Research

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Temporally dynamic habitat suitability predicts genetic relatedness among caribou

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Landscape heterogeneity plays a central role in shaping ecological and evolutionary processes. While species utilization of the landscape is usually viewed as constant within a year, the spatial distribution of individuals is likely to vary in time in relation to particular seasonal needs. Understanding temporal variation in landscape use and genetic connectivity has direct conservation implications. Here, we modelled the daily use of the landscape by caribou in Quebec and Labrador, Canada and tested its ability to explain the genetic relatedness among individuals. We assessed habitat selection using locations of collared individuals in migratory herds and static occurrences from sedentary groups. Connectivity models based on habitat use outperformed a baseline isolation-by-distance model in explaining genetic relatedness, suggesting that variations in landscape features such as snow, vegetation productivity and land use modulate connectivity among populations. Connectivity surfaces derived from habitat use were the best predictors of genetic relatedness. The relationship between connectivity surface and genetic relatedness varied in time and peaked during the rutting period. Landscape permeability in the period of mate searching is especially important to allow gene flow among populations. Our study highlights the importance of considering temporal variations in habitat selection for optimizing connectivity across heterogeneous landscape and counter habitat fragmentation.

1. Introduction

Preserving and restoring connectivity for broad-scale ecological processes, such as dispersal and gene flow, has become a major conservation priority [1]. A major impediment to this goal is the difficulty in predicting how different land use, climate change or reserve design scenarios will affect connectivity. Conservation planning decisions are thus often made without quantifying benefits for the ecological processes they are meant to be conserving. A lack of connectivity can have dramatic consequences on populations, notably because of the reduction of gene flow, which leads to greater inbreeding and loss of genetic diversity through increased genetic drift within fragments [1,2]. The consequences of fragmentation can even lead to the local extirpation or extinction of species [3].

Landscape genetics is a synthetic methodological approach that combines concepts and tools from population genetics, landscape ecology, geography and spatial statistics to guide management decisions in identifying where best to set aside movement corridors, construct habitat linkages and otherwise promote connectivity [4–6]. These methodologies examine how landscape

features affect recurrent microevolutionary processes (including gene flow, genetic drift and selection) in a spatially explicit manner at multiple spatial and temporal scales [5–7].

This qualitative approach, however, has been shown to suffer from lack of repeatability and poor performance in describing actual landscape costs of movements [8]. Some studies have begun to use radio-telemetry data to identify key environmental factors for constructing more objective models of habitat use [9,10]. A method commonly used to study terrestrial wildlife is to build habitat suitability models (HSMs; [11]) to infer a species' preferred habitat. Weckworth et al. [12] have recently demonstrated the superiority of HSMs over the null isolation-by-distance (IBD) model in predicting genetic structure in woodland caribou (Rangifer tarandus). Using HSMs based on radio-telemetry data informing on connectivity may circumvent prior limitations in landscape genetics research. This association is particularly attractive, because genetic data offer a means to validate spatially explicit connectivity models, whereas environmental data can be used to select and score habitat variables used in landscape genetic studies [10]. Collectively, merging HSMs- and genetic-based information allow for better inferences on whether habitat selection actually facilitates or limits gene flow [4] and what specific habitat variables would favour the maintenance of connectivity.

In addition, landscape genetics studies rarely consider annual migrations, variations in seasonal range or habitat use when implementing models (but see [10] for a comparative approach) although animals may use substantially different habitat among seasons [13,14]. This is particularly problematic when species exhibit variable seasonal response to landscape features or do not select the same habitat types all through the year [14,15]. Annual-based analysis of species distribution that show important temporal variations in distribution may lead to model uncertainty [16], thus impeding our ability to infer about the effects of landscape connectivity on gene flow. To circumvent this limitation, HSMs should be developed for multiple time periods expected to be biologically relevant when species behaviour may differ sensibly.

