap}_{k+1}$. $DD\text{gap}_k$ should be maximised when k is equal to the true number of clusters.

Defining seasonality

The optimal number of clusters identified by the multilayer approach can be used to define biological seasons. Each day of the year is associated with a cluster, which defines a given space-use state (i.e. a behavioural mode based on every space-use variable included in the clustering). Because of temporal autocorrelation in space-use trends, neighbouring days generally fall into the same space-use state. The analysis, however, does not take time into account, so that only similar ecological characteristics would lead observations to be grouped together. We thus defined a season as a homogeneous period of time with the same space-use state. Because each state can appear several times during the year, the k space-use states yield $K \geq k$ seasons. The robustness of the delineation of a given season was then assessed using a bootstrap procedure. We constructed 100 sets of individual-year units randomly resampled from the original data set with replacement to obtain the same size as the observed data set. We then ran the K-means clustering for each set with the estimated number of clusters for the entire data set. A distribution of daily weights, corresponding to the likelihood that a given day corresponds to the start of a new season, is then estimated by the number of new seasons within the bootstrap samples starting within a 5-d period around the focal day (i.e. including the 2 d before and the 2 d after). Only seasons starting at a day that fall in the uppermost (top 20%) part of the weight distribution are then retained, and the others dropped. We used a 20% threshold because they represented the most likely changes. To facilitate the interpretation of the results and reduce noise, every season shorter than 5 consecutive days was merged with the preceding season (Results). See Supplementary material Appendix 2 for a detailed illustration of the different steps, as applied to caribou.

Testing for similarity among species

In the context of apparent competition between caribou and moose, we used a measure of potential predation risk – defined as the resource overlap between the predator and the two prey species – as a proxy for the strength of the two trophic interactions, as compared to the niche overlap between caribou and moose (Chesson and Kuang 2008). We determined niche overlap between every pair of species based on habitat use (i.e. every variable except speed and tortuosity), using a simple index of overlap derived from the Jaccard index (Jaccard 1901) that was adapted to continuous data. For each variable and each day, niche overlap is measured as the size of the intersection divided by the size of the union of the two species ranges, based on the minimum and maximum values of the space-use state associated with the current day:

$$J_C(A, B) = \frac{\min[\max(A), \max(B)] - \max[\min(A), \min(B)]}{\max(A, B) - \min(A, B)}$$

Negative values are then set to 0 so that the index varies between 0 (no overlap) and 1 (complete overlap). All indices were then either averaged over the year to obtain a measure of global overlap for each variable, or over all variables to obtain a measure of global overlap for each day.

All statistical analyses were conducted using R 2.11.1 (R Development Core Team), with the R-packages adehabitat (Calenge 2006) for the extraction of movement characteristics and clusterSim (Walesiak and Dudek 2010) for the K-means analysis. Additional functions for computation of the weighted gap statistic and seasonality-related methods are available at: <http://ase-research.org/basille/seasonality/>.

Results

Seasonality in caribou

The weighted gap statistic indicated that the caribou data were structured over time, with $\text{gap}_1 = 0.49 < \text{gap}_2 - sd_2 \sqrt{(1+1/B)} = 0.50$. $DD\text{gap}_k$ revealed the presence of eight space-use modes during the year, corresponding to 13 seasons during the year. Among them, only 8 started at days corresponding to the 20% uppermost bootstrap-weight distribution and were thus retained. In addition, two 2-d periods were removed in April and in May. We ended up with six biological seasons delimited by the following breakpoints: 16 April, 22 May, 28 May, 3 August, 18 September, 28 December (Fig. 2).

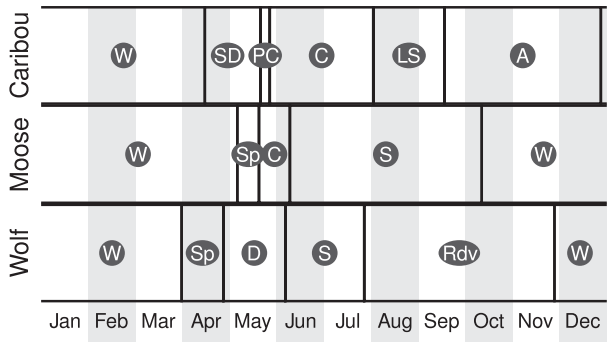

Figure 2. Schematic representation of the biological seasons for caribou, moose, and wolves in the Côte-Nord region of Québec, Canada, in 2005–2010. Legends: W = winter, SD = spring dispersal, PC = pre-calving season, C = calving season, LS = late summer, A = autumn, Sp = spring, S = summer, D = denning period, Rdv = rendezvous.

The first period until mid-April corresponded to a winter season during which caribou travelled at a slow pace. Further, they displayed their strongest use of conifer forests with lichen, and their weakest of deciduous forests and human-disturbed areas (i.e. cuts and areas of high road density) (Supplementary material Appendix 3 for a detailed plot of seasonal characteristics). Winter was followed by spring dispersal, which was characterised by an increase in speed, use of relatively low elevations, and the strongest use of deciduous forests, cuts, and roads. A short season (22 May–27 May), with intermediate characteristics then occurred before the calving season (late May through early August), which was characterised by slow and tortuous movements, high elevations, and a sudden drop in the use of human-disturbed areas. This season was also characterised by the highest use of conifer forests, and the lowest use of conifer forests with lichen. During late summer caribou generally travelled at high speed, made high use of deciduous forests, while they began reducing conifer forest use before winter. During autumn (mid-September to late December), caribou travelled at lower speed than in summer, and displayed their weakest use of conifer forests and a generally high use of conifer forests with lichen.

