Received: 19 September 2024 | Accepted: 4 December 2024

DOI: 10.1002/ecy.70054

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Why does animal home range size decrease with population density?

Juliana Balluffi-Fry[1] | **Yasmine N. Majchrzak**[2] | **Michael J. L. Peers**[2] | **Emily K. Studd**[3] | **Allyson K. Menzies**[4] | **Liam G. Horne**[1] | **Emily Monk**[2] | **Nicole Humeniuk**[1] | **Thomas S. Jung**[5,6] | **Dennis L. Murray**[7] | **Stan Boutin**[1]

[1]Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

[2]Department of Biology, Memorial University, St. John's, Newfoundland, Canada

[3]Department of Biological Sciences, Thompson River University, Kamloops, British Columbia, Canada

[4]Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada

[5]Department of Environment, Government of Yukon, Whitehorse, Yukon, Canada

[6]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada

[7]Department of Biology, Trent University, Peterborough, Ontario, Canada

Correspondence
Juliana Balluffi-Fry
Email: jballuff@ualberta.ca

Funding information
Natural Sciences and Engineering Research Council of Canada; Northern Studies Training Program; University of Alberta Northern Research Award Program; Association of Canadian Universities for Northern Studies; W. Garfield Weston Foundation; Government of Yukon

Handling Editor: Caz M. Taylor

Abstract

Spatial confinement to a home range is theorized to be a more energetically efficient method of acquiring resources than random searching due to spatial memory. Intraspecific studies that have compared home range size at different population densities have found that home ranges shrink as population density increases. This negative trend could be due to increased conspecific competition via population density increase or due to correlations between resource density and population density. We use the 10-year population cycle of snowshoe hares (*Lepus americanus*) and individual-level food-add experiments as a case study to assess whether the mechanism of the relationship between home range size and population density is related to competition from increased conspecific density or confounds between population density and resource density. Over six winters (1 December–31 March) and a 50-fold change in population density, we estimated weekly home range sizes ($n = 464$; 90% minimum convex polygons) of 88 radio-collared hares, of which 26 were food-supplemented. We found a negative relationship between home range size and population density in controls; home ranges decreased by 2.5 ha as hare density increased from 0.24 to 1.2 hare/ha. Food-supplemented hares showed a more negative response to population density than controls (4.0 ± 0.56 ha decrease per 1 hare/ha increase). Our results suggest that the negative trend between home range size and population density is not due to confounds between population and resource density. Likely, there is a trade-off between resource acquisition and some other density-driven constraint when foraging at high densities, which we suggest is a reduction in resource sharing to minimize competition and maintain resource familiarity at high densities.

KEYWORDS
food supplementation, home range size, population cycles, resource availability, snowshoe hare, space use

---

INTRODUCTION

Home range behavior, that is, restricting space use to a certain area, is thought to arise from foraging advantages gained by being familiar with previously used resource patches (Börger et al., 2008; Spencer, 2012). Home range size is assumed to be a function of energy requirements, returns, and expenditures (Enriquez-Urzelai & Boratyński, 2022; Heathcote et al., 2023; Mcnab, 1963) as supported by cross-species comparisons showing that home range size increases with body size in general (Harestad & Bunnel, 1979; Mcnab, 1963). However, within species comparisons, where differences in overall body size are minor, the energetic explanation for the variation of home range size is less clear. Commonly, intraspecific studies have observed a negative relationship between home range size and population density (Aronsson et al., 2016; Erlinge et al., 1990; Sanderson, 1966), but how this trend relates to the energetic explanation for home range size remains understudied.

One potential explanation for the negative relationship between home range size and population density is a confound with resource density (resources/unit area). Intraspecific studies that relate home range size to population density often compare different populations (densities) in different study areas (Bengsen et al., 2016; Stobo-Wilson et al., 2021; Trewhella et al., 1988). In such cases, population density and resource density are likely to be correlated (Fretwell & Lucas, 1970; Kennedy & Gray, 1993). The negative relationship between home range size and conspecific density could be explained by Fretwell's Ideal Free Distribution Model, which argues that animals should fill habitats such that overall fitness (and per capita energy budgets) is equal across habitats (Fretwell & Lucas, 1970). Higher quality habitats (higher resource density) should fill sooner and have higher "carrying capacities" because they provide a higher return per area to individuals, allowing for smaller home ranges and increased density. According to this theory, resource density is the driver of home range size, while conspecific density is only indirectly involved through its correlation with resource density.

A second explanation for the trend is that higher conspecific density increases the energy expenditures associated with foraging, causing home ranges to shrink as a population grows. For non-territorial species, if resource density is constant, an increase in population density would increase the rate of resource consumption, causing a greater difficulty in finding food, that is, greater scramble competition (van Schaik et al., 1983). Further, higher conspecific densities may reduce familiarity with resource patches within home ranges because conspecific exploitation is less predictable and trackable (Spencer, 2012). In either case, this notion hypothesizes that animals reduce their home range size as their population increases to reduce low-return foraging and maintain the required net energy intake to survive.

The correlation between population density and resource density confounds the ability to identify the mechanism behind the relationship between population density and home range size in studies that compare populations (Kjellander et al., 2004; Schoepf et al., 2015). To identify the mechanism here requires a study whereby the population density changes independent of resource density, or better yet, measures how individuals exposed to different resource conditions (food-add experiments) respond to the same changes in density.

The widely recognized population cycle of snowshoe hares offers a unique opportunity to tease apart the drivers of home range size because the density of the same population naturally varies drastically over time in the same location (Krebs et al., 2018; Myers, 2018). Hares can reach peak densities upward of 400 individuals/km^2 and then decline to densities as low as 20 individuals/km^2 (Krebs et al., 2018). Such changes are many times greater than the 2- to 4-fold changes in resource density (Krebs et al., 2001; Smith et al., 1988; see *Methods*). We can say with confidence that hares experience the lowest per capita resource availability during peak densities and the greatest per capita resource availability during the low of the cycle. In addition, snowshoe hares are not territorial and have home ranges that overlap (Richmond et al., 2022). They experience more scramble competition than contest competition (i.e., monopolizing resources by an individual). We conducted individual-level food supplementation experiments on snowshoe hares (*Lepus americanus*) over multiple phases of their population cycle to understand how population density influences home range size without the confound of correlations between resource density and population density. By conducting food supplementation at an individual rather than population scale, we eliminated the potential confound of density increase through immigration to a treatment area (Boutin, 1990; Majchrzak et al., 2022; Quirici et al., 2010).

