Effects of Food Addition and Helminth Removal on Space Use and Spatial Overlap in Wild Rodent Populations

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ABSTRACT

1. Animal space use and spatial overlap can have important consequences for pathogen transmission. Identifying how environmental variability and inter-individual variation affect spatial patterns to drive transmission heterogeneity in wildlife is a priority for effective management of wildlife disease. However, there are few experimental studies investigating how food abundance and macroparasite infection affect transmission opportunities in wildlife.
2. Wild bank voles (*Myodes glareolus*) are a useful study system to investigate spatial patterns of wildlife and are amenable to experimental manipulations. We conducted a replicated, factorial field experiment in which we added food and removed helminths in wild vole populations in natural forest habitat and monitored vole space use and spatial overlap using capture-mark-recapture methods.
3. Using a combination of home range and network analyses, we quantified vole space use and spatial overlap. We then compared the effects of food addition and helminth removal and investigated the impact of season and sex on space use and spatial overlap.
4. We found that space use was impacted by breeding season and sex but not by food addition or helminth removal. Sex-based, seasonal changes in shared space use were more notable with food addition. Food addition also increased the frequency of, and variability in, spatial overlap occurring between individual voles at trapping locations, while helminth removal had no effect.
5. Our work provides empirical evidence quantifying the spatial effects of food abundance and macroparasite infection on wildlife populations. We demonstrate the potential for high food abundance to increase spatial overlap relevant for pathogen transmission. Our findings also suggest that individual contributions to transmission may be heterogeneous

within populations and that season and sex are important covariates to consider when identifying when and with whom transmission is most likely to occur.

KEYWORDS

anthelmintic treatment, disease ecology, *Myodes glareolus*, network analysis, resource provisioning, spatial overlap, transmission, vole

1 INTRODUCTION

How animals use space in their environment and interact with conspecifics is fundamental to understanding transmission of pathogens. However, contributions to transmission are frequently heterogeneous among hosts in a population (Woolhouse et al., 1997). Transmission heterogeneity can result from both environmental variability and inter-individual variation among hosts (VanderWaal & Ezenwa, 2016) and may be influenced by host population density or sex-specific social behavior (Webber & Vander Wal, 2020). Identifying how space use, interactions between animals, and individual-level traits affect transmission continues to be a key goal in disease ecology (Silk et al., 2017) and is necessary for conservation, domestic animal health, and public health, but studies that seek to disentangle the relative contributions of environmental and individual variation to transmission are rare.

Food abundance is a common source of environmental variability that can influence pathogen transmission by altering host space use and spatial overlap (Becker et al., 2015). Variation in food abundance across landscapes can have important impacts on infection prevalence in host populations, either by promoting animal movement through increased attraction of individuals in high food areas or by decreasing movement through increased site fidelity at areas of high food abundance (Becker et al., 2018). When wildlife aggregate around point food sources (e.g. bird

feeders, landfills, crop fields), this facilitates interactions between infected and susceptible hosts and can lead to increased transmission (Forbes et al., 2015).

Individual variation among hosts (e.g. sex, reproductive status, macroparasite infection) can also affect animal space use and spatial overlap with potential consequences for pathogen transmission (VanderWaal & Ezenwa, 2016). For example, testosterone-mediated behavior in mature males can shape social network structure through increased space use and spatial overlap (Dakin et al., 2021) and is hypothesized to be a key driver of commonly observed male bias in infection prevalence (Krasnov et al., 2012). Similarly, frequent interactions among mature individuals during the breeding season can increase transmission opportunities and create seasonal peaks in pathogen transmission (Altizer et al., 2006).

The effects of individual variation in macroparasite infection on animal space use and spatial overlap are not as well understood. Macroparasite infection may require infected hosts to increase their foraging area and thus potential for interactions with conspecifics (Brown et al., 1994). Conversely, infected hosts may decrease their activity, thus decreasing space use and interactions (Lopes et al., 2016). Further, since space use and spatial overlap can influence macroparasite exposure, positive feedbacks between macroparasite exposure and space use can exacerbate or regulate within-population variation in macroparasite burden and movement (Hawley et al., 2021). Despite these findings, further research is needed to understand how individual parasite-induced behaviors scale up to population-level effects on transmission (Hawley & Altizer, 2011).

