# Moving together, foraging apart: effects of the social environment on movement-integrated habitat selection

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# Abstract

Movement links the distribution of habitats with the social environment of animals using those habitats; yet integrating movement, habitat selection, and socioecology remains an opportunity. Here, our objective was to disentangle the roles of habitat selection and social association as drivers of collective movement in a gregarious ungulate. To accomplish this objective, we (1) assessed whether socially familiar individuals form discrete social communities and whether social communities have high spatial, but not necessarily temporal, overlap and (2) modelled the relationship between collective movement and selection of foraging habitats using socially informed integrated step selection analysis. Based on assignment of individuals to social communities and home range overlap analyses, individuals assorted into discrete social communities and these communities had high spatial overlap. By unifying social network analysis with movement ecology, we identified state-dependent social association, where individuals were less cohesive when foraging, but were cohesive when moving collectively between foraging patches. Our study demonstrates that social behaviour and space use are inter-related based on spatial overlap of social communities and state-dependent habitat selection. Movement, habitat selection, and social behaviour are linked in theory. Here, we put these concepts into practice to demonstrate that movement is the glue connecting individual habitat selection to the social environment.



**Keywords:** caribou, integrated step selection analysis, movement ecology, social preference, social network analysis

# 1. Introduction

Movement is defined by a change in spatial location and is the behavioural link between the physical space an animal occupies and the resources available to them [1]. In the context of the social environment, movement represents the connection between the distribution of foraging resources and the social structure of animals that consume those resources [2]. Disentangling the social and spatial drivers of movement is a formidable challenge within behavioural ecology. In many cases, research omits the social contexts within which animals move to, from, and within the areas that contain foraging resources [but see 3,4]. Spatially-explicit models of sociality highlight that some gregarious species aggregate at areas associated with profitable foraging resources [5], while territorial species typically only interact at territory edges [6]. Sharing space, either at foraging sites, territory edges, or elsewhere within an animal's range is required to form the social environment. For example, animals are predicted to select habitat as a function of the profitability and availability of the habitat [7]. A logical extension can be made to conspecifics; individuals form groups based on their familiarity with conspecifics. We aim to quantify the relative importance of habitat and conspecifics by developing a novel socially informed integrated step selection analysis, a movement-based method that accounts for the relative intensity of selection for habitats and neighbours.

For social animals, individual movement shapes social encounters and subsequent interactions with conspecifics that can affect collective movement [8]. Further complicating our understanding of collective movement is the idea that the type, quality, and distribution of habitats on the landscape can constrain or promote collective movement [9]. For example, dense vegetation impedes visibility, which could reduce the probability a group remains together. In addition, individual movement and habitat selection are affected by the distribution of resources.

For example, patchily distributed foraging resources could facilitate large aggregations, whereas homogenously distributed foraging resources could result in a reduction in social associations [10]. The physical space an individual, or group, occupies and the distribution and availability of foraging resources within that space are important drivers of animal movement and the social environment an individual experiences [2].

Animals typically select for habitats that maximize foraging and minimize risk of predation; an important trade-off because most habitats do not accommodate both high quality foraging *and* low predation risk. When animals aggregate in large groups, the per capita risk of predation is lower and individuals in larger groups tend to select more risky habitats, including foraging in open areas [11]. For example, animals in larger groups reduce time spent vigilant [12]. However, not all social groups are equal; some groups contain unfamiliar individuals (i.e., anonymous groups) [13], while others contain familiar individuals [14]. For anonymous and familiar groups, social foraging occurs when the costs and benefits of an individual's foraging behaviour are linked with the foraging behaviour of conspecifics [15]. Social foraging can be most beneficial when social information about foraging resources comes from familiar individuals [16]. For example, when foraging resources are unpredictable, familiar individuals obtain reliable information from conspecifics to increase foraging efficiency [17,18], such that time searching for forage is reduced in favour of more time spent foraging. In the context of movement and habitat selection, theory on social foraging and the benefits of social familiarity provides a framework through which the costs and benefits of collective movement can be explored [15,19].

Apparent social familiarity or preference is the long-term repeated social association due to shared space at the same time. Although individuals often interact with many conspecifics,

non-random repeated social interactions or associations with certain individuals form the basis for social preference [20]. Proximately, long-term social relationships can influence collective movement via the reliability of information transfer about foraging resources or predator risk [21,22], while ultimately they can enhance fitness [23]. The social environment can be influenced by the availability of foraging resources, but social communities can also be composed of individuals with similar physiological or nutritional requirements that occupy the same locations. Apparent social preference may therefore arise as a function of spatial constraints [24], including physical barriers, such as rivers or mountains. Disentangling social preference from spatial constraint could inform our understanding of collective movement and habitat selection [25,26].