We test two competing hypotheses to explain the frequently observed negative relationship between home range size and population density: (1) the resource density hypothesis, whereby higher resource density associated with higher population density allows animals to reduce their home range size when in an area with a higher population density (similar prediction as in Kjellander et al., 2004); and (2) the conspecific competition hypothesis, whereby the increased effort required when foraging among more neighbors causes animals to reduce home range size at higher population densities despite limiting potential resource acquisition (Spencer, 2012). The resource density hypothesis would predict that in our system, where resource density is relatively constant, home range size will not change with population density, and food-supplemented hares will have smaller home ranges than control hares because they require fewer wild resources. The conspecific competition hypothesis would predict that we will find the same negative trend as other studies, and food-supplemented individuals will show a more negative response than control individuals because they have the flexibility to reduce their foraging costs more than controls while maintaining their resource intake.

METHODS

Study area

Our study was conducted in the Kluane region of southwestern Yukon, Canada, where monitoring the density of snowshoe hares has been ongoing for close to 50 years (Krebs et al., 2018). Our study period covered seven winters: between December and March 2015/2016 and 2021/2022. The hare cycle was in the increase in 2015, peaked in the 2016–2017 winter, declined from 2017 to 2019, after which it remained in the low phase (Figure 1, panel A). The study area is bisected by the Alaska Highway but is otherwise comprised of intact boreal forest relatively unaltered by direct human impact. The forest is composed mainly of white spruce (*Picea glauca*) with trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) patchily distributed at lower abundances. During winter, the shrub understory above the snowpack is predominantly willow (*Salix glauca*), which, in addition to spruce branch tips, is the main winter food for snowshoe hares (Krebs et al., 2018; Smith et al., 1988). Dwarf birch (*Betula glandulosa*) is only available in early winter before snow accumulates. Lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) were the main predators of hares during our study period, although great horned owls (*Bubo virginianus*) and northern goshawks (*Accipiter gentilis*) are additional predators (Krebs et al., 2001; Peers et al., 2020).

Animal captures and data collection

We live-trapped snowshoe hares each winter using Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) on multiple trapping grids (600 m × 600 m) within 8 km of one another (Krebs et al., 2001). Trapping grids contained 86 traps, spaced 30–60 m apart, in four trap lines. Grids contained similar habitat and hare densities in any given winter. Hares did not move between grids. Traps were baited with rabbit chow and apple and set at sunset and checked up to 12 h later. Individual ear-tag ID, sex, and body mass (in grams) were recorded for each captured hare. We fitted a sample of captured hares ($n = 108$) with either very high frequency (VHF) collars equipped with mortality sensors (Model SOM2380, Wildlife Materials, Murphysboro, Illinois, USA; or Model MI-2M, Holohil Systems Ltd., Carp, Ontario, Canada) or custom collars which included both a VHF transmitter and a GPS (Technosmart Europe Srl., Rome, Italy; Majchrzak et al., 2022; Shiratsuru et al., 2021). Only hares weighing >1100 g were collared to ensure that collar mass did not exceed 5% of body mass. The GPS fix schedule was set to record locations every 5, 15, or 30 min and had a GPS error of ~15 m (Shiratsuru et al., 2021). All handling and collaring procedures were approved by the University of Alberta Animal Care Committee and conducted in accordance with research permits issued by the Government of Yukon. The raw GPS data were screened for potential erroneous locations prior to analysis.

We used data and methods available through the long-term snowshoe hare monitoring project to associate the home range data with demographic data using methods outlined in Krebs et al. (2018) and Shiratsuru et al. (2023). Hare densities were estimated every September using spatial mark–recapture on three control grids. Hare densities always decline over winter due to predation. Hare survival was routinely monitored using radio telemetry. VHF transmitters were programmed to emit a mortality signal after eight hours of being motionless. Hares were monitored every two days for mortality signals and retrieved if dead. Based on the recorded frequency of mortalities, we calculated daily survival rates using semiparametric Cox proportional hazard models (Graham, 2008; Therneau & Grambsch, 2000) with the "survival" R package (Therneau et al., 2024). We then averaged survival rates for each month of winter (data from Shiratsuru et al., 2023). For each winter, we used the preceding September mark–recapture estimate as the starting density and estimated subsequent monthly hare densities using monthly survival rates:

$$D_{t+1} = D_t \times P_t,$$

where D_{t+1} is the next month's hare density, D_t is the current month's hare density, and P_t is the current month's hare survival rate. We fitted a linear model through monthly hare densities for each winter and used the model to estimate daily hare densities (see Appendix S1: Figure S1 for hare density data).