Here, we explore the landscape genetic structure of caribou in Québec and Labrador. We used ARGOS radio-telemetry data from more than 500 migratory tundra caribou and capture locations of forest-dwelling and mountain caribou to construct HSMs for caribou at the landscape scale. Pathways based on least-cost distance and circuit theory between individuals were constructed, and correlated to levels of genetic relatedness. Using this approach, we addressed the following questions: (i) is habitat suitability a good predictor of gene flow? (ii) do seasonal patterns of habitat selection differ in their ability to predict gene flow? and (iii) how do landscape connectivity models compare with null models of genetic differentiation? Based on caribou ecology, we predicted that (i) models based on locations during the rut will be the best predictors of genetic relatedness as roving males sire offspring (Espmark 1964); (ii) summer models will be better predictors than winter models, because movement is restricted during winter [17] and this is when range overlap between different herds increases [18]; (iii) patterns and predictive ability of models will vary between males and females because of sex-based differences in habitat suitability [19]; (iv) habitat selection models of males will be better than those of females, because gene flow is male-mediated [20]; and (v) the
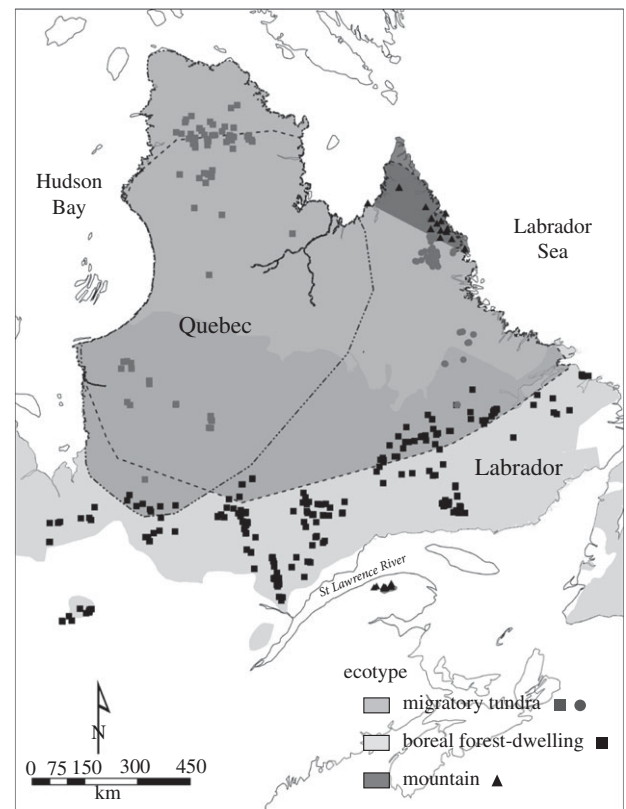

Figure 1. Map of genetic sample locations of caribou in Québec and Labrador, eastern Canada. Grey squares: Rivière-aux-Feuilles migratory herd; grey dots: Rivière-George migratory herd; black squares: forest-dwelling caribou; black triangles: mountain caribou. The annual ranges of migratory herd are delineated by dotted and dashed contour lines for the Rivière-aux-Feuilles and the Rivière-George herds, respectively.

habitat selection models will outperform the null (IBD and isolation-by-barrier, IBB) models of genetic differentiation [12].

2. Methods

(a) Study area and species
Caribou (R. tarandus) rank among the most mobile terrestrial mammals. In eastern North America, three ecotypes are present: migratory caribou, mountain caribou and forest-dwelling sedentary caribou [21]. The migratory barren-ground ecotype undertakes long-distance seasonal migrations of hundreds of kilometres (up to 2500 km) between summer range in the tundra and winter range in the boreal forest. Migratory females breed in late October during the autumn migration. They return to the tundra in spring, aggregate on the way to calving grounds, and in June, they calve on traditional calving grounds. By contrast, the mountain ecotype undertakes altitudinal movements associated with food availability and predation avoidance, but usually stays in the same alpine area. The sedentary ecotype resides in the boreal forest throughout the year, and females perform short-distance migrations in spring to space away from conspecifics and predators [22]. The study area encompassed an approximately 1 365 000 km^2 region in Quebec and Labrador, Canada (figure 1) that represented a broad diversity of ecosystems in eastern North America, ranging from southern boreal forest and mountain habitat (47° north) to northern Arctic tundra (62° north).

(b) Genetic data
We obtained tissue samples of 480 caribou representative of the three ecotypes found in Quebec/Labrador (figure 1 and table 1).

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Table 1. Number of caribou analysed. (For migratory caribou, the number of individuals genotyped and fitted with ARGOS-telemetry collars is given by sex and herd, respectively. Values between brackets indicate number of caribou for which we had both genetic information and ARGOS locations (see text). For sedentary forest-dwelling and mountain caribou, the number of individuals genotyped is given by sex and herd, but for these individuals, sampling location was used for habitat-suitable models.)

sex	ecotype	herd	no. genotyped individuals	no. radio-collared individuals	no. ARGOS fixes
all individuals	migratory	Rivière-George	70 [30]	296 [30]	37 711 [2230]
		Rivière-aux-Feuilles	77 [32]	233 [32]	25 216 [1883]
	forest-dwelling		316	—	—
	mountain	Gaspésie	27	—	—
		Torngat	23	—	—
females only	migratory	Rivière-George	52 [12]	243 [12]	32 560 [952]
		Rivière-aux-Feuilles	58 [13]	162 [13]	19 927 [1168]
	forest-dwelling		268	—	—
	mountain	Gaspésie	16	—	—
		Torngat	16	—	—
males only	migratory	Rivière-George	18 [18]	53 [18]	5151 [1278]
		Rivière-aux-Feuilles	19 [19]	71 [19]	5289 [715]
	forest-dwelling		15	—	—
	mountain	Gaspésie	11	—	—
		Torngat	7	—	—