Seasonality in moose

The weighted gap statistic indicated that the moose data were structured over time, with $\text{gap}_1 = 0.27 < \text{gap}_2 - sd_2\sqrt{(1+1/B)} = 0.56$. $DD\text{gap}_k$ revealed the presence of two space-use modes during the year, corresponding to 4 seasons during the year. All of them started at days corresponding to the 20% uppermost bootstrap-weight distribution and were thus retained. The four biological seasons were delimited by the following breakpoints: 7 May, 21 May, 10 June, 12 October (Fig. 2).

The first period from mid-October until early May corresponded to a long winter season, including autumn, during which moose travelled at a slow pace and at a high elevation, while making strong use of deciduous forests, but little use of conifer forests with lichen and human-disturbed (i.e. cuts and of high road density) (Supplementary material Appendix 4 for a detailed plot of seasonal characteristics). Winter was followed by a short period characterised by an increase in speed, a decrease in the use of conifer forests, as well as the highest use of human-disturbed areas. The calving season (late May through 10 June) was characterised by the strongest use of high elevations, with a sudden drop in the use of cutblocks. During summer (10 June through mid-October), moose travelled at their highest speed, at low elevations, while displaying their strongest use of conifer forests with or without lichens and regenerating cuts, and their weakest of deciduous forests.

Seasonality in wolves

The weighted gap statistic indicated that the wolf data were structured over time, with $\text{gap}_1 = 0.58 < \text{gap}_2 - sd_2\sqrt{(1+1/B)} = 0.66$. $DD\text{gap}_k$ revealed the presence of five space-use modes during the year, corresponding to 14 seasons during the year. Because we only had data for 9 wolves from 4 packs (compared to 29 caribou and 16 moose), we used a threshold of 40% for the bootstrap-weight distribution, and only 11 seasons were thus retained. For the same reason, we removed 6 seasons that were shorter than 10 d: one 8-d period in March, one 5-d and one 9-d period in April, and one 1-d, one 2-d, and one 9-d period in November. We ended up with five seasons delimited by the following breakpoints: 1 April, 28 April, 7 June, 28 July, 28 November (Fig. 2).

The first period until early April corresponded to nomadic periods during which wolves travelled at slow pace, while making their strongest use of high elevations (Supplementary material Appendix 5 for a detailed plot of seasonal characteristics). The short spring season in April was characterised by faster and less tortuous movements, and the use of low elevations compared to winter. The denning season in May was characterised by a lower travel speed than in spring, the strongest use of low elevations, and the lowest use of conifer forest and regenerating cuts. Summer corresponded to the season during which wolves travelled at the highest speed, displayed the highest use of conifer forest with lichen, while also making the lowest use of deciduous forests. Finally, autumn corresponded to the rendezvous period, characterised by the lowest use of conifer forests with lichen, and the highest use of human-disturbed areas.

Interspecific niche overlap

The maximum niche overlap between wolves and caribou during the course of the year was associated with the use of conifer forests with or without lichen (overlap indices of 0.16 and 0.20, respectively, Table 1). All human disturbance variables displayed almost no overlap between wolves and caribou (0–0.04 for cuts and road density). In contrast, the year-round niche overlap was greater between wolves and moose than between wolves and caribou in the use of almost every habitat attribute (Table 1), with the greatest differences for recent cuts (difference of + 0.46), elevation (+ 0.29) and closed-canopy conifer forests (+ 0.28). Conifer forests with lichen were the only land-cover type

Table 1. Measure of niche overlap between caribou, moose and wolves, an assessment based on their concurrent use of habitat attributes (i.e. average elevation, average road density, and proportion of locations located in closed-canopy mature conifer forest, mature conifer forest with lichen, deciduous forest, recent cuts and regenerating cuts). The index varies between 0 (no overlap) and 1 (complete overlap), where complete overlap would occur when both species exhibit the exact same niche. The difference between moose-wolf overlap and caribou-wolf overlap is also provided.

Variable	Caribou–moose	Wolf–caribou	Wolf–moose	Difference
Elevation	0.034	0.131	0.416	+ 0.285
Closed-canopy conifer forests	0.271	0.199	0.483	+ 0.284
Conifer forests with lichen	0.050	0.155	0.000	− 0.155
Deciduous forests	0.000	0.001	0.218	+ 0.216
Recent cuts	0.046	0.048	0.504	+ 0.456
Regenerating cuts	0.042	0.000	0.256	+ 0.256
Road density	0.014	0.000	0.056	+ 0.056
Mean				+ 0.200

for which the overlap was greater with caribou than with moose (Table 1), due to their very limited year-round use by moose (Supplementary material Appendix 4). Niche overlap was lower between caribou and moose than between the predator and either one of its prey for every habitat variable considered (Table 1).

The niche overlap between wolves and caribou was higher in winter, relative to the rest of the year (Fig. 3). In fact, overlap was at a maximum at the end of winter, during the spring dispersal (April and May), and in late summer (August until mid-September), while it was lowest from the calving season until early August and during the rut. Niche overlap between wolves and moose was greater than the overlap between wolves and caribou almost all year-round and followed the same general pattern, except that it decreased, instead of increasing, after winter (Fig. 3). Consequently, differences between both prey in their niche overlap with wolves were the greatest during late calving (June and July), rut, and winter (wolf–moose overlap was 342, 564 and 139% higher than wolf–caribou overlap, respectively, Fig. 3), while they were their lowest during spring dispersal in May, late summer and fall (wolf–moose overlap was 30, 49 and 33% higher than wolf–caribou overlap, respectively, Fig. 3).