Here, we develop a unified framework to bridge the gap between social network analysis and movement ecology. We disentangle the roles of social preference and collective movement on habitat selection behaviour by parameterizing socially informed integrated step selection models (Figure 1). Animal social networks often comprise distinct sub-networks, or social communities, defined by the existence of social preference among discrete clusters of individuals [20]. Using a social ungulate as a model system, our objective was to disentangle the roles of habitat selection and social association as drivers of collective movement in a gregarious ungulate (*Rangifer tarandus*) when the availability and distribution of foraging resources are variable. We calculated three distinct measures of social preference. First, we assigned individuals to social communities based on a community detection algorithm. Second, we assessed the temporal stability of social association among individuals. Third, we estimated spatial overlap of social communities using home range analyses. Due to variance in the distribution of foraging resources on the landscape, we expected that access to social information

via close proximity to conspecifics should influence patterns of selection for foraging resources. Specifically, individuals with stronger social preference should select foraging habitat collectively. The corollary is that individuals should also take short steps in the presence of conspecifics, given that from a movement ecology perspective, shorter steps typically represent foraging behaviour and longer steps represent searching behaviour [27].

# 2. Materials and Methods

*(a) Caribou as a model system*

We investigated patterns of movement, space use, and social behaviour for caribou (*Rangifer tarandus*) on Fogo Island, Newfoundland, Canada. Fogo Island is a small (~237km$^2$) island off the northeastern coast of Newfoundland with a humid continental climate (see Supplementary Materials for details). Between 1964-1967, 26 caribou were introduced to Fogo Island from the Island of Newfoundland [28]. Currently, Fogo Island has a population of approximately 300 caribou (Newfoundland and Labrador Wildlife Division, unpublished data). Caribou live in fission-fusion societies [29] and throughout much of their range caribou forage primarily on lichen, grasses, sedges, and other deciduous browse with access to these resources changing between the seasons [30]. During winter (January to March) the landscape is covered by snow and caribou forage primarily on lichen. Lichen is heterogeneously distributed and access is impeded by snow and ice cover. Caribou dig holes in the snow, termed craters, to access lichen in the winter, often where snow depth is relatively shallow (~30–60 cm deep). Consequently, caribou have limited access to subnivean forage and tend to re-use established craters. To cope with this limitation, caribou use conspecific attraction and social information transfer to gain access to foraging opportunities [31]. In winter, caribou activity budgets suggest that caribou spend ~50% of their time foraging, while ~40% of their time is spent lying down or

ruminating, 7% of their time is spent walking or trotting, and 3% of their time is spent standing [32,33]. In addition, caribou typically avoid forested habitats due to deep snow in forests and lack of access to forage opportunities [34], whereas most open habitats on Fogo Island are windswept in the winter, therefore facilitating foraging and movement [30].

We used GPS location data collected from Fogo Island caribou (2017–2019) to assess the relationship between social behaviour, habitat selection, and movement (see supplementary information for details on collaring procedures). Each relocation was assigned to a given habitat classification that was extracted from Landsat images with 30x30m pixels [35]. Locations were categorized as one of open foraging (lichen barrens), open moving (wetland, rocky outcrops, and water/ice), or closed (conifer scrub, mixed wood, and conifer forest). Adult female caribou (n = 26 individual caribou, n = 72 caribou-years) were immobilized and fitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g). Prior to analyses, we removed all erroneous and outlier GPS locations following Bjørneraas et al. [36]. We did not collar all female caribou in the herds, however, and collared individuals were randomly selected from the population. We therefore assume that our sample of collared animals was randomly distributed. Although associations between collared and uncollared animals were unrecorded, we assumed that our networks (see below) were unbiased representations of the relative degree of social association among all caribou.

*(b) Formulating integrated step selection models*

Integrated step selection analysis (iSSA) simultaneously incorporates movement and habitat selection within a conditional logistic regression framework [see Figure 1; 33]. As in other resource and step selection analyses [38], iSSA models habitat use as a binomial response variable where ‘use’ represents the location an animal was observed and ‘availability’ represents

the geographical area an animal could potentially use but was not necessarily observed (Figure S1). iSSA defines availability based on empirically fitted distributions of step lengths and turn angles [37], where a step is the linear connection between consecutive relocations, and turn angle is the angular deviation between the headings of two consecutive steps [39]. We generated available steps and turn angles based on the distributions informed by observed population-level movement behaviour using the *amt* package in R [40]. First, we sampled step lengths from a gamma distribution of observed step lengths for the study population; values were log-transformed for analysis. The statistical coefficient of log-transformed step length is a modifier of the shape parameter from the gamma distribution originally used to generate available steps [37]. Second, we sampled turn angles (measured in radians) for available steps from observed values between $-\pi$ and $\pi$ following a Von Mises distribution; values were cosine transformed for analysis. The statistical coefficient of cosine transformed turn angle is an unbiased estimator of the concentration parameter of the Von Mises distribution [37,41]. Each observed relocation was paired through a shared start point with 10 available steps generated from step-length and turn-angle distributions and compared in a conditional logistic regression framework (see section *g*). In addition to generating available movement parameters, we also generated an available social environment (see below).