The sampling included: two migratory tundra herds: the Rivière-George ($n = 70$) and the Rivière-aux-Feuilles ($n = 77$) herds; two mountain caribou populations: Torngat Mountains ($n = 23$) and Gaspésie ($n = 27$), as well as 316 sedentary forest-dwelling caribou inhabiting the boreal forest of Québec and Labrador. The genetic data used here are from individuals PCR amplified and genotyped at 16 polymorphic microsatellite loci, following Yannic et al. [23]. We assessed deviation from Hardy–Weinberg equilibrium and linkage disequilibrium using GENEPOP v. 4.0 [24]. Genetic relatedness among all pairs of sampled individuals was calculated using Lynch & Ritland's [25] estimator with COANCESTRY v. 1.0 [26]. The accuracy of relatedness metrics has been shown to vary among datasets (reviews in [27,28]), and more specifically in a landscape genetic context [29]. We selected the Lynch and Ritland's r coefficient index, because this estimator has been proved to be an adequate marker-based estimator of relatedness in natural populations and often outperforms other estimators [25,28].

(c) Model fitting and habitat suitability maps

Using satellite-tracking collars for migratory caribou and sampling locations for forest-dwelling and mountain caribou, we fitted daily HSMs on a sliding window of ± 3 days for the complete dataset and for the sexes separated. To fit the models, we used the locations of 296 caribou (53 males and 243 females) of the Rivière-George herd and 233 caribou (71 males and 162 females) of the Rivière-aux-Feuilles herd fitted with satellite collars (ARGOS, Largo, MD; table 1). At the scale of the study, we used only movements performed by migratory caribou and considered forest-dwelling caribou and mountain caribou as strictly sedentary all year round (table 1). For each Julian day, we derived HSMs for all individuals, for females only and for males only.

We computed environmental layers for the study area. We used generalized linear models (GLM [30]) as implemented in R [31], because they provide parameter estimates that are easy to interpret and allow investigation of the variance explained by each model component. We modelled the distribution of the

caribou using the 12 environmental variables, some being temporally dynamic (snow cover, normalized difference vegetation index (NDVI), temperature, precipitation) others being static (elevation, proportion of the different land cover categories; electronic supplementary material, table S1). Those variables are recognized as important predictors of caribou habitat suitability and are likely to enhance or impede caribou movement [32–34]. We obtained 1095 HSMs, resulting from the combination of Julian days and sex (i.e. from the whole dataset and from the sexes separated). We used k-fold cross-validation to evaluate habitat model performance [35]. We evaluated the predictive performance of each model using a repeated split sampling approach in which models were calibrated over 70% of the data and evaluated over the remaining 30%. This procedure was repeated five times. Because the models were built with pseudo-absences, we used the true skill statistics (TSS) as the predictive performance metric [36,37]. In addition, we compared the habitat model fits estimated with the coefficient of determination R^2.

