Title: Bound together: density-dependent social tethers inhibit fitness

Running Title: Social tethers

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Abstract:

Putative mechanisms affecting fitness that underlie why animals occupy a particular place are often in tension. A tension amplified in social animals, where individuals are often not free to make independent habitat selection or foraging decisions. The ideal free distribution (IFD) is a density-dependent emergent property describing how individuals should distribute themselves to maximize fitness on the landscape. However, IFD is agnostic to an individual's propensity to be social, which is known to influence their habitat selection. Our agent-based model tested whether social behaviour explains undermatching, a distribution pattern where more individuals are found within poorer patches than predicted, under varying densities and competition. Low density and high sociality best explained undermatching. We reveal that in social animals, undermatching is driven by social tethering, which restricts an individual's ability to escape undermatching due to conspecific attraction. Social tethering in small populations has the potential to inhibit population growth – or recovery.

Keywords:

Allee effects, caribou, optimal foraging theory, *Rangifer tarandus*, social foraging, social tethers

Introduction

Competition and sociality are density-dependent phenomena that occur simultaneously, are often in opposition, and manifest at similar scales. The socio-spatial interface—a concept that identifies where social interactions and physical space intersect—has recently spotlighted the need to better test and disentangle the potentially putative interactions of social and spatial behaviour (Webber et al. 2023, Albery et al. 2024). Indeed, without properly assessing social and spatial behaviours in concert, researchers run the risk of erroneously misattributing the fitness implications of one or the other. For example, in social caribou (*Rangifer tarandus*), an individual's ability to specialize its diet is negatively correlated with its social connectivity within its population (Webber et al. 2024), i.e., more social animals have more general diets. Despite the correlation, caribou only accrued fitness benefits through diet specialization, not through their social connectedness. Thus, sociality persists despite the fact that less social animals have greater ability to specialize their diets, and produce more offspring. A finding that recalls the paradox of social aggregations, where the grouping of individuals must result in a density-dependent decrease in fitness, and yet social foraging persists (Giraldeau 1988).

Several classical optimal foraging theories (see Suppl. Mat. A for a glossary of optimal foraging terms) provide a framework for testing how animal choice in patch or habitat selection will be affected by competition, sociality, and population density. For example, the ideal free distribution (IFD, Fretwell and Lucas 1970) has long predicted optimal patch use is agnostic of social dynamics. There has been renewed interest in investigating classical optimal foraging theory in a collective movement and sociality framework. For example, caribou employing two different social strategies (aggregated or disaggregated) were shown to have the same mean fitness as suggested by IFD (Bonar et al. 2020). However, much empirical research revealed suboptimal IFD outcomes, termed undermatching – where more individuals are found within poor-quality patches than expected (see Box 1).

Moreover, social or territorial animals are not free to move among patches – an assumption of IFD, which is because spatial and social arrangements are inherently linked (Webber et al. 2023). Therefore, movement may be constrained by social fences or tethers (Hestbeck 1982) or social resistance (Armansin et al. 2020). Individual proclivity for joining social groups is highly variable between individuals (Schradin 2013, Stamps 1988) and leader follower dynamics may emerge as individuals less affected by conspecifics switch patches for new forage opportunities. Patch switching behaviour has been previously attributed to presence of conspecifics (Jepsen and Topping 2004) and supports the idea that conspecific attraction could contribute to undermatching, particularly when followers switch patches to follow leaders. Additionally, conspecific attraction often results in groups that are larger than would be expected by IFD (Sirovnik et al. 2021). Incorporating social information into movement models has been shown to improve predictions of spatial movement given the significance that conspecifics play in individual decision making (Torney et al. 2018). Competition and conspecific attraction work as opposing spatial forces, where competition repels conspecifics and attraction draws conspecifics closer. Further, the effects of social attraction and competition are known to vary across densities (Webber et al. 2023, Sirovnik et al. 2021). Disentangling how conspecific attraction, competition, and density interact may help explain why undermatching in IFD is so often observed across taxa.

Woodland caribou are an ungulate of conservation concern with complex social dynamics (Bergerud et al. 2007; Peignier et al. 2019). Caribou exist within a fission-fusion society, which means that their social groupings change in size and composition over time as they move across the landscape (Lesmerises et al. 2018; LeGoff et al. 2024). Caribou are also found at a range of densities that offer the opportunity for density-dependent effects to emerge. Caribou, therefore, serve as an exceptional model system for studying fine-scale movement patterns and their interaction with sociality. Yet caribou, especially, at low densities, are often treated as a non-social animal, without considerations for their sociality in regards to population demographic predictions and growth rates (Gunn et al. 2012).

In an agent-based model, Folmer et al. (2012) modeled IFD of leaders (agnostic to conspecifics) and followers (attracted to conspecifics) while incorporating conspecific attraction, indirect (scramble) competition, and knowledge of forage. Their model showed that patches with higher forage availability can be left unoccupied when conspecific attraction is high as animals use conspecifics as a signal of forage quality. Building from Folmer et al. (2012), we investigated how changes in conspecific attraction, competition, and density may explain the mechanisms creating undermatching in IFD. We built agent-based models (ABMs) that allow for fine-tuning of individual-level (conspecific attraction and competition) and population-level (density) parameters. We included depletion of resources into our model to further investigate the importance of conspecific attraction and leader-follower dynamics in changing resource availability.

We propose 3 main patterns as a result of undermatching in social species:

1) individuals visit patches of poor quality at higher rates than when following IFD,
2) individuals move less frequently from poor quality patches than expected from IFD, and
3) individuals move less frequently overall than when following IFD; due to individuals using conspecifics as a signal of resource quality and the loss of efficiency in group movement (Box 1).

First, we investigated the central premise of IFD: that the number of animals per patch would increase proportionally with food availability such that their consumption rates are equivalent. We predicted that with increased conspecific attraction, the number of unique patch visits with high food availability would increase more slowly as more individuals would occupy patches with lower food availability due to conspecific attraction (P1; Fig 1A). We also predicted that with increased conspecific attraction, the length of time at a patch would be higher than what would be predicted given IFD at poor quality patches (P2; Fig 1B). We expected that competition and density would also contribute to undermatching. Social foraging theory suggests that increased competition should result in increased undermatching (Giraldeau and Caraco 1986), but these models do not take into account the opposing forces of attraction and competition, and how that interplays with undermatching. Our model allowed for varying levels of conspecific attraction, competition, and density to disentangle which attribute most contributes to undermatching.

We also expected that the length of time at individual patches, regardless of patch quality, would be longer when conspecific attraction is high (P3; Davis et al. 2022) indicating that individuals are less likely to switch patches even as consumption rate decreases, potentially as a social fence (Fig 1C). However, we expected that this pattern would not hold for high densities, as individuals have more conspecifics to choose to follow. How competition, density, and conspecific attraction intersect with quitting time at a patch were also investigated with our model.

We then investigated how individual consumption rates (as a proxy for fitness, Okuyama 2020) change with density as a function of conspecific attraction and competition. We predicted that consumption rate would decrease with increasing density and increasing competition (as predicted by IFD) at low conspecific attraction (P4; Fig 1D). We also predicted that consumption rate would be parabolic with low consumption rates at both high and low densities with high conspecific attraction as individuals may use the presence of conspecifics as a signal of forage quality (Fig 1).

Methods

Patch environment

We created a spatially-explicit agent-based model (ABM) in NetLogo (v. 6.4.0). An overview, design concepts and details (ODD) protocol (Grimm et al. 2010) can be found in Suppl. Mat. B. We based our model on the caribou population of Fogo Island, NL – an island that is home to a resident population of caribou whose population size has fluctuated from 20 % to 100 % to 50 % with a carrying capacity of 300. We built a 237 km^2 landscape to replicate the total land surface area of Fogo Island. The landscape is a 77 x 77 two-dimensional grid, with 5929 grid cells. Each grid cell represents a 200 x 200 m^2 square patch that contains consumable food. Each patch was randomly assigned a food value between 1 and 10 from a uniform distribution to create a heterogeneous landscape with 10 representing the most food available. We smoothed patch values with a Guassian 2D convolution filter with a kernel range of 5 patches to remove unrealistic differences between adjacent patches. We did not wrap the virtual landscape as caribou on Fogo Island are relatively restricted in movement beyond the edge of the island, although caribou are known to swim to smaller neighbouring islands (Webber et al. 2021).

