

Density-dependent plasticity in territoriality revealed using social network analysis

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Abstract

1. Territories are typically defined as spatially exclusive areas that are defended against conspecifics. Given the spatial nature of territoriality, it is inherently density dependent, but the economics of territoriality also depend on the distribution and abundance of defended resources. Our objectives were to assess the effects of changing population density and food availability on individually based territorial phenotypes.
2. We developed a novel analytical framework that bridges spatially explicit territories with social network analysis to model density-dependent territorial phenotypes. Using the outputs from our data pipeline, we modelled plasticity in territory size and territory intrusion rates in a long-term study population of North American red squirrels *Tamiasciurus hudsonicus*. Red squirrels defend year-round territories around a central hoard (midden) of white spruce *Picea glauca* cones. Importantly, white spruce is a masting species that produces large cone crops every 4–7 years (i.e. mast years) in our study area interspersed with non-mast years when few cones are produced. In the spring following mast years, populations are approximately double in size, but are lower in the spring of non-mast years.
3. We predicted that territory size and intrusion rates would decrease as resource abundance, and consequently population density, increased. By contrast, as resource abundance decreased via depletion, and therefore density decreased, territories should increase in size and intrusions should also increase.
4. As we expected, individual territory size and territorial intrusions were negatively density dependent, such that increased density after mast years resulted in smaller territories and fewer intrusions. When considering between-individual variation in plasticity across a density gradient, individuals responded differently to changes in population density within their lifetime.

5. Our results show that territory size and intrusion rates display negative density dependence. When food becomes available in the autumn of a mast year and density in spring of the following year increases, territories shrink in size to effectively a small area around the midden. While our findings for red squirrels are unique compared to other systems, they serve as a reminder that the direction and strength of fundamental ecological relationships can depend on the nature of the system.

KEY WORDS

intrusion, plasticity, red squirrels, repeatability, social network analysis, territoriality

1 | INTRODUCTION

Territories are spatial areas defended against conspecifics for exclusive access to resources, for example, food, mates or shelter (Brown & Orians, 1970; Maher & Lott, 1995). Territorial defence can be costly in terms of time and energy, and territory owners should therefore seek opportunities to reduce these costs. The defence of a territory is expected to evolve for animals living under energetic constraints if the benefits of exclusive access to space outweigh the costs of maintaining ownership, that is, patrolling boundaries and repelling intruders, and the resulting net benefits exceed those of non-territorial behaviour (Brown, 1964; Krebs, 1980). Within the context of food-based territoriality, the advantages of exclusive access to food are thought to apply to populations where food is limited (Brown, 1964; Carpenter, 1987). The benefits of food-based territoriality therefore depend on the abundance and distribution of the limited food resource being defended. However, in some cases, resources may become hyperabundant and a cessation of territory defence is observed (Adams, 2001). For example, Hawaiian Honeycreepers *Vestiaria coccinea* defend territories at some times, but not others, an outcome which was attributed to an increase in the number of flowers available to consume (Carpenter & MacMillen, 1976). As food productivity increased, territoriality was predicted to disappear because the increase in food availability resulting from defence was inadequate to counterbalance the costs of defence (Carpenter, 1987).

Costs associated with territory defence typically depend on the abundance of potential or realized competitors. As such, territoriality and density are fundamentally linked. Overall, territories typically decrease in size with increasing population density (Both & Visser, 2003), while models of game theory predict that smaller territories are more easily defended when competitor density is high (Morrell & Kokko, 2005; Parker & Knowlton, 1980). As food and competitor density increase, the costs of competition for limited space favour a reduction in territory size (Stamps, 1994). Given long-standing predictions for population-level changes in territoriality as a function of changing density, it is reasonable to expect that individuals adjust their territorial behaviour in response to changing density based on the first principles of adaptive phenotypic

plasticity. In organisms that experience variable environments, the evolution of adaptive phenotypic plasticity is likely to evolve. Adaptive phenotypic plasticity is the ability of a genotype to vary its phenotype across an environmental gradient to maintain or enhance fitness. (Pigliucci, 2005). For example, as the distribution and abundance of food as well as the number of competitors changes throughout the lifetime of an individual, behavioural plasticity can enable the individual to adjust territorial behaviour to match current conditions. As such, within-individual plasticity in territorial traits in response to changes in population density and resource availability could have important consequences for population-level changes in territoriality.

Two measures of territoriality include territory size and territory exclusivity. Territory exclusivity can be energetically costly and has potential to result in heightened risk of predation. The cost function in models of territoriality is described as the relationship between the size of a territory and the cost of territorial defence (Adams, 2001). Although territorial space is often thought to be exclusive (Maher & Lott, 1995), territorial intrusions are common in most systems and represent a measure of territoriality related to competition for resources. Evicting intruders is costly, and some non-physical displays, for example, vocal or chemosensory, at boundary edges are common tactics to reduce the time and energy costs associated with evicting intruders (Adams, 2001). Despite the costs to territory owners and intruders, territory intrusions are common when there is competition for space (Eberhard & Ewald, 1994). Territory size can therefore both affect, and be affected by, food supply and intruder pressure and territory size is predicted to change as a function of variability in food resources and competitor density. As a result, changes in food abundance, and the associated changes in the density of competitors, can affect two key territorial phenotypes: territory size and territorial intrusion rates.

We use behavioural reaction norms (Dingemanse et al., 2010) to quantify among-individual variation in plasticity in territory size, territory intrusion and the propensity with which an individual's territory is intruded upon across a population density and food availability gradient in North American red squirrels (*Tamiasciurus hudsonicus*, hereafter, 'red squirrels') in populations that have been continuously studied since 1989. We examined annual measures of red squirrel territory size, territory intrusions and the propensity

with which an individual's territory is intruded upon. Red squirrels defend individually based year-round territories around a central hoard of white spruce *Picea glauca* cones called a 'midden'; seeds inside these cones are the main food source through winter and during spring reproduction (Fletcher et al., 2013; Ren et al., 2017). White spruce is a masting species that produces large cone crops every 4–7 years (i.e. mast years), which are interspersed with non-mast years when few cones are produced (Lamontagne & Boutin, 2007). In the autumn of mast years, red squirrel populations approximately double in size, but typically decline during non-mast years (Dantzer et al., 2020; McAdam et al., 2019). Unlike systems where food is relatively stable from year-to-year (e.g. large herbivores; Bonenfant et al., 2009), the abundance of food in mast years likely relieves the population from heightened competition that other species typically experience at high density. Moreover, red squirrels are white spruce seed specialists that have relatively low dietary diversity (Fletcher et al., 2010, 2013; Ren et al., 2017), and thus, a low population dietary niche width, an outcome that, in theory, results in heightened intraspecific competition among individuals (Bolnick et al., 2011). Red squirrels live in a highly competitive environment where social interactions are often based on competition for food (Siracusa et al., 2017), although direct observation of antagonistic physical interactions in red squirrels is rare (Dantzer et al., 2012).