Much of our knowledge of how food abundance and macroparasite infection impact pathogen transmission in wildlife comes from studies of laboratory animals under highly controlled conditions (e.g. Budischak et al., 2015; Croft et al., 2011) or observational studies in wildlife

(e.g. Jolles et al., 2008; but see Forbes et al., 2016). However, explicit investigation through rigorous field experiments on wildlife are necessary to understand the effects of environmental and individual variation on transmission in their ecological context. Such research is pertinent and timely because urbanization and other land-use change can influence wildlife disease dynamics (Bradley & Altizer, 2007; Plowright et al., 2021) and are likely to further increase heterogeneity in food abundance and macroparasite burdens in wildlife.

Our goal was to determine the effects of food abundance and macroparasite infection on space use and spatial overlap in wildlife populations. We chose bank voles (*Myodes glareolus*) as a focal study species as they are amenable to experimental manipulation; are a common host for macroparasite infection (e.g. helminths like *Heligmosomoides glareoli*; population-level helminth prevalence approx. 80% in some areas, Haukisalmi & Henttonen, 2000); and have well-documented natural history, particularly with respect to space use behavior of mature voles. Mature males hold territories that are larger than those of females and that overlap with territories of other males and with females. Mature females are territorial toward other mature females but may overlap more with juvenile females and in the non-breeding season. Both food availability and population density are thought to regulate vole territory size (Bondrup-Nielsen & Karlsson, 1985).

Here we experimentally manipulated wild bank vole populations via food addition and removal of intestinal macroparasites (helminths) and monitored individual- and population-level responses. Specifically, we 1) quantified space use and shared space use in the breeding and non-breeding season using home range approximation and 2) quantified spatial overlap between voles each month based on co-location in capture-mark-recapture trapping grids and visualized the population-level clustering of these “overlaps” using network approaches. As abundant food often increases small mammal population density through immigration

(Prevedello et al., 2017), we hypothesized that food addition would result in more spatial overlap that is highly clustered, corresponding to a decrease in vole space use. We hypothesized that helminth infection would increase host movement (because of increased foraging requirements), and thus expected that helminth removal would decrease space use and spatial overlap, resulting in sparser, less clustered networks. Furthermore, we expected space use and spatial overlap to differ by season and sex such that heterogeneity in the number of spatial overlaps per vole would peak during the breeding season when activity is highest and most different by sex and breeding status.

2 MATERIALS AND METHODS

2.1 Study site and experimental design

We conducted a two-factor field experiment in the boreal forests of southern Finland (61.0775°N, 25.0110°E) where bank voles are the dominant rodent species. These forests receive snowfall from approximately November-April, and absence of snow cover makes monitoring and experimental manipulation of voles most feasible from May-October. Twelve study sites were established in old-growth spruce forest patches. All sites were at least two kilometers apart to prevent dispersal between replicate populations. At each site, a standardized trapping grid (100 m x 100 m, 1 hectare) was established of 61 uniquely identified traps spaced 10 meters between grid rows and columns to monitor the vole population (Figure 1).

Sites were randomly assigned to one of four treatment pairings (“treatments”): no manipulation (“unfed-control”; “U-C”); helminth removal but no food addition (“unfed-deworm”; “U-D”); food addition but no helminth removal (“fed-control”, “F-C”); and both food addition and helminth removal (“fed-deworm”; “F-D”). Each treatment was replicated at three sites (Figure 1). Sites assigned to food addition received a feed mix of mouse chow pellets and sunflower seeds

evenly distributed on the trapping grid every two weeks from May through November (if snowfall had not yet accumulated). The supplemental feed mix was dosed at 7.54 kcal/m^2 (following Sweeny et al., 2021) consisting of 7.875 kg of mouse chow pellets (Altromin 1324 10 mm pellets maintenance diet for rats and mice [3227 kcal/kg]; Altromin Spezialfutter GmbH & Co. KG, Lage, Germany) and 7.875 kg sunflower seeds (as fed, 6350 kcal/kg). Voles at deworm sites were given an oral dose of 10 mg/kg Ivermectin and 100 mg/kg Pyrantel on their first capture in a trapping occasion; these doses are known to be effective at treating larval and adult helminth infections (Clerc et al., 2019). Voles at control sites received a matching weight-based dose of sugar water (17.5% sucrose solution) on their first capture in a trapping occasion.

