

# The adaptive value of density-dependent habitat specialization and social network centrality

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May 9, 2022

## Abstract

Density dependence is a fundamental ecological process. Patterns of animal habitat selection and social behaviour are often density-dependent and density-dependent traits should affect reproduction and survival, and subsequently affect fitness and population dynamics. The Ideal Free Distribution and Optimal Foraging Theory present distinct predictions about how the effect of habitat selection on fitness differs across a population density gradient. Using a social ungulate (*Rangifer tarandus*) as a model system, we test competing hypotheses about how (co)variance in habitat specialization, social behaviour, and fitness vary across a population density gradient. Within a behavioural reaction norm framework, we estimated repeatability, phenotypic plasticity, and phenotypic covariance among social behaviours and habitat selection to demonstrate the adaptive value of these phenotypes across a population density gradient. In support of Optimal Foraging Theory, but not the Ideal Free Distribution, we found that at high density habitat specialists had higher fitness than generalists, but were also less social than habitat generalists, suggesting the possibility that specialists were inhibited from being social. Our findings illustrate that social strength and habitat specialization varied consistently among individuals across a density gradient, but that habitat specialists maximized fitness at high density. Taken together, our study provides preliminary support for Optimal Foraging Theory as the driving mechanism for density-dependent habitat specialization.

## INTRODUCTION

Our understanding of animal ecology can be simplified to incorporate five fundamental principles: organisms consume resources, require space to live, interact with members of the same and other species, live in dynamic environments, and copy their genes (Morris 2003). These principles extend directly to our understanding of density dependence in animal populations. Animals consume resources as they are available, but as population density increases, resources become limited and competition among conspecifics influences the ability of animals to use space, interact with conspecifics, and copy their genes. A particularly salient question in the integration of these fundamental principles lies in disentangling apparent social behaviour from shared preferences for habitats or resources and to assess the relative impacts of social behaviour and habitat selection on individual fitness parameters (i.e., survival and reproductive success; Webber and Vander Wal 2018). Patterns of habitat selection (i.e., the non-random use of available habitats; Morris 2003) may vary based on the social environment an animal experiences, for example, an individual's own social phenotype (Webber & Vander Wal 2018) and spatiotemporal variation in population density (Morris 1987). Importantly, individual variation in social phenotypes can also be density-dependent (Bonenfant *et al.* 2009). Our understanding of the adaptive value of density-dependent habitat selection and social phenotypes influences our ability to quantify individual-based traits and assess their influence on fitness components, including survival and reproductive success.

Density dependence of phenotypes influences population dynamics and demographic rates through feedback loops (Pelletier *et al.* 2009) and is important in a behavioural context. For example, for phenotypes that display density-dependent plasticity and affect fitness may feedback to population dynamics through effects of a phenotype on survival or reproductive success, both of which feed into population dynamics and density. Density fluctuates in natural populations, suggesting that individuals should display behavioural plasticity in response to fine-scale spatiotemporal changes in density (Nicolaus *et al.* 2016). For gregarious species, social network centrality (O'Brien *et al.* 2018) and interaction duration (Brashares *et al.* 2010) are density-dependent, and the relationship between these traits and fitness is predicted to change as a function of population density (Webber & Vander Wal 2018). Individuals in social groups should therefore be equipped with adaptive behavioural plasticity to cope with the potential for increased competition as a function of increasing density. The adaptive value of social behaviour and the potential for social plasticity in the context of density dependence is often ignored, yet the relationship between social behaviour and fitness has potential to influence, and be influenced by, population-level density dependence (Webber & Vander Wal 2018; Vander Wal & Webber 2020).