Similar to other study systems, we have previously documented territorial boundaries for red squirrels based on direct observations of territorial defence behaviours, including chasing other squirrels and territorial vocalizations (Boutin & Schweiger, 1988; Lamontagne et al., 2013; Larsen & Boutin, 1995; Price et al., 1986). Although this method of territory mapping yields highly accurate territory boundaries, it is laborious, which limits the scope of data that can be collected in this way. Here, we instead leveraged a large

dataset of spatially explicit observations of red squirrels to infer territories and estimate proxies of territory size and intrusions (see Methods). Although our approach (Figure 1) is not as accurate as directly observing territorial defence behaviour in the field (Boutin & Schweiger, 1988; Larsen & Boutin, 1995; Price et al., 1986), we consistently quantified proxies of territory size and intrusion rate for a large number of individuals ($n = 1029$ unique individuals, $n = 1861$ total measures), which provides a unique opportunity to explore how territorial phenotypes change in space (across two 40 ha study grids) and time (25 years) in response to changes in the environment affecting resource availability and social competition for space.

Given that territory intrusion necessarily influences another individual, it is a dyadic process. However, considering intrusions within a dyadic context is limited to modelling how individuals intrude upon each other's territories and does not account for an individual's cumulative number of intrusions across all territories in the population. Thus, to determine the territorial phenotypes of individual squirrels, we extend the dyadic approach used by Dantzer et al. (2012) to a social network approach (hereafter, intrusion networks). Within an intrusion network, nodes represent individual squirrels and edges represent directional intrusions from an individual squirrel to the territory of another squirrel (Figure 1). Directed social network edges have an initiator and recipient. In the case of the intrusion networks, an edge will be directed from individual A to individual B when A invades the territory of B, and directed from B to A when B invades the territory of A (Figure 1). Our spatially explicit social network approach is a novel analytical framework that provides opportunity to consider territorial intrusion from the perspective of intruders as well as from individuals whose territories are being intruded upon, and while we apply it here to red squirrels, it could be applied to any spatially explicit social system.

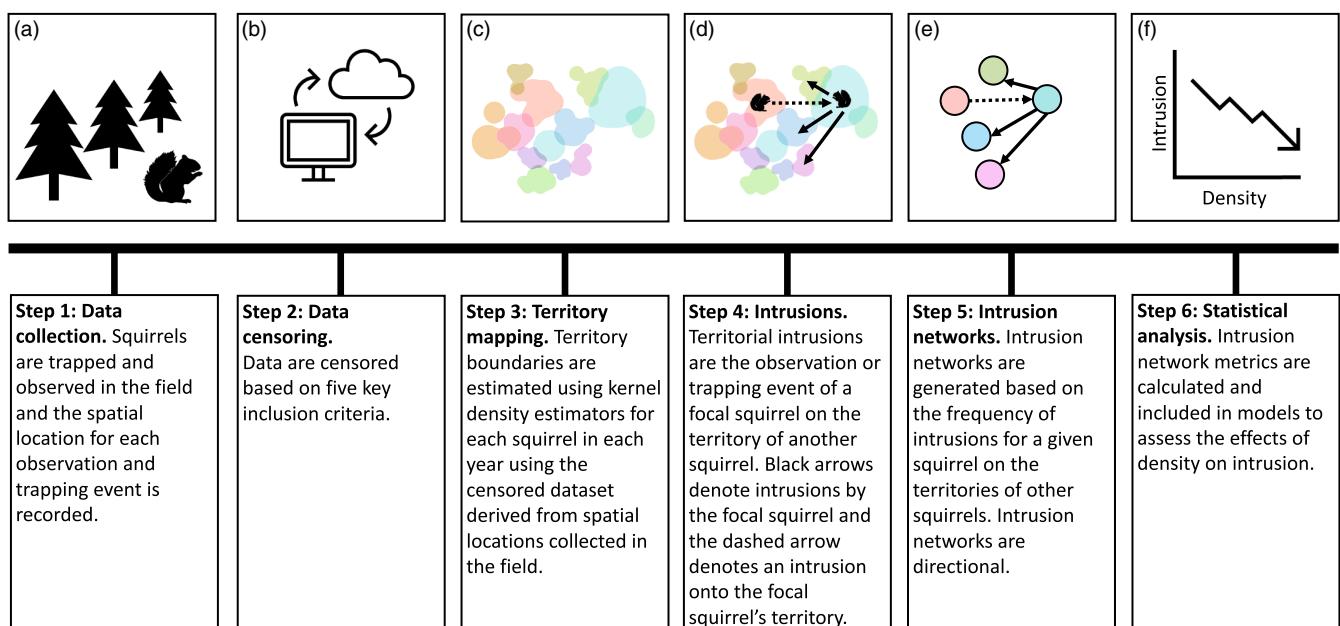


FIGURE 1 Summary of the novel analytical framework from data collection and censoring to territorial mapping and generating intrusion network to statistical analyses.

Following prior work in this system by Dantzer et al. (2012) and Siracusa et al. (2019), we tested the hypothesis that environmental variability, that is, annual changes in the availability of spruce cones and squirrel density, drive among-individual variation in territorial phenotypes through behavioural plasticity. The coupling of two environmental fluctuations (e.g. food and density) makes it difficult to determine which environmental factor is inducing plasticity (Dantzer et al., 2020). One way to disentangle food abundance from population density is through experimental manipulation (Boutin, 1990). While food manipulation can tease apart some aspects of food abundance and population density in the short term, experimental increases in food typically cause increases in density, that subsequently results in increased food competition (Prevedello et al., 2013). In the context of territoriality, the cessation of territory defence can be attributed to an abundant food supply (Carpenter, 1987) and red squirrels are swamped with white spruce cones in the autumn of a mast year (Fletcher et al., 2010). As a result, in the autumn of a mast year, individual squirrels have near unlimited access to resources such that the food-driven density dependence experienced prior to mast years is relieved. At the population level, red squirrels reduce intrusions (Dantzer et al., 2012) and reduce territory sizes (Steury & Murray, 2003) as a function of increasing density. Within-individual plasticity in territorial phenotypes remains an unknown aspect of red squirrel behaviour. Applying a behavioural reaction norm approach provides an opportunity to estimate within-individual behavioural responses in intrusions and territory size to changes in population density. Given negative density dependence at the population-level in intrusion rates and territory size, we predicted that individuals would reduce their rate of territory intrusion as a function of increasing population density and food availability as a plastic adjustment to decreasing territory size at high population density. We, therefore, also predicted that as territories decrease in size, intrusion rates would also decrease in part because individuals with smaller territories are predicted to be better able to defend their territory. However, we predicted that an individual's intrusion rate would be positively correlated with the propensity for their territory to be intruded upon, because more time spent off-territory implies less time spent defending the territory.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

All data were collected as part of the Kluane Red Squirrel Project in south-western Yukon, Canada, that has monitored a wild population of red squirrels continuously since 1989 (Dantzer et al., 2020). We monitored squirrels on two (KL and SU) adjacent 40-ha study areas separated by the Alaska Highway. Both study areas were staked at 30-m intervals, which allowed us to record the spatial location of all squirrel territories and observations. This research was approved by the University of Guelph Animal Care Committee (AUP 1807), the University of Alberta Animal Care and Use Committee for

Biosciences and the University of Michigan Institutional Animal Care and Use Committee (PRO00007805).