Caribou-agent properties

Caribou-agents attempt to maximize their consumption rate on the simulated heterogeneous landscape. We assigned expected consumption rate, C_i, for each patch i based on expected resource availability and competition with Beddington's functional response model (Beddington 1975, Folmer et al. 2012):

$$C_i = aR_i / (1 + ahR_i + qP_i)$$

where R_i is the expected resource availability on patch i, P_i is the number of conspecifics on patch i, q is the competition rate, a is the attack rate, and h is the handling time. Caribou-agents had perfect knowledge of resource availability on their current patch, while they had imperfect information of neighboring patches. Expected resource availability on neighboring patches was calculated by drawing from a left-truncated standard normal distribution with the mean of true resource availability and a standard deviation of 1. The distribution was truncated at 0, i.e., no negative values of expected resource availability were possible. We were interested in how varying competition q affected the expected consumption rate and selected values of 0.1, 0.5, and 1.0 to represent the spectrum from low to high competition. Attack rate a and handling time h were assigned values of 1 following Folmer et al. (2012).

We also incorporated conspecific attraction as an additional cue of resource availability. Conspecific attraction included the number of conspecifics within a patch and the neighboring patches that shared a border or vertex. For instance, a patch found within the centre of the landscape had 8 neighboring patches, while a patch on the edge of the landscape had 5 neighboring patches and a patch at the corner had 3 neighboring patches. We calculated conspecific social attraction, S_i, for each patch i using the equation presented in Folmer et al. (2012):

$$S_i = s * (\Sigma^{N}_{j=0} W_{ij} * P_j) / (1 + \Sigma^{N}_{j=0} W_{ij} * P_j)$$

where N is the number of patches in the landscape, W_{ij} is a matrix that represents the available social environment for each patch, P_j is the number of conspecifics within a patch, and s is the intensity of conspecific attraction. For patch i, we assigned W_{ij} a value of 1 for all neighboring patches and patch i itself. We assigned all other patches a value of 0 for W_{ij}. As per Folmer et al. (2012), we row-normalized the matrix by dividing the value of the matrix by the sum of its row elements in W for all rows so that each row equaled 1. Therefore, conspecific attraction S_i was independent of the number of neighboring patches. We selected intensity of conspecific attraction s values of 0.0, 0.5, and 1.0.

Caribou-agents integrated their expected consumption rate and conspecific social attraction into one metric of total patch attractiveness T_i :

$$T_i = C_i + S_i$$

to determine which patch to move to on the landscape.

Caribou are known to have varying levels of conspecific attraction (Hendrix et al. 2024, Webber et al. 2024). To model this individual variation, we included both leaders and followers in the model. Leaders were agnostic to conspecific attraction, such that $S_i = 0$. We assigned leader-follower proportions as 0.2 and 0.8, respectively. We determined this proportion by assuming there are one or two leaders within an average caribou group. Caribou group sizes average between 7 and 8 individuals in Newfoundland (Webber et al. 2021), which suggests leaders represent between 14 % and 29 % (mean of 20 %) of the population.

Caribou-agent relocations

At the start of the simulation, leader caribou-agents were distributed randomly on the landscape. Follower caribou-agents then distributed themselves to a patch within a radius of 2 patches from a leader. They randomly chose which leader to follow leading to varied group sizes across the landscape. At each time step, each caribou-agent determined their optimal patch location by computing T_i for their current patch and all neighboring patches T_j. Caribou-agents moved to a neighboring patch when $T_j > T_i$, but remained in their initial patch when $T_j < T_i$. After each relocation attempt, each caribou-agent recalculated their consumption rate based on the actual resource availability of their chosen patch and consumed that portion of the patch resources. Each patch relocation attempt represented 1 hour of time, with each caribou-agent attempting relocation 8,760 times, representing 1 year of time. We varied the number of caribou on the landscape to assess density-dependent effects. We chose densities based on previously selected values for modeling caribou which corresponded to 0.4, 2 and 5 caribou/km^2 (Ferraro et al. 2022).

Simulations

We tested 27 scenarios of varying conspecific attraction (0.0, 0.5, 1.0), competition (0.1, 0.5, 1.0), and population density (0.4, 2, and 5 caribou/km^2) in a full factorial design (Fig 2). We replicated each scenario 60 times, resulting in 1,620 trials. We extracted several output variables to assess how density, competition, and conspecific attraction interact to affect the distribution of animals on the landscape and the consequences of that distribution. The output from the scenarios included (1) the final resource count for each patch, (2) the final number of patch visits for each patch, (3) the patch value and residence time for each caribou for each patch visited, (4) mean residence time of caribou on a patch, and (5) mean consumption rate at each time step.

Analysis

We conducted all analyses in R (v. 4.2.2, R Core Team 2024). We calculated means and standard errors for patch visits, residence time per patch value, and overall residence time for all 27 scenarios. To analyze the number of patch visits for each patch, we rounded the final resource count to the tenth decimal place and then calculated the mean of the total patch visits for each of the rounded resource counts across all replicates. To calculate the mean residence time per patch, we also rounded the resource count to the tenth decimal place. We averaged the residence time per patch value across all animals in all replicates. We calculated mean residence time and mean consumption rate by averaging across all patch values in all replicates.

Sensitivity analysis

We conducted sensitivity analyses to understand the importance of variables used in the ABM using the ‘nlrx’ package (Salecker et al. 2019) in R. We used the Morris screening method (Morris 1991, Salecker et al. 2019) to rank the model parameters in their influence on the distribution of residence time, patch visits, and consumption rate. We analyzed four model parameters that we determined could affect the model results: the degree of smoothing on the landscape (kernel range), how fast a caribou-agent searches for forage (attack rate), the degree of uncertainty in the forage value for each patch (theta), and the percentage of the population that are leaders. We did not include handling rate as caribou directly consume all plants, and therefore the handling rate across plant species and patch quality, should be the same. For kernel range, we varied the parameter from 3 to 7 from the assigned value of 5. For attack rate and theta, we varied from 0.5 to 1.5 from the assigned value of 1. For the percentage of population that are leaders, we chose the biologically relevant values from the literature of 14 to 29 %. We also included a full factorial combination of parameters to determine if the results were sensitive to a specific combination. We held conspecific attraction and competition values constant at a moderate value of 0.5. We completed sensitivity analyses at both 0.4 and 5 caribou/km^2 density.

We used the mean absolute value of elementary effects (mustar) to measure the overall influence of each parameter on our results (Salecker et al. 2019). We also used the standard deviation of the values (sigma) to measure higher-order effects including nonlinearity and interaction effects (Campolongo et al. 2007). We created scatterplots from the results to show the relative importance of each parameter to the overall model. The overall effect of changing the values of the parameter was small, given the values of mustar and sigma. We found that for low density scenarios, kernel range had the largest impact on the model, while for high density scenarios, theta had the largest impact. The plots can be found in Suppl. Mat. D.

Results

Our results support our first proposed pattern of undermatching: incorporating social interactions led to caribou-agents visiting low-quality patches more often than predicted by IFD (P1). As patch value increased, patch visits also increased, but we did not see a linear relationship as previously described (Box 1 and Fig 3). Conspecific attraction, competition, and density all changed the shape of the function. For qualitative assessment, we used a conspecific attraction value of 0 to compare against all other scenarios, as our primary hypothesis was that the presence of conspecifics served as an indicator of patch quality, and thus contributed to undermatching. Caribou-agents with higher conspecific attraction visited more patches of poorer quality when compared to non-social caribou-agents. Competition had a smaller impact on the relationship between patch visit and quality, but we did qualitatively observe the highest level of undermatching in low competition scenarios. Low density scenarios led to more undermatching than high density scenarios. Therefore, high conspecific attraction, low competition, and low density produced the highest degree of undermatching (Fig 3).

Conspecific attraction, competition, and density also contributed to changes in variance from the mean of patch visits. We observed increases in variance for high conspecific attraction and low competition scenarios compared to non-social, highly competitive scenarios. Low density scenarios had higher variance compared to high density scenarios.

Our second prediction, that individuals would move less frequently from poor quality patches than expected from IFD (P2), was also supported by our results (Fig 4). As with the first prediction, we used a value of 0 for conspecific attraction to compare against all other scenarios. As patch value increased, with 0 conspecific attraction IFD would predict the longest residence times at high patch values. In our simulations, when conspecific attraction was high and competition was low, caribou-agents spent longer at low patch values suggesting undermatching as with prediction 1. As competition increased, the slope of residence time was more similar across all conspecific attractions and densities. Thus, caribou-agents spent more time in poor quality patches at low densities when compared with high density. Therefore, high conspecific attraction, low competition, and low density produced the highest degree of undermatching.

Our results also supported our third proposed pattern of undermatching. We predicted that social caribou-agents would move between patches less frequently than when following IFD (P3). We found that caribou-agents slightly increased their residence time with increasing density, but only with low competition, and no conspecific attraction (Fig 5). Residence time increased with conspecific attraction but decreased under higher competition. Conspecific attraction had a greater impact on residence time at lower density than higher density (Fig 5).