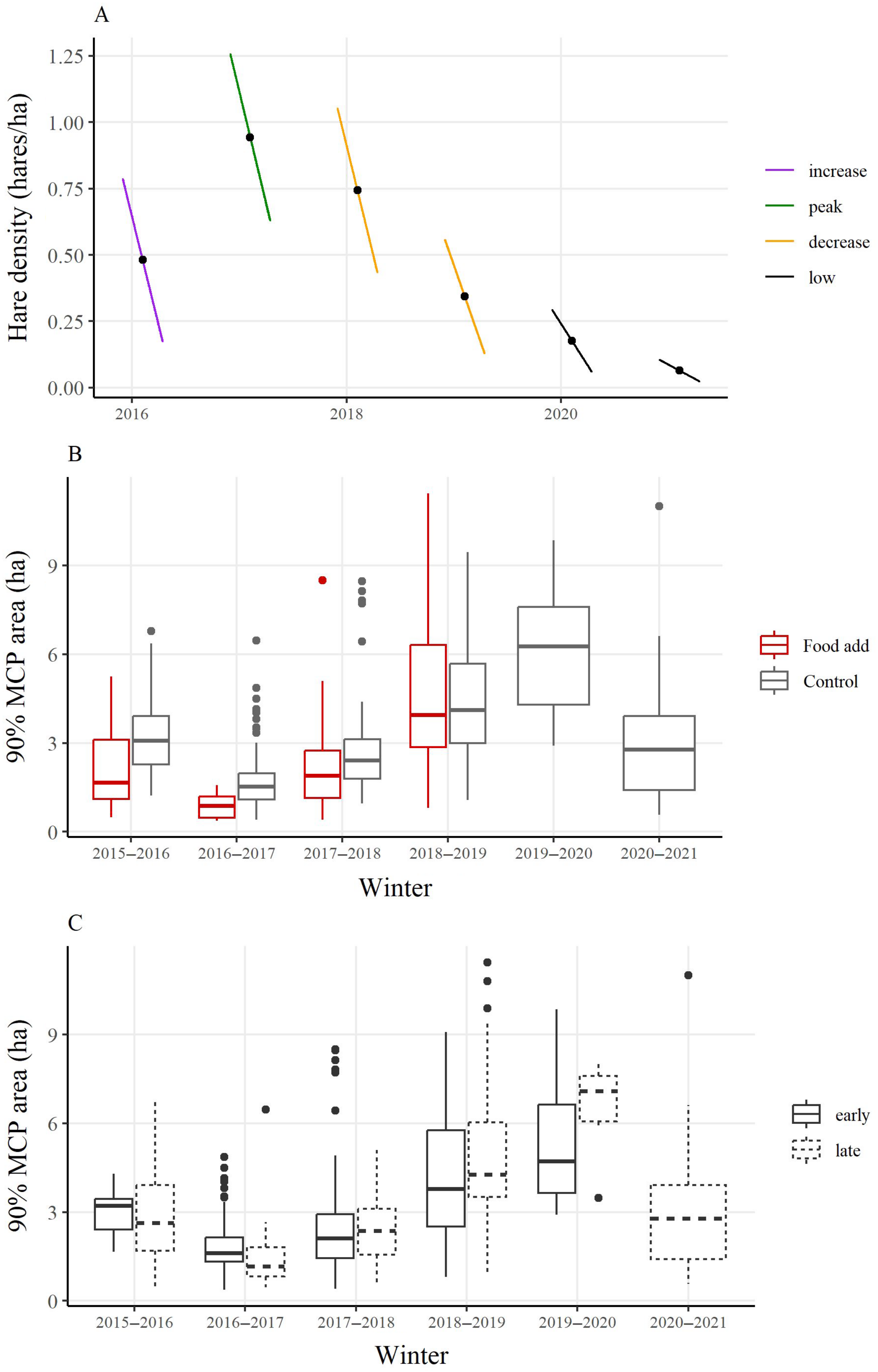

FIGURE 1 (A) Daily hare densities from December to March of each winter (black point represents winter mean population), (B) median hare home range sizes (90% minimum convex polygon [MCP]) by food-add treatment ($n = 464$), and (C) median hare home range sizes (90% MCP) by season, either early winter or late winter ($n = 464$). Winters are categorized into cycle phases. Food-add experiments ended in the spring of 2019. Lower and upper hinges in boxplots represent the first and third quantiles, respectively.

Resource density and food supplementation

Hares feed on the small twigs of willow and birch in winter. We did not measure resource density during our study, but previous studies showed interannual variation in resource changes on the order of 2–4 fold over a hare cycle (Krebs et al., 2001; Smith et al., 1988). Given this, we assumed that changes in overall resource density were small relative to the major changes in hare densities over a cycle. On a seasonal basis, resource density available to hares will decrease over winter because twigs are consumed by hares and availability decreases as snow accumulates. In our study area, snow accumulation begins in October, reaching peak depths in March. We classified GPS data into two seasons: December and January as "early winter" and February and March as "late winter" (see summary of sample sizes of each winter in Appendix S1: Table S1). Due to snow depth, we assume there is greater natural food availability and lower movement costs in early winter than in late winter, so we included season in the analysis.

We experimentally altered resource density by providing rabbit chow to individual female hares. Food supplementation occurred during winter from November 2015 to March 2019 on a subset of collared females ($n = 26$). Individuals were given commercial rabbit chow ad libitum via passive integrated transponder (PIT) tag-enabled automated cat food feeders placed inside their home range (Majchrzak et al., 2022). Rough estimates of home ranges were made via telemetry and trapping of hares in our study areas. A subset of females was randomly selected to receive supplemental food. Only females with PTT tags built into their collars were able to access the feeders. Food-supplemented females occupied home ranges that overlapped with control females that could not access the feeders. Ad libitum rabbit chow provides ample protein to hares, which is hypothesized to be a limiting nutrient for hares in winter (Sinclair et al., 1982). Food-supplemented hares spent no more than one hour per day at their respective feeder and spent most time still foraging on natural browse (Majchrzak et al., 2022), likely to maintain a balanced intake of protein and fiber (Hodges & Sinclair, 2003). Food-supplemented hares had higher survival than controls and were used in the study for as long as they were alive and present on the trapping grids. A previous synopsis of these food-add experiments found that food supplementation did improve hare reproductive fitness by way of increased first litter mass and overwinter survival (Majchrzak et al., 2022).

Home range size calculation

We only used fixes between 1 December and 31 March to capture the winter season, but not mating behavior that begins in April. We categorized fixes into weeks for each individual—winter starting 1 December, eliminating any weeks that did not have a full seven days of data. We estimated weekly home ranges using minimum convex polygons (MCPs) around all fixes using the mcp.area() function of the R package, "adehabitatHR" (Calenge, 2006). We decided to use MCPs because, unlike kernel densities, MCPs require no parameter assignment that can alter home range sizes, making MCPs more reproducible. MCPs are accurate estimates for home range sizes in this study because hare home ranges are too small to be shaped around geographical features like lakes or mountains, which are scenarios when kernel densities would be the more appropriate tool. MCPs have been found to be more accurate than kernel densities for estimating home range sizes in other small-bodied species (Row & Blouin-Demers, 2006). We calculated MCPs for 90%, 75%, and 50% of GPS points, and results for all three were highly correlated ($r > 0.78$). We completed subsequent home range size analyses with just the 90% MCP results. Weekly home ranges were calculated using an average of 298 fixes (38–1564).