During the spring and summer of each year, we monitored the survival and reproduction of individually marked squirrels using regular live trapping (Figure 1a; Dantzer et al., 2020; McAdam et al., 2007). We marked squirrels with unique metal ear tags and unique combinations of coloured wires or pipe cleaners threaded through the tags to identify individuals from a distance (Dantzer et al., 2020). Long-term monitoring protocols included an annual census of the entire population in May of each year to quantify territory ownership and population density (Dantzer et al., 2020). We calculated density based on the number of squirrels enumerated during the spring census divided by 40 ha (i.e. the area of each grid). During the May census in each year, we recorded the location of each individual's primary cache of spruce cones (i.e. midden) which is typically located near the centre of its territory. We used the midden location as a measure of the spatial location of each individual's territory in each year. With the exception of females occasionally bequeathing their territory to one of their offspring (Berteaux & Boutin, 2000; Lane et al., 2015; Price & Boutin, 1993), squirrels defend the same territory for their entire life and are reluctant to change their territory when new ones become available (Larsen & Boutin, 1995).

2.2 | Territory mapping and measuring intrusions

To account for error associated with trapping and behavioural observations, we jittered all spatial locations based on the resolution with which we measured the location of these data. We measured the spatial locations of behavioural observations to the nearest 3 m, but trapping locations are recorded to the nearest 15 m. As a result, we jittered trapping data based on an error of ± 15 m and behavioural observation data based on an error of ± 3 m. Behaviours were recorded when squirrels were observed in the field or through instantaneous sampling at 30-s intervals of radio collared (model PD-2C, 4 g; Holohil Systems Limited) squirrels (for details see Dantzer et al., 2012). Previously published studies that mapped squirrel territories in our system targeted individual squirrels and intensively observed and recorded the locations of territorial defence behaviours in the field (Donald & Boutin, 2011; Lamontagne et al., 2013). These studies explicitly mapped territory boundaries over 4 years (2002–2004 and 2008; Table S2). Our approach was to infer territories for a large number of individual squirrels in as many years as possible. Biologically, squirrel territories do not overlap (Price et al., 1986), but our territory estimates of territory size have potential to overlap due to the nature of our data collection and the analytical procedures describe above. We therefore followed a series of conservative data inclusion criteria and validations to reduce bias associated with estimating territories.

Our data inclusion criteria consisted of four steps (Figure 1b; for sample sizes, see Figure S1). First, we removed the observations of squirrels that occurred outside of the study area as the precise spatial locations for these observations were not recorded by observers

in the field. Second, based on sensitivity analyses to determine the minimum number of spatial locations required to accurately estimate territory size, we included individuals with a combination of at least 20 behavioural observations and trapping events in each year (Figure S2). A year was defined based on all observations and trapping events that occurred between 15 March and 1 September. We chose March 15 as the start date because data collection began no later than March 15 in all years. Third, in some cases, observers conducted focal observations on specific individuals for other projects and recorded a large number of behavioural observations within a single day (range = 0–132 observations per squirrel per day). For cases where >30 observations were collected per day, we randomly selected 30 observations for that individual on that day. We chose 30 observations as the threshold for inclusion because ~95% of data averaged across individuals fell under 30 observations/day. Finally, we removed all grid-year combinations with fewer than 10 unique squirrels after applying the criteria listed above (Figure S1). After applying these inclusion criteria, we determined that data collected between 1989 and 1995 did not meet our criteria for inclusion and so these years were removed. We were left with territories generated for 1029 individual squirrels ($n = 1861$ squirrel-years; $n = 144,430$ spatial locations) between 1996 and 2020 (Figure 1c; Figure S1). We used these data to estimate territory size for each individual squirrel based on the 30% isopleths from fixed kernel density estimates for each individual squirrel in each year with the *href* smoothing parameter in the ADEHABITATR package in R (Calenge, 2011). We selected 30% isopleths as a conservative measure of an individual's territory boundary (for details, see Appendix S2). Given the nature of our data inclusion criteria, our estimates of territory size are likely underestimates of the true size of an individual's territory based on mapping of territorial defence behaviours typically used to estimate territory boundaries (Figure S4). Our estimates of territory size are therefore considered proxies for the full size of an individual's territory, but rather represent an individually variable area around each squirrel's midden.

We had a three-step procedure to measure territorial intrusions in red squirrels (Figure 1d). First, we estimated territories based on 30% isopleths (described above and Appendix S2). Second, once territories were estimated for each individual in each year, we determined whether the spatial location of each trapping event and behavioural observation was within an individual's own territory, within the territory of another squirrel or outside any territories. Third, we considered instances of an individual squirrel within the territory of another squirrel as an intrusion, but we excluded juveniles captured or observed on their mother's territory within a year (Dantzer et al., 2012). Territorial intrusions, therefore, occurred when any squirrel was trapped or observed on a territory that was owned by another squirrel.

Once territories and intrusions were estimated, we developed a temporal moving window approach for territory ownership to remove potential false positives in our determination of intrusion events. For example, if a territory owner died and the territory was subsequently taken over by a new squirrel, the spatial overlap of locations for these two squirrels would be mistakenly interpreted as intrusions unless

the timing of these observations was considered. Territory mapping for individual squirrels was flexible within a given year to account for the possibility of the death of a territory owner and recruitment of a new individual into the vacated territory. Notably, squirrels with an already established territory rarely move (Berteaux & Boutin, 2000; Larsen & Boutin, 1995) and territories are typically taken over by new individuals relatively quickly following the death of the previous owner (Price et al., 1986; Siracusa et al., 2017). We used a hierarchical approach to develop our temporal moving window (Figure S1). First, based on our complete population censuses in each spring, we determined the location of each individual's midden (Dantzer et al., 2020). Based on the assignment of middens to squirrel territories, we determined whether a squirrel held the same territory in consecutive years. Second, in cases where an individual squirrel did not own a territory in either the previous or subsequent years, we used trapping and observation data to determine the earliest and latest days that each squirrel was either trapped or observed on its own territory each year. Thus, our inference was based on two sources of data: midden ownership obtained during spring censuses and spatially and temporally explicit trapping and observation data collected throughout the year. Based on our hierarchical approach, we assigned territory intrusions to one of three categories. Instances where a squirrel was observed on the territory of another squirrel during the period of territory ownership were considered 'true' intrusions. When a territory owner did not own their territory in the previous year, we omitted any instances when a squirrel was observed 'on' a territory before the owner's earliest observed day within a given year. Finally, when a territory owner did not own their territory in the subsequent year, we omitted any instances when a squirrel was observed 'on' a territory after the owner's last observed day within a given year (Figure S1). This procedure was designed to discriminate instances where a squirrel was observed in a location that was previously, or not yet owned by another squirrel, from 'true' instances of intrusion where the squirrel was observed in that location during the tenure of the owner of that location.