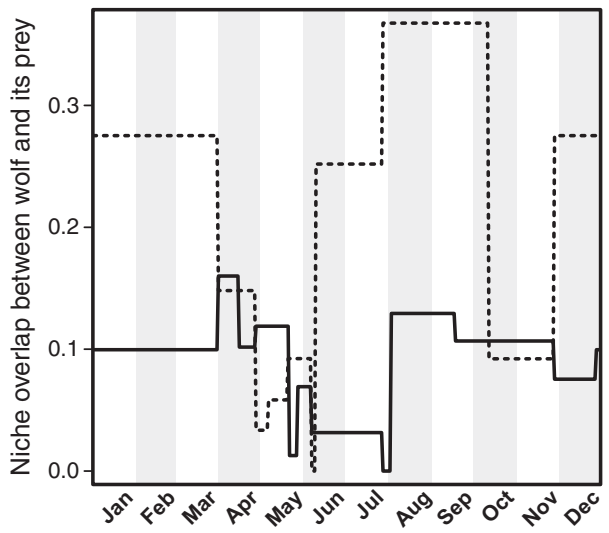

Figure 3. Temporal changes in niche overlap between wolves and caribou (solid line), and between wolves and moose (dashed line), based on temporal patterns of habitat use (i.e. average elevation, average road density, and proportion of locations located in closed-canopy mature conifer forest, mature conifer forest with lichen, deciduous forest, recent cuts and regenerating cuts). The index varies between 0 (no overlap) and 1 (complete overlap), where complete overlap would occur when wolves and a prey exhibit the exact same niche. The index is generally higher for wolf/moose than for wolf/caribou, indicating that wolves had generally a stronger niche overlap with moose than with caribou.

Discussion

In this paper, we developed a framework which merges cluster analysis with niche overlap indices to reveal temporal variation in the relative strength of predator–prey interactions, thereby revealing seasonal food-web properties in a system of large mammals. This approach has the flexibility needed to be applicable to a broad range of systems of interacting species. Indeed, the multivariate technique does not require restrictive assumptions, such as seasons that are necessarily delineated by changes in movement rate only, as the method can integrate multiple measurements of space use (e.g. movement measurements and habitat use) necessary to understand trade-offs shaping food webs. We applied this framework to define a total of seven biological seasons for caribou, and five for both moose and wolves. These seasons reflected the closer temporal match in space-use patterns that wolves have with moose, its primary prey, than with caribou, its alternative prey (Fig. 3). Food-web properties thus emerged from our approach, with the strength of trophic interactions reflecting a closer match in seasonal patterns and a stronger predator–prey relationship.

While traditional techniques to delineate seasons may suffice in the context of some ecological studies, the generic definition that is generally provided can mask food-web properties. For example, using movement characteristics alone to delineate seasons would have failed to expose important temporal variation in resource use and, hence, in trophic interactions. With Courbin et al.'s (2009) approach, for example, no distinction was made between early summer and late summer for caribou in the same study area. We showed, however, that caribou clearly increased their use of deciduous forests over the summer and, consequently, their potential predation risk (Supplementary material Appendix 3). Likewise, Ferguson and Elkie (2004) were unable to disentangle between late summer and autumn, while caribou display contrasted use of conifer forests with or without lichen and deciduous forests. Lastly, an expert-based definition of seasons, focusing on wolf movement ecology, led Houle et al. (2010) to define the entire denning period as a single biological season; however, we showed that, during the pre- and post-denning seasons, wolves display strong differences in their use of conifer forests, a key component of caribou habitat during this period. Our study presents a more comprehensive method that can delineate biological seasons based on changes in space-use patterns, thereby providing a clearer picture of niche overlap among species, which is fundamental to assessing the strength of trophic

links within food webs. Finally, while we aimed to define general biological seasons across years for each species, the same approach could be used to delineate annual seasons, and thus study inter-annual variation in space use in dynamic environments.

Prey should move in a landscape while attempting to acquire the maximum amount of resources with the minimum risk (Hugie and Dill 1994, Lima and Bednekoff 1999), whereas predators should focus their hunting efforts in areas where they are most likely to make a kill (Lima 2002), such as in areas of high prey density. Despite the predator–prey behavioural response race (Sih 1984), habitat-use patterns by cursorial predators, such as wolves, need to somewhat match those of their prey, i.e. the predation process is dependent on predator–prey sympatric use of space for an encounter to occur (Schmitz et al. 2004). Therefore, the predator's search behaviour ought to yield similarities in habitat use with its prey (Sih 1998). For example, wolf distribution tends to closely match elk *Cervus elaphus* distribution in winter, when pups do not restrict the movements of the adults (Mao et al. 2005). Moreover, the behavioural response race between predators and prey in a multi-prey system can give rise to spatial structure in the intensity of trophic interactions, as highlighted in Alberta and British Columbia where caribou were spatially separated from wolves and moose (Seip 1992, James et al. 2004). This spatial segregation is consistent with the closer niche overlap observed between wolves and moose than with caribou. Black bears can also have a significant impact on neonatal caribou and moose survival (Ballard 1994, Bastille-Rousseau et al. 2011). However, they were present at low densities in the area (Courtois et al. 2007, Courbin et al. 2009), and bears predate ungulate neonates only during a brief period of approximately 4–6 weeks after calving. The impact of black bears on seasonal patterns for the two ungulates was thus expected to be limited in our study system, during most seasons.