*(c) Social network analysis*

We used the R [42] package *spatsoc* [43] to generate proximity-based social association networks from GPS location data. Nodes in the networks were represented by individual caribou and edges were represented by the frequency of association based on proximity between individuals. We generated social networks at two scales based on proximity of locations between individual caribou: (1) seasonal winter networks to assign individuals to social communities and

assess long-term social preference and (2) weekly networks to assess the role of short-term social preference on patterns of habitat selection (section *b*). Social communities represent a subset of individuals within a network that are more closely connected with each other than with the rest of the network. For networks at both seasonal and weekly scales, we assumed association between two individuals when simultaneous locations (i.e. GPS relocations that occurred within 5 minutes of each other) were within 50 m of one another [29,31]. We selected the 50 m threshold based on the standard distance applied to assign individuals to groups in studies of ungulate group size and social behaviour [44]. We applied the 'chain rule', where each discrete GPS fix was buffered by 50 m and we considered individuals in the same group if 50 m buffers for two or more individuals were contiguous, even if some individuals were beyond 50 m of one another. We weighted edges of social networks by the strength of association between dyads of caribou using the simple ratio index [45], SRI:

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

where $x$ is the number of times individuals A and B were within 50 m of each other, $y_A$ is the number of fixes from individual A when individual B did not have a simultaneous fix (i.e. within 5 minutes), $y_B$ is the number of fixes from individual B when individual A did not have a simultaneous fix, and $y_{AB}$ is the number of simultaneous fixes from individuals A and B that were separated by >50 m [46]. We constructed social networks with the *igraph* package in R [47]. Nodes in our networks therefore represented individuals and edges represented associations between individuals.

*(d) Detecting social communities: long-term social preference*

For seasonal winter social networks, we used a community detection algorithm to define social communities [48]. We assessed social community structure for each winter to determine

the broadest extent of social structure. Modularity is a commonly used measure that defines how well-connected social communities are to one another. It is calculated from the weighted proportion of edges that occur within a community, minus the expected proportion of edges, if edges were distributed randomly in the network [48]. A modularity value close to 1 indicates a network with a strong clustered structure in which interactions of individuals belonging to different clusters do not occur. We quantified modularity (*Q*) for observed annual winter networks. To ensure observed social structure did not occur at random, we compared these values to null models [24]. Specifically, we generated null models based on GPS fixes to reduce potential for type II error typically associated with node-based permutations [49]. Following Spiegel et al. [24], we re-ordered daily GPS movement trajectories for each individual while maintaining the temporal path sequence within each time block (e.g., day 1 and day 2 may be swapped). This technique is a robust network randomization procedure for GPS data because: 1) it maintains the spatial aspects of an individual's movement; 2) by randomizing movement trajectories of individuals independent of one another, temporal dependencies of movement are decoupled [24]. We repeated this procedure 100 times for annual winter networks and re-calculated modularity at each iteration. We then compared observed modularity (*Q*) values to the null distribution and determined whether the observed *Q* value fell within the 95% confidence interval of the distribution of *Q* values [20].

In addition to comparing observed *Q* values from annual winter networks to a null distribution, we also calculated a community assortativity coefficient ($R_{com}$) to assess confidence in the assignment of an individual to a given community [50]. Specifically, $R_{com} = 0$ indicates no confidence in the assignment of an individual to a community, while $R_{com} = 1$ indicates certainty in the assignment of an individual to its community.

*(e) Weekly networks and lagged association rates: short-term social preference*

We iteratively generated weekly social networks using a moving window approach and calculated the observed SRI to be included as a covariate in iSSA models (see section *b*). The first network was calculated for 1 January to 7 January, the second was 2 January to 8 January, and so on. Weekly networks contained 84 relocations per individual (12 relocations per day). For each of these networks we used dyadic values of SRI as a proxy for short-term social preference. We used a three-step process. First, to incorporate SRI within the iSSA framework, we determined the identity and distance (m) of each individual's nearest neighbour at each relocation [43]. Second, for each focal individual and their nearest neighbour at each relocation, we matched the dyadic SRI value for the prior week. For example, for individual A at 12:00 on 8 January, we determined the nearest neighbour was individual B and we extracted the dyadic SRI value for these individuals for the previous week. Third, we repeated steps one and two for all 'available' relocations defined by random steps generated in the iSSA (section *b*). Therefore, each individual at each relocation had an observed weekly dyadic SRI value and a series of available weekly dyadic SRI values (see section *b*).