Habitat selection is also density-dependent and affects fitness. Density-dependent habitat selection occurs when individuals select habitat based on both habitat quality and the density of individuals present (Fretwell & Lucas 1969; Morris 1987). Habitat selection analyses are used to predict how populations, or individuals, select certain habitats compared to their availability (McLoughlin *et al.* 2010). Habitat selection phenotypes vary among individuals (Leclerc *et al.* 2016) and across densities. Two distinct bodies of literature provide predictions about how habitat and resource selection have evolved as a function of variation in population density. The Ideal Free Distribution (IFD) suggests the available resources on a habitat patch can sustain a specific number of individuals, which leads to equal fitness across unequal densities (Bradbury *et al.* 2015). Density-dependent habitat selection is an extension of IFD theory and predicts that individuals at high population density will be generalist consumers because competition for high quality resources is high, while at low population density individuals will be specialist consumers (Fortin *et al.* 2008). For example, red deer (*Cervus elaphus*) were grassland specialists at low density but habitat generalists, as well as dietary generalists, at high density (McLoughlin *et al.* 2006). By contrast, Optimal Foraging Theory (OFT) suggests that competition at high population density is expected to increase individual specialization – i.e., the proportion of an individual's diet or resource use relative to the population's overall resource base (Svanbäck & Bolnick 2007; Tinker *et al.* 2008; Carlson *et al.* 2021). For example, individual banded mongoose (*Mungos mungo*) increased their foraging specialization as group size and competition increased (Sheppard *et al.* 2018). Given these diverging predictions in habitat specialization it is also possible that individuals may display plasticity in their ability to specialize within their lifetime (Bolnick *et al.* 2003; Araújo *et al.* 2011).

Plasticity is defined as variation in a given trait, including behavioural traits, as a function of variation in internal or external stimuli (Stamps 2016). Within-individual behavioural plasticity, or flexibility, refers to the extent to which an individual's behaviour changes in different situations or in response to a given stimulus and this type of behavioural plasticity has been widely applied to the field of animal personality (Stamps 2016). Animal personality traits, defined as consistent individual differences in behaviour, are expected to persist through space and time and this variation may be adaptive (Smith & Blumstein 2008). The concept of individual differences in behaviour can be quantified using three parameters: 1) behavioural plasticity: the ability of individuals to alter phenotypes as a function of the environment; 2) behavioural syndromes: correlated suites of behaviours across time or space; and 3) behavioural repeatability: the proportion of phenotypic variance attributable to among-individual differences (Dingemanse *et al.* 2010). These parameters are examples of ways to operationalize the adaptive potential of behavioural phenotypes, such as social behaviour and habitat specialization, at individual or population-levels.

Here, we empirically quantified social associations, habitat specialization, and fitness in six herds of a social ungulate (*Rangifer tarandus*) living across a population density gradient through space and time. First, we used proximity-based social network analysis to estimate social graph strength, which is the sum of weighted associations in a social network. Second, we estimated individual habitat specialization, measured as the proportional similarity in resource use between individuals and the population. Third, we estimated fitness

based on calf survival, an important fitness proxy in ungulates (Gaillard *et al.* 2000). We then used multivariate behavioural reaction norms (BRNs) to estimate plasticity of social strength and habitat specialization across a population density gradient, covariance between social strength, habitat specialization, and fitness, and repeatability of all traits. We first tested predictions associated with IFD and OFT (for details on each prediction see Table 1). First, independent of IFD and OFT, we predicted that individual values of social strength should increase with population density (P1). According to IFD and OFT, the relationship between habitat specialization and population density should differ, such that the IFD predicts individuals (or populations) should specialize as population density increases (P2a), while the OFT predicts individuals should generalize as population density increases (P2b). We did not expect the relationship between social strength and habitat specialization to vary for the IFD or OFT, so we predicted a positive relationship, such that more social individuals are habitat generalists (P3a and P3b). We predicted that social strength and habitat specialization would be repeatable through space and time (P4a and P4b). The IFD predicts that at lower density, fitness would be highest for more social individuals, while at higher density fitness would be highest for less social individuals (P5a), while the OFT does not have an intuitive directional prediction for the relationship between social strength and fitness across a density gradient (P5b). Finally, based on the IFD, we predicted that at lower density, fitness would be highest for individuals with a high degree of habitat specialization, while at higher density, fitness would be highest for individuals with a high degree of habitat generalization (P6a). By contrast, based on Optimal Foraging Theory, we predicted that at lower density, fitness would be highest for individuals with a high degree of habitat generalization, while at higher density, fitness would be highest for individuals with a high degree of habitat specialization (P6b). For details on all predictions see Table 1.