The probability of detecting an intrusion is affected by the frequency of trapping or observation. Individual squirrels vary in their trappability (Boon et al., 2008), and a few squirrels require many traps be set over multiple days to capture them. We acknowledge the possibility that trapping effort may bias intrusion rates for some squirrels. Specifically, it is possible that targeted trapping for certain squirrels may artificially inflate the rate at which we measure intrusions on their territory. Given our large sample sizes of trapping events ($n = 30,469$) and behavioural observations ($n = 113,961$), we expected that these events likely make up a relatively small number of intrusions (see Appendix S3 for further explanation and details about this assumption; Table 1).

2.3 | Generating intrusion networks

Based on the intrusion of individual squirrels onto the territories of other individuals, we generated intrusion networks (Figure 1e).

TABLE 1 Summary of assumptions and potential weaknesses associated with our analyses along with references to relevant supplementary materials

Assumption and potential weaknesses	Justification	Relevant appendix, figure or table
Insufficient data for individual squirrels to estimate territory size and intrusion rates in each year	Data were iteratively removed from a subset of individuals to determine the minimum number of locations required to estimate robust territory sizes	Appendix S1; Figure S2
Using fixed temporal windows to generate intrusion networks (15 March–1 September) has potential to capture territorial intrusions for the purposes of both mating and food competition	Mating can occur from January to July (occasionally even later) but most mating happens between March and May (McAdam et al., 2019). Given the inter-annual variability in the timing of mating, removal of data after the mating season would result in limited data for many years (including all post-mast years) and a new set of assumptions about data inclusion	Appendix S1
Territories estimated using spatial locations, and not specific territorial behaviours, overestimates territory size	We generated a sensitivity analysis to determine the most appropriate kernel density estimator (KDE) percentage for territories. We selected 30% KDEs as territories generated using this percentage were significantly smaller than those generated using higher percentages. We also compared territory size estimated using methods in this study to previously published measures of territory size	Table S1; Table S2; Figure S3; Figure S4
Behavioural observations or trapping events represent true intrusions	Outcomes from models using intrusion events based only on behavioural observations (as opposed to observation and trapping) result in qualitatively similar interpretations, i.e. that out-intrusion-strength and in-intrusion-strength decrease as a function of population density	Figures S10 and S11
Variability among behavioural observation and trapping data in different years may confound the effect of density on intrusions measured using these data	No relationship between population density and behavioural observation or trapping data suggests these data are not confounded with density and can therefore be used as estimates for intrusion and any effect of density on intrusion is biological as opposed to a logistical or methodological confound	Table S3; Figure S12
Trapping effort is not accounted for in measures of territorial intrusion. For example, it may take days to catch some squirrels and only hours to catch others	It is possible that variation in effort, i.e. number of traps set on for a squirrel that is difficult to trap, results in inflated intrusions on the territory of a squirrel being intensively trapped. Given our large sample size of behavioural observations ($n = 114,137$) compared to trapping events ($n = 33,550$), and our validation that trapping effort measured as the number of squirrels trapped per year did not differ as a function of density, we posit that the number of times an individual was trapped is a reasonable, albeit imperfect, proxy for trapping effort	Figure S12

Nodes represented individual squirrels and edges were directed and represented the frequency of territory intrusion events between a pair of individuals. To account for sampling differences among individuals, we generated a territoriality intrusion index for each dyad in each year and grid. The territoriality intrusion index is similar to the simple ratio index (Cairns & Schwager, 1987) and is calculated as $I_{ij} / (I_{ij} + N_i)$, where I_{ij} represents the number of intrusions by individual i onto the territory of individual j and N_i represents the total

number of observations for the intruding individual. We calculated two social network metrics: out-strength and in-strength. Out-strength (hereafter out-intrusion-strength) is defined as the sum of all intrusions for an individual and higher values indicate that the individual more frequently intruded on the territories of others, while in-strength (hereafter, in-intrusion-strength), is defined as the sum of all intrusions onto an individual's territory and higher values indicate that the individual's territory was intruded upon more frequently

(Figure 1f) (Webber & Vander Wal, 2019). We calculated out- and in-intrusion-strength for each individual squirrel in each year.

2.4 | Statistical analysis

During exploratory analysis, we observed that one of the two study areas in 1 year (KL grid in 2006, hereafter KL-2006) was a clear outlier. After further examination, we determined median territories on KL-2006 were 13.04 ha, which was ~ 50 times larger than an average year (median = 0.26 ha, $SD \pm 1.05$ ha, but see results for variation in territory size between sexes and mast vs. non-mast years), suggesting the possibility that squirrels abandoned territorial defence for home ranges in KL-2006. We therefore considered KL-2006 an outlier and removed these data from all subsequent analyses but further discuss this unique observation later.

We used behavioural reaction norms to model the potential for density-dependent changes in territory size, out-intrusion-strength (frequency of intrusions by a focal individual) and in-intrusion-strength (frequency of intrusions onto the territory of a focal individual). We employed three bivariate Bayesian mixed models in the MCMCGLMM R package (Hadfield, 2010) to quantify covariance between out-intrusion-strength, in-intrusion-strength and territory size as well as plasticity of these traits as a function of population density where the random intercept term reflects among-individual variation and the random slope term reflects phenotypic plasticity (Dingemanse et al., 2010). Our models were fitted with out-intrusion-strength and territory size as co-response variables; out-intrusion-strength and in-intrusion-strength as co-response variables; and in-intrusion-strength and territory size as co-response variables. We used three separate bivariate models instead of a single trivariate model because of convergence issues with the trivariate model. All models included grid (KL or SU), age, sex, spring density, mast year (yes or no) and mean-centred and scaled year as fixed effect covariates. All three territorial phenotypes were mean-centred and scaled to improve model fit. To account for the possibility that individuals may vary in their slopes (i.e. an Individual \times Environment interaction), we included squirrel ID as a random effect where slopes varied among individuals in the effect that spring density had on each trait. To assess within-individual consistency of territorial phenotypes, we also estimated repeatability (see Appendix S4).

Finally, we used weakly informative priors for the random effects ($V = 1$, $nu = 1$, $alpha.V = 25^2$). 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. We also performed three runs of our model to ensure different chains reached the same qualitative result.

3 | RESULTS

Over 25 years, we estimated annual territory size and quantified intrusions for 1029 individual squirrels ($n = 455$ males; $n = 574$ females; total of 1861 squirrel-years), and on average, we monitored individuals for 2 years ($SD \pm 1.15$, range = 1–8). Intrusions were clustered spatially (Figure 2). Population density fluctuated annually, with peaks in density in the spring following spruce mast events in the previous autumn (Figure 3). The estimated median territory size and number of intrusions differed between females and males, but the magnitude of this difference depended upon whether, or not, it was a spruce mast year. In mast years, males (0.48 ha, $SD \pm 0.88$ ha) had larger median territory sizes than females (0.22 ha, $SD \pm 0.63$ ha), while the median number of intrusions by males (7 per year, $SD \pm 7.9$) was higher than the median number of intrusions by females (4 per year, $SD \pm 6.2$). Similarly, the median number of times a territory was intruded upon by males (8 per year, $SD \pm 6.1$) was higher than the median number of times a territory was intruded upon by females (4 per year, $SD \pm 3.7$). In non-mast years, median territory size for males (0.17 ha, $SD \pm 0.62$ ha) was larger than median territory size for females was (0.10 ha, $SD \pm 0.40$ ha), while the median number of intrusions by males (2 per year, $SD \pm 5.9$) was similar to the median number of intrusions by females (1 per year, $SD \pm 4.0$). Similarly, the median number of times a territory was intruded upon by males (2 per year, $SD \pm 5.1$) was similar to the median number of times a territory was intruded upon by females (1 per year, $SD \pm 2.8$). Overall, these results highlight that in both mast and non-mast years, males have larger territories, intrude on the territories of other squirrels more frequently and have territories that are intruded upon more frequently by other squirrels.