(d) Statistical analyses

We first constructed two null landscape genetics models. The first, an IBD model, was created by calculating Geodesic distances between individuals based on great circle distances according to the 'Vincenty (ellipsoid) method using the package 'geosphere' 1.2–27 implemented in R. The second, an IBB model, took into account the effect of the St Lawrence River, which is an impassable barrier dividing the study area (figure 1). If the compared individuals were separated by the river they were coded with a 1, with other individuals coded with a 0 [38]. We next examined the influence of connectivity; landscape connectivity models were based on conductance surfaces from 10 km cells using the HSM maps. Least-cost paths were calculated between all individuals using the costDistance function implemented in the 'gdistance' 1.1–4 package of R; this produces a single, pairwise conductance score between each pair of individuals (hereafter referred to as 'least-cost path'). We finally used circuit
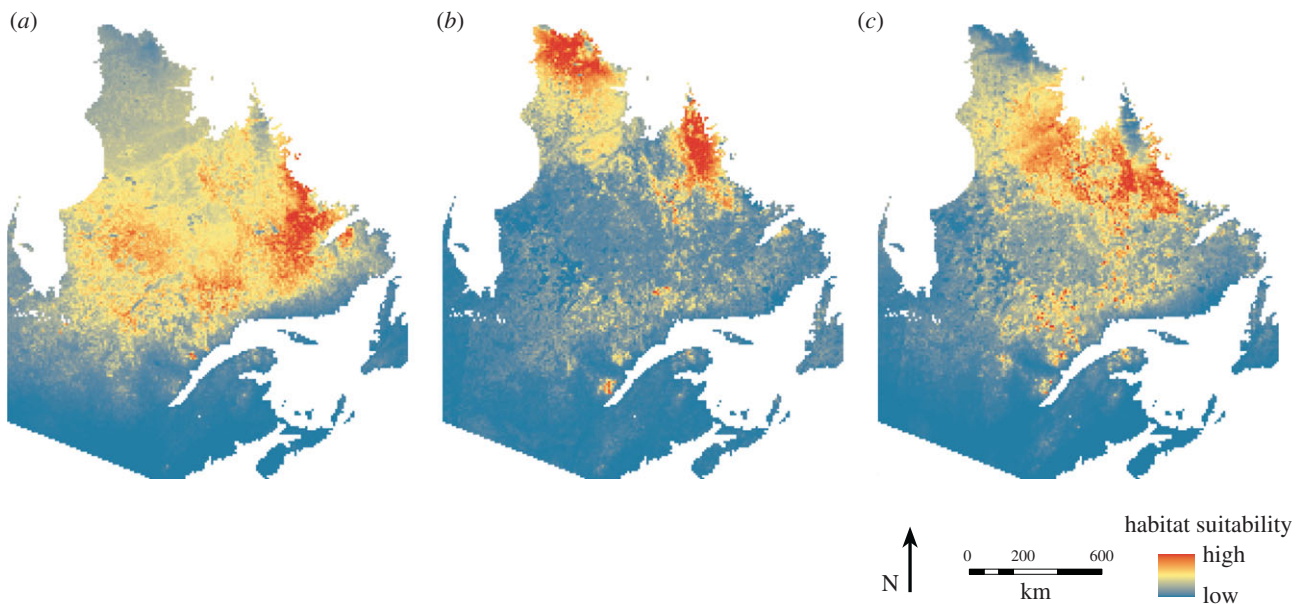
Figure 2. Maps of suitable surfaces for caribou in Québec/Labrador. (*a*) The winter habitat suitability model (HSM) map, (*b*) The calving season HSM map, and (*c*) the rutting period HSM map. (Online version in colour.)

theory [39,40], which does not rely on a single pathway to estimate connectivity distances between all individuals (hereafter referred to as 'circuit theory'). This distance reflects the average travel time from origin to goal following a (Brownian) random walk [39,40]. Using the same conductance matrix used for estimating least-cost distance, we calculated the connectivity distance between all individuals using the *commuteDistance* function implemented in 'gdistance'. This function is related to the procedure implemented in CIRCUITSCAPE [40]. Connections were allowed between all eight surrounding cells of each pixel. Based on the assumption that the model with the best support should exhibit not only the highest simple correlation with genetic distance, but also a significant, positive partial correlation with genetic distance after controlling for each of the competing models, we employed causal modelling to identify the most influential variables associated with gene flow within a multiple hypothesis-testing framework as applied by Cushman *et al.* [41]. We evaluated the significance of correlations and partial correlations using Mantel [42] and partial Mantel tests, computed using the R library 'ecodist' [43] with 10 000 randomizations.

We evaluated the predictive power of models using a repeated split sampling approach in which models were calibrated over 70% of the data and evaluated over the remaining 30%. This procedure was repeated 10 times for the whole dataset and for the sexes separated. We then tested the effect of geographical distances (i.e. geodesic distance, least-cost-path or circuit connectivity) and biological seasons (see the electronic supplementary material, figure S6) on the Mantel's r coefficients using GLMs in R. We used Spearman rank–order correlation as the predictive performance metric between predicted values obtained by GLMs on the training datasets and the observed values obtained from the test datasets. As GLM does not provide R^2-values, we computed the explained variance as: $R^2 = 1 - (A/B)$, where $A = \text{sum } [(\text{values}_{observed} - \text{values}_{predicted})^2]$ and $B = \text{sum } [(\text{values}_{observed} - \text{mean}(\text{values}_{observed}))^2]$ to estimate the proportion of variance explained by our models.

Among the 296 migratory caribou used to fit the daily HSMs, we had a 16 locus genotype for a subset of individuals only ($n = 62$). Similarly, we did not have the daily locations of all genotyped migratory caribou. To overcome this problem, for each focal day, we randomly sampled $n_{leaf} = 77$ and $n_{Geor} = 70$ ARGOS-satellite positions for the Rivière-aux-Feuilles and Rivière-George herds,

respectively (table 1). Then, we randomly assigned a 16 locus genotype to these daily locations. For forest-dwelling and mountain caribou, geographical sampling corresponded strictly to the genetic sampling. To ensure that this procedure did not affect the results, we repeated the analyses with a subset of the data ($n = 140$), including the 62 satellite-collared caribou, for which we had a corresponding genotype.