## Methods

### *Study Area and Species*

We used global positioning system (GPS) location data collected from six caribou herds in Newfoundland, Canada (Figure S1, for details see Appendix S1). Caribou population density in Newfoundland has fluctuated over time, such that herds peaked in size in the 1990s and declined in size in the 2000s (Figure S2; Bastille-Rousseau *et al.* 2013). Adult female caribou from all herds were immobilized and fitted with GPS collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g, see Appendix S1 for details). Collars were deployed on 127 adult female caribou for one to three years, and collars were often re-deployed on the same individuals for up to seven years (mean  $\pm$  SD =  $3.2 \pm 1.7$ ) between 2007 and 2013. The number of collared individuals varied between herds, but the proportion of collared individuals in each herd was similar (Figure S3). Collars were programmed to collect location fixes every two hours. Prior to analyses, we removed all erroneous and outlier GPS fixes following Bjørneraas *et al.* (2010). Each relocation was assigned to a given habitat classification that was extracted from Landsat images with 30 x 30 m pixels. Locations were categorized as one of eight habitat types: lichen barrens, wetland, rocky outcrops, water/ice, conifer scrub, mixed wood, or conifer forest (Integrated-Informatics 2014). To assess potential for seasonal differences in social behaviour and habitat selection, we delineated GPS fixes into discrete 70-day periods to reflect winter (1 December–10 February) and calving (21 May–31 July), which we then used for all subsequent analyses. These seasons correspond with previously identified seasonal periods that were identified based on caribou movement and life-history (Bastille-Rousseau *et al.* 2016). We chose to include winter and calving seasons because winter represents a resource limited season where adult female caribou form groups to optimize access to foraging resources (Webber & Vander Wal 2021). Calving is a period when females aggregate on calving grounds or in large social groups and select habitat to reduce the risk of calf predation (Bonar *et al.* 2020). All animal capture and handling procedures were consistent with the American Society of Mammologists guidelines (Sikes & Mammalogists 2016).

### *Population density estimates*

Population size was estimated based on intermittent aerial surveys for each herd (Figure S2; Mahoney *et al.* 1998). We estimated the area occupied by each herd in each season and year by pooling GPS relocation data for all individuals and subsequently calculating the area of the 100% minimum convex polygon in the

*adehabitatHR* package in R (Calenge 2006). We then estimated population density for each herd in each year and season by dividing the total number of animals estimated by the area occupied by the herd. To ensure convergence of subsequent models, population density was scaled and mean centered by herd to preserve variation in density among herds.

### *Social network analysis*

We used the *spatsoc* package (Robitaille *et al.* 2019) to generate proximity-based social networks from GPS telemetry data. Traditional designation of caribou herds in Newfoundland assigns animals to specific herds, however, because of winter spatial overlap for some herds (Schaefer & Mahoney 2013), we constructed a single network for all collared animals in each year-by-season combination. We generated social networks based on proximity of GPS fixes for individual caribou. We assumed association between two individuals if simultaneous GPS fixes, i.e., recorded within 5 minutes of each other, were within 50 m of one another (Lesmerises *et al.* 2018). We applied the ‘chain rule’, where each discrete spatiotemporal 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 (Kasozi & Montgomery 2020). We weighted edges of social networks by the strength of association between dyads using the simple ratio index (SRI, for details on calculating the SRI see Appendix S2). The SRI is a shared dyadic value that measures the number of times the dyad were observed together, while accounting for the amount of data for each individual (Cairns & Schwager 1987). Given recent discussion regarding the use of effect sizes and Bayesian inference to model social networks (Franks *et al.* 2021), we did not generate null models and estimate effects of covariates on social network strength in a multi-variate regression framework. Rather, we developed a parallel set of univariate frequentist models and developed data-stream permutations to assess whether the relationships between social graph strength and covariates were non-random (for details see Appendix S2; Figures S4 and S5).

### *Estimating habitat specialization*

Our study area was separated into eight habitat types based on landcover classification: conifer forest, conifer scrub, mixed-wood forest, deciduous forest, wetland, lichen barrens, rocky barrens, and water/ice (Table S2). Using the number of spatial relocations for a given individual in each habitat type, we estimated the proportional specialization index ( $PS_i$ ):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where  $p_{ij}$  describes the proportion of the  $j$  th habitat type for individual  $i$ , and  $q_j$  describes the proportion of the  $j$  th habitat type at the population level. Values of  $PS_i$  closer to one reflect individuals that select habitats in direct proportion to the population, i.e., habitat generalists, whereas values of  $PS_i$  closer to zero reflect individuals that are habitat specialists. We calculated the  $PS_i$  using the *RInSp* package in R (Zaccarelli *et al.* 2013). A value of  $PS_i$  was calculated for each individual in each year-by-season combination and represented the degree to which that individual specialized on any given habitat type. To confirm habitat specialization was related to habitat selection, we generated resource selection functions and compared the  $PS_i$  to habitat selection coefficients for the dominant habitat types (see Appendix S3, Figure S6).