Some of the concordance in biological seasons among caribou, moose and wolves simply reflected a similar and concurrent response to abiotic elements of the environment. For example, all species had lower speed and more tortuous paths during winter (December–April) than during other seasons. This observation could be explained by the increased energetic costs of moving through snow that is experienced by all three species (Kelsall 1969, Telfer and Kelsall 1984, Fancy and White 1985). However, the behaviours underlying seasonal patterns that were most revealing of trophic interactions were those linked to the use of potential resources. For example, the presence of snow reduces browse availability for ungulates in winter (Visscher et al. 2006), and their distribution could then be heavily constrained by the distribution of resource-rich patches. Accordingly, the use of mature conifer forests with lichen was highest in winter for caribou, when it constitutes their primary source of food (Johnson et al. 2001, Briand et al. 2009).

Wolves also made strong use of these forests, to the extent of being the only important source of overlap with caribou, which led to extensive niche overlap during winter. However, niche overlap was even stronger between moose and wolves at this time of the year. Moose made intensive use of high elevations and deciduous stands where they can find abundant deciduous browse, an essential food in winter (Bryant and Kuropat 1980, Routledge and Roese 2004). The hunting tactics of wolves led them to the same areas, which created a much stronger niche overlap with moose than with caribou in winter (Fig. 3). Temporal changes in the 'relative' strength of niche overlap should reflect changes in the strength of trophic links, as these changes reflect temporal variation in the probability of predator–prey encounters, which is a critical component of the predation process. Indeed, only 17% of caribou mortalities occurred during winter in the same study area (Courtois et al. 2007). The much greater overlap between wolves and moose during the same period could have resulted in de facto dilution effects and, therefore, in relatively low predation risk for caribou (Bednekoff and Lima 1998). In contrast, space use of caribou in spring was characterised by a sudden increase in movement speed and by the highest use of disturbed areas (i.e. cuts and roads) in the year, which resulted in relatively strong niche overlap with their predator. During this biological season, niche overlap of wolves was only 30% higher with moose than with caribou, i.e. the lowest difference in the year. As a result, caribou faced their greatest risk of wolf predation during spring dispersal, with 56% of mortalities in the study area occurring during this season (Courtois et al. 2007), confirming that the niche overlap captured the predation risk for the prey. This result is particularly important in the case of mobile predators, which can show a rapid aggregative numerical response to an increase in prey availability, hence amplifying the effect of predation (Holt and Kotler 1987).

This temporal variation in the overlap of biological seasons is of concern for the conservation of forest-dwelling caribou, a species threatened across North American boreal ecosystems. Wolf populations are generally closely linked to the level of moose populations (Peterson et al. 1984, Messier 1994), a relationship consistent with the stronger niche overlap that we observed between wolves and moose than between wolves and caribou for most of the year. Nevertheless, the periodic increases in predation rate that caribou experience during the course of the year can have a substantial impact on their populations. First, caribou populations are generally under top-down control (Seip 1992, Wittmer et al. 2005b). Second, even if caribou populations were to reach low levels, negative feedback on wolf populations is not necessarily expected due to the presence of moose. In multiple-prey systems, generalist predators can escape such feedback by switching between prey, which can result in a density-independent numerical response with respect to each prey species (Courchamp et al. 2009) that can dramatically impact the rarer prey (Wittmer et al. 2005a, McLellan et al. 2010).

Additionally, forest harvesting can exacerbate the situation. The interactions among wolves, moose, and caribou in managed forests are closely linked to human activities. While caribou do not directly compete with moose for resources (Table 1), they may suffer from apparent competition with them, with asymmetrical interactions (Chaneton and Bonsall 2000) being mediated by wolves, in a fashion that shared three characteristics generally associated with endangerment of the alternative prey (DeCesare et al. 2010): 1) a common predator showing generalist behaviours; 2) a preferred prey

showing a numerical response to habitat disturbance; and 3) human-induced changes to the ecosystem favouring the preferred prey, and exacerbating predator effects on the alternative one. This situation fits the caribou–moose–wolf system well: logging has a strong negative impact on caribou (Smith et al. 2000, Courtois et al. 2007, Vors et al. 2007, Hins et al. 2009), while it can be beneficial to moose and, therefore, to wolves (Seip 1992, James et al. 2004, Wittmer et al. 2007). In our study, moose and wolves apparently coped with higher levels of human disturbance than did caribou: moose spent 5–14 times and wolves 12–25 times more time in human-disturbed areas (i.e. cuts and roads) than caribou during most seasons. Depending on its frequency and intensity, disturbance has the potential to severely affect species interactions and community structure by modulating the effects of predation in apparent competition (Kneitel and Chase 2004). By defining biological seasons, our study outlines some of the behavioural mechanisms modulating the strength of direct and indirect interactions within the caribou–moose–wolf food web during the course of the year.