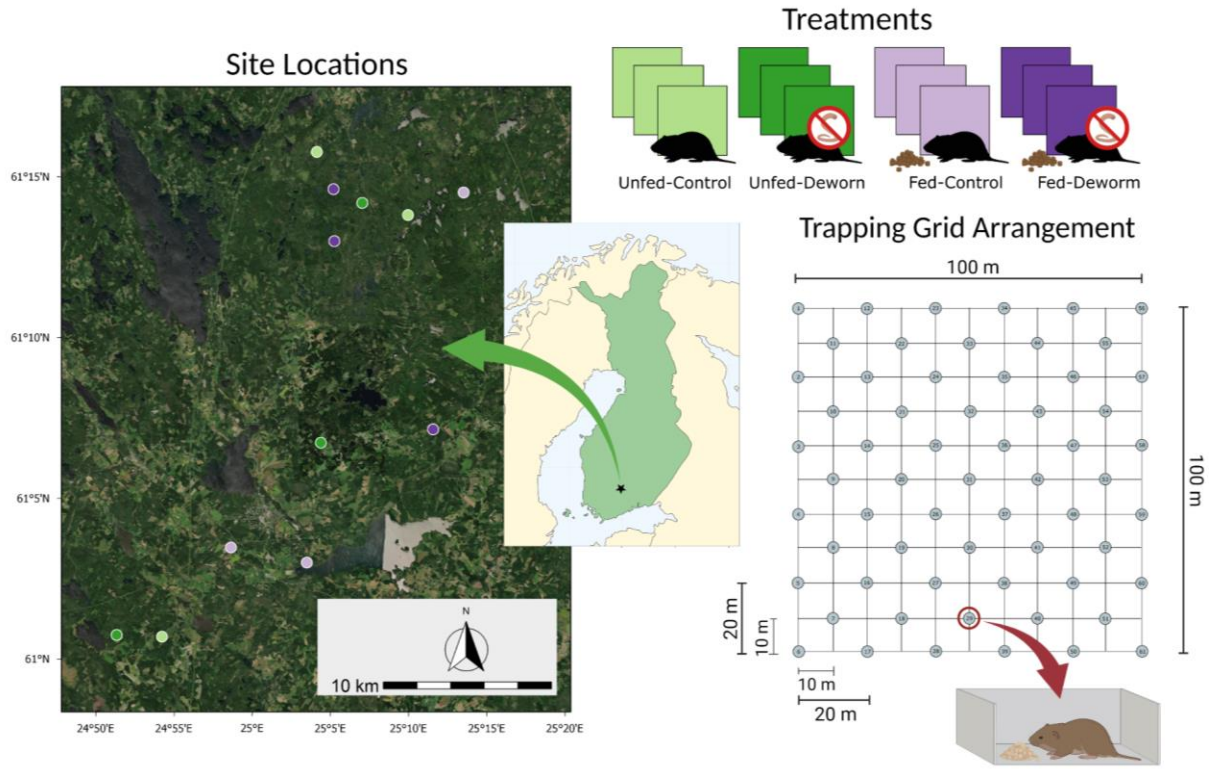

Figure 1. Field study design and experimental set-up. ("Site Locations") Twelve field sites were established in southern Finland. ("Treatments") Sites were assigned one of four treatment pairings: unfed-control, unfed-deworm, fed-control, and fed-deworm and each treatment was replicated at three sites each. ("Trapping Grid Arrangement") The trapping grid included 61

traps in 11 rows and 11 columns. Rows and columns were spaced 10 meters apart and traps (dots) were placed in an offset arrangement with 20 meters to the next trap in the same row and column and 14.14 meters to the next trap on the diagonal.

2.2 Data collection

Vole populations were longitudinally monitored via capture-mark-recapture methods. Every four weeks from May-October 2021, Ugglan multi-capture live traps (Grahnab, Sweden) were baited with whole oats and set for 48 hours (a “trapping occasion”). Traps were checked each morning and evening at approximately 0600 and 1600 (four checks per trapping occasion) and captured animals were processed and then released at the point of capture. Six trapping occasions were conducted at each site (total trap events: 17,568). Upon first capture, all voles were injected with a Passive Integrated Transponder (“PIT tag”; “Skinny” PIT Tag, Oregon RFID, USA) for unique identification. The trap number, PIT tag number, body mass, sex, and reproductive status were recorded for each vole on their first capture each trapping occasion. If a vole was recaptured in a given trapping occasion, only the trap number and PIT tag number were recorded, and the vole was released at the capture location. Reproductive status was categorized as a binary measure (reproductive or non-reproductive). Females were considered reproductive if they were lactating or pregnant. Males were considered reproductive if they had scrotal testes. Reproductive status within the breeding or non-breeding seasons was summarized on an “all or nothing” basis: if a vole was ever recorded as reproductive during a trapping occasion within the season, it was recorded as reproductive in that season. Body mass was used to categorize voles into two age classes: sub-adult (≤ 17 g) or adult (>17 g) (Balčiauskienė et al., 2009; Balčiauskienė & Balčiauskas, 2009).