### *Fitness estimates*

We used calf mortality as a proxy for fitness for adult female caribou. Following DeMars *et al.* (2013) and Bonar *et al.* (2018) we retrospectively assessed calf mortality using a movement-based approach. Unlike other cervids, caribou only have a single calf per year. Parturition is associated with reduced movement rate in caribou, and we used inter-fix step length from GPS collared caribou to infer parturition and calf mortality (for details on validation see Bonar *et al.* 2018 and application in Bonar *et al.* 2020). We applied a population-based method using a moving window approach to evaluate three-day average movement rates of adult females to estimate parturition status (DeMars *et al.* 2013), and an individual-based method that used maximum likelihood estimation and GPS inter-fix step length of adult females to estimate calf mortality up

to four weeks in age. Mothers that do not give birth have a consistent daily average movement through time, while mothers that give birth decrease step length immediately after birth and slowly return to daily average movement rates (see Fig. 2 from Bonar *et al.* 2018). In cases where calf mortality occurs, the mother will return to daily average movement rate almost immediately after calf mortality (see Fig. 2 from Bonar *et al.* 2018). The majority of calf mortality in our study was due to predation (Mahoney *et al.* 2016). Based on results from these models, we estimated calf mortality for each individual caribou in each year, i.e., annual reproductive success, and used this value as a proxy for fitness (for details see Bonar *et al.* 2018).

### *Statistical analysis: behavioural reaction norms*

Behavioural reaction norms (BRNs) estimate behavioural repeatability and plasticity. BRNs generate two key parameters: 1) the reaction norm slope, which corresponds to phenotypic plasticity; and 2) the reaction norm intercept, which corresponds to consistent individual differences in behaviour, which are used to estimate repeatability (Dingemanse *et al.* 2010). We employed a multivariate mixed model (R package ‘MCMCglmm’: Hadfield 2010) to quantify BRN components, i.e., repeatability and plasticity, for resource specialization, social strength, and fitness as a function of population density. We used multi-variate models to avoid the common problem of ‘stats-on-stats’, where best linear unbiased predictors (BLUPs) are extracted from one or more mixed models and used to represent an individual’s phenotype in subsequent statistical models (for details see Hadfield *et al.* 2010; Houslay & Wilson 2017). Although BLUPs can be problematic if used in the context of ‘stats-on-stats’, our use of tri- and bi-variate models limits this issue by assessing the relationship between variables of interest and accounting for potential confounds in the same model (Houslay & Wilson 2017). To facilitate model convergence, we scaled and centered social strength and habitat specialization to a mean of zero.

We developed five multi-variate models. First, we parameterized a tri-variate global model that included calf survival, social strength, and habitat specialization as co-response variables. In this model, we included year, season, scaled population density, and herd as fixed effects. Individual identity and mean and center-scaled population density were included as random effects, where individual values of social strength and habitat specialization varied as a function of population density. Next, we parameterized four bi-variate models with calf survival and either social strength or habitat specialization as co-response variables for subsets of the data delineated based on either low- or high-density herds. Specifically, based on the distribution of scaled population density, we delineated the lowest quartile (i.e., lowest 25% of population density values) as low density data, and the highest quartile (i.e., the highest 75% of population density values) as high density data. We chose to separate data based on the lowest 25% and highest 75% values of population density to ensure there was no potential for error in assigning individuals to a density category or overlap of individuals in each herd, whereas if we used the upper and lower 50% as categories this would have been possible).