Undermatching should correspond with decreased fitness for individuals. We used consumption rate as a metric of fitness. We predicted that for non-social caribou, consumption rate would be highest at low densities as there are fewer individuals with whom to share resources (P4), which our results supported. We predicted that for social caribou, consumption rate would be lowest at both low and high densities, with a peak at moderate density (P4). We expected the low consumption rate at low density because caribou-agents are attracted to conspecifics that might be bad indicators of forage quality. There would also be less forage to share amongst the gathered caribou-agents. Instead, we found that consumption rate decreased with increasing density, competition, and conspecific attraction (Fig 5). The decrease in consumption rate due to conspecific attraction and competition was density-dependent as the decrease was greatest at high density scenarios. It appears that the effect of conspecific attraction was buffered by competition. For example, at moderate attraction across all densities, consumption rate was higher at high rates of competition compared to moderate competition. Further, at high conspecific attraction, the relative change in consumption rate was smaller between moderate and high competition than between low and high competition.

Discussion

The socio-spatial interface provides us with a fresh perspective from which to test why animals may undermatch their optimal habitat use, i.e., occupying lower quality habitat than predicted by the ideal free distribution. We created an agent-based model that expands on IFD, incorporating sociality not only in a competitive context as studied previously, but also positive conspecific attraction and their density-dependent effects. Using these advances, we investigated 3 patterns of undermatching in IFD. We found that social non-competitive caribou-agents at low densities were more likely to visit resource poor patches than non-social caribou-agents (P1; Fig 3), move less from poor patches (P2; Fig 4), and move less overall (P3; Fig 5). Social attraction also affected consumption rate – a proxy for fitness – where social caribou-agents at high densities had the lowest consumption rate (P4; Fig 5). In contrast, competition appeared to buffer the effects of conspecific attraction in both undermatching and consumption rate. These results highlight that the tension between social behaviour and competition at the fine-scale socio-spatial interface can negatively impact fitness through undermatching.

The idea that conspecifics impact movement is not novel, but illustrating that through a classical framework such as IFD is novel. The presence of multimodal oscillations for patch visits (P1) and residence time (P2) as patch value increased (Fig 3) emerged as an unexpected, but central, finding. The oscillations support our hypothesis that conspecific attraction contributes to undermatching in IFD. While unexpected, our robust sensitivity analysis provides confidence that this was an emergent property of the model, rather than an artifact (Suppl. Mat. D). The oscillations suggest that caribou-agents attempted to move to more attractive food patches by assessing expected consumptive rates, but the presence of conspecifics pulled caribou-agents back towards areas that had poorer food availability but high conspecific presence - creating undermatching via a social ‘tether’.

The social resistance (Armansin et al. 2020) or social fences hypothesis (Hestbeck 1982) suggests that individuals are prevented from moving into new locations due to aggression, especially as density increases. In contrast, we posit that conspecifics can also serve as a social ‘tether’ that continues to draw individuals back to a suboptimal area and that increased density allows individuals to move between groups. In our model, the strongest of multimodal oscillations occurred at low density (0.4 caribou/km^2) but disappeared at high density (5.0

caribou/km^2). As density increases, individuals have more neighbors from which to choose, reducing the strength of the social tethers. Thus, high densities could be a condition for fission-fusion societies to occur, as many groups on a landscape can allow individuals to move more flexibly between groups. An increased fission-fusion dynamic at higher densities allows any given social tether to dissipate, providing the agents with access to other groups and patches, and consequently more opportunities to escape patches where they would be undermatched. Social tethers may have been demonstrated in other social herds. For example, in plains bison (*Bison bison*), individuals with increased social connectivity have smaller home ranges, i.e., more intensely occupy smaller patches (Merkle et al. 2024). Hypothetically, the connection between patches and social connectivity in bison could indicate the presence of a social tether in an empirical system.

Social tethers may contribute to Allee effects at low densities through the creation of fitness sinks. An Allee effect is an inverse density-dependent relationship between population growth rate and density, where at low densities, a decrease in growth rate is observed. Social species are hypothesized to be at an increased risk for Allee effects (Stephens & Sutherland 1999). Our model suggests that social tethers may be a mechanism underlying this increased risk as individuals caught by these tethers are unable to escape to patches of better forage quality, leading to a decrease in their consumption rate, and ultimately their fitness. Caribou populations are in decline worldwide. The benefits of sociality, like predator avoidance, likely evolved for caribou at higher densities than currently observed. In our model, at low densities, these benefits of sociality are not apparent. Caribou-agents get caught at local maxima because there are not enough neighbours to indicate better habitat or pull them away from pockets of high density. The lowest density we explored was 0.4 caribou/km^2 based on Newfoundland estimates, but it has been reported that densities can reach as low as 0.02 caribou/km^2 (Environment Canada 2011). These very low density populations are unlikely to benefit from social interactions, resulting in maladapted social strategies. Social behaviour has been previously shown to result in decreased fitness (Sigaud et al. 2016). Through a conceptual density-dependent movement model, it has been suggested that in barren-ground caribou Allee effects at low densities result in decreased spatial fidelity for calving grounds and decreased calf survival due to a loss of anti-predator strategies and unfamiliarity with the landscape (Gunn et al. 2012). Gunn et al. (2012) also suggest that the movement away from typical calving grounds is driven by conspecific attraction to these new areas. Our work aligns with these findings in that normal social strategies are drawing individuals to areas of the landscape that correlate with lower survival (or in our case a proxy of survival) at low densities. Collectively, these results highlight the importance of considering not only low densities of populations, but also the decrease in the number of social units and that larger numbers of individuals are needed for population success than previously understood (vonHoldt et al. 2025).

Despite the low-density scenarios showing the highest degree of undermatching in IFD, with most animals at patches with poorer quality, we did not observe a comparable decrease in consumption rate (P4; Fig 5). It is likely that our model had abundant food available even when patch choice was not optimal. There may be circumstances where the average consumption rate is better for high density scenarios. For example, more individuals on a sparse landscape are more likely to find forage faster than only a few individuals. Caribou are known to be more social in winter when food is patchier, likely as an increased foraging strategy (Peignier et al. 2019). Our model could be used to explore this concept by creating resource hotspots, and measuring how quickly they are found, and at what point in time consumption rates are comparable between densities. These results also highlight Giraldeau's (1988) apparent paradox, where in all social scenarios, consumption rate was lower than for all non-social scenarios, which ignores the benefits of social grouping not incorporated in the model.

While our ABM included variation in conspecific attraction, competition, and density to explore undermatching and consumption rate, further variations could be explored. Caribou foraging behaviour changes seasonally, which we did not include. Caribou are known to dig craters during the winter to access vegetation, and these craters become despotic, i.e., defend local resources (Barrette and Vandal 1986; Schaefer and Mahoney 2001). An expansion on our model could change both the availability of forage on the landscape to mimic crater distribution, and modify competition to be direct interference that impacts caribou-agent movement to explore the behavioural changes between seasons. We also held conspecific attraction as constant over a trial, but social attraction is known to change within individuals over time (Webber et al. 2024). An individual being able to weigh the costs and benefits of sociality and modulate their social attraction as a response would provide increased nuance to sociality as a factor of spatial distribution. Lastly, as sociality is often a response to predation risk via the dilution effect (Turner & Pitcher 1986) or many eyes hypothesis (Lima 1995), including predators in the model would further elucidate the possible fitness benefits of conspecific attraction. However, one could interpret our current model as implicitly valuing predation risk assigned to the landscape grid simply as an overall attraction score, where low scores could symbolize high predation risk. Behavioural decisions to limit risk then result in social individuals collecting on poor patches as an anti-predator strategy (Lima and Dill 1990). Further expansions could elucidate other nuances; our model provides a groundwork for these ideas.

The social-spatial interface (Webber and Vander Wal 2018, Albery et al. 2024) helps reframe long held hypotheses. Whether it is bison whose collective decision making shapes their habitat selection and results in increased adult mortality (Sigaud et al. 2017) or caribou where social connectedness inhibits habitat selection specialization and offspring survival (Webber et al. 2024b), tension between spatial and social behaviours have clear implications on fitness for which the mechanisms remain unresolved. Our agent-based model interrogates these plausible mechanisms. The model integrates the social-spatial interface with IFD, testing the extent to which social behaviour – across densities, degrees of attraction, and variation in competition – contributes to undermatching and its fitness implications. Indeed, the effect of conspecific attraction on spatial distribution depended on density, such that habitat undermatching was most pronounced at low densities. Social tethers emerged where animals are trapped or return to areas of poor resource availability due to the presence of conspecifics. The implications of which are marked for small populations of social animals, where tethers will exacerbate undermatching and may induce Allee Effects. We spotlight the importance of including sociality explicitly when modeling movement, and especially density-dependent movement.