3. Results

(a) Habitat suitability models

Predictive power of the daily models was high. The mean TSS index from fivefold cross-validation was 0.62 (CI$_{95\%}$: 0.61–0.63), indicating that the model adequately predicted habitat use by caribou. The explained deviance ranged from 0.16 to 0.46 (R^2 mean: 0.29, CI$_{95\%}$: 0.28–0.30). Both the predictive power (TSS) and the coefficient of determination of the models (R^2) were not constant over time, with a maximum around Julian day 200 and lower values during the winter, indicating that habitat selection in regards to the environmental features included in the models was more pronounced in summer than in winter (figure 2). Similarly, the relative contribution of each variable to the models changed over the seasons (electronic supplementary material, figure S1). All variables except altitude were particularly good predictors of caribou habitat selection during the calving period, and snow cover also influenced habitat selection during the rut and autumn migration. Altitude consistently had a low influence on caribou habitat selection throughout the year.

(b) Genotyping and metrics of relatedness

All markers were in Hardy–Weinberg equilibrium, with none of 120 comparisons showing evidence of linkage disequilibrium after Bonferroni correction [44]. Diversity statistics for each locus are found in the electronic supplementary material.
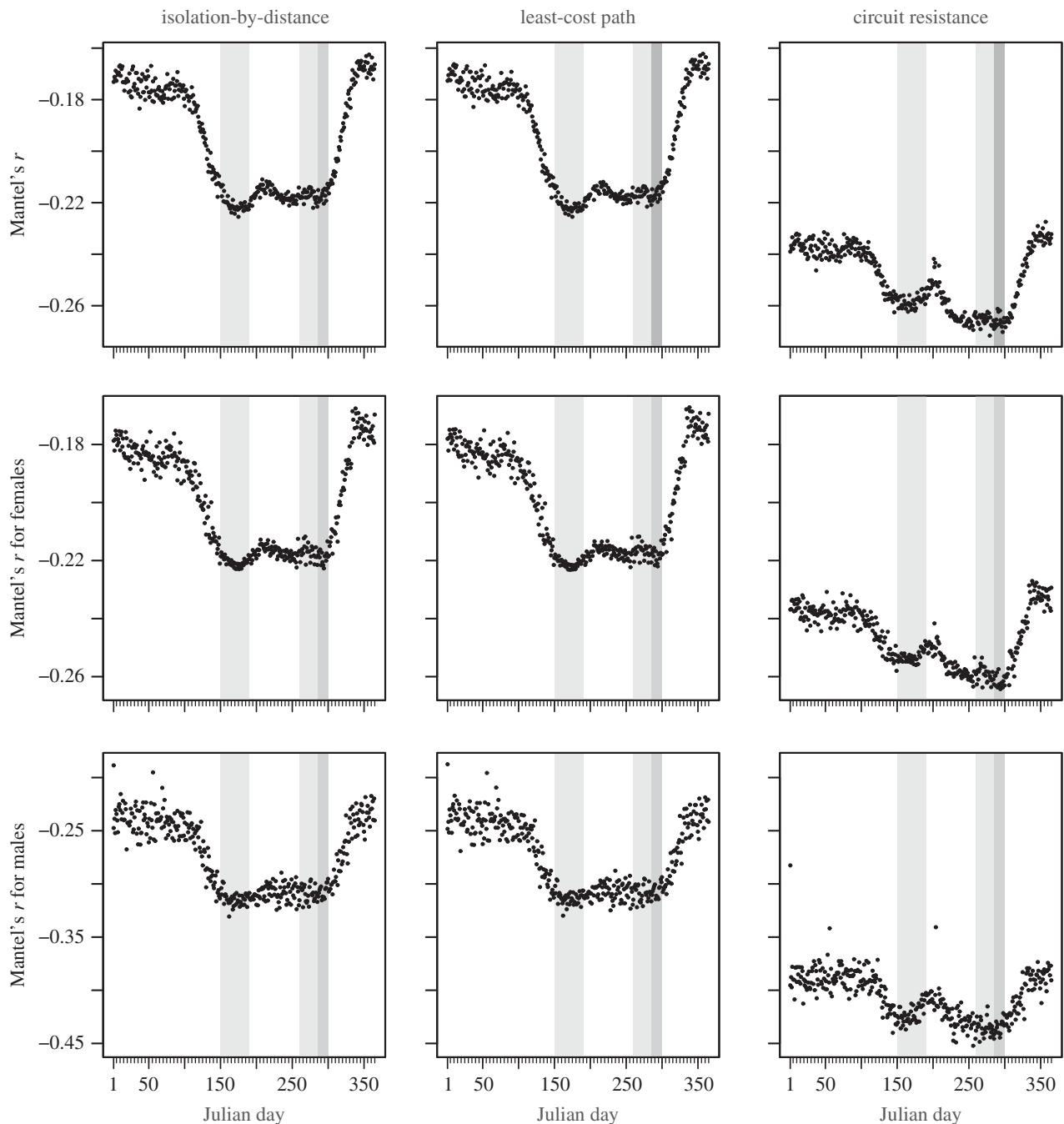
Figure 3. Temporal changes in correlation coefficient (Mantel's *r*) between genetic distance (i.e. relatedness among individuals) and geographical distance. Plots of genetic relatedness (Lynch & Ritland [25] relationship coefficient) against geodesic distance, least-cost path and circuit theory for the whole dataset and for the sexes separated. Grey boxes delimit the calving period (Julian days 155–190) and the rut period (Julian days 260–300) for forest-dwelling caribou [45] and migratory caribou [18]. Dark grey box shows the rutting peak for migratory caribou (Julian days 285–300; [18]).