Using results from the global model, we evaluated repeatability ( $r$ ) of BRN intercepts for habitat specialization and social strength as the amount of between-individual variance ( $V_{ind}$ ) attributable to the residual variance among groups ( $V_{res}$ ) for each trait (Dingemanse & Dochtermann 2013):

$$r = \frac{V_{ind}}{(V_{ind} + V_{res})}$$

Within the global model, repeatability was estimated for social strength and habitat specialization during winter and calving seasons. We also examined correlations between habitat specialization, social strength, and fitness. Among-individual variance in resource specialization and social strength may differ based on whether population density is low or high, relative to the overall average. We therefore varied residuals in the model by season because of differences in social tendencies and habitat selection for caribou across seasons (Bastille-Rousseau *et al.* 2016; Peignier *et al.* 2019). Thus, we calculated  $V_{res}$  and  $r$  for habitat specialization and social strength, for each season separately. Finally, we used uninformative priors (Wilson *et al.* 2010) and coded variance ( $s^2$ ) as  $s^2/2$  and degree of belief as four for fixed and random effects. We fitted all models with Gaussian error structure for response variables. We ran all models for 420,000 iterations, a thinning

length of 100, and a burn-in of 20,000 to form posterior distributions. The importance of fixed and random effects was judged by the distance of the mode of the posterior distribution from zero, and the spread of the 95% credible intervals. We evaluated convergence by visually investigating chains, assessing the Heidelberger convergence diagnostic (Heidelberger & Welch 1983), and checking that auto-correlation between successive samples of the MCMC chain was below 0.1. Finally, we performed three runs of our model to ensure different chains reached the same qualitative result. All analyses were conducted in R version 4.0.2 (R Core Team 2020).

## Results

We collected data for 127 individual caribou. In total, we calculated an average of  $6.0 \pm 3.5$  (range: 1–14) measures of social strength, habitat specialization, and reproductive success per individual, for a total of 752 measures of these variables across all years, seasons, and herds. Due to variation in length of time that collars were deployed on individuals seasonal networks were larger in winter (average:  $66 \pm 21$  individuals, range = 35–90) than during calving (average:  $53 \pm 26$  individuals, range = 15–81). On average, social strength was higher in winter (mean =  $0.012 \pm 0.001$ ) than calving (average:  $0.005 \pm 0.006$ ). Average habitat specialization indices were the same in winter (average:  $0.72 \pm 0.08$ ) and calving (average:  $0.72 \pm 0.13$ ). Habitat specialization was positively correlated with habitat selection coefficients generated from resource selection coefficients for the four most common habitat types. Given that the  $PS_i$  measures specialization of a given resource relative to the population, a positive relationship between selection and specialization suggests that specialists tend to select for a single habitat type and neither select, nor avoid, other available habitat types, while generalists tend to neither select, nor avoid, all habitat types (Table S3; Table S4; Figure S6). Because caribou have strong selection for lichen, there were few, if any, caribou that specialized on lichen (Figure S6), whereas some individuals specialized on, and had strong selection for, other habitat types. With regards to fitness, calf survival was 61% (241/393 annual reproductive events) over the course of our study.

We found support for our first hypothesis that social strength and habitat specialization would increase as a function of population density gradient (Prediction 1). Individuals varied their behavioural response to changes in population density, but in general, individuals became more social as population density increased (P1, Figure 1a, Figure S7). In addition, individuals also varied in their habitat selection patterns as population density changed, where most individuals tended to become habitat specialists as density increased (P2a, Figure 1b, Figure S8). Although the direction of behavioural change in habitat specialization was similar for most individuals, we observed variation in the magnitude of change, suggesting an individual by environmental interaction.

We found mixed support for predictions on phenotypic covariance (P3) and repeatability (P4). In our global model, we found strong phenotypic covariance between social strength and habitat specialization (0.52, 95% Credible Interval: 0.21, 0.79), suggesting that habitat generalists were more social and habitat specialists were less social (Figure 2). After taking herd, season, and year into account as fixed effects, we found that social strength was moderately repeatable during calving ( $r = 0.25$ , 95% CI: 0.15, 0.37), but not winter ( $r = 0.03$ , 95% CI: 0.015, 0.05). By contrast, habitat specialization was moderately repeatable in winter ( $r = 0.20$ , 95% CI: 0.11, 0.29), but not during calving ( $r = 0.09$ , 95% CI: 0.05, 0.14, Table 2).