<u>Box 1: A Primer on Undermatching:</u>

Fretwell and Lucas (1969) proposed the ideal free distribution (IFD) as one model to describe density-dependent habitat selection. The IFD model suggests that individuals within a species will distribute themselves among patches such that all individuals have equal fitness. The model is density-dependent because the density of individuals between patches will vary as the patches differ in resource quality and the introduction of new individuals into each patch results in a decrease in fitness for all individuals within the patch (Fretwell and Lucas 1969, Morris 1988). The IFD assumes that individuals (1) move between patches without cost, (2) are of equal competitive ability, and (3) have omniscient knowledge of resource quality and conspecific densities (Fretwell and Lucas 1969). Many studies that investigated IFD observed a phenomenon known as "undermatching" where more individuals are found within the poor-quality patch than expected (Fig 1A). Perception limitations (Abrahams 1986), unequal competitors (Sutherland et al. 1988, Holmgren 1995, van der Meer 1997), interference competition (Sutherland 1983), travel costs (Baum and Kraft 1998), and resource replenishment rates (Kennedy and Gray 1993) have been hypothesized to explain the high occurrences of undermatching.

Here we explore how conspecific attraction can further explain undermatching. Social species are known to violate the assumptions of IFD. Specifically, moving as a group is costly when compared to solitary movement (Klarevas-Irby et al. 2025) and individuals use their neighbours as an indicator of forage quality due to imperfect knowledge (Jepsen and Topping 2004). We use patch visits and residence time as an indicator of undermatching (Fig 1). Due to the increased cost of movement for group movement, we predicted that the number of patch visits for social individuals would be lower than solitary individuals, while the overall patch residence time would increase for social individuals compared to solitary individuals. **end of box 1**

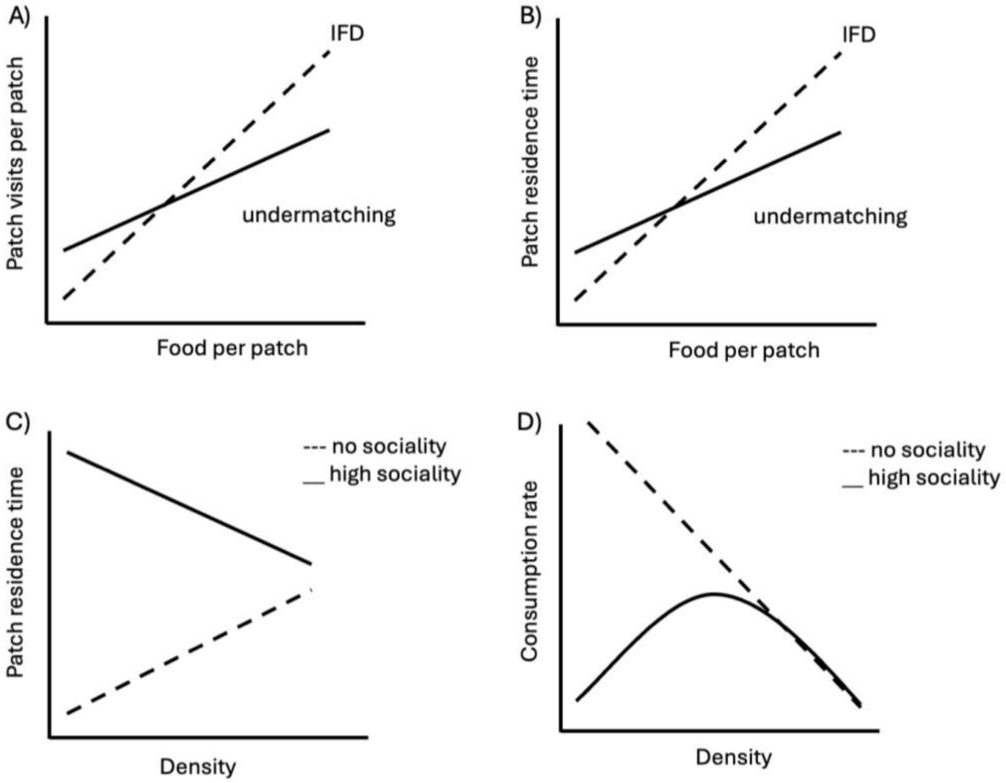

Figure 1. A) In the ideal free distribution model, individuals are expected to distribute among patches in a 1:1 relationship with food availability (dashed line). When individuals are found in patches at higher rates than food availability, undermatching occurs (solid line). Therefore, patch visits should also scale linearly with food availability as more individuals should visit patches with more food. B) Patch residence time should equally increase with food per patch. C) Patch residence time should increase with density as there are fewer places for individuals to move to with more conspecifics. Increased conspecific attraction should increase residence time, such that at high densities there is convergence of residence time with no conspecific attraction as the social landscape becomes homogenous. D) Slopes of consumption rate as a function of density at low (left) and high (right) conspecific attraction. Solid lines represent predictions based on low and high conspecific attraction, while the dashed line represents IFD expectations.

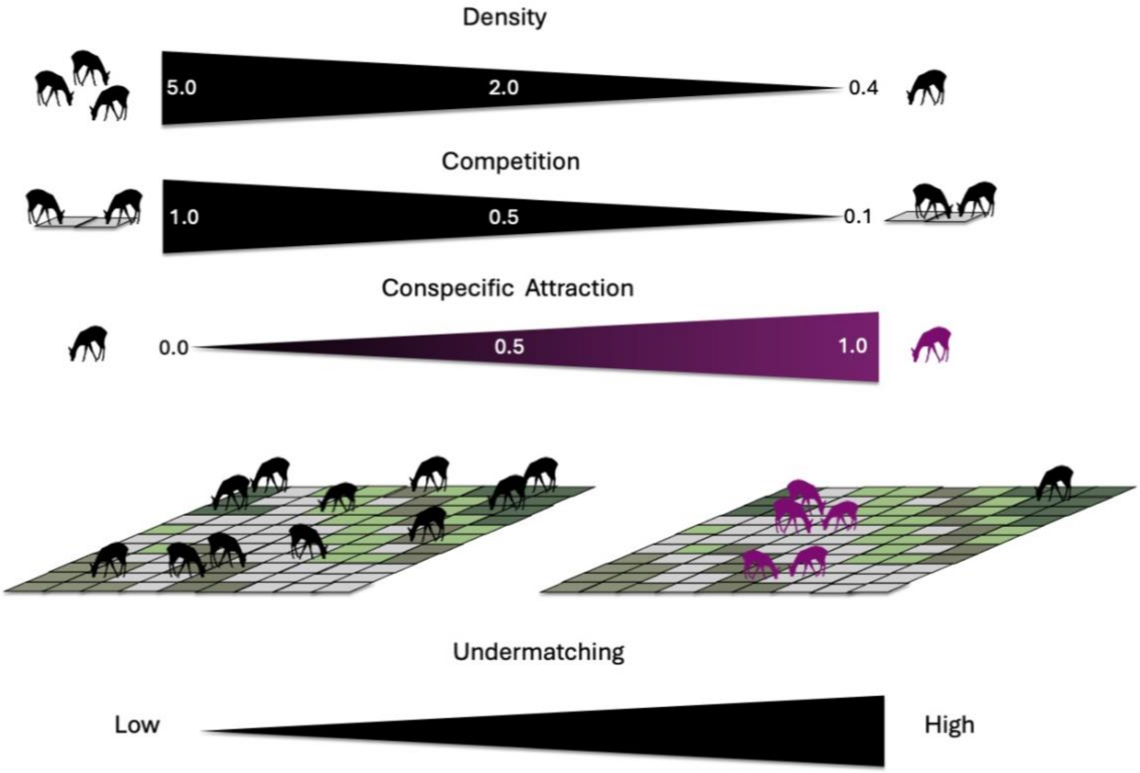

Figure 2: Diagram of varying levels of caribou density, conspecific attraction, and competition analyzed in the model and their impact on undermatching. We included 3 density levels that represent caribou/km^2, ranging from 0.4 to 5.0. The intensity of competition ranges from 0.1 to 1.0 and is represented by distance between caribou-agents, with low competition caribou sharing a patch, and high competition caribou foraging on separate patches. Conspecific attraction ranges from 0.0 to 1.0 and is represented by a change in colour from black (non-social) to purple (high social attraction). The varying levels resulted in 27 scenarios with 60 replicates for each combination. Highest undermatching occurred under low density, low competition, and high conspecific attraction.

