

Research article

Evidence of migratory coupling between grey wolves and migratory caribou

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Large-scale animal migrations influence population and community dynamics along with ecosystem functioning. The migratory coupling concept posits that movement of migrant prey can lead to large-scale movements of predators. In northern ecosystems, spatial patterns and behavioral responses of grey wolf to spatio-temporal changes in its primary prey distribution, the migratory caribou, remain poorly documented. We used a long-term GPS dataset (2011–2021) of 59 wolves and 431 migratory caribou from the declining Rivière-aux-Feuilles herd (QC, Canada) to investigate movement patterns and space use of wolves related to caribou seasonal distribution. Wolves home ranges overlapped with areas used by caribou year-round, especially in May and winter. Wolves exhibited three annual tactics: sedentary (17%), long-distance migration (> 700 km) between wintering areas and the tundra (36%), and a medium-distance migration, stopping their northward movement near the treeline (47%). Migratory wolves started spring migration northward earlier than caribou, intercepting their prey on their way to calving grounds, but departed southward for fall migration later than caribou, tracking them on their way back to wintering areas. Wolves near or overlapping areas used by caribou exhibited lower monthly movement rates compared to wolves located further away. Overlap of home range among wolves was higher during migrations and winter but decreased in summer when wolves rear pups and caribou are dispersed on summer grounds. We provide evidence of migratory coupling between grey wolves and migratory caribou, with most wolves adjusting their space use patterns to match their primary prey distribution. Although predation pressure may affect the dynamics of declining caribou herds, the global decline of that prey may in turn impact predators on the long-term, potentially enhancing intraspecific competition for new resources. Highlighting this migratory coupling is a key step to develop appropriate conservation and management measures for both guilds in the context of large-scale migratory prey decline.

Keywords: *Canis lupus*, migration, movements, predator–prey interactions, *Rangifer tarandus*, space use



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Introduction

Long-distance animal migration is among the most spectacular and biologically significant phenomena in nature and is widespread in many taxa and systems (Joly et al. 2019, Teitelbaum and Mueller 2019). Migration is thought to maximize fitness by increasing the probability of encountering suitable seasonal habitat for reproduction or foraging activities, enabling animals to reduce intra- and inter-specific competition as well as predation risk, and tracking vegetation green-up in some species (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2009, Avgar et al. 2014, Buchan et al. 2020). Many studies have focused on the movement patterns and space use of long-distance migratory prey species (Furey et al. 2018, Joly et al. 2019), but there is little information about the behavioral responses of predators to the migration of their main prey (Walton et al. 2001, Gelin et al. 2017, Walton et al. 2017, Furey et al. 2018).

Large carnivores exploiting long-distance migratory prey can exhibit several behavioral tactics. Some predators perform long-distance movements following their prey along their migratory routes, defined as migratory coupling (Pierce et al. 1999, Walton et al. 2001, Furey et al. 2018). Others can be sedentary and switch to alternative prey species when their primary prey migrates (Danell et al. 2006, Walton et al. 2017). The tactics used by large carnivores can also vary among individuals within the same population (Ballard et al. 1997, Musiani et al. 2007) leading to difficulties to fully grasp their spatial responses to changing distribution of resources and their potential impact on the migratory prey. Nevertheless, evaluating interactions between predators and their migratory prey is essential to fully understand the factors influencing the population dynamics and distribution of both guilds, and ensure efficient conservation and management planning.

The grey wolf *Canis lupus* is one of the most spatially widespread large mammalian carnivores (Mech and Boitani 2004). Its feeding ecology, social behavior, and spatial distribution have been studied extensively in North America and Europe (Mech and Boitani 2003, Newsome et al. 2016, Martin et al. 2018, Ordiz et al. 2020, Orning et al. 2021). In North America, the grey wolf is mostly considered a highly territorial (Mech 1994, 1970) generalist species (Mech and Boitani 2004, Newsome et al. 2016). Its distribution closely reflects the availability of large prey such as ungulates (Metz et al. 2012, Newsome et al. 2016, Kittle et al. 2017, Martin et al. 2018). Wolf ecology is, however, not as well documented at the northernmost limit of the species distribution range compared to wolves in other regions. Nonetheless, a few studies have shown that wolves do not defend a stable annual territory in the tundra and may face great variation in the availability of their primary prey leading to seasonal variations in their home range size (Walton et al. 2001, Hansen et al. 2013).

In northern Québec (Canada), the migratory caribou *Rangifer tarandus* of the Rivière-aux-Feuilles herd (RFH) perform some of the longest terrestrial migrations worldwide

(Furey et al. 2018, Joly et al. 2019). Their wintering areas are located at the southern limit of their distribution range in the boreal forest (Taillon et al. 2012a, b, Le Corre et al. 2017). They perform a synchronized northward spring migration (ca 700 km) to reach their calving grounds in the arctic tundra between mid-April and mid-June (Fig. 1; Taillon et al. 2012a, b, Leclerc et al. 2021). During summer, migratory caribou remain in the arctic tundra seeking a productive habitat to forage (Couturier et al. 2009, Taillon et al. 2012a, b, Le Corre et al. 2017). Afterwards, caribou perform a southward fall migration from the end of September to early December, during which the rut occurs (Le Corre et al. 2017). During migrations, the extent and phenology of caribou movements are negatively influenced by higher precipitations, lower ice availability and increased snow depth (Leblond et al. 2016, Le Corre et al. 2017, Leclerc et al. 2021). During the last decades, the RFH has experienced a population decline from ca 628 000 individuals in 2001 to ca 199 000 in 2016 (Taillon et al. 2016). The processes explaining the observed population decline are still poorly understood but predation by grey wolves could be involved, in addition to climate changes, habitat loss and human activity (Plante et al. 2018). Moreover, some studies suggest that behavioral tactics of wolves could increase their efficiency and allow them to maintain a high predation rate even when their main prey declines (Mech and Boitani 2003).

Most studies investigating the movements of grey wolves in relation to their prey have been conducted in the boreal forest during winter when tracks and carcasses are easier to monitor, and when wolves hunt larger prey species (Mech and Boitani 2003, Kuzyk et al. 2006, Mumma et al. 2017, Droghini and Boutin 2018). The movement ecology of wolves outside the winter period is less documented although this information is key to fully understand the spatial and temporal dynamics of predator–prey interactions, especially for migratory prey species. Our general objective was to quantify year-round movement behavior and space use of grey wolves in northern Québec and evaluate the relationships between wolf movements and access to their main prey, the migratory caribou (Fig. 2). Knowing that several behavioral tactics can be expressed within a population, we first expected to observe variable behavioral tactics, from sedentary to migratory wolves (Fig. 2_{H1}; Pierce et al. 1999, Walton et al. 2001, Hansen et al. 2013, Gelin et al. 2017). Given the key role of migratory caribou in the feeding ecology of wolves (Bonin et al. 2020, 2023), we predicted that most grey wolves would be moving with migratory caribou herds and remain highly associated with them year-round (Furey et al. 2018). Because migratory movements of predators and their prey may be asynchronous when constrained by their specific phenological cycle (Hansen et al. 2013, Klaczek et al. 2015), we then hypothesized that seasonal variation would drive the spatial interactions between wolves and caribou (Fig. 2_{H2}). We expected asynchronous migration departure times between wolves and caribou, predicting that grey wolves would leave their wintering ranges earlier than migratory caribou to establish their den because pups are usually born in early May while caribou