(c) Landscape genetic models

The null IBD models along with the HSMs based on least-cost path and circuit theory models are presented in figure 3 and table 2. Circuit theory models improved the IBD models by 17–18% for females and 33–35% for males. By contrast, least-cost path models yielded no or weaker improvements to the null IBD models (figure 4 and table 2). The best predictors of genetic relatedness were circuit theory models centred on the calving (Julian days 155–190) and the rut (Julian days 260–300) habitat selection, whereas winter-based models (Julian days 355–110) were the poorest (figure 3). Sex-based models showed similar trends, except that male models explained more variance in relatedness than female models (table 2). The IBB model that accounted for the effect of the St Lawrence River separating different herds explained a significant part of

the genetic distance among individuals (Mantel *r*: −0.125, *p* < 0.001, *β* = −0.055). The analyses performed on the data subset (*n* = 140), notably including the 62 satellite-collared caribou, for which we had a genotype, and the random subset of forest-dwelling and mountain caribou (*n* = 78) did not alter the overall results obtained with the whole dataset (electronic supplementary material, figure S2). The best predictors of genetic relatedness were still circuit theory models centred on the calving and the rutting habitat suitability, whereas winter-based models were the poorest. Predictive power of the models was high (see the electronic supplementary material). Repeated split sampling approach indicated a high congruence between predicted and observed Mantel's *r* coefficients for the whole and female datasets, and to a lesser extent for the male dataset owing to the lower sample size for males

Table 2. Results from distance and landscape-based connectivity models (least-cost paths and circuit theory) in caribou, along with the null models of differentiation looking for a correlation between geographical distance and genetic relatedness. (Simple Mantel' r and p-values are provided; all daily models are highly significant (*$p < 0.0001$; $n = 365$). The slopes are calculated from linear regressions between geographical and genetic distances.)

model[a]		Mantel's r	p	slope	p
IBB	barrier	-0.06	<0.0001	-0.02	<0.0001
IBD	distance	-0.20 ± 0.02	$<0.0001^*$	$-4.58 \times 10^{-8} \pm 3.86 \times 10^{-9}$	$<0.0001^*$
	distance F	-0.20 ± 0.02	$<0.0001^*$	$-4.62 \times 10^{-8} \pm 3.33 \times 10^{-9}$	$<0.0001^*$
	distance M	-0.28 ± 0.03	$<0.0001^*$	$-7.67 \times 10^{-8} \pm 7.62 \times 10^{-9}$	$<0.0001^*$
least-cost path	least-cost path	-0.19 ± 0.03	$<0.0001^*$	$-4.28 \times 10^{-4} \pm 5.65 \times 10^{-5}$	$<0.0001^*$
	least-cost path F	-0.20 ± 0.02	$<0.0001^*$	$-4.34 \times 10^{-4} \pm 3.73 \times 10^{-5}$	$<0.0001^*$
	least-cost path M	-0.27 ± 0.04	$<0.0001^*$	$-7.25 \times 10^{-4} \pm 8.55 \times 10^{-5}$	$<0.0001^*$
circuit theory	circuit theory	-0.25 ± 0.01	$<0.0001^*$	$-5.25 \times 10^{-7} \pm 3.61 \times 10^{-8}$	$<0.0001^*$
	circuit theory F	-0.25 ± 0.01	$<0.0001^*$	$-5.04 \times 10^{-7} \pm 3.23 \times 10^{-8}$	$<0.0001^*$
	circuit theory M	-0.41 ± 0.02	$<0.0001^*$	$-9.18 \times 10^{-7} \pm 6.59 \times 10^{-8}$	$<0.0001^*$