3.1 | Within-individual plasticity

At the population level, we observed negative density dependence for all three territorial traits, such that territories became smaller, intrusion rates decreased and the propensity for a territory owner's territory to be intruded upon all decreased with increasing squirrel population density (Figure 4; Table 2). Our behavioural reaction norm models included an individual by environment interaction (Figure 4), such that slopes for individual phenotypes differed in their degree of density dependence. Most individuals reduced the size of their territories and reduced intrusions as population density increased, although there was some variation in this relationship (Figure 4a,c,e). While traditional behavioural reaction norms focus on how phenotypes vary across an environmental gradient, we also examined how territorial phenotypes varied temporally as squirrel density

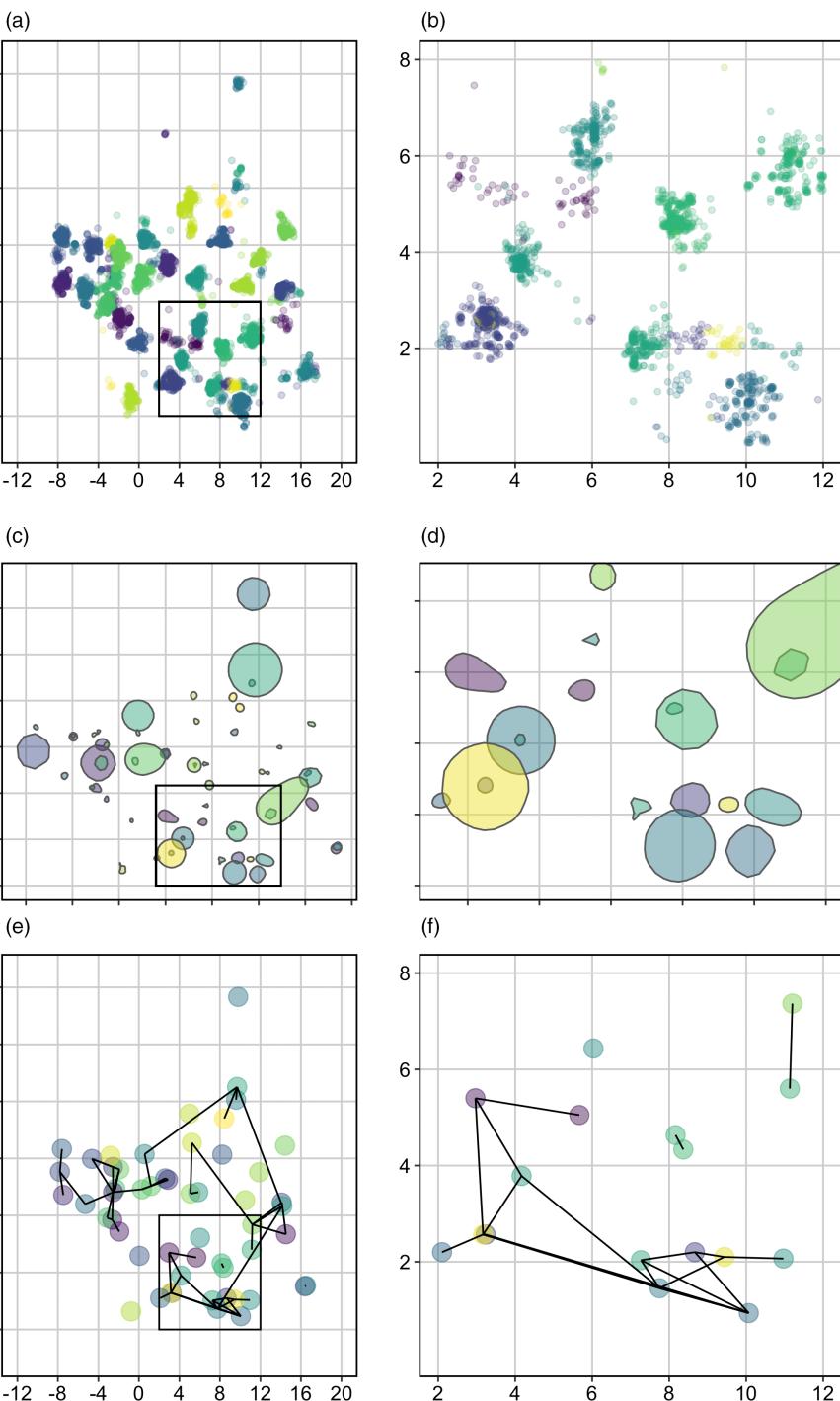


FIGURE 2 Demonstration of our novel analytical framework that transforms (a) raw squirrel spatial locations to (c) territorial kernels to (e) intrusion networks based on the intrusion of squirrels on the territories of conspecifics. For clarity, panels (b), (d) and (f) are zoomed in sections of panels (a), (c) and (e) respectively. Data presented were collected in 2015 on the KL grid. Note, colours represent individual squirrels are consistent across panels and points on panels (a) and (b) represent the locations of individual squirrels, polygons on panels (c) and (d) represent the locations of territories for individual's squirrels and nodes on panels (e) and (f) represent the centre of each individual's territory and edges connecting nodes represent intrusion events from one territory owner to another.

fluctuated as a function of food availability (Figure 4). Specifically, we found that individuals predictably increase intrusion rates and territory sizes in the season leading up to autumn mast events (i.e. in the spring and summer of mast years when there is low density and low resource abundance), followed by drastic reductions in intrusion rates and territory sizes following mast years (i.e. in the year following an autumn mast when there is high density and high resource abundance; Table 2). Notably, we found similar trends when we examined within-individual plasticity in intrusion rates and territory size for males and females (Figure S9) and when we only considered

intrusions based on behavioural observations or trapping events separately (Figure S11).

We also found that males tended to have larger territories, higher out-intrusion-strength and higher in-intrusion-strength than females (Table 2; Figure S9). Meanwhile, there was no effect of age on territory size, though older individuals tended to have higher out-intrusion-strength, but lower in-intrusion-strength (Table 2). Finally, squirrels on KL and SU had similar sized territories, but squirrels on KL had higher out-intrusion-strength and higher in-intrusion-strength than squirrels on SU (Table 2).