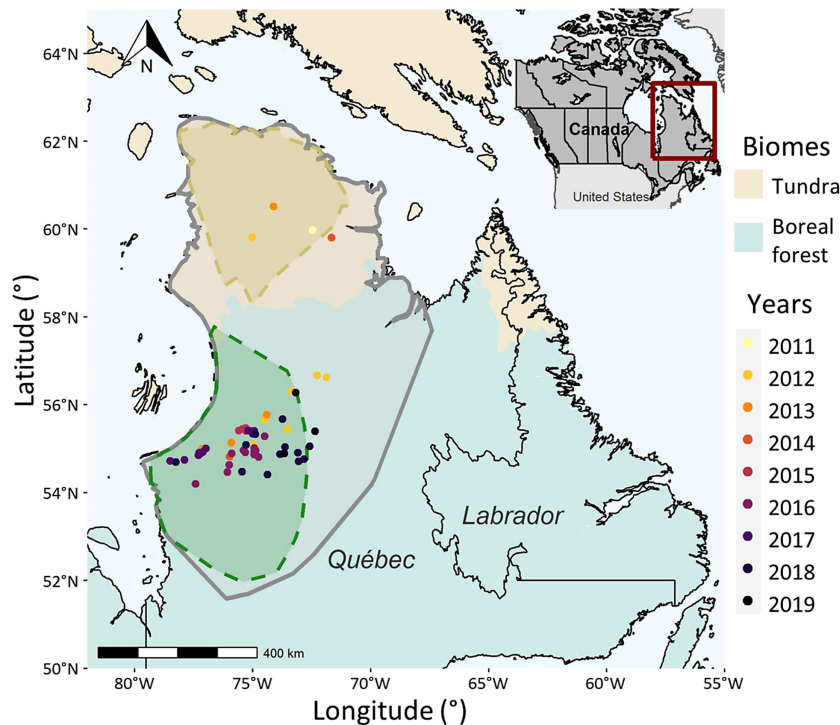


Figure 1. Study area in northern Québec, Canada. The map background represents the boreal zone (boreal forest and forest tundra south, in green) and the tundra (north, in beige), with the delineation of the treeline around 58°N between the two zones. The two-colored polygons with dashed contours are the seasonal ranges of migratory caribou (winter in green, south; summer in yellow, north) and the large grey polygon stands for the annual range of the Rivière-aux-Feuilles migratory caribou herd. The colored locations correspond to the first location of each individual wolf after capture, with a color code corresponding to the year of capture. We delimited the seasonal and annual ranges of migratory caribou using the maximum convex polygon 90% based on GPS locations of females and males in 2011–2019 between December and February for the winter range and mid-May to mid-July for summer (MFFP unpubl.). The limit of the treeline at 58°N was used in subsequent analyses to determine wolf movement tactics.

calving occurs in June (Walton et al. 2001). We also predicted that wolves would start their fall migration later than migratory caribou, to benefit from late migrants which could be alone and potentially more vulnerable. In addition, we predicted that wolf home ranges would have greater overlap with the area used by caribou during winter when the availability of alternative prey species is limited and caribou are more vulnerable to predation because their movements are constrained by snow (Le Corre et al. 2017, Droghini and Boutin 2018, Gable et al. 2018). We also hypothesized that predator movement rate would vary depending on the availability of their main prey in their ranges (Fig. 2_{H3}; Whittington et al. 2011, Martin et al. 2018, Ordiz et al. 2020). Therefore, we evaluated variations in grey wolf movement rate in relation to the proximity of caribou. We expected grey wolves to increase their hunting effort when they are closer to areas used by caribou, traveling shorter distances with less straight movement paths compared to wolves located further away from caribou. Finally, we hypothesized that territoriality behavior and territory size of wolves would vary during periods of reduced prey availability (Fig. 2_{H4}; Kauffman et al. 2007, Elbroch et al. 2016). We consequently predicted that wolf home ranges would be smaller during the denning period when they take care of pups and stay close to the den (Walton et al.

2001), but that their size would increase during the migration periods. We also expected wolves to be more tolerant of conspecifics during these long-distance movements and consequently have higher home range overlap with conspecifics during migration (Elbroch et al. 2016).

Material and methods

Study area

We collected data on grey wolf movements in northern Québec in the annual range of the Rivière-aux-Feuilles migratory caribou herd (RFH; Fig. 1). The north of the study area is located in the arctic tundra and is composed of polar and sub-polar tundra, grasslands and shrublands dominated by lichens and mosses. The boreal forest covering the southern portion of the study area is composed of temperate and sub-polar shrublands and coniferous forests (Leboeuf et al. 2018). The elevation in the tundra ranges from 0 to 682 m (mean = 206 m) while it ranges from 0 to 1500 m (mean = 356 m) in the southern boreal portion (Bertheaux et al. 2018). The mean temperature during the coldest and warmest trimesters in northern Québec are respectively on average −19.5 and 11.0°C, with

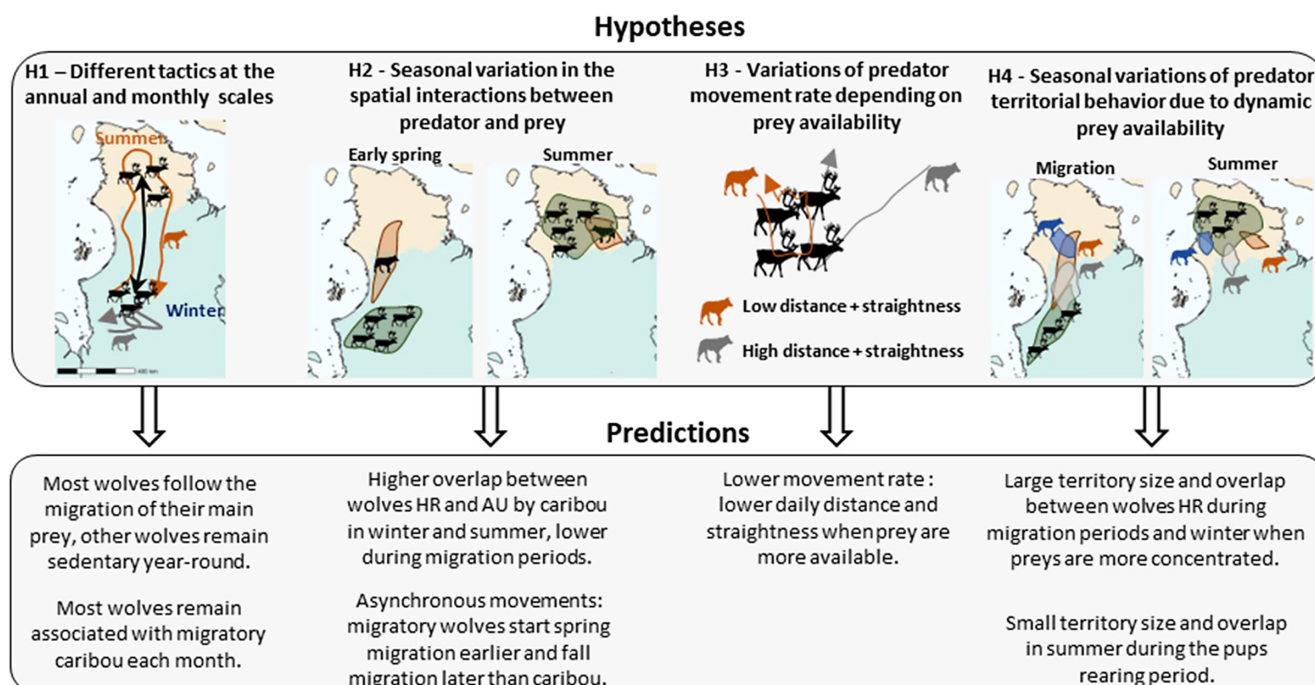


Figure 2. Conceptual figure representing the different hypotheses and predictions tested to explain wolf movements in relation to migratory caribou space use. 'HR' stands for 'home-range', 'AU' for 'area used'.

an annual average of 3.6°C (Berteaux et al. 2018). In addition to the migratory caribou, muskoxen *Ovibos moschatus*, moose *Alces alces*, beaver *Castor canadensis* and other small mammals inhabit the study area and are part of the diet of grey wolves (Bonin et al. 2023). Grey wolf population size is unknown but expected to be stable in the RFH range (Ministère de l'Environnement, de la Lutte aux changements climatiques, de la Faune et des Parcs, MELCCFP unpubl.).