In addition to incorporating social preference directly within iSSA models, we also assessed social preference by estimating within-season temporal patterns in associations between individuals by calculating the lagged association rate (LAR). We calculated the LAR within each seasonal proximity-based social network using the *asnipe* package in R [51]. We calculated LARs for each winter by generating social networks following the procedure described above (section *e*) using GPS relocations. LARs measure the probability that pairs of individuals associating at a given relocation would still associate at subsequent relocations [52]. We compared within-season LARs for individuals in the same annual winter social community to

LARs for individuals in different annual winter social communities to assess potential for within-season patterns of association among individuals.

*(f) Home range overlap between social communities*

To determine spatial overlap of social communities we estimated home ranges for winter social communities using the area of the 95% isopleths from fixed kernel density estimates [53] for each social community in each year with the *href* smoothing parameter in the *adehabitatHR* package in R. Data from all individuals in a given social community were pooled to estimate the community home range. We estimated home range overlap between social communities with the utilization distribution overlap index (UDOI), where higher values of UDOI represent a greater proportion of overlap and lower values represent lower proportion of overlap [54].

*(g) Modelling collective movement and habitat selection*

We fitted three separate iSSA models using the *glmmTMB* package in R to fit conditional logistic regressions [55]. We fit iSSA models with a series of fixed and random effects following Muff et al. [55], through which we take advantage of the fact that the conditional logistic regression model is a likelihood-equivalent to a Poisson model with stratum□specific fixed intercepts. Specifically, our first model was a 'core model' [39] which is an informed null model that includes covariates expected to influence patterns of habitat selection regardless of collective movement (Table S1). The core model contained three fixed effects: habitat type, the natural log-transformed step length, cosine transformed turn angle, and interactions between habitat and log-transformed step length and cosine-transformed turn angle. We also modelled individual-specific slopes for log-transformed step length and habitat within the random effect structure of the model. We included three distinct habitat types in our models: forest, open-foraging, and open-movement. The forest category included coniferous forest, conifer scrub, broadleaf forest, and

mixed-wood forest habitat types; open-foraging included lichen habitat; and open-movement included wetland, rocky barrens, frozen lakes, and anthropogenic habitat types. The core model was an informed null model that we used as the foundation on to add hypothesis-testing covariates.

Our second model tested covariates included in the core model and nearest neighbour distance as a fixed effect. Nearest neighbour distance (m) was measured as the distance between a focal individual and the nearest collared conspecific and was calculated for all used and available steps in *spatsoc* [43]. Nearest neighbour distance was transformed using the natural logarithm (ln) and included in interactions with cosine transformed turn angle, ln step length, and habitat type within the fixed effect structure of the model (Table S1). In addition, we also included individual-specific slopes for nearest neighbour distance, the interaction between log-transformed step length and nearest neighbour distance, and the interaction between habitat type and nearest neighbour distance within the random effect structure of the model.

Our third model also tested covariates included in the core model, nearest neighbour distance, and weekly dyadic simple ratio index (section *c*). Specifically, we incorporated weekly dyadic SRI values for each observed and available step. Dyadic SRI was included in interactions with turn angle, step length, and habitat type (Table S1).

*(h) Calculating effect sizes*

We calculated population-level relative selection strength (RSS) to demonstrate how habitat features influenced selection [56]. Specifically, we calculated the strength for selecting one step over another that differ in the habitat value where those steps end. RSS was calculated for each habitat type (i.e., forest, lichen, or open habitats) as a function of nearest neighbour distance and the shared dyadic simple ratio index between nearest neighbours.

# 3. Results

We found that individuals associated with members of multiple communities and associations were stronger among members a given community. Depending on the year, social networks comprised 2–6 social communities and although community assortativity ($R_{com}$) was similar across years, there was high certainty (range = 0.95–1.00) of an individual's assignment to a given community in a given year (Table 1). In addition, lagged association rates (LAR) within each winter confirmed temporal stability of community assortment, where association rates for members of the same winter community remained higher than association rates for members of different communities in each year (Figure 2). Seasonal winter values of modularity (*Q*) were significantly lower than the distribution of *Q* generated from null models (Figure S2), suggesting that although social networks were structured into communities, inter-community social associations are common (Table 1). In support of our expectation, we observed relatively high spatial overlap between different winter social communities (average UDOI = 0.37, SD = 0.34, range = 0–0.98; Figure S3; Table S2), thus facilitating the potential for association between social communities.