When testing the relationship among social strength, habitat specialization, and fitness, we found support for Optimal Foraging Theory. In our global model, there was a positive relationship between habitat specialization and social strength, where more social individuals were habitat generalists (P3a and P3b, 0.50, 95% CI: 0.17, 0.71, Table 3). In our global model, there was a weak negative relationship between habitat specialization and fitness ( $-0.29$ , 95% CI:  $-0.59$ , 0.03), but no relationship between social strength and fitness ( $-0.03$ , 95% CI:  $-0.36$ , 0.29, Table 3). When we modeled high and low density separately, there was no effect of social strength on fitness at either low or high density (P5a and P5b, Table 3). In support of Optimal Foraging Theory (P6b), and in contrast to the IFD (P6a), we found negative covariance between habitat specialization and fitness at high density ( $-0.62$ , 95% CI:  $-0.99$ ,  $-0.01$ , Table 3), but no relationship between habitat specialization and fitness and low density (0.02, 95% CI:  $-0.81$ , 0.94, Table 3).

## Discussion

Animals live by five fundamental principles that are distilled into resources, space use, competition, environmental variation, and reproduction (Morris 2003). We examined these principles by testing competing hypotheses about the relationships among habitat specialization, sociality, population density, and fitness. According to the Ideal Free Distribution, resource specialists maximize fitness at low population density (Fortin *et al.* 2008), while Optimal Foraging Theory posits that resource specialists maximize fitness at high population density (Tinker *et al.* 2008). The apparent tension between these two hypotheses could be mediated by consideration of variation in the social environment experienced by individuals (e.g. Sheppard *et al.* 2018). An increase in social connections across a population density gradient could influence individuals' propensity to successfully generalize or specialize. At high density, when individuals tend to be more social and compete more for limited resources, individuals may specialize on different available resources to reduce competition (Newsome *et al.* 2015). Here, we highlight that individual habitat specialization is density-dependent following predictions associated with optimal foraging, and the relationship between habitat specialization and fitness is moderated by individual social phenotypes.

Overall, we found support for our predictions associated with the Optimal Foraging Theory, where individuals tended to specialize on one habitat at high population density (P6b). In banded mongooses, sea otters (*Enhydra lutris*), and stickleback (*Gasterosteus aculeatus*), individuals and populations tended to specialize at high population densities (Svanbäck & Bolnick 2007; Tinker *et al.* 2008; Sheppard *et al.* 2018). In addition to these empirical studies, our results support theory suggesting that population density is a mechanism driving variation in individual habitat specialization (Bolnick *et al.* 2003; Araújo *et al.* 2011). The relationship between habitat specialization and fitness according to Optimal Foraging Theory assumes that individuals specialize on profitable resources and that this profitability results in increased fitness. Indeed, we found that higher fitness was achieved for habitat specialists at high density. Given that individuals consistently adjusted their habitat specialization behaviour as density changed, and that at high densities specialists had higher fitness, fluctuating selection should favour variation in habitat specialization phenotypes. A potential mechanism explaining among-individual variation in habitat specialization is a mutual interest in avoiding competition in heterogeneous or patchy environments (Laskowski & Bell 2013). Given the adaptive value of habitat specialization, plasticity in habitat specialization from low to high density could be maintained as individuals alter their behaviour to adjust to environmental conditions.

In support of our prediction associated with the IFD, we found positive phenotypic covariance between social strength and habitat specialization, such that more social individuals were habitat generalists (P3a, Table 3). Individual dietary and resource specialization are known to be strongly driven by competition (Bolnick *et al.* 2003). In a more competitive social environment, IFD theory predicts that individuals should generalize on resources or habitats to reduce competition. Social individuals may be constrained from specializing due to the competition associated with group living at high density. Moreover, theory of density dependence predicts that at high population density, reproductive success will be relatively low (Fowler 1981), and only a small proportion of individuals will successfully rear calves. Habitat generalists tend to be more social – a tactic that does not immediately affect fitness. More social habitat generalists presumably obtain other benefits of group-living, such as increased vigilance or access to information about foraging resources. Although we were unable to test for life-history trade-offs, it is possible individuals that are more social prioritize survival, as opposed to reproductive success, a trade-off that could have implications for population dynamics. Given observed plasticity in social behaviour and habitat specialization, these contrasting strategies present an apparent tension for individuals to simultaneously be habitat specialists *and* be highly connected in the social network.