Data collection

In February and March of 2011–2019, we captured 59 adult grey wolves within the RFH range from a helicopter and using either a net gun or a tranquilizer dart gun with Telazol (10 mg kg⁻¹). We equipped grey wolves with GPS collars (Lotek, Vectronic, Telonics) programmed to record a location every 1:00–5:00 h depending on the collar model and year (Supporting information). Individual grey wolves monitoring lasted on average 419 ± 227 days (mean ± SD). We defined each wolf-year as 1 April–31 March of the following year.

We captured caribou in the RFH range between December and March each year as part of the long-term population monitoring conducted by the MELCCFP and Caribou Ungava. We captured caribou from a helicopter with a net gun and equipped them with GPS collars (Vectronic). GPS collars were set to record a location every 1:00–13:00 h. A total of 431 females from the RFH were monitored for 741.5 days on average.

For both caribou and wolves, we avoided to capture several individuals in the same group, and we distributed the

capture effort over a large spatial extent (thousands of km²). Therefore, and as supported by the visual examination of movement patterns, we consider each grey wolf as independent and not belonging to the same wolf pack. Animal capture and handling procedures complied with the Canadian Council on Animal Care guidelines and were approved by the MELCCFP and Laval University Animal Care committees (Certificate no. 2011-039, 2014-011, 2019-242; CPA-FAUNE 16-01, 17-04, 18-24, 19-06, 19-17).

GPS data cleaning and processing

All data cleaning, processing and analyses were conducted in R ver. 4.1.1 (www.r-project.org). We processed GPS locations of wolves and caribou to remove points corresponding to duplicated date-time and locations, as well as outlier date-time or locations based on unlikely movement rates (speed between two consecutive locations > 30 km h⁻¹). We further manually investigated all wolf movements faster than 10 km h⁻¹ to evaluate unrealistic locations, leading us to remove three locations that showed unusual trajectory and speed compared to the previous and subsequent locations. We used caribou GPS data (Leclerc et al. 2021 for further details on GPS data processing) to assess large-scale space use patterns. We randomly selected one location per day per caribou to standardize the influence of individuals with different collar schedules. Because most of the wolves GPS collars were programmed to record one location every four hours (Supporting information), we resampled wolf locations every four hours for collars with one and two hours schedules. We could not, however, resample locations at four hour intervals

for individuals with a GPS collar programmed to record one location every five hours ($n=2$ wolves). Therefore, we used data from six randomly selected individuals with one hour relocations, resampled their track every four and five hours and found a very high correlation ($R^2=0.99$) between total distances travelled computed with both resampled subsets (Supporting information). Consequently, we kept the data of the two wolves with five hours location intervals in the analyses and included the number of locations recorded as a control variable in the models.

Annual tactics, monthly home ranges and movement metrics

We evaluated the movement patterns and space use of wolves in relation to the space use of caribou at the monthly and annual scales. To ensure analysed data were representative of wolf behavior despite missing wolf locations, we used all months for which a wolf track contained at least 50% of the expected GPS locations within the month. This threshold was determined based on the data analysis detailed in the Supporting information, and allows to represent at least 90% of the total home-range area expected using all locations (Girard et al. 2002).

Using the *kernelUD* functions in 'adehabitat' R package ver. 0.4.19 (Calenge and Fortmann-Roe 2021), we computed the monthly 95% kernel individual home range (HR) of wolves and the area used by the caribou population (AU, kernel 95%) by pooling all daily GPS locations of caribou within a month. To detect the different tactics exhibited by wolves and the variations in the spatial interactions between wolves and caribou (Fig. 2_{H1-H2}), we calculated the proportion of overlap between wolf monthly HRs and the monthly AU by migratory caribou (Supporting information). We further derived the proportion of wolves overlapping with the AU by caribou in each month (Supporting information).

To assess if wolves exhibited different space use tactics in relation to caribou migration at an annual scale (Fig. 2_{H1}), we evaluated the annual movements displayed by each wolf with ≥ 10 consecutive months (each month having more than 15 days of monitoring) of GPS monitoring. We visually inspected the spatial distribution of each GPS track and metric of wolf movements described above to assign a tactic to each wolf. As we expected some wolves to perform a long migration and others to remain sedentary, we discriminated migratory versus sedentary wolves looking at obvious and long north-south movements along with an increase in the monthly proportion of overlap between wolves' home-ranges (HRs) and the area used (AU) by caribou. Sedentary wolves were expected to remain in a restricted range throughout the year and therefore their HR should not overlap with migratory caribou year-round. As most of the wolves were captured during winter in the south of the study area, within or near RFH wintering range (Fig. 1), they could thus exhibit either a sedentary or migratory tactic. We calculated the straight-line distance between the most distant latitudes of each wolf-track to assess the latitudinal distance travelled in each tactic.

We used four movement metrics to evaluate the variation in movement rate and spatial interactions between the two species (Fig. 2_{H2-H3}). We calculated the mean daily distance travelled by wolves every month by dividing the total distance travelled in the month (Supporting information) by the number of days in the month. We calculated the monthly straightness (Supporting information) as the ratio between the straight-line distance between the first and last location in the month and the total distance travelled during the month. We computed a monthly 'delta-distance' of each wolf to the AU by migratory caribou as the difference in the distance to the AU by migratory caribou between the final and initial monthly locations for each wolf (Supporting information). This variable allowed us to determine whether individuals tended to move further away (delta-distance > 0), closer (delta-distance < 0) or if they remained at a similar distance (delta-distance around 0) to the AU by caribou within the course of a month (Fig. 2_{H2}). In addition, we calculated the mean monthly distance of wolves to the AU by migratory caribou (Supporting information) by determining the nearest distance between each location of a wolf during the month and the monthly AU by caribou, and then dividing the sum of all distances by the number of locations recorded during that month. If a location was within the monthly AU by migratory caribou, the distance was set to 0. We used this explanatory variable to determine at which distance wolves overlapping (or not) with the AU by migratory caribou were on average from the AU by migratory caribou (Fig. 2_{H2}). We then investigated the relationships between the two movement rate metrics (mean daily distance and straightness) and 1) a binomial factor of overlap or not with the AU by caribou, 2) the proportion of overlap between wolf HRs and the AU by caribou and 3) the mean distance to AU by caribou to assess variations in wolves' movements according to their spatial interactions with caribou (Fig. 2_{H2-H3}).