We removed any statistical outliers (z-score >3), which were abnormally large home ranges ($n = 16$; 2.2% of the sample). We also removed three home ranges that were less than 0.1 ha (0.4% of the sample). These three cases were likely unrecorded mortalities. After cleaning, the weekly home ranges of food-supplemented and "control" individuals were assigned the average hare density (in hares per hectare) for that week and were classified into seasons (early winter and late winter). In total, we analyzed GPS data from 88 individuals, totaling 464 weekly home ranges. Within our sample, 20 individuals were male, and 68 were female. Of the females, 26 were food-supplemented while collared. We had a sample of 234 home ranges in early winter and 230 in late winter. There was a low sample size of food-supplemented home ranges in the winter of 2016/17 because of difficulty acquiring adequate GPS batteries and some collar malfunctioning (Appendix S1: Table S1).

Statistical analysis

All models were run using the lmer() function of the R package, "lme4" and used hare ID as a random effect (Bates et al., 2015). First, we ran a model to test how home ranges respond to population density with only control individuals from all years of the study ($n = 324$). Next, we developed seven linear mixed models, all of which used control and food-supplemented individual home ranges from 2015 to 2019 when food supplementation experiments were run ($n = 443$). These models tested how home range size (90% MCP) responded to population density (in hares per hectare) but considered food availability differently. We compared the models using Akaike information criterion (AIC). We interpreted results based solely on these models. We tested how hare density influenced home range size without considering food availability in the "Density" model. Next, we tested how hare density interacted with seasonal changes in food availability to affect home range size in the "Season" model. We made season a binary factor and interacted it with hare density. Thirdly, we tested how hare density interacted with food-add treatment; that is, food supplementation, to influence home range size in the "Treatment" model. This model interacted hare density with food-add treatment. Lastly, we conducted a three-way interaction between season, food-add treatment, and hare density to assess how all cases of food availability affect home range size in the "Season-treatment" model ($n = 443$). We ran a "Null" model (random effect only) and two additional models to test the effects of season ("Season test model") and food treatment ("Treatment" test model) without considering population density.

RESULTS

Daily hare densities ranged from a minimum of 0.024 to a maximum of 1.26 hares/ha, starting at a winter median of 0.48 hare/ha during the increase in the 2015–2016 winter, reaching 0.94 hare/ha during the peak in 2016–2017, and decreasing to 0.065 hare/ha in the low of 2020–2021 (Figure 1A). Meanwhile, hare home range areas (90% MCPs) ranged from an annual average of 0.38 to 11.43 ha from 2015 to 2021. The mean areas (±SD) of 90%, 75%, and 50% weekly home ranges (MCPs) were 2.76 ± 1.96 ha, 1.84 ± 1.5 ha, and 1.01 ± 0.98 ha, respectively. Snowshoe hare home ranges were largest during the low phase (2019–2020) and smallest at the peak of the cycle (2016–2017; Figure 1B,C). Sex did not have a significant effect on home range sizes of control individuals ($p = 0.25$, $f = 1.34$, df = 322). Neither food treatment nor season on its own (test models) was found to affect home range size (Table 1). We also found no difference between the home ranges of food-supplemented females and control females ($p = 0.85$, $f = 0.037$, df = 317).

We found a negative relationship between home range size and population density when we tested control individuals only from 2015 to 2021 (−1.5 ± 0.3 ha per 1 hare/ha increase). As hare density increased from 0.24 to 1.2 hares/ha, hare home ranges shrunk from 3.78 to 2.28 ha (Figure 2). The models that included both food-supplemented and control individuals (all individuals in years with food-add experiments; $n = 443$) continued to show a negative trend. Our seasonal model, which interacted hare density with season (early vs. late winter), found a negative relationship for both seasons and no significant interaction between season and hare density (−3.34 ± 0.47; Figure 3A; Table 1). Our food treatment model found that as hare density increased

TABLE 1 Results and corrected Akaike information criterion (AIC_c) comparison of linear mixed models that tested how snowshoe hare home range size (90% minimum convex polygon [MCP]) responds to hare density and resource availability in the form of food-add treatment (food add vs. control) and season (late winter vs. early winter), which fluctuates in a 10-year population cycle.

Model	Intercept	Density	Season	Food	Season × density	Food × density	Food × season	Food × season × density	R^2_m	R^2_c	ΔAIC_c
Season-treatment	6.61 ± 0.62	**−5.16 ± 0.74**	**−1.59 ± 0.75**	−1.32 ± 0.88	1.42 ± 1.14	**2.47 ± 0.99**	0.66 ± 1.02	−1.43 ± 1.39	0.18	0.59	0
Season	5.64 ± 0.44	**−3.34 ± 0.47**	**−1.07 ± 0.49**		0.24 ± 0.62				0.18	0.56	7.56
Treatment	5.51 ± 0.44	**−4.02 ± 0.56**		**−1.55 ± 0.52**		**2.54 ± 0.66**			0.14	0.59	16.33
Density	4.39 ± 0.26	**−2.19 ± 0.29**							0.13	0.54	26.46
Null	2.87 ± 0.18								0	0.54	75.29
Treatment test	3.02 ± 0.29			−0.22 ± 0.33					0	0.55	77.29
Season test	2.83 ± 0.19		0.07 ± 0.16						0	0.54	78.98

Note: All models include individual as a random effect. We also included a "Null" model, which only includes the individual random effect, and two test models, "Season Test" and "Treatment Test," which test the effects of food treatment and season on home range size without considering population density. Beta coefficients (±SD) for each term, ΔAIC_c, marginal R^2 (R^2_m), and conditional R^2 (R^2_c) of models are reported. Significant terms are bolded ($|T| > 2.00$).