All trapping and handling of wild bank voles was conducted under approval of the University of Arkansas Institutional Animal Care and Use Committee (IACUC #19105) and the Finnish Animal

Ethics Board (ESAVI-17810-2019). Access to forest sites was provided by private landowners and by Metsähallitus Metsätalous Oy (MH 6302/2019).

2.3 Data analysis

Quantifying transmission-relevant interactions and visualizing heterogeneity in these interactions can suggest how individuals in a population may differentially contribute to pathogen transmission (Craft & Caillaud, 2011). Spatiotemporal overlap is a common and flexible approach that can approximate transmission opportunities for a range of pathogens (e.g. Godfrey et al., 2010; Porphyre et al., 2008) under the assumption that spatial overlap and interaction frequency are directly correlated (Robert et al., 2012). Transmission-relevant overlap may be approximated finely in small areas and short time windows (e.g. co-occurrence at a point-location) or more broadly over large areas and long time windows (e.g. home range overlap), depending on the host-pathogen system and research question of interest (Mistrick et al., 2022). Bank voles are host to a variety of microparasites with confirmed or suspected zoonotic potential (e.g. cowpox [*Vaccinia* virus], Puumala hantavirus, Ljungan virus), many of which are primarily shed in excreta and can remain infectious in the environment for days to weeks (e.g. Puumala hantavirus, Kallio et al., 2006), providing a biologically relevant temporal window to approximate transmission via environmental contamination.

To understand general patterns of space use by season and sex and how this might impact transmission opportunities, a home range approach was used to quantify space use and shared space use for voles repeatedly captured in the breeding or non-breeding season. To quantify transmission opportunities more specifically and how these may vary with space use and the experimental manipulations, co-occurrence at trap locations was used to approximate transmission-relevant spatial overlap between voles. When interactions like spatial overlap are heterogeneous among individuals, network analysis is a useful method to visualize their

frequency and distribution within a population and predict how transmission may occur (Bansal et al., 2007). In spatial overlap networks, points (nodes) represent individual animals and connections between nodes (edges) signify spatiotemporal overlap. Constructing and comparing networks for populations experiencing varying ecological conditions enables researchers to explore how environmental variability affects opportunities for pathogen transmission.

2.3.1 Space use

Vole space use was quantified by aggregating the data from each trapping occasion into a summer (May-August) and an autumn season (September-October). These divisions were chosen to capture changes in vole space use between the summer breeding season and autumn non-breeding season (breeding season May-September in southern Finland; Kaikusalo, 1972). Home range estimators require repeated observations of individuals; therefore the space use analysis was conducted with a subset of the full vole capture dataset. Only voles that were captured at least five times in a given season (hereafter “seasonal residents”) were used for this analysis. Voles that were only captured one to four times in a season were not considered seasonal residents. However, the autumn and summer seasons were considered separately so any vole could be considered, for example, a seasonal resident in autumn but not in summer. The sex, reproductive status, and age class of the seasonal residents in each treatment and season was noted. A 100% minimum convex polygon (“capture polygon”) containing all capture locations in a given season was constructed for each seasonal resident using the ‘adehabitatHR’ R package (Calenge, 2006). Space use was quantified as the area of a seasonal resident’s capture polygon in hectares. Shared space use was quantified both as the number of neighbor voles whose capture polygon overlapped that of a focal vole (“number of capture polygon overlaps”) and the proportion of the focal vole’s capture polygon that was shared with each neighbor vole (“proportion of capture polygon overlap”). Proportion overlap was directed

and was calculated for each individual per pair of voles with overlapping capture polygons and the sexes of the focal and neighbor voles for each pairing were noted. Space use and shared space use were compared using nonparametric rank-sum tests (Mann-Whitney U test for two groups; Kruskal-Wallis test for multiple groups).