Finally, to explore variations in territoriality of wolves throughout the year (Fig. 2_{H4}), we calculated the area of overlap among the monthly HRs of wolves monitored during the same month (Supporting information). We subsequently derived the mean proportion of wolves with their HR overlapping with at least one other wolf during each month of the year (Supporting information). As we only included wolves with at least 10 consecutive months of data in the analysis, changes in the area of overlap between neighbors within a year could be interpreted with confidence. We did not, however, monitored all neighboring wolves such that the results do not represent the absolute value of overlap and should be interpreted with caution.

Statistical analyses

All models were performed using Bayesian mixed models with the *brm* function from the 'brms' package ver. 2.16.3 (Bürkner 2021). For each model, we ran three Markov chains of 24 000 iterations each. In each chain, the first 4000 iterations were discarded as burn-in and we used a thinning rate of four for the remaining 20 000 iterations, which gave us

Table 1. Summary of each model tested along with its accompanying hypotheses and predictions (Fig. 2), including the response and explanatory variables, the random effect, and the family of statistical model used. 'HR' = home-range; 'AU' = area used; 'Nb_loc' = number of locations recorded during the month; 'HR_prop' = the proportion of overlap between the HR of wolves and AU by caribou; 'Mean_dist' = the monthly mean distance between the wolf and the AU by caribou (Fig. 3); 'Over_not' = a factor indicating whether the wolf HR overlapped or not with the AU by caribou in the given month; 'Nb_wolf' = number of wolves monitored during the given month. The first prediction of the first hypothesis (H1) was not tested using a model but was visually determined (Material and methods section in 'Annual tactics, monthly home ranges and movement metrics').

Hypotheses	Predictions	Response variables	Explanatory variables	Random effects	Family
H1 – Different tactics at the annual and monthly scales	Most wolves follow the migration of their main prey, other wolves remain sedentary year-round. Most wolves remain associated with migratory caribou each month	Proportion of wolves' HR area overlap with AU by caribou (interval]0,1]) (Supporting information)	Month + Sex + Nb_loc	ID + Year	Beta
H2 – Seasonal variation in the spatial interactions between predator and prey	Higher overlap between the HR of wolves and AU by caribou in winter and summer, lower overlap during the migration period Wolves leave winter areas earlier and summer areas later than caribou	Proportion of wolves' HR area overlap with AU by caribou (interval]0,1]) (Supporting information) Delta-distance (Supporting information)	Month + Sex + Nb_loc	ID + Year	Beta
H3 – Variations of predator movement rates depending on prey availability	Lower movement rate and greater path tortuosity when preys are more available	Mean daily distance (Supporting information)	Month + Sex + Nb_loc + HR_prop + Mean_dist*Over_not	ID + Year	Gaussian
H4 – Seasonal variation of territoriality during a period of varying prey availability	Wolves' HR area smaller during the denning period, higher during the migration period Territoriality decreases during the migration period	Monthly straightness (interval]0,1]) (Supporting information) Log(Home-range area) Proportion of HR area overlap with the HR of other wolves (interval]0,1]) (Supporting information)	Month + Sex + Nb_loc + HR_prop + Mean_dist*Over_not Month + Sex + Nb_loc	ID + Year	Beta
			Month + Sex + Nb_loc + Nb_wolf	ID + Year	Gaussian

5000 values for posterior distributions per chain. We checked for the convergence of each parameter with the Gelman and Rubin (1992) diagnostics ($R_{hat} < 1.1$) and the Pareto k diagnostic. Finally, we conducted posterior predictive checks drawing simulated values from the joint posterior predictive distribution of replicated data and comparing these samples to the observed data for each parameter of the models using the *pp_check* function, and by checking that the credible interval (CI) of the fit of the models was each time included within the limits of the posterior predictive distribution (Gelman et al. 2013).

We modelled the 1) delta-distance to AU by migratory caribou, 2) proportion of overlap between wolf HRs and AU by migratory caribou and 3) proportion of overlap among individual wolf HRs (Supporting information) using their monthly values, according to sex and month as factors (Table 1). Sex was used to investigate potential differences in movement rate of wolves especially in spring and summer after the pups are born and when females might spend more time near the den while the rest of the pack is more likely to hunt farther from the den (Theuerkauf et al. 2003, Schmidt et al. 2008). To assess variation in movement behavior according to space use and interactions between wolves and migratory caribou, we tested if the mean daily distance and straightness of wolf movements (Table 1) was influenced by the month, sex, proportion of overlap between wolf HRs and AU by caribou. We also added the interaction between the mean distance to AU by caribou and a dummy variable indicating the overlap or not between a wolf and the AU by migratory caribou. We found no correlation between the different movement variables tested and no collinearity among explanatory variables with all variance inflation factors < 2 (VIF function from the 'usdm' package ver. 1.1-18, Naimi 2017).

We used beta-regressions for modeling the proportion of HR overlap and straightness as they are bounded between 0 and 1. We used the method of Smithson and Verkuilen (2006) to transform the [0,1] values into]0,1[interval to respect one of the beta-regression assumptions. We modelled the mean daily distance and the delta-distance to AU by caribou using a gaussian family distribution, and we log-transformed wolf HRs.

In all models, we added the number of locations recorded in the month as a covariable to account for potential biases due to gaps in the GPS recordings. We ran all models with wolf IDs and year as random intercepts (Table 1). For the HR overlap among wolves, we added the number of wolves monitored during the month in the model to account for varying sample size. Unless otherwise indicated, results of the models are reported as the mean and the 95% credible interval (95 % CI). The final dataset used to run all models are available in the Supporting information.

Results

The final dataset included 59 unique wolf IDs for 98 wolf-years and 765 wolf-months (Supporting information). Among

them, 47 wolf-years (from 33 unique IDs) were monitored for at least 10 months and were used to determine the annual tactics exhibited by grey wolves (Results section 'Determination of annual space use tactics'). For all the models, > 99.9% of the Pareto k estimates were smaller than 0.7, indicating that models were not misspecified (Vehtari et al. 2017).

Determination of annual space use tactics

Among the wolves monitored over the entire year (47 wolf-years [20 female-years, 27 male-years] from 33 unique IDs [13 unique females, 20 unique males]), we detected eight sedentary wolves that did not exhibit long north-south movements but instead remained in a geographically restricted range all year long. The latitudinal straight-line distance they traveled was on average 276.0 ± 98.8 km (mean \pm SD; Fig. 3, Supporting information). We observed 39 migratory wolves performing large north-south movements, but we detected two different tactics among them: a long-distance ($n=17$) and a medium-distance ($n=22$) migratory tactics based on the northernmost or the southernmost wolf locations. Wolves departing from the winter range of migratory caribou and reaching caribou summer range in the tundra (north of 58°N ; Fig. 1) were categorized as long-distance migratory wolves (mean latitudinal straight-line distance = 700.1 ± 117.5 km; Fig. 3, Supporting information). Wolves performing north-south movements, but stopping their northward movement near the treeline (at ca 58°N ; Fig. 1) or stopping their southward movement and staying north of the core

caribou winter range (56°N) were categorized as medium-distance migratory wolves (mean latitudinal straight-line distance = 551.4 ± 109.5 km; Fig. 3, Supporting information).

The proportion of female-years exhibiting each of the three tactics was similar (35.0% for the mid- and long-distance tactics and 30.0% for the sedentary tactic; Fig. 3b), while more variability was detected in male-years which mainly exhibited the medium-distance tactic (55.6%) or the long-distance tactic (37.0%) with only 7.4% being sedentary. We monitored 11 wolves (unique IDs) for two years or more and six of these wolves used the same tactic throughout the monitoring period while five of them changed their tactic (Supporting information). All wolves that changed tactic initially showed a long-distance migratory tactic and switch to a medium-distance migratory tactic or a sedentary tactic in the following years.