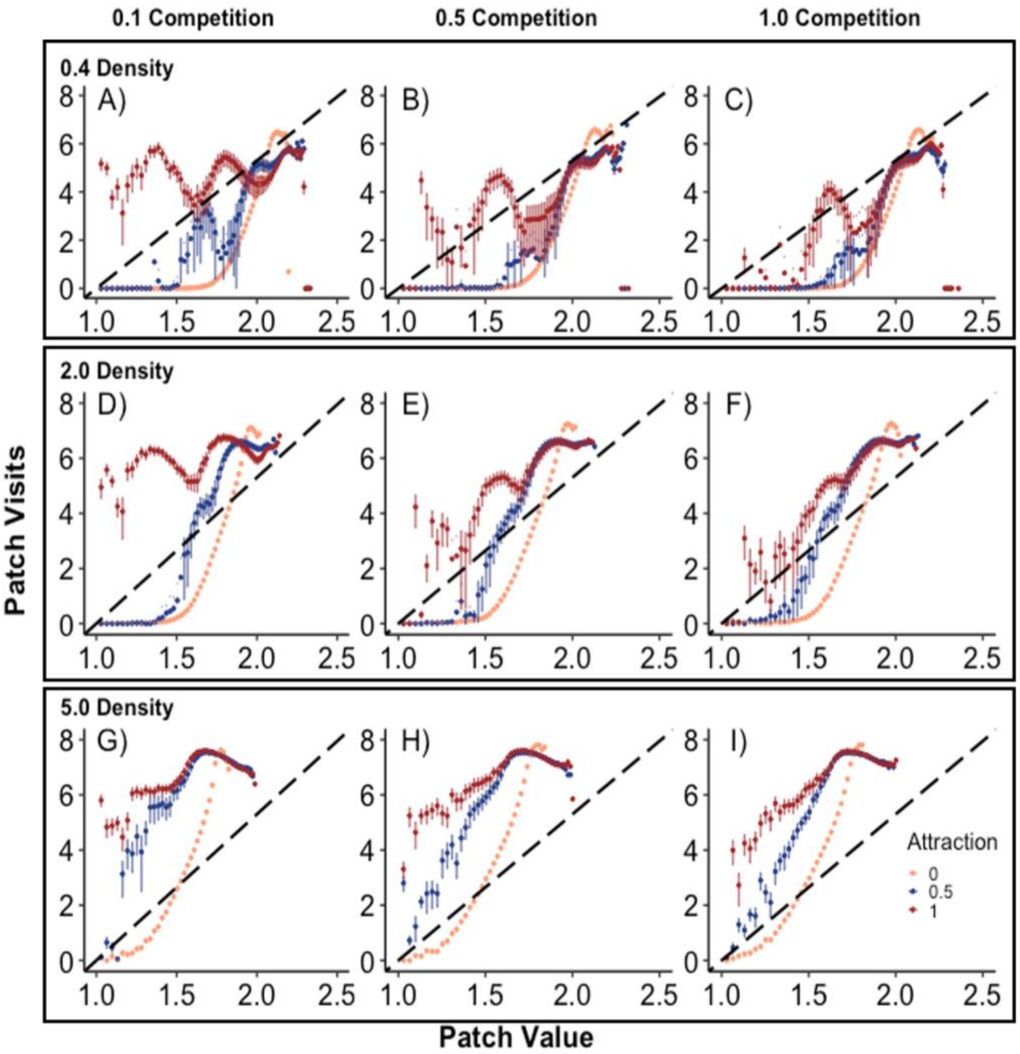

Figure 3. Mean values of the log of patch visits against the log of patch resource values across varying conspecific attraction, density, and competition. Density increases from top to bottom, with 0.4 caribou/km^2 in top row and 5 caribou/km^2 in the bottom row. Competition increases from left to right along columns from 0.1 to 1. Colour within each plot reflects the degree of conspecific attraction from 0 to 1. Mean patch visits were calculated from 60 replicates of each scenario. The dashed line represents the expected relationship in IFD. Error bars represent one SE. Social caribou-agents visited patches of poorer quality at higher rates than non-social agents, with a multimodal oscillation pattern emerging at low density. Increased competition decreased the degree of undermatching when conspecific attraction and density were held constant.

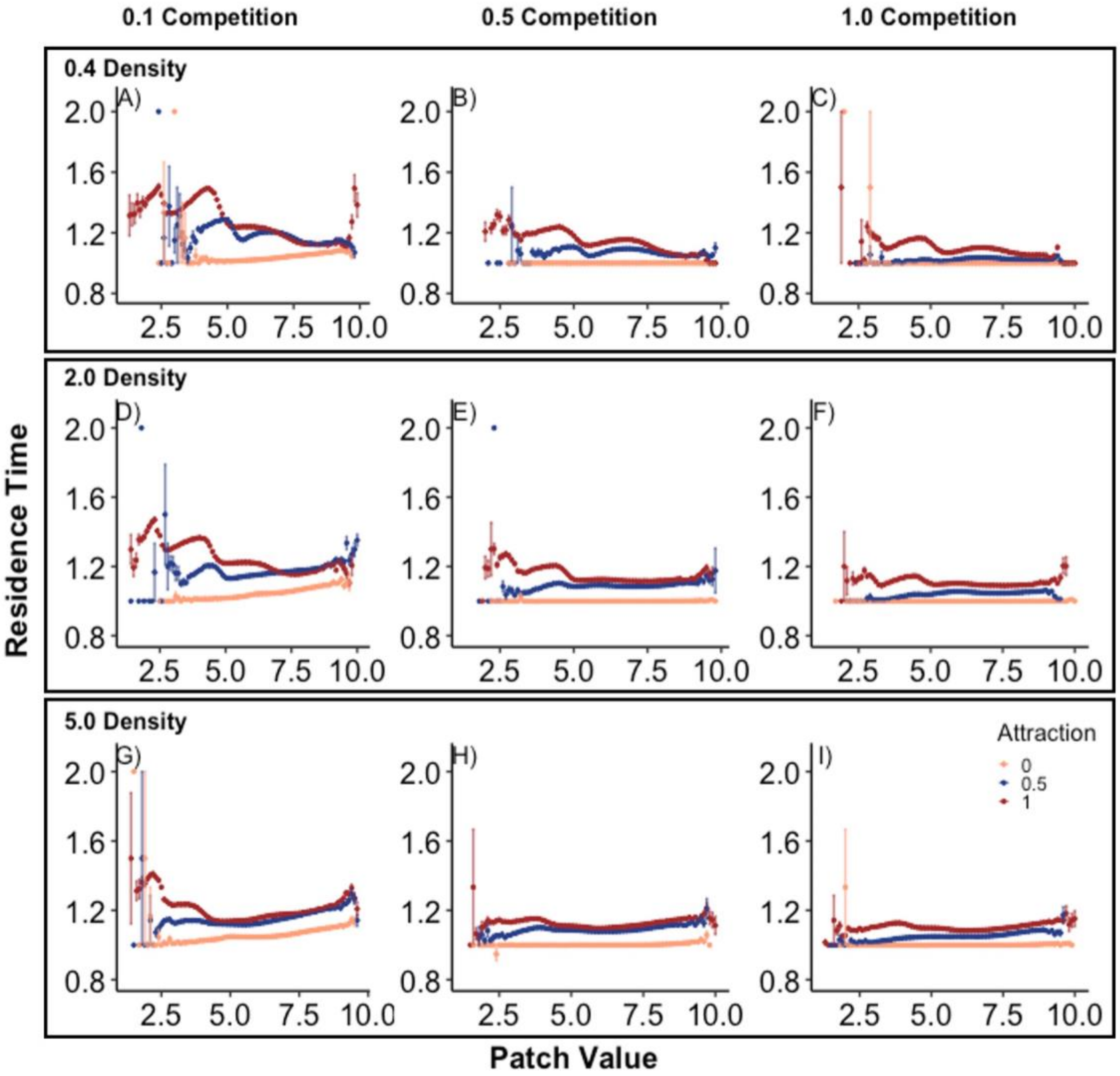

Figure 4. Mean values of the residence time per patch against patch resource value across varying conspecific attraction, density, and competition. We removed residence times of zero for ease of interpretation. The figures with zeros included can be found in the Suppl. Materials C. Density increases from top to bottom, with 0.4 caribou/km^2 in top row and 5 caribou/km^2 in the bottom row. Competition increases from left to right along columns from 0.1 to 1. Colour within each plot reflects the degree of conspecific attraction from 0 to 1. Residence times represent the mean number of time steps spent at a patch before relocating. Residence times were calculated from 60 replicates of each scenario. Error bars represent one SE.