[a]Models for which the sex (F for female and M for male) is not denoted are based on all individuals.
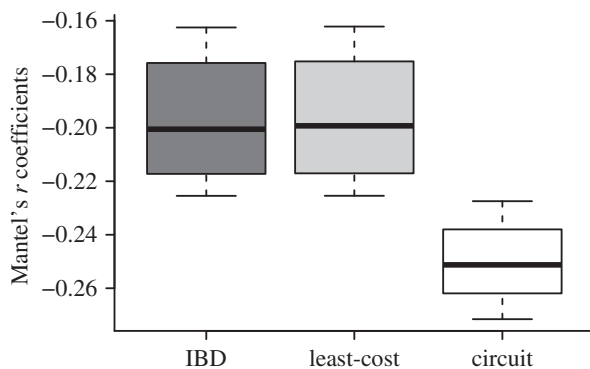
Figure 4. The relative Mantel's r coefficients estimated from the correlation of genetic versus the three geographical distances between pairs of caribou: geodesic distance (IBD), least-cost path and circuit theory, respectively.

(see the electronic supplementary material, table S4 and figure S7). Both geographical distance (i.e. geodesic distance, least-cost-path or circuit connectivity) and biological season (see the electronic supplementary material, figure S6) covariates explained 94% of the variance of the Mantel's r coefficients for the whole dataset (electronic supplementary material, table S4).

4. Discussion

When assessing population connectivity, temporal variation in species habitat utilization is rarely considered, even if behaviour may vary among seasons within a year [33]. Here, we showed that the genetic distances among caribou, which reflect the extent of genetic exchanges over time, were best explained by landscape features than simple linear distances, and that this relationship varied within the year. Daily HSMs indicated that characteristics of the landscape separating populations best explain genetic distances during the rutting period, when genetic exchanges are most likely. Our dynamic temporal approach provided new insights into three interrelated components: (i) what habitats caribou are selecting, (ii) whether these patterns of habitat selection predict genetic relatedness, and (iii) which season is the best predictor of genetic relatedness for males and females. This information can then be used to design areas optimizing population exchanges during periods of the year when they are most needed.

Movement patterns reflect interactions between animals and their environment [46,47] and understanding them often requires consideration of the temporal dynamic nature of environmental conditions among seasons [48,49]. For example, the spatial distribution of Thomson's gazelles *Gazella thomsonii* in Africa continually changing from month to month, like a shifting mosaic [50]. Similarly, home-range size of red deer *Cervus elaphus* at multiple temporal scales is driven by temporally dynamic variables such as temperature, precipitation, day length and snow cover [51]. Hence, studies of animal movements can greatly benefit from the incorporation of temporally dynamic environmental variables. Only a handful of studies have used HSMs based on satellite-radio-telemetry in a landscape genetics framework despite its recognized use [4], and none of these models explicitly used the telemetry data to select and score habitat variables for HSMs with the intent of predicting genetic relatedness throughout the year (but see [10,12]). Using this combined method, here we showed the usefulness of a spatio-temporal approach to determine the most relevant period and most relevant area for optimizing connectivity among populations. Overall, the combined use of individual locations obtained with satellite telemetry and genetic data increases the capability of landscape genetics in elucidating the relationships between landscape heterogeneity and genetic differentiation in space and time.

Our analyses showed changes in habitat selection and an increase of the correlation between habitat selection and relatedness during the rut. Avgar *et al.* [33] demonstrated changes in rates of movement in caribou according to seasonal environmental conditions. Comparisons among the movement characteristics of different ungulate species suggest that major classes of movements, such as migration and nomadism, might reflect an adaptation to the spatio-temporal dynamics of resource distribution across the landscape [48,52]. Here, we further showed that HSMs during the rut were the best

correlates of genetic distance, probably because the composition of groups is changing more at that time than during other periods [53,54], and males move between female groups to find mates and sire offspring [55]. Excursions by migratory individuals into the ranges of sedentary and mountain caribou during the rut have also been revealed by radio-telemetry [18], suggesting possibilities of gene flow between ecotypes. Field observations of rutting caribou indicate that during herding, mating is greatly intensified and the general pattern of courtship behaviour exhibited in static groups does not occur [54]. The maintenance of movements, as well as high density, appears to be important for changes to caribou during the rutting season. Our results suggest strong relationships between relatedness and habitat selection while controlling for the distance (causal modelling in the electronic supplementary material, figure S3 and table S3), implying clear habitat preferences during the rutting period. This result could be explained by the gathering of animals of the same herds (higher relatedness within herds than among herds) after a period of nomadism and interherd range overlap during the summer [18].