Seasonal variation in space use and association of grey wolves with migratory caribou

We observed seasonal variation in the proportion of grey wolves with their home range (HR) overlapping the area used (AU) by migratory caribou with the maximum number of wolves overlapping AU by caribou during winter and spring, and the minimum in summer (Fig. 4a). More than 74% of wolves were overlapping AU by migratory caribou in all months outside June and July. The proportion of overlap between wolf HRs and the AU by migratory caribou followed a similar pattern (Fig. 4b, Supporting information),

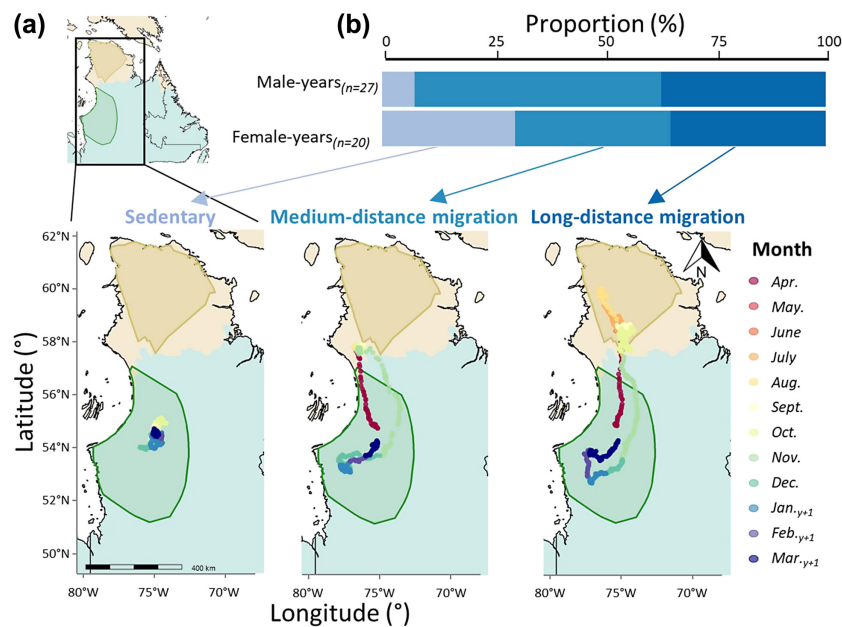


Figure 3. (a) Examples of annual GPS tracks of grey wolves in the Rivière-aux-Feuilles caribou range, exhibiting one of the three tactics: sedentary (bottom-left map), medium-distance migration (bottom-middle map) and long-distance migration (bottom-right map). The GPS locations are colored by month. The map background represents the boreal zone (boreal forest and forest tundra south, in green) and the tundra (north, in beige), with the delineation of the treeline around 58°N between the two zones. The two colored polygons are the seasonal ranges of migratory caribou (winter in green, south; summer in yellow, north); and (b) proportion of wolves of both sexes (13 unique females representing 20 female-years, and 20 unique males representing 27 male-years) exhibiting each of the three tactics (from light blue to dark blue): sedentary, medium-distance migration and long-distance migration.

with the highest overlap in May (mean = 71.4, 95% credible interval [CI] = [64.2, 77.9]; Fig. 4b) and the lowest in July (mean = 35.0%, CI = [27.2, 43.3]).

Grey wolves tended to move north and away from migratory caribou in April (Fig. 4c, Supporting information), when the delta-distance was the greatest (mean = 27.3 km, CI = [10.9, 43.9]), and generally moved towards caribou in June, July, November and December with the minimal delta-distance reached in November (mean = -94.2 km, CI = [-113.3, -75.8]; Fig. 4c). The number of locations recorded and sex had no effect on the proportion of overlap between wolf HRs and the AU of migratory caribou, or the delta-distance (Supporting information).

Seasonal movement rate according to the degree of interaction with migratory caribou

On average, wolves that did not have their monthly HR overlapping with the AU by caribou traveled shorter mean daily distance ($\beta = -4.6 \text{ km day}^{-1}$, CI = [-7.2, -2.0]) and exhibited lower monthly straightness ($\beta = -0.6$, CI = [-1.0, -0.2]) compared to wolves overlapping with AU by caribou (Fig. 5a–b; Supporting information). Wolves whose monthly HR overlapped with the AU by caribou showed

higher (although not significant) daily distance and monthly straightness as their mean monthly distance to AU by caribou increased (Fig. 5c–d). Wolves with their HR overlapping the AU by caribou travelled shorter distances with increasing HR overlap ($\beta = -0.03 \text{ km}$, CI = [-0.05, -0.01]; Supporting information). The proportion of HR overlap did not have any effect on the monthly straightness of wolves' movements (Supporting information). In addition, wolves that were on average closer to the monthly AU by caribou covered less daily distance and had lower straightness than wolves that were further away during that month (Fig. 5c–d; Supporting information). The mean daily distance covered by wolves was highest in July (mean = 23.9 km day⁻¹, CI = [17.7, 30.2]; Fig. 5a), lowest in January (mean = 11.5 km day⁻¹, CI = [6.0, 16.3]), and remained low until March. The mean distance traveled daily was comparable during the spring and fall migrations (mean of April and May = 17.6 km day⁻¹, CI = [12.2, 22.2]; mean of September and November = 17.0 km day⁻¹, CI = [11.4, 22.7]). The monthly straightness was low in spring, late summer and winter (Fig. 5b), but it was high in July (mean = 0.4, CI = [0.3, 0.5]), and reached a peak during the fall migration (mean in November = 0.5, CI = [0.4, 0.6]).