We showed that the strength of food-web links can be inferred from the synchrony of seasonal changes in space-use behaviours. Trophic interactions strongly depend on the game played between predator and prey. Efficient ways to detect cycles from assemblages of behaviours in cyclic environments should therefore also enlighten structural properties of food webs. Our study emphasises temporal and spatial patterns in food-web hierarchy such as an increasing risk of predation for caribou during spring in relation to a high use of disturbed areas. Many generalist predators, from fishes (e.g. red drum *Sciaenops ocellatus*, Scharf and Schlicht 2000) to mammals (e.g. arctic fox *Alopex lagopus*, Fay and Stephenson 1989), feed upon multiple prey at a rate reflecting seasonal changes in their availability. In this study, wolves prey upon two ungulate species, which initiates the conditions for top-down control of predation (Jiang and Morin 2005) and that elicits both density- and trait-mediated effects, which in turn can have consequences on plant species coexistence (Calcagno et al. 2011). In the end, by adjusting their space-use behaviours, caribou are able to temporally mitigate to some degree this top-down control during the year. Most food webs are characterised by temporal variation in their properties (Moore and de Ruiter 1991, DeAngelis 1992); our study thus demonstrates how the study of trophic interactions can benefit from comprehensive definitions of biological seasons.

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Supplementary material (Appendix E7367 at <www.oikosoffice.lu.se/appendix>). Appendix 1–5.

Ecography

E7367
Basille, M., Fortin, D., Dussault, C., Ouellet, J.-P. and Courtois, R. 2012. Ecologically based definition of seasons clarifies predator–prey interactions. – Ecography 35: xxx–xxx.

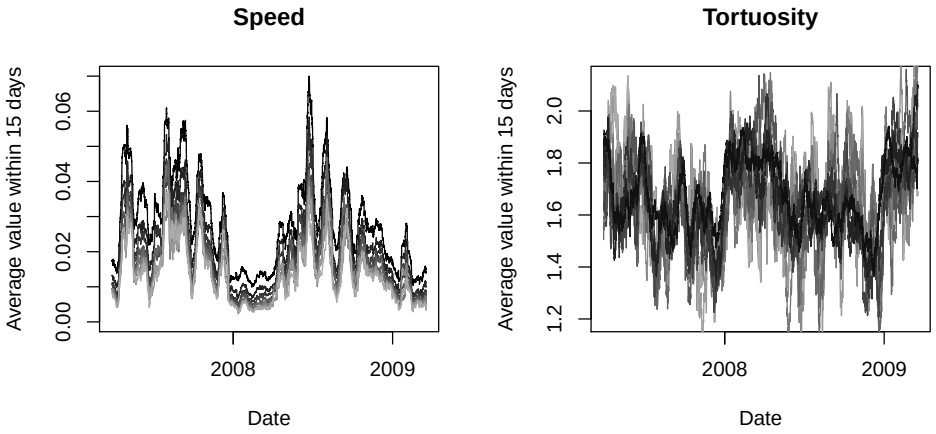
Supplementary material

Appendix 1–5

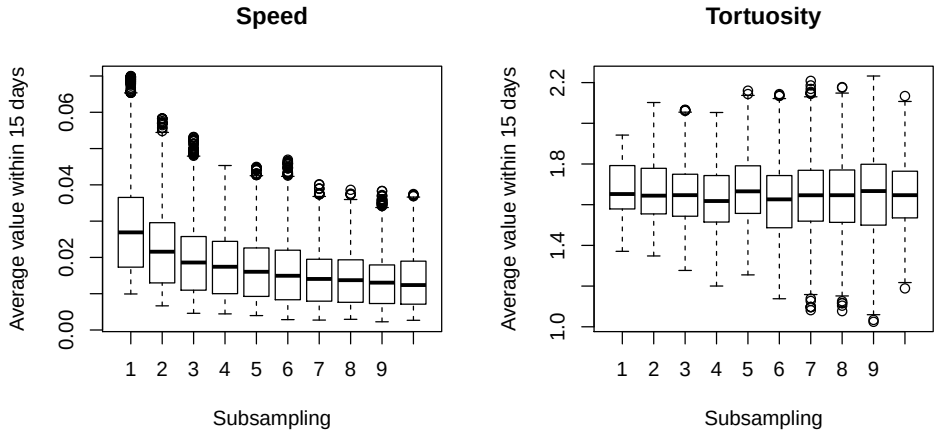
Supplementary material: Expanded results of seasonality

1 Impact of sampling frequency

We assessed variation in movement pattern due to the different monitoring schedules, by subsampling our finest-scale data (one location every 1 hour) to one location every 2 to 10 hours. We computed the average speed and tortuosity in a 15-day moving window as indicated in the manuscript. Temporal patterns were the same for every subsample. We illustrate the outcome based on one individual relocated every 1 hour. We first show the average speed (left) and tortuosity (right) in a 15-day moving window from the beginning to the end of the monitoring period. The subsamples are displayed with decreasing levels of grey, from black (one location every 1 hour) to light grey (one location every 10 hours):



The amplitude decreases for speed with higher subsampling (left), while the variance increases for angles (right):