The best HSMs in terms of fit and predictive power were obtained for the rutting and calving periods. These observations are in agreement with the observed high fidelity to calving [56,57] and rutting spaces exhibited by forest-dwelling caribou, and the high fidelity to calving ground displayed by migratory caribou [58,59]. Return to traditional calving grounds has been regarded as one of the most consistent behaviours of migratory caribou [58,60]. Fidelity to calving grounds is stronger than for other portions of the annual range. Spatial fidelity of females to calving grounds may confer ecological benefits such as familiarity to resources and topography, early access to vegetation green-up and predator avoidance [61,62]. Our results demonstrated that habitat selection during the calving period was a good predictor of relatedness among female caribou, and surprisingly also among males.

By contrast, the predictive power of the HSMs as well as the relationship with genetic distance were lowest during the winter. Caribou from different herds may winter in the same areas (leading to shorter geographical distances and lower genetic relatedness among individuals), especially migratory caribou that can spend most of the winter season in the boreal forest, in the vicinity of forest-dwelling caribou [18]. The location of migratory caribou herds in winter is highly variable, making it notoriously hard to predict [56,63]. Winter areas occupied by the two migratory caribou herds have changed substantially over the past 20 years (M. Le Corre, C. Dussault and S. D. Côte 2014, unpublished data). In addition, the winter range is approximately 20 times larger than the summer range, and not all regions of the winter range are occupied every year [63]. Lower correlation between habitat selection and relatedness in winter is also reflective of changes in habitat permeability with season. Permeability is for instance positively correlated with water cover during the winter months; lakes may enhance movement when frozen during winter yet impede it during the summer, and may also serve as movement corridors in winter. Ice cover has been shown to enhance movement for caribou in northern Ontario, where higher movement rates were observed in winter [33]. Conversely, least-cost paths did not improve IBD in explaining the observed patterns of relatedness in time and space. Circuit theory integrates all possible pathways into distance calculations and wider habitat swaths connecting individuals, whereas least-cost distances are measured along a

single optimal pathway [39,64], most likely very similar to geodesic distance over long distances (see the electronic supplementary material, figure S2).

The least-cost paths did not explain as much variance as the circuit-theory-based approach (figure 4). We attribute these differences to the fact that the scale of the study was too large for least-cost paths to be effective [4,65] or that the HSMs-based models produced accurate connectivity surfaces and the circuit theory paths were a good representation of those actually used by the animals. This latter point highlights perhaps the strongest asset of our approach, which is that the circuit theory values were based on HSM coefficients inferred from actual animal location data. As a result, they have meaningful biological interpretations and, as evidenced by our study, show that habitat selection is a good predictor of gene flow. Conversely, least-cost paths did not improve IBD for inferring gene flow. Circuit theory integrates all possible pathways into distance calculations, whereas least-cost distances are measured along a single optimal pathway [39]. Moreover, circuit theory is a measure of isolation assuming a random walk, whereas least-cost distances presumably reflect the route of choice if a disperser has complete knowledge of the landscape it is traversing. Random walk is more likely reflective of caribou movement behaviour than straight paths [33,63], at least during some parts of the year (see also [66]).

5. Conclusion

Landscape features exist at multiple spatial and temporal scales, and these naturally affect spatial genetic structure and our ability to make inferences about gene flow. We have demonstrated how it is possible to use an extensive dataset of ARGOS-telemetry, remote-sensed environmental variables and genetic information to link daily local conditions experienced by individual animals across a vast landscape with genetic relatedness. In particular, our study highlights the importance of considering temporal variation in individual habitat utilization for inferring the influence of landscape features on spatial patterns of genetic variation. Most landscape genetic approaches (but see [10]) used static animal locations to infer the effect of landscape on gene flow, but we have demonstrated the influence of both daily habitat selection and seasonal behaviour on gene flow.

The approach presented here has several potential applications. First, protection of habitat must consider the dynamic use of space by species. As a behaviour-based indicator for habitat preference, our approach might inform the creation of corridors for fauna or the protection of critical habitats that optimize connectivity among populations and counter habitat fragmentation.

Our approach allows mapping of the most suitable habitats during the periods when connectivity is the most critical for gene flow among populations. Effective protection of critical habitats, such as the calving grounds of ungulates, has received much attention [60,67]. Rutting ranges, however, have a limited and relatively well-defined geographical extent, often with high densities of animals, but are not targeted by legislated protection. Habitat-dependent movement rates could also help with the development of spatially explicit models of gene flow across novel or altered landscapes. In addition, our approach has been tested on a large migratory species, and although it should be applicable to virtually any taxon, it should be

evaluated for other species models and at other spatial scales. Fuelled by rapid advancement in telemetry, remote sensing technologies and availability of genetic information, this approach could significantly help improving our understanding and conservation of wide-ranging wildlife species.

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