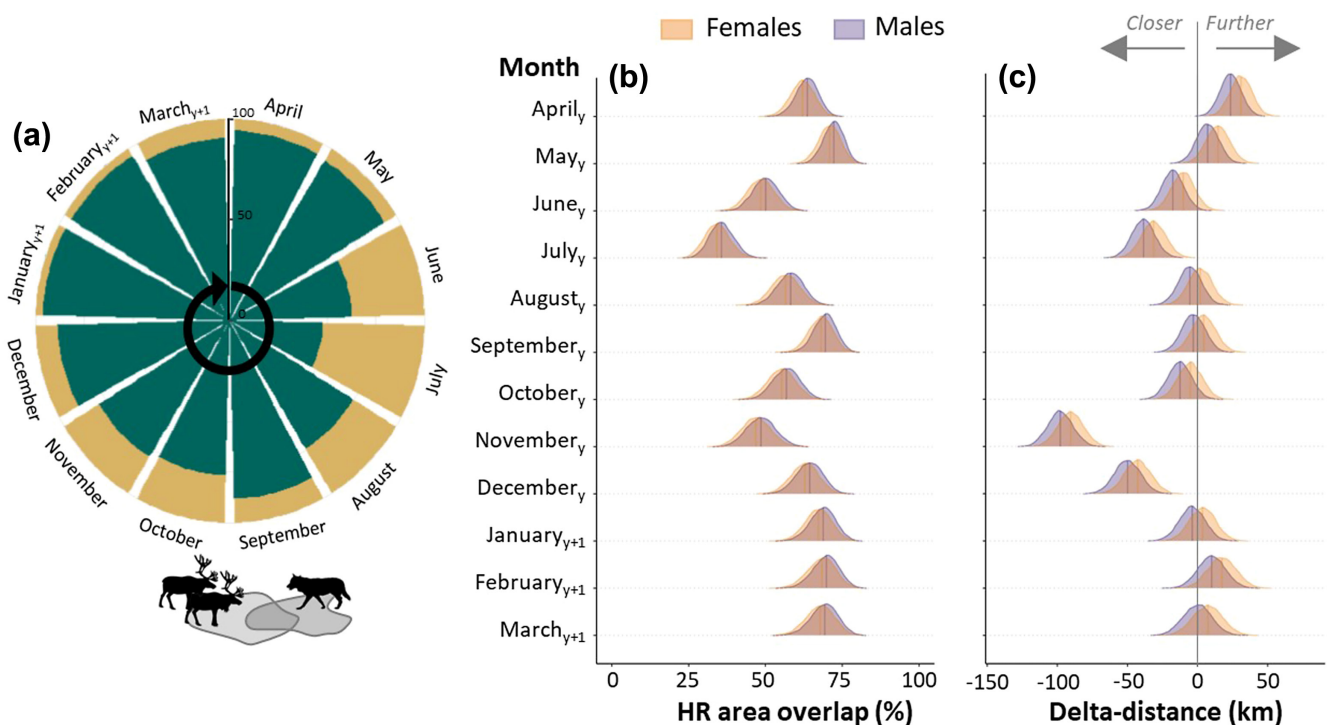


Figure 4. (a) Monthly proportion of wolves with home-range (HR) overlapping the area used (AU) by migratory caribou in green, or not overlapping in yellow (in %); (b) posterior predictions from April of the year_y to March of the next year_{y+1} of the proportion of overlap between wolf HR and the AU by migratory caribou (in %); and (c) posterior predictions from April of the year_y to March of the next year_{y+1} of the delta-distance (i.e. the difference in the distance to the AU by migratory caribou between the final and initial monthly locations for each wolf, in km; see the Supporting information, and section 'Annual tactics, monthly home ranges and movement metrics' in Material and methods), with the two arrows at the top representing whether wolves moved closer (delta-distance < 0) or further (delta-distance > 0) or if they remained at a similar distance (delta-distance near 0) from the AU by caribou during the month. In (b) and (c), the color codes for the posterior predictions correspond to females (orange) and males (purple).

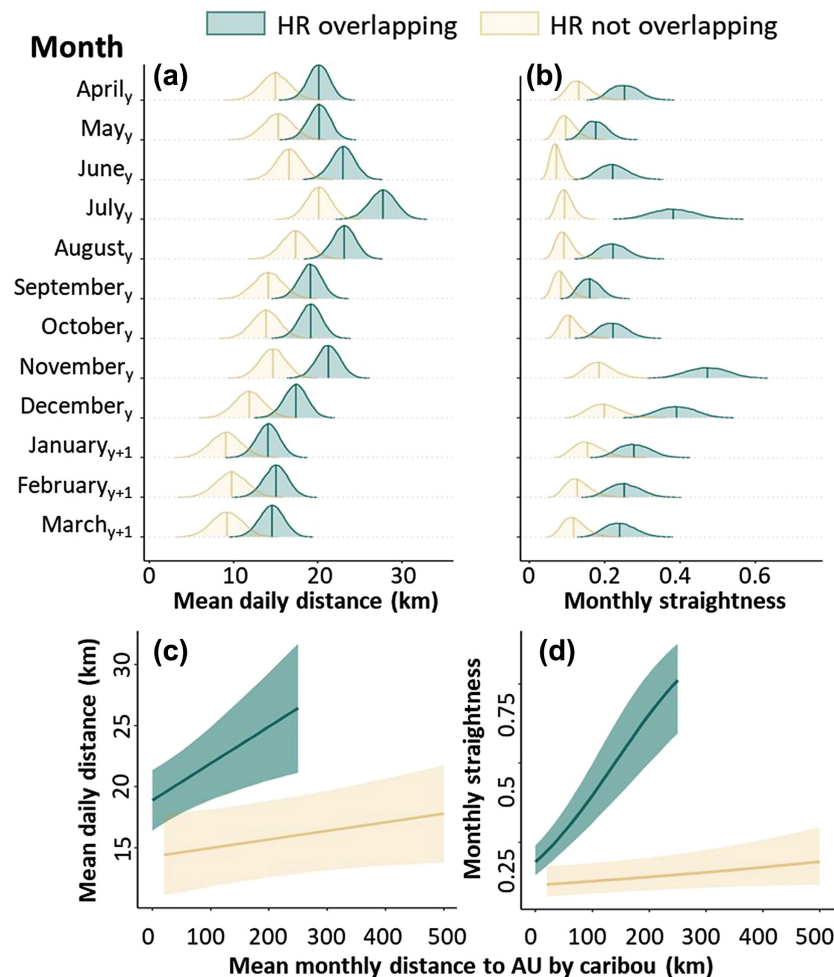


Figure 5. Posterior predictions of wolves' (a) mean daily distance per month (in km) and (b) monthly straightness, from April of the year_y to March of the next year_{y+1}, and relationship between (c) the mean daily distance (in km) and (d) the monthly straightness of wolves' movements with the monthly mean distance to the area used (AU) by migratory caribou (in km). The color code represents the prediction for grey wolves having their home-range (HR) overlapping the AU by migratory caribou in a given month (in green), and grey wolves that did not overlap the AU by migratory caribou (in yellow).

Variation of territoriality behavior

Wolf HRs were larger in November (Fig. 6a, Supporting information) and smaller in June with stable values during summer. Home ranges of males were larger than those of females ($\beta=0.4$ [on log-transformed scale, Supporting information], $CI=[0.01, 0.9]$). Monthly HRs overlapped with the home ranges of other wolves more than 60% of the time (Fig. 6b). The highest proportion of overlap among wolves was in April (92.0%; Fig. 6b) and the lowest proportion in June (60.5%; Fig. 6b). The monthly proportion of HR area overlap among wolves did not differ between sexes (Supporting information), nor according to the number of wolves monitored within the same month. The proportion of the HR of wolves overlapping was high during spring, late fall, and winter (April: mean=61.6%, $CI=[42.0, 79.0]$;

November: mean=65.7%, $CI=[44.3, 83.9]$; Fig. 6c), but remained low between June and October (Fig. 6c).

Discussion

Our study sought to improve the understanding of seasonal space use and movement patterns of grey wolves in response to the space use of their main prey in subarctic and arctic environments. Wolves exhibited variations in their behavioral tactics and movement patterns in response to the seasonal variation of migratory caribou availability. We highlighted a gradient of annual tactics used by wolves (Fig. 2_{HI}, 3, Supporting information) from sedentary individuals to wolves that migrate with caribou (Fig. 3, Supporting information). As we expected, the movement patterns of wolves