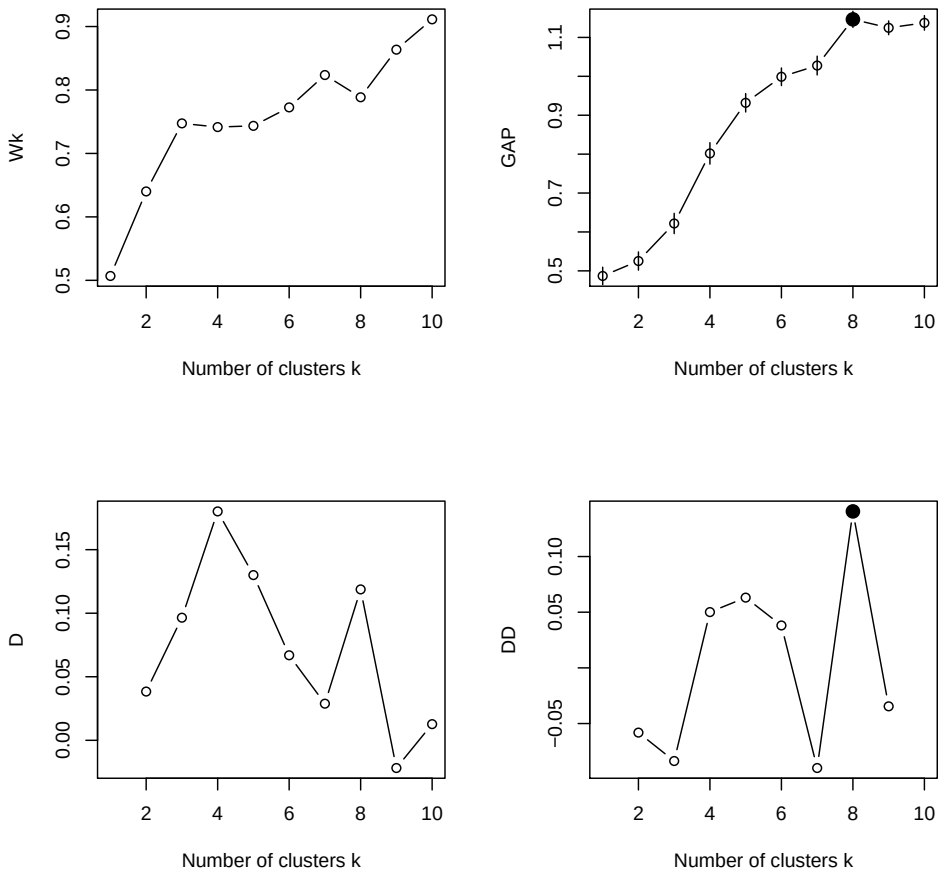
Nevertheless, this was not an issue in our analyses, since the range standardisation levelled out temporal patterns, so that subsamples at 1 hour or 8 hours provided the same results. In the end, this shows that the approach is robust to our level of variation in sampling frequency.

2 A detailed analysis of seasonality: the example of caribou

We start with a 365×9 data frame, with one row per Julian day and one column per space-use variable. The K-means is first run iteratively on this data frame, from 1 to 10 clusters. The "multilayer" approach is then used to choose the number of clusters (see the section *Statistical analyses* of the paper). We first compute W_k as $W_k = \sum_{m=1}^{k} \frac{1}{2n_m(n_m-1)} D_m$ where $D_m = \sum_{i,i' \in m} d_{i,i'}$ is the sum of pairwise distances. The weighted gap statistic is then computed as $\text{gap}_k = E^*\{\log(W_{kb})\} - \log(W_k) = (1/B)\sum_{b=1}^{B} \log(W^*_{kb}) - \log(W_k)$. A structure in the data set is revealed if $\text{gap}_1 < \text{gap}_2 - sd_2\sqrt{(1+1/B)}$, where $sd_2 = [(1/B)\{\sum_{b=1}^{B} \log(W^*_{2b}) - (1/B)\sum_{b=1}^{B} \log(W^*_{2b})\}^2]^{1/2}$. Finally, differences of weighted

gap, and differences of difference weighted gap are defined as $D\text{gap}_k = \text{gap}_k - \text{gap}_{k-1}$, and $DD\text{gap}_k = D\text{gap}_k - D\text{gap}_{k+1}$.

To guide the decision, the results can be presented as follows:



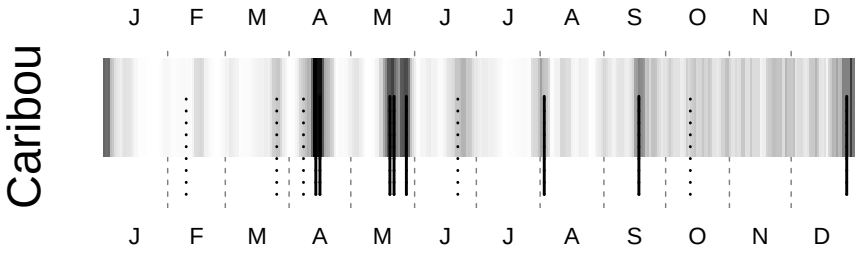
For each plot, the X-axis gives the number of clusters used in the K-means, and the corresponding W_k, weighted gap statistic, $D\text{gap}_k$, and $DD\text{gap}_k$. For the weighted gap statistic, the black dot indicates the estimated number of clusters (in this case, 8 clusters), such as $\text{gap}_k > \text{gap}_{k+1} - sd_{k+1}\sqrt{(1 + 1/B)}$. As the gap statistic tends to overestimate the real number of clusters, the "multilayer" approach provides another criterion of choice: $DD\text{gap}_k$ should be maximised when k is equal to the true number of

clusters. The black dot for the $DD\text{gap}_k$ plot thus indicates the maximum value (in this case, also at 8 clusters).