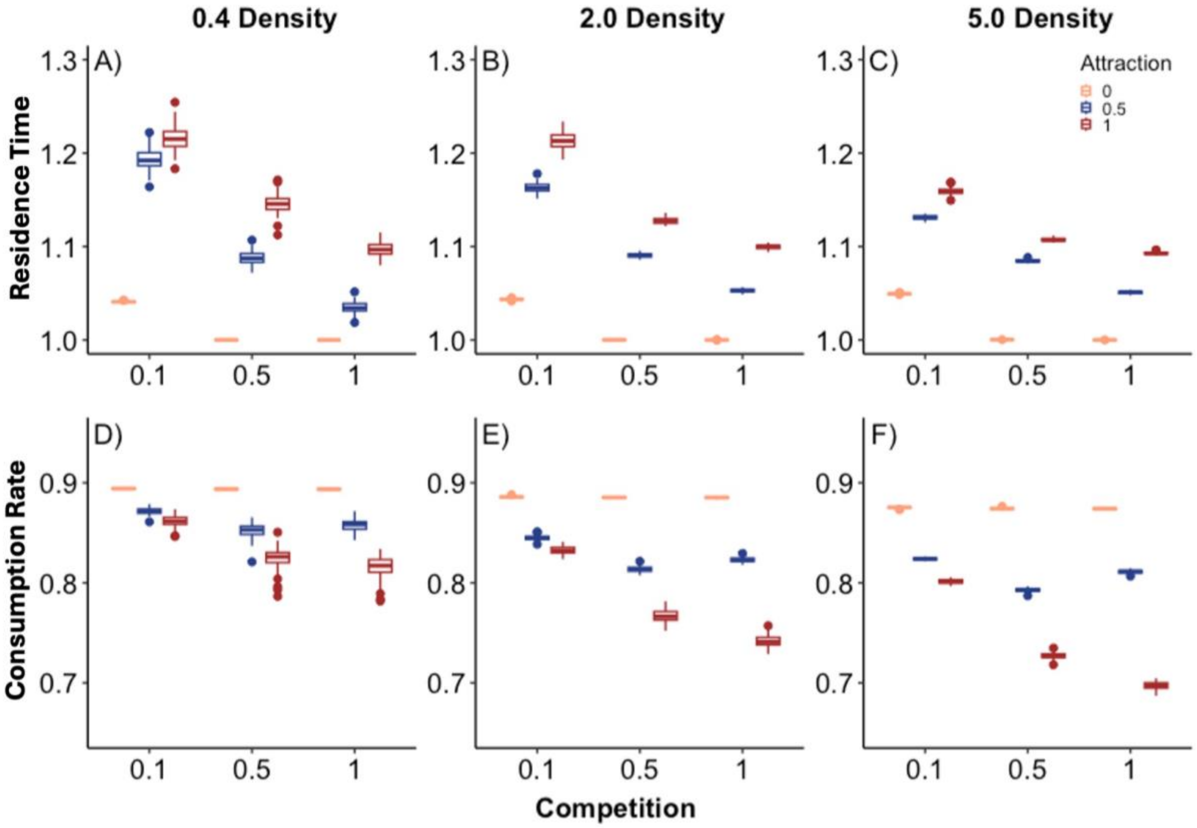

Figure 5. Boxplots of mean residence time (A,B,C) and mean consumption rate (D,E,F) for 3 levels of conspecific attraction (0, 0.5, and 1) and competition (0.1, 0.5, 1.0) across 3 densities [0.4 (A,D), 2.0 (B,E), 5.0 (C,F) caribou/km^2]. Residence times represent the mean number of time steps spent at a patch before relocating. Error bars represent one SE. Mean residence times and consumption rates were calculated from 60 replicates of each scenario.

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Supplementary Materials

A. Glossary

Term	Definition	Reference
Attack rate	The rate at which an individual finds prey (probability of encounter)	King & Marshall 2022
Consumption rate	The rate that prey or forage is consumed based on search rate and handling time of prey	King & Marshall 2022
Fitness	A multi-component measure of an individual's ability to pass their genotype onto the next generation. Components of fitness often include adult survival and annual reproductive rate	Uboni et al. 2017
Free	Individuals can move between patches without travel costs or competitive exclusion	Sutherland 1983
Ideal	Individuals are omniscient in their knowledge of resource abundance and conspecific density within each patch	Sutherland 1983
Handling time	The time it takes to consume prey through capture and ingestion	King & Marshall 2022
Marginal value theorem	The optimal time for an individual to leave a patch based on consumption rate and diminishing returns	Davis et al. 2022
Patch	A spatially bounded area that differs from its surroundings in some aspect of resource availability that can be depleted	Cassini 2013
Quitting time	The point at which an individual chooses to leave a patch and forage in a new patch	Mella et al. 2018
Residence time (patch exploitation time)	The length of time an individual spends in a patch before moving to a new patch	Davis et al. 2022
Resource	A substance, object, or energy source required for maintenance, growth, or reproduction	Cassini 2013
Spatial landscape	The arrangement of habitat patches across a defined area	Cassini 2013
Undermatching	A phenomenon of IFD when more individuals are within the poorer patch than would be expected by resource abundance	Baum & Kraft 1998

B. Overview, Design Concepts, and Details Protocol:

Full code and data for the NetLogo simulations are available at:
https://github.com/jmkusch/Social-Undermatching-In-IFD .

We followed the ODD protocol (overview, design concepts, details) for describing individual-based models (Grimm et al. 2010).

Purpose

The purpose of this model is to investigate how social attraction, interference competition, and density influence spatial distribution and consumption rate of caribou. We proposed that undermatching from the ideal free distribution (IFD) occurs through 3 mechanisms: 1) that caribou visit patches of poorer quality at higher rates than expected, 2) that caribou spend longer on patches of poorer quality than expected, and 3) caribou spend longer per patch overall than expected compared to IFD due to individuals using conspecifics as a signal of resource quality.

Entities, state variables, and scales

We created a spatially-explicit agent-based model (ABM) in NetLogo (v. 6.4.0).

Caribou-agents - We modeled our agents on caribou (*Rangifer tarandus*) that move between patches and consume available food on these patches. Before the simulation, each caribou-agent is assigned a role as leader or follower (described below) that determines to what degree they are influenced by conspecifics. Caribou-agents attempt to maximize their consumption rate on the simulated heterogeneous landscape (C_i). We also incorporated conspecific social attraction as an additional cue of resource availability (S_i). Caribou-agents integrated their expected consumption rate and conspecific social attraction into one metric of total patch attractiveness T_i:

$$T_i = C_i + S_i$$

to determine which patch to move to on the landscape. After moving onto a patch, caribou-agents consume a portion of the available food, such that consumption affects the patch attractiveness for the next caribou-agent that encounters that patch.

Patch environment - We based our model off the caribou population of Fogo Island, NL – an island that is home to a resident population of caribou whose population size has fluctuated. We built a 237 km^2 landscape to replicate the total land surface area of Fogo Island. The landscape is a 77 x 77 two-dimensional grid, with 5929 grid cells. Each grid cell represents a 200 x 200 m^2 square patch that contains consumable food. Caribou are expected to move less than 200 m/hr in habitats with increased forage availability, and more than 200 m/hr with decreased forage availability (Webber et al. 2024). In contrast, caribou are considered a social group when they are located within 50 m of another (Kasozi and Montgomery 2020; Webber and Vander Wal 2021). However, it is likely that their perception of conspecifics extends beyond this distance. Roe deer (*Capreolus capreolus*) have been shown to perceive conspecifics at least 200 m away, with fusion events occurring when individuals are up to 200 m away (Pays et al. 2007). Thus, we determined that 200 m x 200 m was an appropriate patch size. We did not wrap the virtual landscape as caribou on Fogo Island are relatively restricted in movement beyond the edge of the island. Each patch is randomly assigned a food value between 1 and 10 from a uniform distribution to create a heterogeneous landscape. We smoothed patch values with a Guassian 2D convolution filter with a width of 5 patches to remove unrealistic differences between adjacent patches. The model represents 1 year of time, each time step representing 1 hour of time with 8760 total timesteps. We ran the model for 1 year to simulate the period of time from green up with maximum food availability, to decreasing availability over winter due to consumption, and to avoid adding caribou-agents to the model due to reproduction.

Process overview and scheduling

To start the model, users determine the density, social attraction, and competition interference for the trial.