We found that models including nearest neighbour distance and the simple ratio index covariates were higher ranked compared to the core and nearest neighbour distance models (Table S3). We found mixed support for our second set of predictions. In contrast to our expectation, individuals avoided conspecifics while selecting foraging lichen habitat ($\beta$ = 0.021, 95% CI: 0.0033, 0.038; Figure 3; Table S3). Although individuals tended to move away from conspecifics during foraging ($\beta$ = 0.239, 95% CI: 0.007, 0.041), on average, individuals selected nearest neighbours (regardless of distance) that had higher dyadic values of the simple ratio index ($\beta$ = 2.91, 95% CI: 2.77, 3.06; Figure 3; Table S3). These findings suggest that although

individuals selected foraging habitat further from conspecifics, they had stronger shared values of the SRI for their nearest neighbours. We also found support for our expectation of collective movement, although there was no effect of social proximity on turning angles. Specifically, individuals took shorter steps when they were in close proximity to conspecifics ($\beta = -0.02$, 95% CI: –0.0254, –0.0148), even though individuals took longer steps when they shared a higher dyadic SRI value with their nearest neighbours ($\beta = 0.151$, 95% CI: 0.131, 0.172; Figure 3; Table S3). These findings suggest individuals tend to move shorter distances in close proximity to any conspecifics, but further distances when they had stronger shared values of the SRI for their nearest neighbours.

# 4. Discussion

Our study examined apparent social preference in the context of shared space use using socially informed integrated step selection analysis. We present a framework that unifies social networks within a traditional movement ecology and habitat selection framework. Although individual social associations were well mixed at the population level, we found that social networks were structured into discrete communities. Despite spatial overlap between different social communities, which suggests an opportunity for individuals to interact with members of other communities, we highlight two forms of within-community social preference, including long-term temporal stability of associations among individuals, as well as an effect of short-term social preference on habitat selection. Further, we found that individuals tended to select foraging habitat spaced away from conspecifics, but moved between foraging habitats with conspecifics, suggesting collective movement is state-dependent. The processes underlying community structure appear to be social, and not spatial. Based on our unification of social

network analysis with integrated step selection analyses, we highlight the influence of collective movement and preferred associations on habitat selection and foraging.

Testing social preference as a driver of movement and habitat selection required establishing the existence of discrete communities and long-term social associations within the population-level network. Indeed, the formation of discrete social communities, in combination with our lagged association analysis, confirmed the existence of temporal stability in social associations for members of the same social community. The formation of non-random social communities was driven in part by social preference, but aspects of space use, including shared space, could also influence the stability of social communities [57]. We found high spatial overlap between social communities, suggesting that physical barriers on the landscape do not explain the formation of discrete social communities. For social communities to emerge from a well-mixed population, individuals in different communities must have high spatial, but low temporal overlap in shared geographical space, thus revealing the importance of space and time in the formation of social communities [58]. Disentangling space and time within the social environment reveals distinct social communities and groups of individuals that are more likely to associate than simply by chance [24]. On resource limited landscapes, individuals are expected to aggregate in close proximity to those resources, for example, elephants (*Loxodonta africana*) aggregate near water-holes, which are a limiting resource [5]. At the population-level, social networks were highly connected, thus providing the impetus to quantify socially informed patterns in movement and habitat selection.

Our findings reveal state-dependent social associations, where selection for nearest neighbours was reduced when foraging, but strongest when moving between foraging patches. Individuals are more likely to trust social information from familiar individuals, but the potential

costs are an increase in competition at foraging patches. Individuals may balance the trade-off between competition and access to information by sharing information about the general location of foraging patches in transit but spacing apart at patches to reduce competition. Specifically, when individuals were in closer proximity to one another they selected foraging resources, which is typically open, allowing them to remain in visual and vocal contact, thereby facilitating social cohesion during foraging despite physically spacing apart [59]. Individuals also took longer steps when they had high social preference for their nearest neighbour, indicating increased movement when nearest neighbours are familiar with each other. Under the assumption that shorter steps represent foraging behaviour and longer steps represent searching behaviour [27], our results suggest familiar individuals move between foraging patches together. Our results reveal potential behavioural mechanisms (i.e., foraging or moving) that influence the frequency and magnitude of social associations.

The emergent geometry of collective movement and spatial arrangement of individuals in a group appears to change as individuals adjust their behaviour based on the availability of resources and the presence of familiar conspecifics [60]. Assame macaques (*Macaca assamensis*) distance from one another during foraging, but move collectively between foraging sites [61], while individual giraffes (*Giraffa camelopardalis*) show social preference for conspecifics during foraging, but not during movement [22]. Interestingly, macaques foraged in closer proximity to individuals of similar dominance rank, while for giraffes it was unclear whether observed social preference was the result of passive or active assortment. For caribou, dominance hierarchies are linear and typically driven by body size [62,63], suggesting that social preference in caribou could also be related to dominance. Our ability to delineate aspects of the social environment between collective movement and habitat selection within a unified

framework is useful for disentangling passive or active assortment, for example dominance rank, conspecific attraction, or the transfer of information about foraging resources.