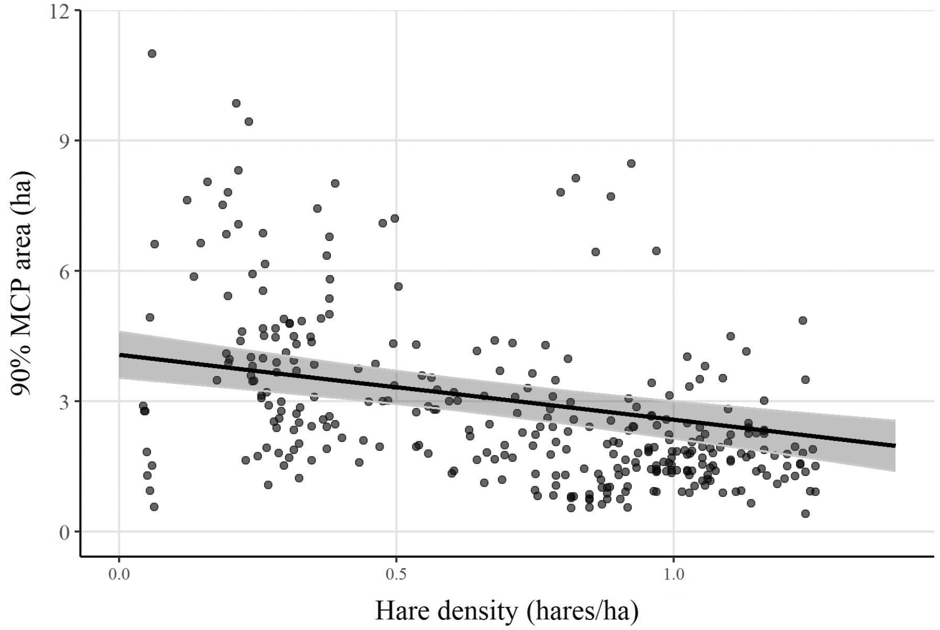

FIGURE 2 Snowshoe hare home range size (90% minimum convex polygon [MCP]) in response to hare density, excluding food-add individuals ($n = 324$). The trend line and confidence interval are shown.

from 0.24 to 1.2 hares/ha, controls slightly decreased their home ranges from 3.66 to 2.18 ha, and food-adds substantially decreased their home ranges from 4.70 to 0.69 ha (Figure 3B). All terms in the food treatment model—hare density, food treatment, and their interaction—were significant ($t > 2$) in predicting home range size (Table 1). The model that interacted food treatment, season, and hare density was the top ranked model according to AIC_c (Table 1). It also found a negative relationship between home range size and density (-5.16 ± 0.74 ha per hare/ha increase). Regardless of scenario, season, or food treatment, home ranges decreased with hare density (Figure 3C). The interaction between food treatment and density remained significant ($t > 2$; Table 1), with food-adds in early winter showing the most negative response and controls in early winter showing the least negative response (Figure 3). The interaction between all three terms was not significant (Table 1).

DISCUSSION

Animal home ranges often decrease in size when population density is higher (Sanderson, 1966). Here, we tested two notions: (1) that studies frequently observe this negative relationship because resource density and population density are correlated, with animals responding to greater resource density rather than conspecific density; or (2) higher conspecific competition at higher densities causes animals to reduce home range size as a way of reducing foraging costs. Our findings support the conspecific competition hypothesis. We found that snowshoe hares reduced their home range size as their population density increased dramatically, regardless of how we controlled resource availability. Here, we further discuss the type of conspecific competition that might be at play in a non-territorial species. We suggest that animals decrease their home range size as population density increases to minimize resource sharing and maintain familiarity of resources when there are more neighbors and greater home range overlap.

Our control model found the same negative trend between home range size and population density as other studies (Figure 2), refuting the resource density hypothesis' prediction that home range size would not change with population density (Mitchell & Powell, 2004). During our study period, food density remained relatively constant compared with the roughly 50-fold change in hare density (Smith et al., 1988). Thus, only per capita resource availability correlated with population density (Smith et al., 1988). The negative response we found provides evidence that potential correlations between resource density and population density are not why animal space use decreases with population density. This finding supports the work of other studies that shared similar objectives to ours but manipulated the density of a population (Kjellander et al., 2004; Schoepf et al., 2015).