We then proceed with the K-means with 8 clusters. Each Julian day is associated with a given cluster, and consecutive days from the same cluster define a season. The clustering gives the following breakpoints between seasons:

February 10, March 26, April 08, April 14, April 16, May 20, May 22,
May 28, June 22, August 03, September 18, October 13, December 28

We then computed the bootstrap-weight distribution to evaluate the robustness of the delineation, and checked whether the previous breakpoints fell in the top 20 % part of the weight distribution. In the following figures, the weight for each day is displayed with a level of grey, the darker the higher. Seasons that were retained, or dropped, are symbolised by a solid line, or a dashed line, respectively:

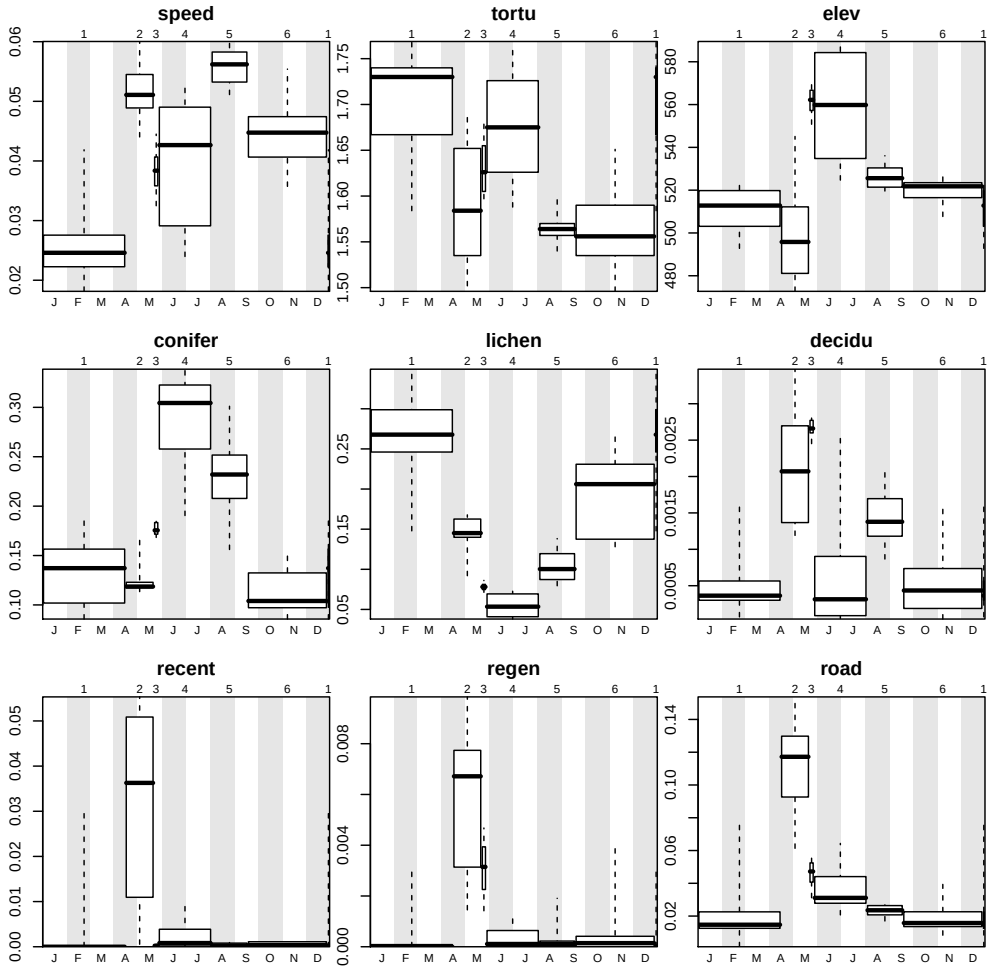


Among every season, only 8 started at days corresponding to the 20 % uppermost bootstrap-weight distribution and were thus retained, while seasons starting at March 26, April 08, April 14, June 22, and October 13 were dropped. Finally, we then remove every season shorter than 5 consecutive days. In this case, two 2-day periods were removed in April (April 14–April 15) and in May (May 20–May 21). We ended up with six biological seasons delimited by the following breakpoints:

April 16, May 22, May 28, August 03, September 18, December 28

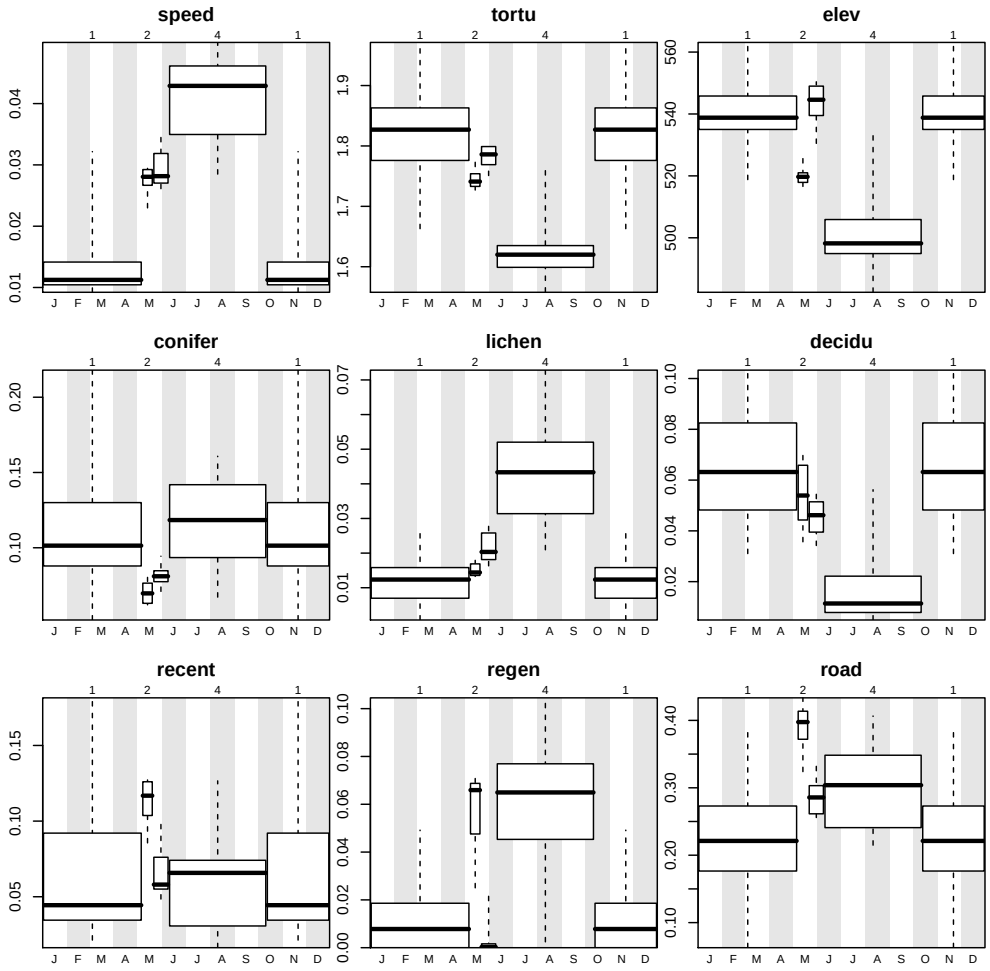
3 Detailed characteristics of sites used by caribou