We assumed that dispersed foraging is a function of competition among individual caribou for craters in the winter [62] and movement in groups could reflect the use of social information about foraging sites [29] or predation [64]. Craters can vary in size and distribution [30]; however, craters may only be large enough for a single individual to forage at a time [65]. Solitary foraging is therefore most beneficial but foraging in close proximity to preferred conspecifics may be an exception. We propose that while caribou generally have larger group sizes in winter [31,66] groups may be sparsely distributed in space to reduce fine-scale competition at individual cratering sites. Groups may spread out such that competition at foraging sites is limited, but group members can retain visual contact. Furthermore, female caribou have antlers, which unlike males, persist into winter. Females are hypothesized to use their antlers to defend craters and exert dominance over both males and females without antlers [62,67]. This interpretation is corroborated by theory used to explain fission-fusion dynamics, where individuals are expected to split and merge through space and time to reduce conflict and competition during foraging.

We demonstrate assortment of individuals into distinct social communities, despite high range overlap with individuals in other communities. Integrating space and time revealed fine-scale processes that form social communities and the socially mediated nature of movement ecology and habitat selection. Within a unified socially informed integrated step selection framework, we bridge the theoretical and methodological gap between social network analysis [68], movement ecology [69], and habitat selection [70]. We also demonstrate how social association is context-dependent, where individuals spaced out during foraging, but moved

collectively between foraging patches. Our synthesis of integrated step selection analysis with social networks to test hypotheses is an important step towards identifying the roles of physical space and animal space use as factors influencing the social environment [9]. Moreover, individual variation in phenotypes attributable to movement or habitat selection may affect how individuals experience the social environment [71]. Movement, habitat selection, and social behaviour are clearly linked; as van Moorter et al. [1] described movement as the ‘glue’ connecting habitat selection to the physical location of a given set of habitats, we posit that movement is the glue connecting collective habitat selection to the social environment.

**Ethics.** All animal captures and handling procedures were consistent with the American Society of Mammologist guidelines and were approved by Memorial University Animal Use Protocol No. 20152067.

**Data accessibility.** All code and data used for statistical analysis and figures will become available upon acceptance.

**Authors contributions.** QMRW and EVW conceived the ideas and designed method; QMRW conducted fieldwork QMRW and generated social networks; QMRW, CMP, and KAK conducted movement and spatial analysis; QMRW led the writing of the manuscript; EVW developed the research program. All authors contributed critically to drafts and gave final approval for publication.

**Competing interests.** We have no competing interests.

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**Table 1.** Summary of winter community assignment for three caribou social networks (2017–2019), including the number of individuals (N), number of communities, community size, modularity (*Q*), and the community assortativity coefficient ($R_{com}$ = 0 indicates no confidence in community assignment; $R_{com}$ = 1 indicates certainty in community assignment).

| **Year** | **N** | **Community** | **Community size** | **Home range area (km$^2$)** | ***Q*** | **$R_{com}$** |
|---|---|---|---|---|---|---|
| 2017 | 10 | 1 | 3 | 84.71 | 0.13 | 0.95 |
| | | 2 | 7 | 43.43 | | |
| 2018 | 16 | 1 | 5 | 113.09 | 0.17 | 1.00 |
| | | 2 | 7 | 77.31 | | |
| | | 3 | 1 | 13.84 | | |
| | | 4 | 1 | 23.11 | | |
| | | 5 | 1 | 4.94 | | |
| | | 6 | 1 | 19.06 | | |
| 2019 | 12 | 1 | 2 | 32.39 | 0.13 | 1.00 |
| | | 2 | 9 | 33.87 | | |
| | | 3 | 1 | 1.26 | | |