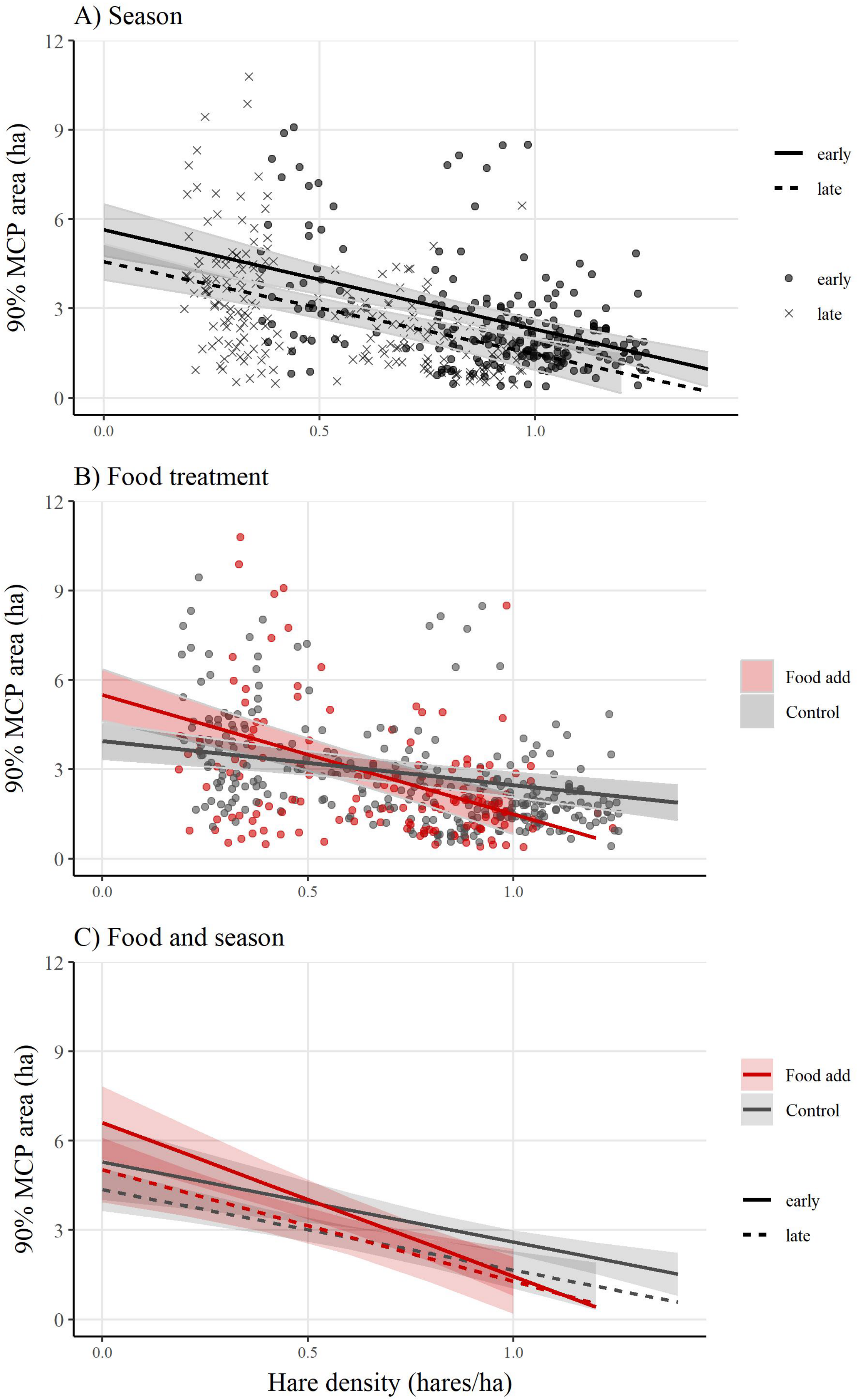

FIGURE 3 Legend on next page.

When we controlled resource availability, we continued to observe a negative relationship between home range size and population density, as in our initial test. Hares in early and late winter showed very similar magnitudes of change in response to population density, with late winter home ranges being smaller than early winter overall (Figure 3A). We speculate that hares may be restricted by movement costs associated with deeper snow in late winter; however, when the effect of season was tested alone, it did not impact home range size (Table 1). Similarly, food supplementation did not affect home range size unless population density was included (Table 1). Hare space use is likely more sensitive to changes in conspecific density than changes in resource density (i.e., food supplementation) or movement costs (i.e., snow depth) alone.

The interaction between food supplementation and population density supports the second hypothesis that conspecific competition causes animals to shrink their space use at high densities, and the advantages of reducing this expenditure are at odds with energy requirements. We found that food-supplemented hares had smaller home ranges than control hares at highest densities, indicating that it may be advantageous to use less space when there are more conspecifics competing for resources, and this strategy is further enabled by food supplementation. Differences in resource availability between early (i.e., more food) and late winter (i.e., less food) may not have been significant enough to mimic the same interaction as food supplementation or were diminished by the opposing factor of potential movement costs associated with snow depth. Food-supplemented females still foraged on natural foods, but did so at a lesser rate than controls (accelerometer data; foraging includes searching for browse; Majchrzak et al., 2022). Foraging rate also declined as the cycle moved from the increase to the decrease phase (Majchrzak et al., 2022). Thus, home range size and foraging rate may be inversely correlated across the cycle. More work should investigate the interactions between foraging rate, space use, and the population cycle.

Many competition-based explanations for population density and home range size dynamics are based on territoriality and exclusivity, but they do not suit our case study findings well. For territorial species, having more neighbors increases the cost of defending a territory, so a simple cost–benefit analysis would predict territory size to decrease as population density increases (Fortier & Tamarin, 1998; Sells & Mitchell, 2020). For animals with exclusive home ranges, similar notions exist that increased neighbor density would cause animals to shrink their space use to maintain resource exclusivity (Jetz et al., 2004). A study similar to ours that experimentally manipulated roe deer (*Capreolus capreolus*) densities found the same negative response in home range size (Kjellander et al., 2004). It suggested that the decreases in home range size were due to increased social interactions and feeding displacements. Another experiment suggested that increased contest competition is the mechanism behind decreases in space use at high density (Schoepf et al., 2015). In our case, hares are non-territorial and nonaggressive species and likely only experience scramble competition. Snowshoe hares have overlapping home ranges (Richmond et al., 2022). Likely, more indirect forms of competition are at play in our case study.

We find it likely that familiarity and memory of the spatial distributions are mechanisms of the negative relationship between home range size and population density (see Spencer, 2012 for how memory contributes to non-territorial but exclusive home ranges). This explanation does not involve direct competition or territoriality and leans on the evolutionary explanation for home range behavior: knowledge of resources (Börger et al., 2008; Spencer, 2012). Animals use memory, not perception, to track changes in the abundance and quality of patches and make subsequent foraging decisions based on this information (Ford, 1983; Ranc et al., 2021). If an individual shares a patch with conspecific, as snowshoe hares do at peak densities, the resource levels of patches in a home range depend on neighbors in addition to the individual. Therefore, we postulate that as population density increases, the number of individuals using the same space increases, and therefore so does the rate of change in patch resource levels. The individual must then visit a patch more frequently to maintain familiarity with current resource levels, which leads to a reduction in home range as a result (similar idea to Spencer, 2012).

FIGURE 3 The relationship between snowshoe hare home range size (90% minimum convex polygon [MCP]) and hare density (hares/ha) under different resource conditions ($n = 443$): (A) in early winter (solid line and solid points) and late winter (dashed line and cross-points), (B) under food-add treatment (red line and points) and control conditions (black line and points), and (C) under food-add treatment in early winter (solid red line) and late winter (dashed red line), and under control conditions in early winter (solid black line) and late winter (dashed black line). Trend lines and confidence intervals are shown for the "season" model (panel A), "treatment" model (panel B), and "season-treatment" model (panel C).

Supporting this notion, there is evidence that individual home range size correlates with cognitive ability (Heathcote et al., 2023). Future studies could test this mechanism with foraging experiments or fine-scaled movement analyses. For a non-territorial species like hares, and all species for that matter, incorporating memory and familiarity may help explain home range size dynamics, adding to the cost–benefit analysis.