The K-means associated with the multilayer approach results in 6 seasons during the year for caribou, which characteristics can be seen on the following plot (note that the winter season overlaps the end and the beginning of the year, so that the last and the first boxplot should be read as only one season):

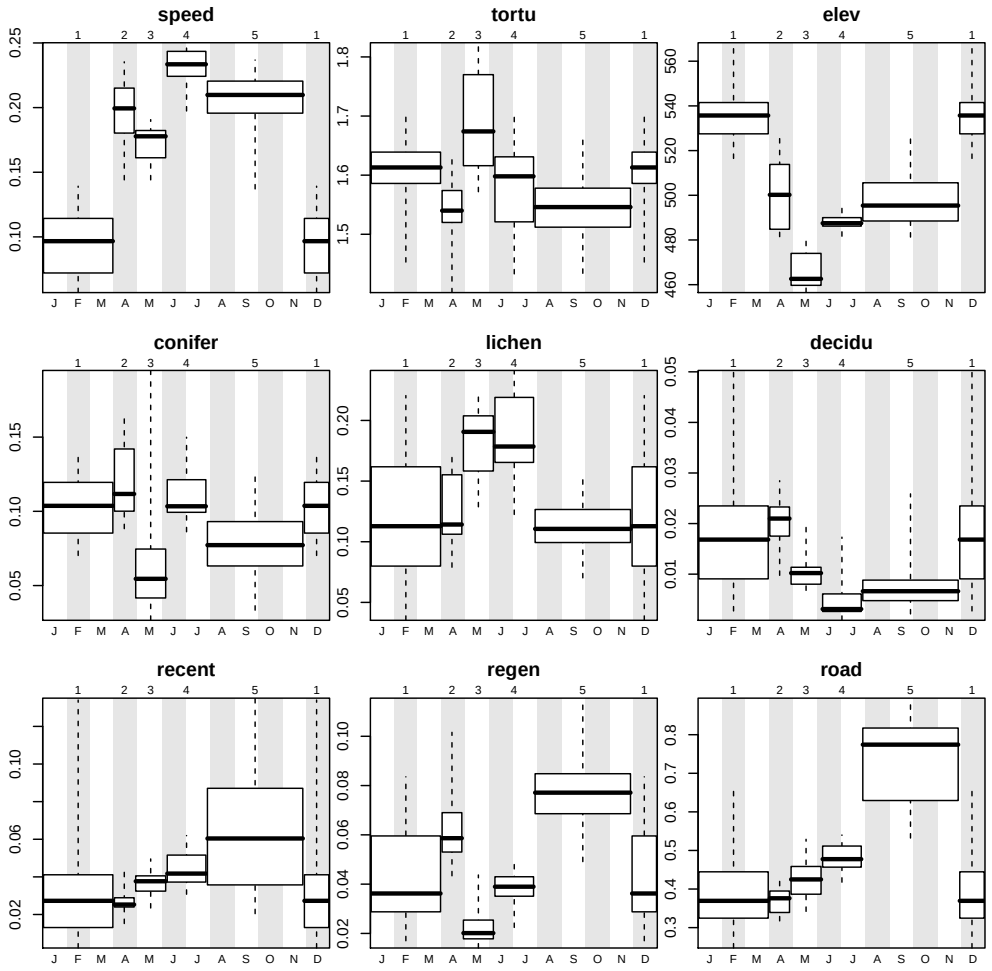


4 Detailed characteristics of sites used by moose

The K-means associated with the multilayer approach results in 4 seasons during the year for moose, which characteristics can be seen on the following plot (note that the winter season overlaps the end and the beginning of the year, so that the last and the first boxplot should be read as only one season):



5 Detailed characteristics of sites used by wolves

The K-means associated with the multilayer approach results in 5 seasons during the year for wolves, which characteristics can be seen on the following plot (note that the

winter season overlaps the end and the beginning of the year, so that the last and the first boxplot should be read as only one season):