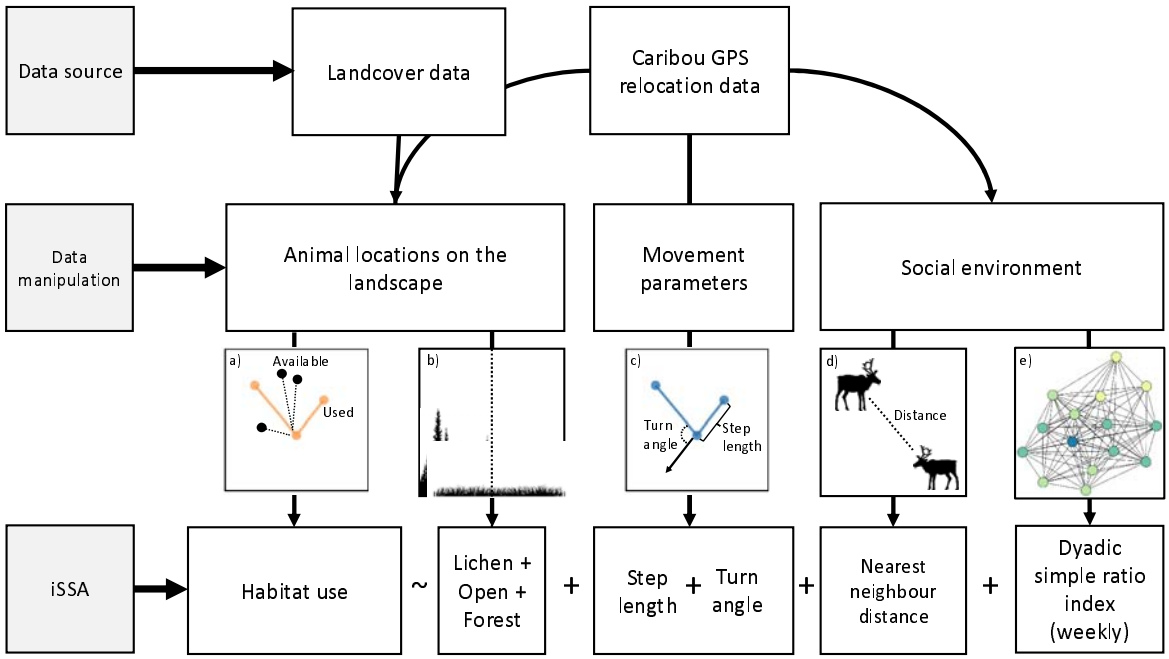


**Figure 1.** Summary of the data pipeline used to generate integrated step selection analysis (iSSA) models. Primary data sources were landcover data and caribou GPS relocation data, which were combined to determine the physical locations of animals on the landscape. The pairing of animal locations and landcover data was used to generate the comparison of used to available points (panel a), which is the response variable in iSSA models, as well as the habitat type in which a given relocation occurred: lichen (defined in text as open-forage), open (defined in text as open-movement), and forest (panel b). Caribou relocation data were also used to generate two movement parameters (panel c) and aspects of the social environment (panels d and f). Movement parameters included turn angle, which is the angular deviation between the headings of two consecutive steps, and step length, which is the linear distance between consecutive relocations. The social environment included nearest neighbour distance (panel d) and weekly social networks and the dyadic simple ratio index generated based on a moving-window as a proxy for short-term social preference (panel e). The bottom row represents a graphical formulation of our iSSA models, where habitat use (1:10 ratio of used to available

relocations) was regressed against habitat type (lichen, open, and forest), movement parameters (step length and turn angle), nearest neighbour distance, and weekly dyadic simple ratio index.

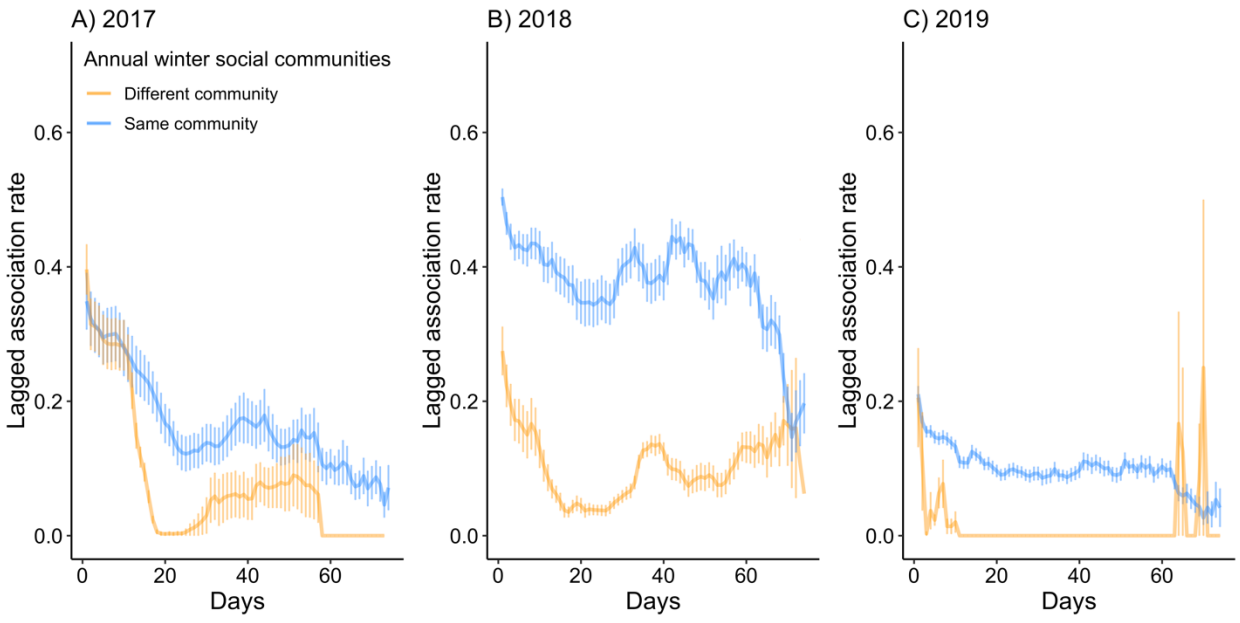


**Figure 2.** Observed lagged association rate (LAR) for caribou in the same (blue lines) and different (orange) annual winter social communities, calculated as the probability that any pair of individuals associated on a given day, are still associated on subsequent days. Note, the time period for LAR analysis and social community assignment was 1 January to 16 March. Error bars represent the standard error of all pairwise association rates calculated on each day. Individuals in the same social communities (blue lines) generally had higher lagged association rates, suggesting they were more likely to associate together over time.