Our results suggest that smaller home ranges provide a higher energy balance than larger home ranges at high densities. The mechanism for this result must be at odds with per capita resource acquisition, because food-supplemented hares take a more conservative space use approach than control hares do at high densities (Sinclair et al., 1982). We speculate that if densities become high enough, home ranges could become so small that they do not supply individuals with enough resources, leading to a negative energy balance. Smaller home ranges at higher densities could potentially contribute to indirect food limitation at the peak of their cycle, possibly contributing to lower survival and breeding outcomes that happen as the population crashes (Hodges et al., 2006; Majchrzak et al., 2022; Smith et al., 1988). While conspecific competition increases with increases in population densities, the direct link to patterns in home range size, particularly for non-territorial circumstances, is less studied. Incorporating memory and familiarity into studies on home range size may be an avenue to help explain patterns of animal space use across more species.

AUTHOR CONTRIBUTIONS

Yasmine N. Majchrzak, Michael J. L. Peers, Emily K. Studd, and Allyson K. Menzies collected the data. Juliana Balluffi-Fry, Stan Boutin, Liam G. Horne, Emily Monk, Nicole Humeniuk, Yasmine N. Majchrzak, Michael J. L. Peers, Emily K. Studd, and Allyson K. Menzies conceptualized the study. Juliana Balluffi-Fry led the analysis and writing. Liam G. Horne contributed to data analysis. Nicole Humeniuk, Emily Monk, and Liam G. Horne contributed to the writing. Stan Boutin, Liam G. Horne, Emily Monk, Nicole Humeniuk, Yasmine N. Majchrzak, Michael J. L. Peers, Emily K. Studd, Allyson K. Menzies, Thomas S. Jung, and Dennis L. Murray revised the manuscript.

ACKNOWLEDGMENTS

We would like to thank the many field technicians who helped collect the data and Shotaro Shiratsuru, who led data collection in 2019 as a graduate student. We also thank Alec Robitaille for helping with the GPS cleaning and analysis. We extend our gratitude to Agnes MacDonald and her family for long-term access to her trapline, and the Champagne and Aishihik First Nations and Kluane First Nation for allowing our work within their traditional territory. This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Northern Studies Training Program, the University of Alberta Northern Research Award Program, the Association of Canadian Universities for Northern Studies, The W. Garfield Weston Foundation, and the Government of Yukon.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Balluffi-Fry, 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.14775700.

ORCID

Juliana Balluffi-Fry https://orcid.org/0000-0002-2365-1055

Thomas S. Jung https://orcid.org/0000-0003-2681-6852

REFERENCES

Aronsson, M., M. Low, J. V. López-Bao, J. Persson, J. Odden, J. D. C. Linnell, and H. Andrén. 2016. “Intensity of Space Use Reveals Conditional Sex-Specific Effects of Prey and Conspecific Density on Home Range Size.” *Ecology and Evolution* 6: 2957–67.

Balluffi-Fry, J. 2025. “Why Does Animal Home Range Size Decrease with Population Density? Repository.” In Ecology. Zenodo. https://doi.org/10.5281/zenodo.14775700.

Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software* 45: 361–373.

Bengsen, A. J., D. Algar, G. Ballard, T. Buckmaster, S. Comer, P. J. S. Fleming, J. A. Friend, et al. 2016. “Feral Cat Home-Range Size Varies Predictably with Landscape Productivity and Population Density.” *Journal of Zoology* 298: 112–120.

Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. “Are there General Mechanisms of Animal Home Range Behaviour? A Review and Prospects for Future Research.” *Ecology Letters* 11: 637–650.

Boutin, S. 1990. “Food Supplementation Experiments with Terrestrial Vertebrates: Patterns, Problems, and the Future.” *Canadian Journal of Zoology* 68: 203–220.

Calenge, C. 2006. “The Package ‘Adehabitat’ for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals.” *Ecological Modelling* 197: 516–19.

Enriquez-Urzelai, U., and Z. Boratyński. 2022. “Energetic Dissociation of Individual and Species Ranges.” *Biology Letters* 18: 20210374.

Erlinge, S., I. Hoogenboom, J. Agrell, J. Nelson, and M. Sandell. 1990. “Density-Related Home-Range Size and Overlap in Adult Field Voles (*Microtus agrestis*) in Southern Sweden.” *Journal of Mammalogy* 71: 597–603.

Ford, R. G. 1983. “Home Range in a Patchy Environment: Optimal Foraging Predictions.” *American Zoologist* 23: 315–326.

Fortier, G. M., and R. H. Tamarin. 1998. “Movement of Meadow Voles in Response to Food and Density Manipulations: A Test of the Food-Defense and Pup-Defense Hypotheses.” *Journal of Mammalogy* 79: 337–345.

Fretwell, S. D., and H. L. Lucas. 1970. “On Territorial Behaviour and Other Factors Influencing Habitat Distribution in Birds.” *Acta Biotheoretica* 19: 16–36.

Graham, M. H. 2008. “Confronting Multicollinearity in Ecological Multiple Regressions.” *Ecology* 84: 2809–15.

Harestad, A. S., and F. L. Bunnel. 1979. “Home Range and Body Weight—A Reevaluation.” *Ecology* 60: 389–402.

Heathcote, R. J. P., M. A. Whiteside, C. E. Beardsworth, J. O. Van Horik, P. R. Laker, S. Toledo, Y. Orchan, R. Nathan, and J. R. Madden. 2023. “Spatial Memory Predicts Home Range Size and Predation Risk in Pheasants.” *Nature Ecology & Evolution* 7: 461–471.

Hodges, K. E., R. Boonstra, and C. J. Krebs. 2006. “Overwinter Mass Loss of Snowshoe Hares in the Yukon: Starvation, Stress, Adaptation or Artefact?” *Journal of Animal Ecology* 75: 1–13.

Hodges, K. E., and A. R. E. Sinclair. 2003. “Does Predation Risk Cause Snowshoe Hares to Modify Their Diets?” *Canadian Journal of Zoology* 81: 1973–85.

Jetz, W., C. Carbone, J. Fulford, and J. H. Brown. 2004. “The Scaling of Animal Space Use.” *Science* 306: 266–68.

Kennedy, M., and R. D. Gray. 1993. “Can Ecological Theory Predict the Distribution of Foraging Animals? A Critical Analysis of Experiments on the Ideal Free Distribution.” *Oikos* 68: 158–166.