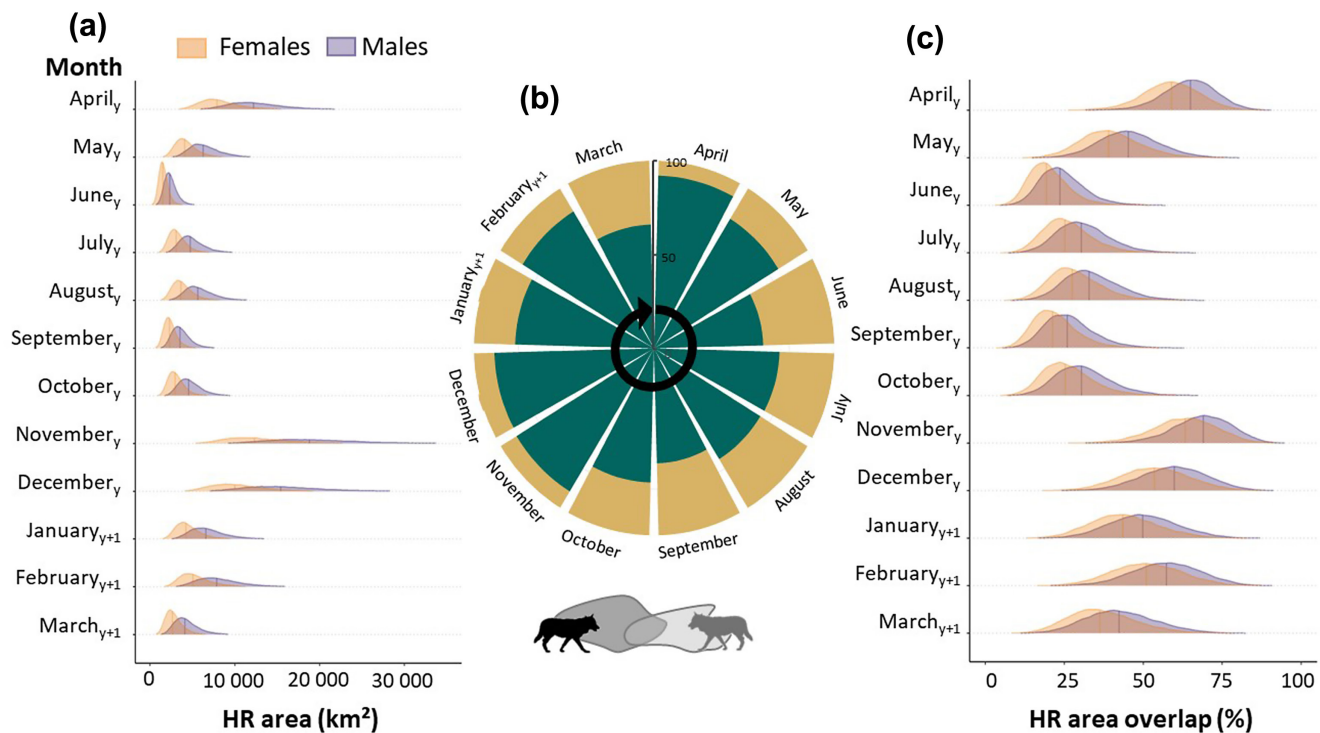


Figure 6. (a) Predicted posteriors of the monthly home range (HR) area (in km²) of wolves from April of the year_y to March of the next year_{y+1}, with females in orange and males in purple; (b) proportion of wolves (in %) with their HR overlapping the HR of other wolves in the same month (in green) or not (in yellow); and (c) predicted posteriors of the proportion of monthly HR overlap among wolves (in %) for males and females (same color code as a).

varied monthly and seemed to be related to spatial interactions with caribou and conspecifics (Fig. 2_{H2-H3}).

Migratory coupling between grey wolves and migratory caribou

Our results revealed migratory coupling between migratory caribou and grey wolves. The migratory caribou of the Rivière-aux-Feuilles herd (RFH) move back and forth between their winter and summer ranges located more than 700 km apart (Taillon et al. 2012a, b, 2016, Leclerc et al. 2021). Our study highlighted the influence of the spatial dynamics of this migrant prey on large-scale movements of its main predator, the grey wolf. Migratory coupling suggests that grey wolves can take advantage of high prey availability year-round, as suggested by Bonin et al. (2023) who recently confirmed the annual presence of migratory caribou in the diet of wolves. During winter, migratory caribou are concentrated at the southern limit of their annual range (Taillon et al. 2016, Le Corre et al. 2020). The larger proportion of migratory caribou found in the diet of wolves in winter compared to other species (Bonin et al. 2023) support our results, with grey wolves sharing large wintering grounds with migratory caribou between January and March (Fig. 4b) and remaining spatially close to their main prey (Fig. 4c). During that period, the large number of wolves with overlapping home-ranges (HRs) and the large proportion of the HR area overlapping among them (Fig. 6) suggest that wolves

exhibit a high tolerance to conspecifics, potentially because of the high abundance and vulnerability of prey. During winter, grey wolves had relatively large HRs, traveled short daily distances and performed less straight movement paths (Fig. 5). Similar movement patterns of wolves were also observed in the Białowieża Primeval Forest (Jedrzejewski et al. 2001) and in the western Arctic (Walton et al. 2001), and might be explained by movements of prey within their wintering habitats (Jakes et al. 2018, Le Corre et al. 2020). In our study, the movements of caribou would therefore lead wolves to cover large areas during winter while travelling short distances at a daily scale because of constraining environmental conditions, particularly snow.

The mating season of grey wolf occurs between February and March and females give birth to pups between the end of April and mid-May (Mech 1970, Hénault and Jolicœur 2003, Villemure 2003). In the Arctic, wolves have been shown to move from their winter ranges to their denning areas near the treeline where they restrict their movements around the den by late April (Walton et al. 2001, Klaczek et al. 2015). Our results support these observations, as wolves in the range of the RFH using medium-distance or long-distance migratory tactics started to move northward in April. The increased distance between wolves and caribou observed in April (Fig. 4c) indicates that wolves started their migration before the caribou. In addition, the highest proportion of wolves and the overlap of HRs among wolves (Fig. 6b–c) observed in April suggest that wolves may be more tolerant

to conspecifics during that period of large-scale movements where large territory would be nearly impossible to defend (Ballard et al. 1997, Walton et al. 2001, Kauffman et al. 2007, Elbroch et al. 2016). The timing of these movements highlights a lag between the onset of the migration by wolves and caribou, as caribou do not initiate migration before mid-April and arrive on calving grounds in early June (Leclerc et al. 2021).

While sedentary wolves remained south during summer, in the vicinity of the caribou wintering range, we found two tactics among migratory wolves in spring and summer: those remaining near the treeline all summer long (the medium-distance migration) and those that migrated further north (long-distance migration, Fig. 3, Supporting information). Den site selection near treeline may highlight a tradeoff between benefiting from favourable den sites supported by roots and shrubs (Heard and Williams 1992) and offering protection for pups, and remaining in the vicinity of the caribou summer range and migration routes to maintain potential access to their main prey during the pup rearing period (Heard and Williams 1992, Hansen et al. 2013, Klaczek et al. 2015, Furey et al. 2018). We observed that most migratory wolves (medium- or long-distance) seemed to reach the northernmost part of their range in May (Supporting information) when they settled for the denning and summer seasons. The mean overlap between wolves' HR area and the AU by migratory caribou also increased in May (Fig. 4b), revealing that migratory wolves regain access to caribou while the prey migrate north to reach the calving grounds. The decrease of wolves' HR size and overlap with conspecifics in May (Fig. 6) is consistent with the restriction of movements around the den sites during the pup rearing season (Jedrzejewski et al. 2001, Walton et al. 2001). The migratory caribou calving peak occurs between 6 and 14 June (Taillon et al. 2012a, Vuillaume 2023). Between the arrival of wolves at the den in May and the caribou calving peak in June, wolves may benefit from alternative prey such as moose or small mammals (Bonin et al. 2023) or from patches of caribou that arrived earlier than the rest of the population or remained north year-round (MELCFFP unpubl.). Caribou calving peak can act as a pulsed resource for wolves rearing pups (Bastille-Rousseau et al. 2016), offering a sudden abundance of vulnerable prey during a season of high energetic demands. After the calving peak, migratory caribou disperse further north in their summer range (Taillon et al. 2012a, b). In July, we observed an increase in the movement rate of wolves (Fig. 5a–b) which are also travelling closer to the AU by migratory caribou (Fig. 4c). These results support studies in western Alaska (USA), in the Northwest Territories and western Nunavut, Canada (Ballard et al. 1997, Walton et al. 2001), that reported dispersal of wolves during summer once pups are more mobile. These movements may enable wolves to get closer to ungulate summer ranges. Wolves then remained close to caribou summer ranges from August to October, as suggested by the low and stable distance to AU by migratory caribou (Fig. 4c) and the increase of the HR overlap with AU by caribou (Fig. 4b), along with the decrease in