3.2 | Phenotypic covariance

In support of our prediction, we found strong positive among-individual correlation between out-intrusion-strength and territory

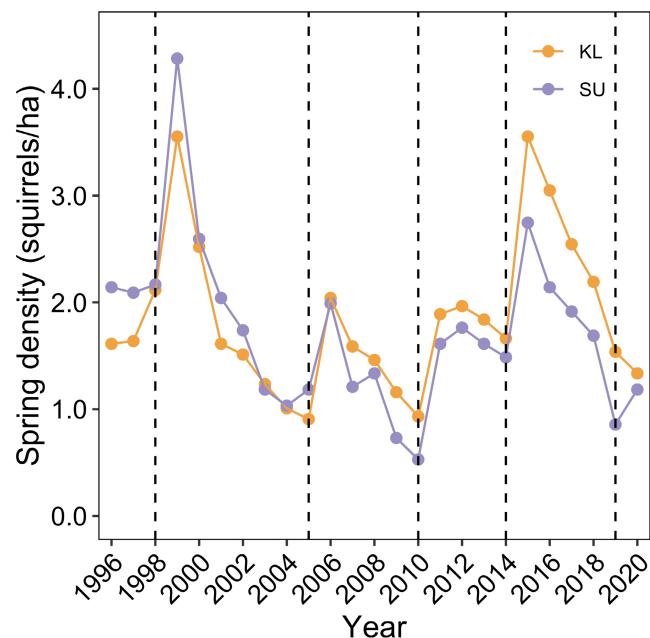


FIGURE 3 Changes in population density (squirrels/ha) between 1996 and 2020 for KL and SU grids used in our study. Vertical dashed lines represent mast events.

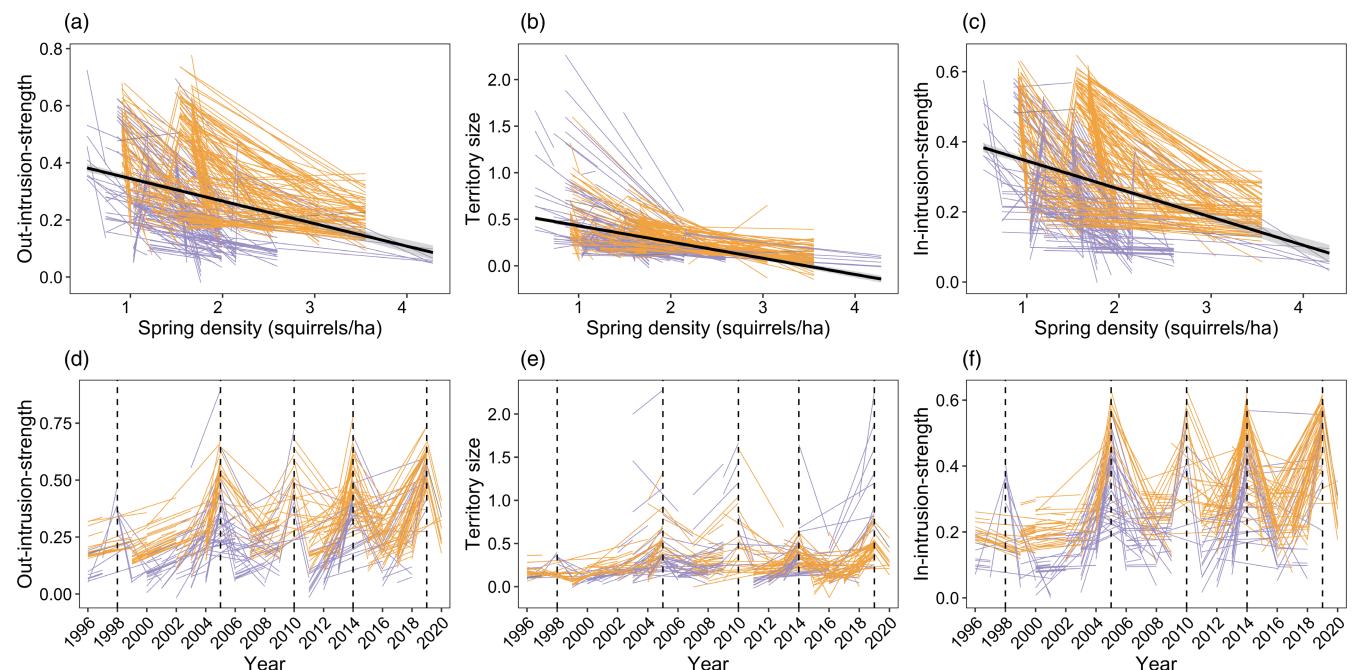


FIGURE 4 Behavioural reaction norm slopes for (a) out-intrusion-strength (frequency of intrusions by a focal individual); (b) territory size; (c) in-intrusion-strength (frequency of intrusions onto the territory of a focal individual) as a function of changes in population density (squirrels/ha). We also present the change in behavioural reaction norm slopes through time for (d) out-intrusion-strength; (e) territory size; (f) in-intrusion-strength between 1996 and 2020. For panels (d), (e) and (f), vertical dashed lines represent mast years. Note, slopes were plotted as a function of density (panels a-c) and time (panels d-f), although slopes presented in corresponding panels (i.e. a and d) were estimated in the same model (Table 2). Orange lines denote squirrels on the KL grid and purple lines denote squirrels on the SU grid.

size (correlation = 0.995; 95% credible intervals = 0.982, 0.999), suggesting that squirrels with small territories intrude on other territories less frequently or that squirrels that are less likely to intrude have smaller territories. We also found support for our prediction that an individual's intrusion rate would be positively correlated with the propensity for their territory to be intruded on. Specifically, in-intrusion-strength and out-intrusion-strength were positively correlated (correlation = 0.93; 95% CI = 0.74, 0.99), suggesting that individuals with higher intrusion rates were also more likely to have their territories intruded upon. Finally, in-intrusion-strength and territory size were also positively correlated (correlation = 0.87; 95% credible intervals = 0.57, 0.99), suggesting that individuals with smaller territories also tended to be intruded upon less or that individuals that had their territories intruded on less were likely to have smaller territories.

4 | DISCUSSION

Using a novel analytical framework that combines spatially explicit territories and social network analyses, we observed within-individual density-dependent plasticity in three territorial phenotypes. As expected, territory size, out-intrusion-strength (frequency of intrusions by a focal individual) and in-intrusion-strength (frequency of intrusions onto the territory of a focal individual) decreased as a function of population density at the population level. However, when considering among-individual variation in plasticity

TABLE 2 Summary of three bivariate behavioural reaction norm models assessing the effects of population density, mast events (reference category is mast), age, sex (reference category is female) and grid (reference category is KL) on territory size, out-intrusion-strength (frequency of intrusions by a focal individual) and in-intrusion-strength (frequency of intrusions onto the territory of a focal individual) in a wild population of red squirrels. 95% credible intervals are displayed in brackets for each posterior mean