Kjellander, P., A. J. M. Hewison, O. Liberg, J.-M. Angibault, E. Bideau, and B. Cargnelutti. 2004. “Experimental Evidence for Density-Dependence of Home-Range Size in Roe Deer (*Capreolus capreolus* L.): A Comparison of Two Long-Term Studies.” *Oecologia* 139: 478–485.

Krebs, C. J., R. Boonstra, and S. Boutin. 2018. “Using Experimentation to Understand the 10-Year Snowshoe Hare Cycle in the Boreal Forest of North America.” *Journal of Animal Ecology* 87: 87–100.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001. *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. Oxford: Oxford University Press.

Majchrzak, Y. N., M. J. L. Peers, E. K. Studd, A. K. Menzies, P. D. Walker, S. Shiratsuru, L. K. McCaw, et al. 2022. “Balancing Food Acquisition and Predation Risk Drives Demographic Changes in Snowshoe Hare Population Cycles.” *Ecology Letters* 25: 981–991.

Mcnab, B. K. 1963. “Bioenergetics and the Determination of Home Range Size.” *The American Naturalist* 97: 133–140.

Mitchell, M. S., and R. A. Powell. 2004. “A Mechanistic Home Range Model for Optimal Use of Spatially Distributed Resources.” *Ecological Modelling* 177: 209–232.

Myers, J. H. 2018. “Population Cycles: Generalities, Exceptions and Remaining Mysteries.” *Proceedings of the Royal Society B: Biological Sciences* 285: 20172841.

Peers, M. J. L., Y. N. Majchrzak, A. K. Menzies, E. K. Studd, G. Bastille-Rousseau, R. Boonstra, M. Humphries, et al. 2020. “Climate Change Increases Predation Risk for a Keystone Species of the Boreal Forest.” *Nature Climate Change* 10: 1149–53.

Quirici, V., R. A. Castro, L. Ortiz-Tolhuysen, A. S. Chesh, J. R. Burger, E. Miranda, A. Cortés, L. D. Hayes, and L. A. Ebensperger. 2010. “Seasonal Variation in the Range Areas of the Diurnal Rodent *Octodon degus*.” *Journal of Mammalogy* 91: 458–466.

Ranc, N., P. R. Moorcroft, F. Ossi, and F. Cagnacci. 2021. “Experimental Evidence of Memory-Based Foraging Decisions in a Large Wild Mammal.” *Proceedings of the National Academy of Sciences* 118: e2014856118.

Richmond, I. C., J. Balluffi-Fry, E. Vander Wal, S. J. Leroux, M. Rizzuto, T. R. Heckford, J. L. Kennah, G. R. Riefesel, and Y. F. Wiersma. 2022. “Individual Snowshoe Hares Manage Risk Differently: Integrating Stoichiometric Distribution Models and Foraging Ecology.” *Journal of Mammalogy* 103: 196–208.

Row, J. R., and G. Blouin-Demers. 2006. “Kernels Are Not Accurate Estimators of Home-Range Size for Herpetofauna.” *Copeia* 2006: 797–802.

Sanderson, G. C. 1966. “The Study of Mammal Movements: A Review.” *The Journal of Wildlife Management* 30: 215–235.

Schoepf, I., G. Schmohl, B. König, N. Pillay, and C. Schradin. 2015. “Manipulation of Population Density and Food Availability Affects Home Range Sizes of African Striped Mouse Females.” *Animal Behaviour* 99: 53–60.

Sells, S. N., and M. S. Mitchell. 2020. “The Economics of Territory Selection.” *Ecological Modelling* 438: 109329.

Shiratsuru, S., Y. N. Majchrzak, M. J. L. Peers, E. K. Studd, A. K. Menzies, R. Derbyshire, M. M. Humphries, C. J. Krebs, D. L. Murray, and S. Boutin. 2021. “Food Availability and Long-Term Predation Risk Interactively Affect Antipredator Response.” *Ecology* 102: e03456.

Shiratsuru, S., E. K. Studd, S. Boutin, M. J. L. Peers, Y. N. Majchrzak, A. K. Menzies, R. Derbyshire, et al. 2023. “When Death Comes: Linking Predator–Prey Activity Patterns to Timing of Mortality to Understand Predation Risk.” *Proceedings of the Royal Society B: Biological Sciences* 290: 20230661.

Sinclair, A. R. E., C. J. Krebs, and J. N. M. Smith. 1982. “Diet Quality and Food Limitation in Herbivores: The Case of the Snowshoe Hare.” *Canadian Journal of Zoology* 60: 889–897.

Smith, J. N. M., C. J. Krebs, A. R. E. Sinclair, and R. Boonstra. 1988. “Population Biology of Snowshoe Hares. II. Interactions with Winter Food Plants.” *Journal of Animal Ecology* 57: 269–286.

Spencer, W. D. 2012. “Home Ranges and the Value of Spatial Information.” *Journal of Mammalogy* 93: 929–947.

Stobo-Wilson, A. M., T. Cremona, B. P. Murphy, and S. M. Carthew. 2021. “Resource Availability Drives Variation in a Marsupial Glider’s Home-Range Size.” *Journal of Zoology* 315: 199–212.

Therneau, T. M., and P. M. Grambsch. 2000. *Modeling Survival Data: Extending the Cox Model*. New York, NY: Springer US.

Therneau, T. M. 2024. “A Package for Survival Analysis in R.” https://CRAN.R-project.org/package=survival.

Trewhella, W. J., S. Harris, and F. E. McAllister. 1988. “Dispersal Distance, Home-Range Size and Population Density in the Red Fox (*Vulpes vulpes*): A Quantitative Analysis.” *The Journal of Applied Ecology* 25: 423.

van Schaik, C. P., M. A. Noordwijk, R. J. de Boer, and I. den Tonkelaar. 1983. “The Effect of Group Size on Time Budgets and Social Behaviour in Wild Long-Tailed Macaques (*Macaca fascicularis*).” *Behavioral Ecology and Sociobiology* 13: 173–181.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Balluffi-Fry, Juliana, Yasmine N. Majchrzak, Michael J. L. Peers, Emily K. Studd, Allyson K. Menzies, Liam G. Horne, Emily Monk, et al. 2025. “Why Does Animal Home Range Size Decrease with Population Density?” *Ecology* 106(4): e70054. https://doi.org/10.1002/ecy.70054