Our integration of individual habitat specialization within a behavioural reaction norm framework highlights the ability for individuals to adjust their specialization phenotypes across a population density gradient. While plasticity in morphological traits is known to influence dietary specialization (Svanbäck & Eklöv 2006), behavioural plasticity of habitat specialization is less well understood. Despite relatively few empirical studies, plasticity in individual specialization reflects a natural extension from the expectations of individual niche

specialization theory (Bolnick *et al.* 2003; Araújo *et al.* 2011), which posits contrary predictions to the IFD. Individuals that experience a range of population densities within their lifetime should vary in their habitat specialization-generalization phenotype across densities (Dingemanse *et al.* 2010; Nicolaus *et al.* 2016). We found that individual caribou generally became more specialized as population density increased, suggesting within-individual plasticity – a strategy that represents an individual’s ability to acclimate to changing environmental conditions. Since reproductive success is frequently depressed at high density (Charnov 1976; Morris 1989), our results suggest that the most specialized individuals have greatest reproductive success, although it is possible that other ecological or behavioural factors could influence reproductive success. The ability for individuals to modulate their specialization behaviour across population densities therefore likely has adaptive consequences (Mathot *et al.* 2012).

Consistent with results from a recent meta-analysis of spatial phenotypes (Stuber *et al.* 2022), we found that habitat specialization was moderately repeatable, suggesting that the most specialized individuals at low population densities remain the most specialized at a higher density. Similarly, in bottlenose dolphins (*Tursiops aduncus*), the same measure of habitat specialization (the proportional similarity index) was repeatable through time (Strickland *et al.* 2021). Behavioural repeatability is important in an evolutionary context because repeatability represents the upper limit of heritability (Dochtermann *et al.* 2015), and ultimately, the adaptive value of habitat specialization suggests the potential for this trait to undergo natural selection (Stuber *et al.* 2022; Vander Wal *et al.* 2022).

Animals use space, select habitat, and occupy social positions that maximize their fitness. By integrating theory of density dependence with competing hypotheses associated with the Ideal Free Distribution and Optimal Foraging Theory, we delineate the effects of social and spatial phenotypes as drivers of fitness. We present evidence supporting predictions of the Optimal Foraging Theory that highlight the adaptive value of individual habitat specialization was greatest at high population density. Within the context of social eco-evolutionary dynamics (Shizuka & Johnson 2020; Vander Wal & Webber 2020), our study addresses two of the criteria outlined as prerequisites for eco-evolutionary dynamics (Fussmann *et al.* 2007). First, previous work in this system has identified fluctuations in population density through time (Bastille-Rousseau *et al.* 2013) and although we only included data from seven years, we observed slight differences in the distribution of habitat specialization as a function of population density (Figure 1). Second, we identified an effect of habitat specialization on fitness at high, but not low, density (Figure 3). Although estimating eco-evolutionary dynamics for behaviour remains elusive, we satisfy some of the baseline expectations of an eco-evolutionary correlation. Next steps include identifying a plausible mechanistic link between an evolutionary, e.g. change in trait distribution, and ecological, e.g. lambda, process (Fussmann *et al.* 2007). It is clear that density dependence is a fundamental ecological process, and we highlight the effects of population density on the relationship between behavioural phenotypes and fitness.

## Acknowledgements

We respectfully acknowledge the territory in which data were collected and analyzed as the ancestral homelands of the Beothuk and the Island of Newfoundland as the ancestral homelands of the Mi’kmaq and Beothuk. We thank G. Albery and members of the Wildlife Evolutionary Ecology Lab for helpful comments on previous versions of this manuscript. We also thank members of the Newfoundland and Labrador Wildlife Division, including S. Moores, B. Adams, W. Barney, and J. Neville, for facilitating animal captures and for logistical support in the field. We thank T. Bergerud and S. Mahoney for their vision in initiating much of the work on caribou in Newfoundland. Funding for this study was provided by a Natural Sciences and Engineering Research Council (NSERC) Vanier Canada Graduate Scholarship to QMRW, NSERC Canada Graduate Scholarships to MPL and MB, and a NSERC Discovery Grant to EVW.