the mean daily distance traveled and straightness (Fig. 5a–b). Bonin et al. (2023) reported a decrease in the proportion of migratory caribou and an increase of other species in the diet of wolves during summer, suggesting reduced use of caribou at that time. Our results suggest that during summer, most wolves remained associated with their migratory prey, but this association was not as strong as during other times of the year (i.e. December–May, Fig. 4b), which may indicate a greater use of alternative prey species.

The fall migration of caribou can be divided into two phases: the pre-migration when caribou start to leave their summer ranges moving southward before making a pause for the rut (peaking around 23 October (Boulet et al. 2007), and the fall migration after the rutting period to reach their winter range (Le Corre et al. 2017, 2020). The onset of southward movements by caribou resulted in an increase of overlap with the home ranges of wolves in September (Fig. 4b). This overlap later decreased in October and November when migratory caribou moved further south. Wolves started to migrate south in November, when they travelled greater distances to get closer to migratory caribou, as suggested by the high negative delta-distance (Fig. 4c), the increase in straightness, the length of daily movements (Fig. 5a–b), and the increase of their HR size and proportion of overlap with conspecifics (Fig. 6). This delay between the departure of caribou and wolves during fall suggests that grey wolves tracked migrant prey, instead of intercepting them as observed during the spring migration, highlighting two distinct tactics of migratory coupling (Furey et al. 2018).

We found that wolves that were on average far from the AU by caribou but had their HR overlapping the AU by caribou exhibited higher movement rates than individuals that were closer to the caribou, regardless of whether their HR overlapped or not with the AU by caribou (Fig. 5b–c). These results may suggest that wolves at the vicinity of the AU by caribou benefited from the availability of their main prey and adopted a hunting behavior, traveling shorter distances but in a more sinuous way. Wolves with their monthly HR not overlapping the AU by caribou but remaining close to it may still consume caribou, benefitting from more isolated, and possibly more vulnerable, prey patches at the periphery of the main AU by caribou (Bergman et al. 2006, Kittle et al. 2017, Schlägel et al. 2017). Wolves with their monthly HR not overlapping the AU by caribou and remaining far from caribou may exhibit higher movement rates due to lower availability of prey, searching for alternative prey species or small caribou groups at the periphery of the core area used by caribou.

Sedentary tactic and reduced interactions with migratory caribou

We observed that even if some wolves migrated with their prey, a smaller proportion of wolves displayed less frequent spatial interactions with caribou or even adopted an annual sedentary tactic (Fig. 3, 4a, Supporting information). Other studies highlighted sedentary behavior of large carnivores even

if their primary prey migrate, such as for the Eurasian lynx *Lynx lynx* in Norway (Walton et al. 2017), cougar *Puma concolor* in Patagonia (Gelin et al. 2017), or grey wolf in Alaska, USA, and forested regions of Canada (Ballard et al. 1997, Musiani et al. 2007). In these systems, predators switched their diet and consumed more alternative prey species when the main prey migrated. Bonin et al. (2023) reported differences in the diet of grey wolves in Nunavik (northern portion of our study area) and Eeyou Istchee (southern portion of our study area). The diet of wolves in Eeyou Istchee was mostly composed of small mammals such as beavers *Castor canadensis*, lemmings *Lemmus* spp., and hares *Lepus* sp., as well as caribou in summer and fall, while they mostly consumed moose *Alces alces* during winter, in contrast to wolves in Nunavik which mostly relied on caribou year-round. We found that grey wolves not associated with migratory caribou exhibited lower movement rates during all seasons (Fig. 5, Supporting information). This result, combined with the known dietary niche (Bonin et al. 2023), suggests that grey wolves remaining sedentary year-round in southern areas relied on alternative prey species when caribou migrated north (Ballard et al. 1997, Bonin et al. 2023). The sedentary tactic was the least observed, but it can allow wolves to maintain a territory throughout the year (Ballard et al. 1997, Mosser and Packer 2009), although it may not support a large population density during periods of lower prey availability. Contrastingly, the migratory tactic is probably more energetically costly, but likely enables the persistence of a larger population density.

The role of migratory coupling for conservation and management

Our results provide evidence that most grey wolves adjusted their space use and movement behavior to match the spatio-temporal distribution and availability of their main prey, the migratory caribou. Wolf behaviors, however, were not homogenous. Some wolves remained sedentary while others migrated with caribou. Future studies should further investigate whether and how sex, age, breeding status and pack size influence the relationships between wolves and their main prey. In addition, assessing interannual variations in the space use and movement behavior of grey wolves is a first step to better understand the response of wolves to long-term fluctuations in the availability of their primary prey. The benefit of migratory coupling for predators may vary with prey abundance and may push predators to alter their behavior to maintain interactions with their migratory prey. Most of the wolves we monitored adjusted their space use to maintain access to caribou all year-long. Variations in the abundance of migratory caribou might also have consequences for grey wolf abundance in northern Québec, as observed in the Northwest Territories and Nunavut (Canada) where wolf densities decreased with the decline of the Bathurst caribou herd (Klaczek et al. 2016). It is crucial to investigate the potential ecological consequences of environmental changes and declines of prey populations on the movement behavior and spatial patterns of wolves, and on the migratory coupling

dynamics. To adopt efficient management and conservation measures on migratory caribou, it is necessary to understand to which extent migratory coupling supports the predator populations and their potential impact on declining migratory prey.

Speculations

In our study, we could not quantify the effect of prey density on space use or movement rates of wolves. Yet, while studying a declining migratory caribou herd, caribou density would be necessary to assess to which extent the predator population may be supported by the remaining availability of prey, but also to quantify the effect of predation pressure on the prey population dynamics. Grey wolves are associated with a type II functional response, suggesting that encounter rate limits kill rate at low prey densities, while kill rate is limited by handling time at high prey densities (Holling 1959, Martin et al. 2018). Few studies highlighted that wolves could maintain a high capture rate in presence of low prey density and can even preferentially select areas with low rather than high prey densities (Bergman et al. 2006, Schlägel et al. 2017). We thus speculate that predation pressure may affect migratory caribou population dynamics, even at low caribou density, while wolves may switch to alternative prey. The energetical cost of finding alternative prey, that may not be highly available in our study area, may, however, lead to intra-specific competition and thus result in a decline of the predator population.

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Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting); **Joëlle Taillon**: Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Christian Dussault**: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Julien Hénault Richard**: Conceptualization (equal); Data curation (supporting); Investigation (supporting); Methodology (supporting); Project administration (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Steeve D. Côté**: Conceptualization (lead); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.63xsj3v81> (Michelot et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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