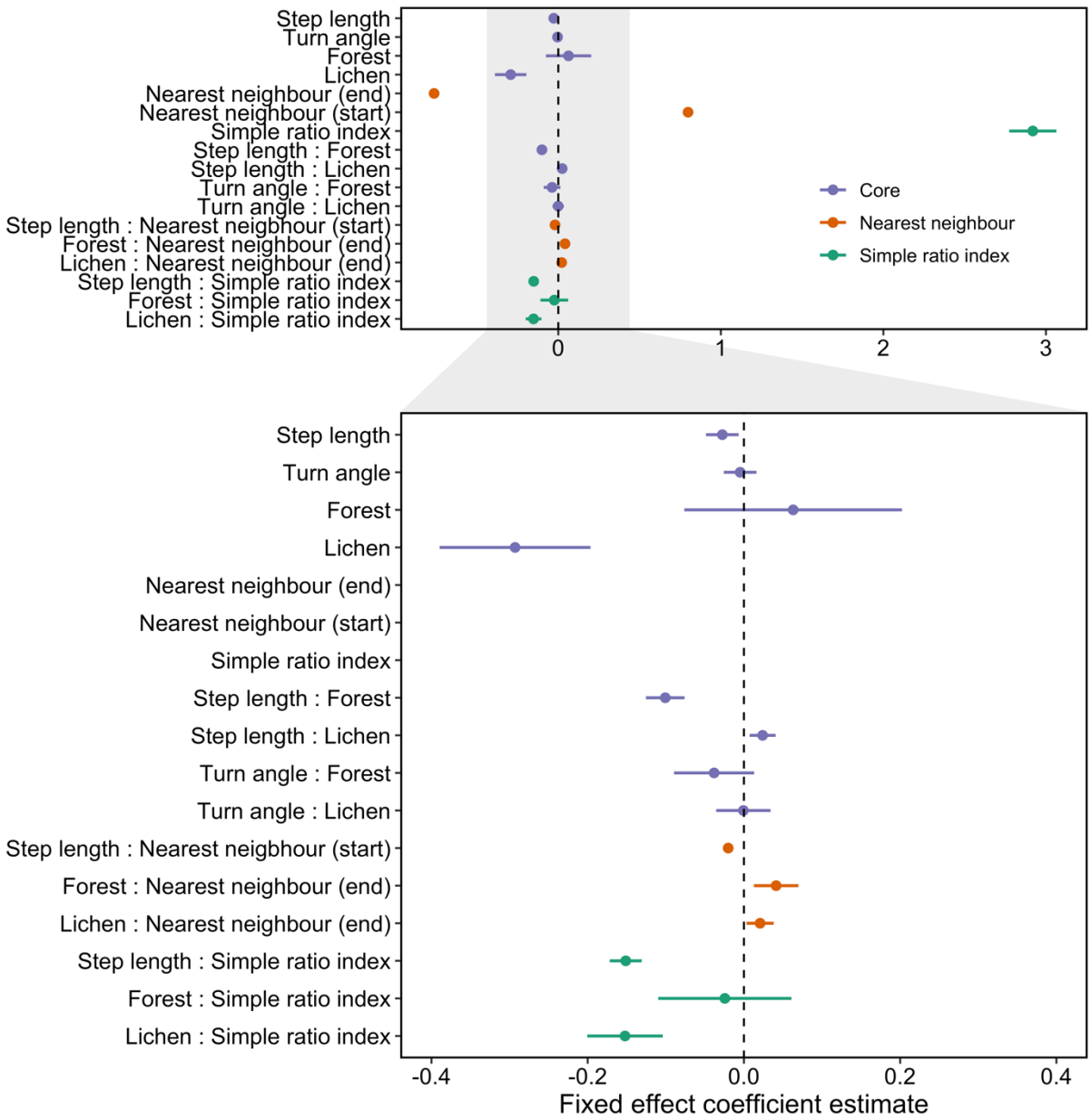


**Figure 3.** Habitat selection coefficients and 95% confidence intervals for the top integrated step selection model. Coefficients that do not overlap zero are deemed significant (see Table S3). Colours represent the model in which each variable or interaction was introduced and once introduced into a model a given variable was included in subsequent models. Purple coefficients represent variables initially included in the core model, orange coefficients represent variables initially introduced in the nearest neighbour model, and green coefficients represent variables

initially introduced in the simple ratio index. Note, step length, nearest neighbour distances (both start and end), and the simple ratio index were log-transformed and turn angle was cosine transformed.

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