Model 1:		Out-intrusion-strength		In-intrusion-strength	
Variable		Posterior mean (95% CI)	p-value	Posterior mean (95% CI)	p-value
Intercept		0.45 (0.28, 0.61)	<0.001	1.11 (0.97, 1.25)	<0.001
Grid (SU)		-0.20 (-0.30, -0.10)	0.005	-0.31 (-0.39, -0.22)	<0.001
Sex (M)		0.15 (0.05, 0.25)	<0.001	0.19 (0.10, 0.26)	<0.001
Age		0.04 (0.01, 0.06)	0.005	-0.03 (-0.06, -0.01)	0.002
Density		-0.06 (-0.12, 0.01)	0.10	-0.10 (-0.16, -0.05)	<0.001
Mast (no mast)		-0.56 (-0.67, -0.45)	<0.001	-1.07 (-1.16, -0.98)	<0.001
Year		0.12 (0.07, 0.16)	<0.001	0.22 (0.18, 0.26)	<0.001
Model 2:		Out-intrusion-strength		Territory size	
Variable		Posterior mean (95% CI)	p-value	Posterior mean (95% CI)	p-value
Intercept		0.48 (0.31, 0.65)	<0.001	0.67 (0.49, 0.84)	<0.001
Grid (SU)		-0.24 (-0.35, -0.14)	<0.001	-0.08 (-0.18, 0.02)	0.12
Sex (M)		0.08 (-0.02, 0.18)	0.12	0.15 (0.05, 0.25)	0.002
Age		0.03 (0.002, 0.05)	0.04	0.02 (-0.01, 0.04)	0.24
Density		-0.04 (-0.11, 0.03)	0.23	-0.21 (-0.28, -0.13)	<0.001
Mast (no mast)		-0.54 (-0.60, -0.40)	<0.001	-0.50 (-0.60, -0.41)	<0.001
Year		0.11 (0.06, 0.16)	<0.001	0.07 (0.03, 0.12)	0.001
Model 3:		In-intrusion-Strength		Territory size	
Variable		Posterior mean (95% CI)	p-value	Posterior mean (95% CI)	p-value
Intercept		1.11 (0.97, 1.24)	<0.001	0.65 (0.46, 0.81)	<0.001
Grid (SU)		-0.33 (-0.40, -0.24)	<0.001	-0.08 (-0.18, 0.01)	0.10
Sex (M)		0.17 (0.09, 0.24)	<0.001	0.16 (0.07, 0.26)	<0.001
Age		-0.04 (-0.06, -0.01)	0.002	0.02 (-0.01, 0.04)	0.23
Density		-0.09 (-0.15, -0.04)	<0.001	-0.21 (-0.28, -0.14)	<0.001
Mast (no mast)		-1.06 (-1.15, -0.97)	<0.001	-0.49 (-0.59, -0.39)	<0.001
Year		0.22 (0.18, 0.25)	<0.001	0.06 (0.02, 0.11)	0.007

in territorial phenotypes across a density gradient, we found evidence that individuals responded differently to changes in population density within their lifetime. Unlike many other territorial systems, red squirrel territory size and intrusion rates decrease with population density. Competition at high density is relaxed due to the influx of resources, an outcome which results in a reduction in both territory intrusions and size.

The typical expectation for the relationship between competition and density is that there is increased competition for a decreasing pool of resources at high density (Bonenfant et al., 2009; Gurevitch et al., 1992). For territorial species, this includes an increase in intruder pressure as a function of increasing density (Heske et al., 1988; Morrell & Kokko, 2005). The norm for most territorial species, such as wolves *Canis lupus*, is an increase in aggression among territorial packs as a function of increasing density (Cassidy et al., 2015; Cubaynes et al., 2014). Meanwhile, the relationship between intrusion pressure and density for squirrels is opposite; we

demonstrate that individually based intrusion rates decrease as a function of increasing density. Squirrel density is closely linked to white spruce mast events, such that in mast years, density is typically low but recruitment (i.e. production of offspring and their survival) is very high leading to high density in the spring after a mast year (Boutin et al., 2006). After mast years, resources are highly abundant and available because squirrels can use cones cached in the mast year in subsequent years, but these resources slowly become depleted over time until the next mast year. Territoriality for wolves and lions *Panthera leo* is dependent spatially on prey biomass (Mosser et al., 2009), whereas territoriality in squirrels is dependent temporally on the size of its cache of white spruce. Our result, therefore, highlight the potential importance of temporal resource variability for driving territoriality.

Our analyses highlight consistent within-individual increases in intrusion rates and territory size leading up to and including mast years, followed by reductions in intrusion rates and territory size

immediately following mast years (Figure 4). Two non-mutually exclusive explanations exist for these trends: food competition and breeding competition. First, prior to cones becoming available in the autumn of a mast year, the pool of available resources is very low and competition for food is high (Lamontagne & Boutin, 2007). The benefits of territoriality do not exceed the costs if there are no resources to defend or if resources lost to pilferage are negligible relative to the resources that will become available in the upcoming mast event. As a result, at low-density individuals may shift space use tactics to occupying undefended home ranges.

Territories fall under the macroecological definition of home ranges, which are broadly defined as the spatial expression of behaviours animals perform to survive and reproduce (Burt, 1943). Most definitions of home ranges exclude defence of an area. Notably, one study area (KL) in 1 year (2006) was an extreme example of how squirrels shift space use from defending territories to occupying home ranges (see Appendix S5). In mast years, breeding often lasts throughout the summer (Williams et al., 2013), resulting in males intruding on female territories for breeding rather than food competition. While food competition is likely the primary driver of the patterns we observed, future work could disentangle the drivers of density-dependent intrusion by determining when males intrude for the purposes of mating versus food competition (see Appendix S1 for brief discussion of mating vs. food competition). Intrusion rates (i.e. out-intrusion-strength and in-intrusion-strength) and territory size are therefore both density dependent and tied to the availability of food.

While both territory size and territorial intrusion rates decreased with density for both males and females, we also found positive phenotypic covariance between out-intrusion-strength and territory size. As estimated territories become larger, they are intuitively more difficult to defend. Moreover, individuals are less likely to leave their territory at high density when food is abundant (following a mast) because resources are available to all individuals, while the costs of losing cones from pilferage are lower because cones are hyperabundant. In addition, individuals reduce their activity at high density to a defendable core area with a midden (Studd et al., 2020); a strategy that means territories are small and more easily defendable against potential intrusions from juveniles in search of possible settlement locations (Larsen & Boutin, 1994). The negative relationship between density and out-intrusion-strength for red squirrels is an exception to the standard expectation of a positive relationship between density and other territorial phenotypes, for example, a positive relationship between aggression and territory size as predicted by the social fence hypothesis (Hestbeck, 1982).

Our behavioural reaction norm results indicate that individuals varied in the slopes of territorial phenotypes across a density gradient. Considering the relationship between territoriality and density through time reveals how territorial phenotypes change as a function of white spruce seed availability, which is the primary driver of density in our system (Dantzer et al., 2020). While the magnitude of plasticity in territorial phenotypes varied among individuals, territory size and out-intrusion-strength were highly repeatable (see

Appendix S4) and the direction of plasticity through time was consistent among individuals; that is, out-intrusion-strength was low and territories were small immediately following mast years, and out-intrusion-strength was high and territories were large during mast years. Variation in out-intrusion-strength likely emerges from variation in territory size and these traits are biologically and mathematically linked.