**Table 1:** Summary of predictions.

General prediction	Prediction associated with Ideal Free Distribution	Prediction associated with Optimal Foraging Theory
P1: Density-dependent social strength. As density increases, individuals are expected to increase their social network strength.	P1a: No directional prediction.	P1b: No directional prediction.
P2: Density-dependent habitat specialization.	P2a: As density increases, individuals are expected to become habitat specialists (Fortin <i>et al.</i> 2008).	P2b: As density increases, individuals are expected to become habitat generalists (Pyke <i>et al.</i> 1977).
P3: Phenotypic covariance between social strength and habitat specialization (Webber & Vander Wal 2018).	P3a: More social individuals are expected to be habitat generalists.	P3b: More social individuals are expected to be habitat specialists.
P4: Repeatability of social strength and habitat specialization, such that behavioural traits are expected to be consistent through space and time (Bell <i>et al.</i> 2009).	P4a: Ideal Free Distribution is agnostic to the identity of individuals.	P4b: Within the framework of Optimal Foraging Theory and behavioural ecology theory, individual behaviours are expected to be consistent through space and time.
P5: Adaptive value of density-dependent social strength (Webber & Vander Wal 2018).	P5a: Low density: higher fitness for more social individuals High density: higher fitness for less social individuals	P5b: No directional predictions.
P6: Adaptive value of density-dependent habitat specialization.	P6a: Low density: higher fitness for habitat specialists High density: higher fitness for habitat generalists (McLoughlin <i>et al.</i> 2006; Fortin <i>et al.</i> 2008).	P6b: Low density: higher fitness for habitat generalists High density: higher fitness for habitat specialists Tinker <i>et al.</i> (2008).

**Table 2:** Summary of repeatability ( $r$ ) estimates for caribou social strength and habitat specialization. Repeatability measures are a ratio between the proportion between-individual variance attributable to the residual variance ( $V_{res}$ ) and therefore does not go below zero. High repeatability values are typically values are  $>0.4$ , moderate values of repeatability are between 0.2 and 0.4, and low values of repeatability are  $<0.20$  (Bell *et al.* 2009). Values in brackets represent 95% credible intervals extracted from MCMC models.

Trait	Season	Median ( $\pm$ SD)	Repeatability	$V_{res}$
Social strength	Calving	0.005 $\pm$ 0.006	0.25 (0.15, 0.37)	1.54
	Winter	0.012 $\pm$ 0.015	0.028 (0.015, 0.05)	0.15
Habitat specialization	Calving	0.72 $\pm$ 0.13	0.09 (0.04, 0.14)	1.07
	Winter	0.72 $\pm$ 0.08	0.20 (0.11, 0.29)	0.44

**Table 3:** Phenotypic covariance among behavioural reaction norm intercepts for social strength, habitat specialization, and fitness in models with all data and separated into separate datasets where only data in the lowest 25% quantile, and highest 75% quantile, of population density were included. Numbers in brackets are 95% credible intervals and phenotypic covariance is considered significant if credible intervals do not overlap zero.

Trait combination	All data	Low density (25% quantile)	High density (75% quantile)
Social strength, habitat specialization	<b>0.50 (0.17, 0.78)</b>	–	–
Social strength, fitness	–0.03 (–0.36, 0.29)	–0.34 (–0.99, 0.86)	0.40 (–0.84, 0.99)
Habitat specialization, fitness	–0.29 (–0.59, 0.03)	0.02 (–0.81, 0.94)	<b>–0.62 (–0.99, –0.01)</b>

## Figure captions

**Figure 1:** Behavioural reaction norms testing the relationship between population density and A) social network strength and B) habitat specialization for caribou (*Rangifer tarandus*; n = 127) in Newfoundland. Each line represents an individual behavioural response to changes in population density and crossing of lines represents individual differences in plasticity (i.e., an individual-environment interaction).

**Figure 2:** phenotypic covariance between social strength and habitat specialization in caribou (*Rangifer tarandus*, n = 127) in Newfoundland.

**Figure 3:** phenotypic covariance between reproductive success and habitat specialization at relatively high (orange points) and relatively low (blue points) population density for caribou (*Rangifer tarandus*, n = 127) in Newfoundland. At high density, more specialized individuals also tended to have an overall higher fitness value, whereas there was no effect of habitat specialization on fitness at low density. Note, both variables are extracted from best linear unbiased predictors (BLUPs) extracted from mixed models for visualization.

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