At the start of the simulation, the patch values representing consumable food on the landscape are randomly generated and smoothed. Caribou-agents are then generated and randomly assigned a role as leader (20%) or follower (80%). We determined this proportion by assuming there are one or two leaders within an average caribou group. Caribou group sizes average between 7 and 8 individuals in Newfoundland (Webber et al. 2021), which suggests leaders represent between 14 % and 29 % (mean of 20 %) of the population. Leader caribou-agents are distributed randomly on the landscape. Follower caribou-agents then distribute themselves to a patch within a radius of 2 patches from a leader. They randomly choose which leader to follow so group size varies across the landscape.

At each time step, each caribou-agent:

(1) determines their optimal patch location by computing T_i for their current patch and all neighboring patches T_j. Caribou-agents moved to a neighboring patch when $T_j > T_i$, but remained in their initial patch if all $T_j < T_i$. The caribou-agents move sequentially, but in a random order for each time step.

After each relocation attempt each caribou agent:

(2) recalculates their consumption rate based on the actual resource availability and conspecifics present on their chosen patch and
(3) consumes that portion of the patch resources.
(4) records the amount of food consumed from which patch, and
(5) records their residence time on a patch

The patch environment then:

(6) updates how much food is available on each patch and
(7) records the number of caribou-agents that landed on it.

Design concepts

<u>Basic principles</u> - The ideal free distribution assumes that individuals will distribute on the landscape such that all individuals have equal fitness. However, this theory does not consider that animals are social and influence the movement of each other. Further, understanding the role of density-dependence is difficult as variable densities are not always naturally present in nature.

We propose that the social attraction between conspecifics can result in undermatching, where individuals are found in poorer habitats more often than when they are alone as individuals because they use their neighbours as an indicator of resource abundance. We hypothesize that this impact is more pronounced at low densities as there are fewer individuals to gain resource information from.

Emergence - The patches visited by each caribou is emergent from their selection amongst patches that is dependent on the value of the food patch which is consumed over time, and the number of conspecifics nearby. As the user varies density, interference, and social attraction the choice of patch also changes in an emergent way.

Adaptation - If follower caribou-agents are not currently in a patch with conspecifics or have conspecifics in neighboring patches, then the followers act as leaders, where they only consider food patch values in their calculation of patch attractiveness. When followers find neighboring conspecifics, they return to behaving like followers.

Objectives - The objective for each caribou-agent is to move to the most attractive patch and consume the greatest number of resources. For leader caribou-agents, the attractiveness of the patch is determined by the expected consumption rate. For follower caribou-agents, the attractiveness of a patch is a function of both expected consumption rate and social attractiveness. All caribou-agents compare between their current patch and neighboring patches that share a vertex to decide if they should relocate or stay put.

Learning - None.

Prediction - Caribou-agents predict the consumption rate on neighboring patches to compare to their actual consumption rate on their current patch. When caribou-agents determine consumption rates for neighboring patches, they draw patch food values from a normal distribution centered on the actual food patch value and standard deviation of 1 which is left-truncated at 0. The predicted consumption rate contributes to the overall attractiveness of the patch.

Sensing - Caribou-agents can sense the number of conspecifics on their current patch and neighboring patches. Follower caribou-agents are attracted to these conspecifics, while both leader and follower caribou-agents experience repulsion on a smaller scale. Caribou-agents also sense the value of the food patch they are currently on, while they sense an estimated value (see above) for neighboring patches.

Interaction - Caribou-agents interact with each other by having passive attraction and repulsion. Follower caribou-agents incorporate social attraction into their overall attraction to a patch by counting the number of conspecifics on the patch. All caribou-agents include interference competition as a repulsive effect in their calculation of patch attractiveness based on the number of caribou-agents on the patch. Caribou-agents interact with the patch environment by consuming food at each time step.

Stochasticity - When the patch landscape is created, each patch food value is randomly drawn from a uniform distribution between 1 and 10. Each caribou-agent is assigned a role of leader or follower by randomly drawing a value between 0 and 1. Caribou-agents that draw a value less than 0.2 are assigned the role of leader, while those equal or above are followers. The initial placement of leader caribou-agents on the landscape is also randomly generated, and followers choose randomly among the available leaders to be placed within 2 patch lengths of the leader. When caribou-agents determine consumption rates for each patch, they draw patch food values based on prediction that involves a stochastic process (see above). For each time step, the order that the caribou-agents move on the landscape is randomly generated such that no one agent moves first each time.

Collectives - Groups of caribou emerge as follower caribou-agents choose patches with consideration of conspecifics already being present. Larger numbers of caribou-agents on a patch result in a more attractive patch.

Observation - We extracted several output variables to assess how density, conspecific interference, and social attraction interact to affect the distribution of animals on the landscape and the consequences of that distribution. The output from the scenarios included (1) the final resource count for each patch, (2) the final number of patch visits for each patch, (3) mean residence time of caribou on a patch, (4) the patch value and residence time for each caribou for each patch visited, and (5) mean consumption rate at each time step.

Initialization

To initialize the model, users determine the density (0.4, 2.0, and 5.0 caribou/km^2), social attraction (0.0, 0.5, 1.0), and competition interference (0.1, 0.5, 1.0) for the trial.

At the start of the simulation, the landscape is randomly generated and smoothed. Each patch is randomly assigned a food value between 1 and 10 from a uniform distribution to create a heterogeneous landscape. We smooth patch values with a Guassian 2D convolution filter with a kernel range of 5 patches to remove unrealistic differences between adjacent patches.

Caribou-agents are then generated and randomly assigned a role as leader or follower. We assigned leader-follower proportions as 0.2 and 0.8, respectively. We determined this proportion by assuming there are one or two leaders within an average caribou group. Caribou group sizes average between 7 and 8 individuals in Newfoundland (Webber et al. 2021), which suggests leaders represent between 14 % and 29 % (mean of 20 %) of the population. Leader caribou-agents are distributed randomly on the landscape. Follower caribou-agents then distribute themselves to a patch within a radius of 2 patches from a leader. They randomly choose which leader to follow so group size varies across the landscape.

Input data

This model does not incorporate input data.

Submodels

Compute Total Patch Attractiveness (T_i): Total patch attractiveness is calculated from summing the expected consumption rate and conspecific social attractiveness of each patch:

$$T_i = C_i + S_i$$

which determines which patch to move to on the landscape. Leaders were agnostic to social attraction, such that $S_i = 0$.

We assigned expected consumption rate, C_i, for each patch i based on expected resource availability and conspecific interference with Beddington's functional response model (Beddington 1975, Folmer et al. 2012):

$$C_i = \frac{aR_i}{1 + ahR_i + qP_i}$$

where R_i is the expected resource availability on patch i, P_i is the number of conspecifics on patch i, q is the interference rate, a is the attack rate, and h is the handling time. Caribou-agents had perfect knowledge of resource availability on their current patch, while they had imperfect information of neighboring patches. We were interested in how varying conspecific interference q affected expected consumption rate and selected values of 0.1, 0.5, and 1.0 to represent the spectrum from low to high interference. Attack rate a and handling time h were assigned values of 1 following Folmer et al. (2012).

Conspecific social attraction included the number of conspecifics within a patch and the neighboring patches that shared a border or vertex. For instance, a patch found within the centre of the landscape had 8 neighboring patches, while a patch on the edge of the landscape had 5 neighboring patches and a patch at the corner had 3 neighboring patches. We calculated social attraction, S_i, for each patch i using the equation presented in Folmer et al. (2012):

$$S_i = s \frac{\sum_{j=0}^{N} W_{ij}P_j}{1 + \sum_{j=0}^{N} W_{ij}P_j}$$

where N is the number of patches in the landscape, W_{ij} is a matrix that represents the available social environment for each patch, P_j is the number of conspecifics within a patch, and s is the intensity of social attraction. For patch i, we assigned W_{ij} a value of 1 for all neighboring patches and patch i itself. We assigned all other patches a value of 0 for W_{ij}. As per Folmer et al. (2012), we row-normalized the matrix by dividing the value of the matrix by the sum of its row elements in W for all rows so that each row equaled 1. Therefore, social attraction S_i is independent of the number of neighboring patches. We selected intensity of social attraction s values of 0.0, 0.5, and 1.0.

Relocation attempt: Caribou-agents attempt to relocate at each time step by determining their optimal patch location. Caribou-agents compute T_i for their current patch and all neighboring patches T_j. Caribou-agents moved to a neighboring patch when $T_j > T_i$, but remained in their initial patch when $T_j < T_i$.