Despite the potential benefits of securing additional food, intrusions on another territory can be costly because squirrels leave their own territory vulnerable to pilferage (Donald & Boutin, 2011; Gerhardt, 2005), they risk altercations with other territory owners (Dantzer et al., 2012) and they may require travelling outside their social neighbourhood (Siracusa et al., 2017). Thus, for the cost to be worthwhile, squirrels presumably select which territory to intrude upon. For example, squirrels may avoid intruding on the territories of kin (Wilson et al., 2015) or familiar individuals in their social neighbourhood (Siracusa et al., 2017) using territorial vocalizations to identify relatives or familiar individuals. They may instead intrude on the most vulnerable territories of non-kin or unfamiliar individuals. Importantly, our analyses of territoriality and territory intrusions are a network-based approach that considers annual territorial phenotypes for each individual but does not consider the characteristics or potential relationships between an intruder and the owner of the territory they are intruding upon. The potential for non-random intrusion rates among individuals that assess the role of sex-based intrusions, relatedness and social familiarity could reveal further complexities in the social lives of squirrels (Siracusa et al., 2021). For example, squirrels that are more related on average to their neighbours do not have higher fitness, but familiarity with neighbours increases survival and annual reproductive success (Siracusa et al., 2021). The benefits of having familiar neighbours suggest that intrusion among familiar neighbours may be maladaptive and generate instability in cooperative relationships.

Although we did not explicitly develop predictions about the effect of sex or age on territorial phenotypes, we found that males tended to have larger territories, intruded on other territories more frequently and were also more likely to have their territories intruded on. While we did not include specific data from mating chases in our measures of territory size or intrusion (Lane et al., 2009), males were more likely than females to intrude on the territories of females, presumably for breeding opportunities. In general, males of other species tend to intrude more on other territories and demonstrate stronger responses to intruders on their own territory. For example, male great tits *Parus major* had stronger vocal responses to intruders than females (Snijders et al., 2017), while dominant male meerkats *Suricata suricatta* had stronger responses to the scent of intruding males than to resident males (Mares et al., 2011). These patterns are consistent with the idea that reproductive conflict with competitors is an important driver of territorial response. Given the time period we used to quantify intrusions (i.e. 15 March–1 September), our measures of intrusion and territory size are influenced by the effect of males intruding on a females' territories for the purposes of mating

(Lane et al., 2009, 2010). Unlike Lane et al. (2009), who compared home range size during the mating season to home range size in the post-mating season, we pooled data from the entire season to estimate territory size. Male red squirrels typically have very large home ranges during mating (average 5.6 ha) compared to the post-mating (average 0.62 ha) seasons (Lane et al., 2009). However, although mating chases may be incorporated into our measures of territory size for males, average male territory size in our study (0.62 ha in mast years, 0.17 ha in non-mast years) was an order of magnitude smaller than mating season estimates obtained by Lane et al. (2009). By contrast, we also compared territory size using our territorial kernel methods to observational methods previously used in our system (Donald & Boutin, 2011; Lamontagne et al., 2013). Overall, our measures of territory size were highly conservative and were significantly lower than observation methods (Table S2; Figure S4).

We observed a positive relationship between age and out-intrusion-strength, suggesting that older individuals tend to intrude on other territories more frequently. Notably, juvenile mortality is very high, but for squirrels that survive to at least 1 year of age, median age is 3.5 years old (McAdam et al., 2007). An increase in food abundance results in higher squirrel density (Dantzer et al., 2020), while predator exclusion does not increase density (Stuart-Smith & Boutin, 1995). In terms of individual squirrels, predator pressure increases for adults and juveniles without territories, largely because individuals with no stored food or depleted food stores are more likely to take greater risks and increase risk of predation (Hendrix et al., 2020; Stuart-Smith & Boutin, 1995). Given that senescence affects life-history traits and other territorial phenotypes in squirrels (Descamps et al., 2008; Siracusa et al., 2021), future work could examine the potential relationships between territorial phenotypes, fitness and senescence in red squirrels and other territorial species.

Our intrusion networks leveraged a large dataset of squirrel spatial locations to infer competition in a socially and spatially complex system. Territorial space is highly valuable due to the midden(s) located within each territory, and thus, intrusion represents a breach of space that might be akin to ignoring social distancing mandates or antagonistic physical interactions in other species. Squirrel social networks are, therefore, spatially restricted to the area adjacent to the territories of owners, a result that is corroborated by prior work in our system suggesting that risk of intrusion is higher among neighbours (Siracusa et al., 2017, 2021). While territories were similar in size across study areas, intrusion phenotypes varied between study areas. Despite similarities in forest and understorey composition, one possible explanation is the slight differences in the availability of resources between these sites (Dantzer et al., 2020). Although our methods provided the opportunity to infer effects of food availability and density on territorial phenotypes, we acknowledge the assumption that our measures of territorial phenotypes are proxies for the true measures of these traits. Despite these assumptions, our analyses confirm our understanding of density-dependent territoriality in red squirrels (Dantzer et al., 2012; Steury & Murray, 2003).

5 | CONCLUSIONS

Social and spatial behaviours in many animals are density dependent (Webber & Vander Wal, 2018). Our work on North American red squirrels provides support for the prediction that territorial intrusion and territory size decrease as a function of population density—presumably because white spruce mast events positively affect population density in this system (Dantzer et al., 2020). By contrast, in other territorial systems, for example, wolves and lions, consumers deplete food sources at high population density, thus resulting in food scarcity and an increase in territorial intrusions. In other territorial systems, there is a lag between peak prey and predator density; when predator density peaks, prey are already declining, leading to higher competition and presumably increased territorial intrusions. In red squirrels, anticipatory reproduction means the increase in density and food are synchronous, which effectively eliminates food competition (and therefore territorial intrusions) at high density. Food availability and density are therefore inherently linked as drivers of territoriality for red squirrels, and indeed for all systems. To test the generality of our results, we posit that future work on the density dependence of territoriality could address similar questions for other territorial consumers that are reliant on periodic resource pulses. For example, granivorous rodents or birds that rely on seed masting may provide a good test of our hypotheses in other systems. While we applied our method (Figure 1) to red squirrels, similar principles likely apply across territorial systems. In nearly all animal populations, density changes through time, resources become available, and, in territorial systems, resources are subsequently defended. Given the ubiquity of density dependence, we expect territorial intrusion behaviour will vary as a function of resource availability and population density in all systems. Our unique findings for red squirrels, however, serve as a reminder that the direction and strength of these fundamental relationships can depend on the nature of the system in question.

AUTHOR CONTRIBUTIONS

Quinn Webber and Andrew McAdam conceived the ideas and designed methodology; Ben Dantzer, Jeff Lane, Stan Boutin and Andrew McAdam facilitated collection of the data; Quinn Webber analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All code are publicly available, while data used for analyses and to generate figures are available on Zenodo Digital Repository <https://doi.org/10.5281/zenodo.7300015> (Webber et al., 2022). Raw data are available upon request.

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SUPPORTING INFORMATION

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