Consumption: Caribou-agents consumed a portion of the food patch based on the actual food present, and not based on their predicted rate. Caribou-agents re-calculated consumption rate, C_i, upon arrival at the new patch. This recalculation is not necessary when they stayed on their original patch. To avoid total depletion of a patch, consumption for each caribou is the calculated consumption rate divided by 1000. After each time step, the amount consumed is added to the running total of all previous time steps.

Depletion: The food patch value is decreased by the same amount as consumed by the caribou-agents. The true amount of food available from each patch is updated at each time step so that caribou-agents calculate their actual consumption rate from a continuously depleting patch.

Residence Time: Caribou-agents record how long they spent on a patch by comparing their current patch with the patch from the previous time step. If the patches had different x and/or y values, their residence time is reset to 0. If the patches had the same x and y values, their residence time increases by 1.

C. Supplementary Figure

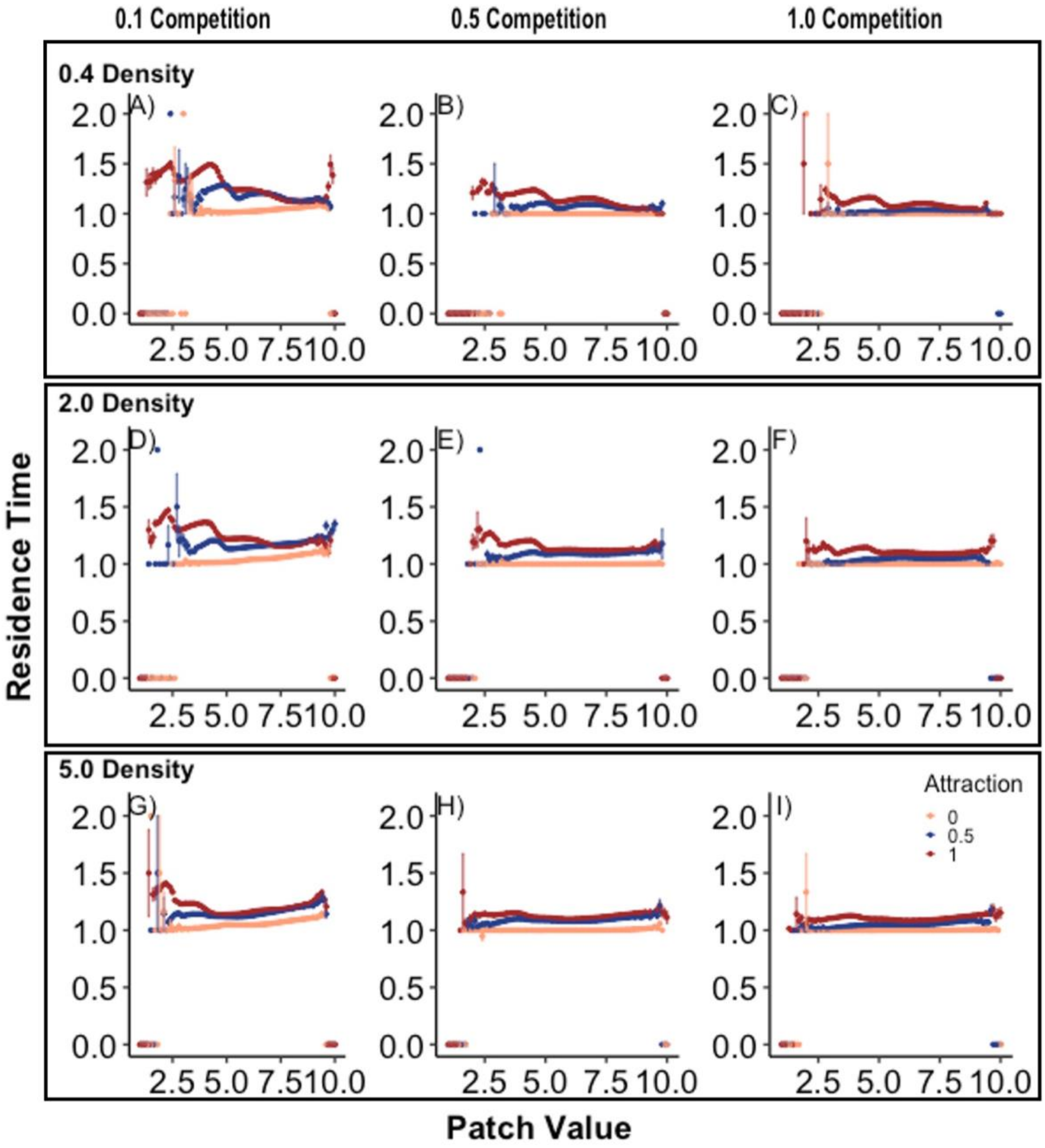

Figure S1. Mean values of the residence time per patch against patch resource value across varying social attraction, density, and competitive interference. Density increases from top to bottom, with 0.4 caribou/km^2 in top row and 5 caribou/km^2 in the bottom row. Interference increases from left to right along columns from 0.1 to 1. Colour within each plot reflects the degree of social attraction from 0 to 1. Residence times represent the mean number of time steps spent at a patch before relocating. Residence times were calculated from 60 replicates of each scenario. Error bars represent standard error.

D. Sensitivity Analysis

The parameters that affected the model were slightly different across low and high density. In both cases, the percentage of leaders to followers and the attack rate had a relatively limited effect. Kernel range had the greatest impact at low density, which suggests that smoothing of the landscape has some influence on caribou-agent movement. For the high density scenarios, the degree of imperfect knowledge was the most influential. The difference between the scenarios suggests that landscape heterogeneity is most important when there are few conspecifics to use as indicators of habitat but that imperfect forage information is most important when many conspecifics are present and may not be helpful in determining forage quality. Overall, the values for both sigma and mustar are rather small suggesting that the overall impact of these metrics is minimal.

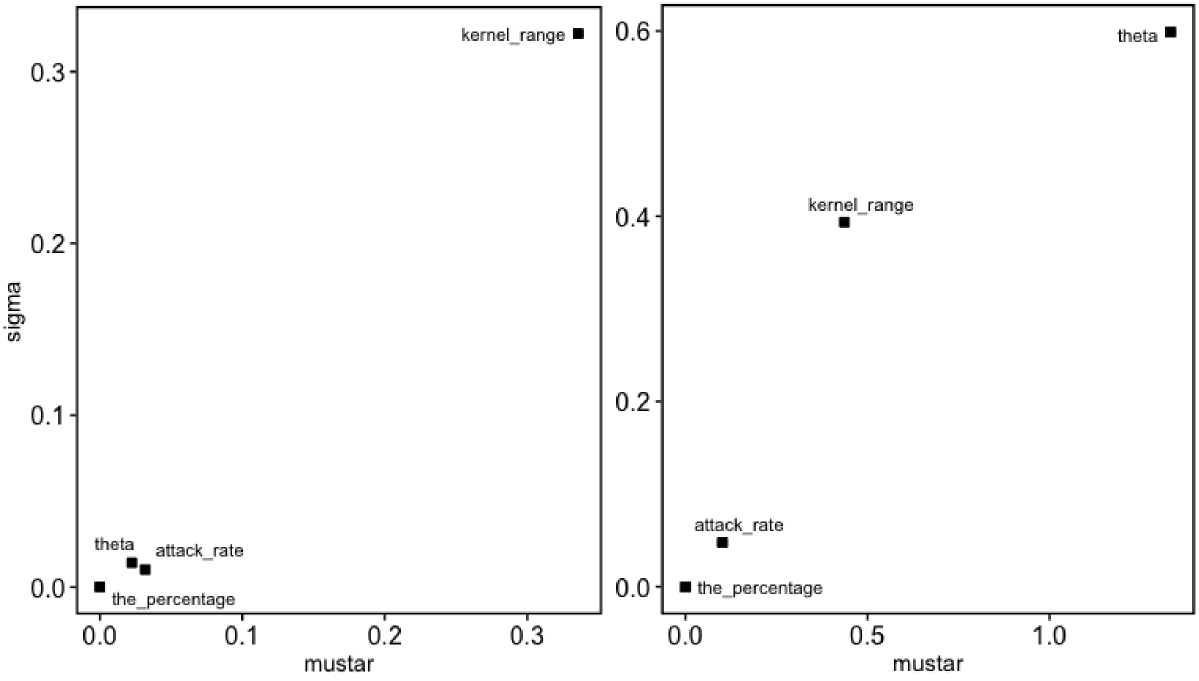

Figure S2. Sensitivity analysis conducted with the Morris method showing variation in model parameters of caribou impacts on patch visits and residence time for low density (left) and high density (right). Mustar is the mean absolute value of the elementary effects. Sigma is the standard deviation of the elementary effects.