2.3.2 Spatial overlap

Spatial overlap networks were constructed for each site and trapping occasion from June-October (capture numbers in May were very low (zero to five animals per site), prohibiting network construction for all sites so the May data were dropped from this analysis). Spatial overlap was visualized as a series of five networks per site, each representing a separate trapping occasion (hereafter called “month”). This method was chosen to capture the temporal dynamics of network structure and account for animal interactions that vary through time due to changing population size, demographics, or seasonal behaviors (Pinter-Wollman et al., 2014). Networks were constructed using the ‘CMRnet’ R package (Silk et al., 2021). Spatial overlap was defined as two voles captured in the same or immediately adjacent trap (within 15 meters) during a trapping occasion to align with similar studies of rodent spatial overlap (Perkins et al., 2009) and to align with a biologically relevant temporal window for transmission (48 hours). Because edges were approximated via spatial overlap, edges were undirected. Edges shown in the main text are unweighted (edges represent the occurrence of spatial overlap between two voles). An analysis of degree with edges weighted by the frequency of overlap between pairs of voles is included in the Supporting Information: Weighted degree.

Network metrics provide quantifiable measures to summarize information at both the node level (e.g. the number of and heterogeneity in overlaps per individual) and at the network level (e.g. how the overlaps are clustered in the population) (Croft et al., 2008). Both node- and network-level metrics (Table 1) were calculated using the ‘igraph’ R package (Csardi & Nepusz, 2006).

Table 1. Description of network metrics and their biological relevance.

Network Metric		Network Definition	Biological Relevance
Node Level	Unweighted degree	Number of edges connected to a focal node	Number of unique neighbor voles a focal vole spatially overlapped with
	Weighted degree *(see Supplement: Weighted Degree)*	Number of edges connected to a focal node by the weight of each edge; weight represents strength of interaction	Number of spatial overlaps observed for a focal vole, considering the number of repeat overlaps between each vole pair
Network Level	Degree distribution	Frequency distribution of degree counts in a network (weighted or unweighted)	Quantifies the heterogeneity in spatial overlap in the population, high heterogeneity is often associated with super-spreader events
	Network Size	Total number of nodes in the network	Number of voles observed during a trapping occasion at a given site
	Modularity	Extent to which nodes in the network are organized into highly connected clusters that minimally interact with nodes outside their cluster (value scaled 0-1)	Extent to which spatial overlap is clustered among groups of voles that overlap frequently with each other but minimally with other groups of voles at their site
	Betweenness Centralization	Extent to which nodes are connected linearly in a chain or connected to a central hub node like spokes in a wheel (value scaled 0-1)	Extent to which certain voles may be serving as “hubs” in their network to connect many other voles; high centralization suggests short paths across the network

Network data are inherently non-independent and many network metrics are closely related and are influenced by network size, limiting the ability to make direct comparisons between networks of varying size (Farine & Whitehead, 2015). To understand how network size was affected by

treatment and contextualize potential confounding factors influencing network metrics, we investigated the factors affecting network size using a linear mixed-effects model fit by restricted maximum likelihood (REML) using the 'lme4' package (Bates et al., 2015). We modeled the main effects of food addition (unfed/fed), helminth removal (control/deworm), and month. Site was included as a random effect to account for multiple measures at each site and variation between replicate sites within a treatment. Network size was log-transformed to normalize distribution of the data.

We quantified the mean and standard deviation of network clustering metrics (i.e. modularity and betweenness centralization) by month to explore differences between treatments. Unweighted degree for all voles at each site in a given month was visualized as a frequency distribution to identify heterogeneity in the number of spatial overlaps per vole. Differences in degree and network clustering metrics between sites and treatments were compared using Kruskal-Wallis tests with Dunn tests (Benjamini-Hochberg correction) for post hoc comparisons.

Heterogeneity in degree is an important feature of networks that can suggest heterogeneity in transmission, particularly if a small proportion of the population has the largest number of connections (Lloyd-Smith et al., 2005). We defined "super-overlappers" as voles with an unweighted degree greater than 1.5 times the interquartile range of degree values of their site in a given month. As such, the degree value of a super-overlapper was determined in relation to the population at its site in a given month, not by an arbitrary threshold, and therefore the actual degree value of super-overlappers differs between populations and months. Super-overlappers were identified for each site in each month and the sex and reproductive status of these individuals was noted.

All data analysis was conducted in program R version 4.1.2 (R Core Team, 2021).

3 RESULTS

We captured 770 unique voles totaling 2086 capture events from the 12 sites during the May-October study period. Of these, 456 individuals (59.2%) were captured at least twice (mean captures per vole: 2.71 ± 2.30 [range: 1-17]).

3.1 Space use

In total, 95 voles (95/770, 12.3% of all voles captured) were seasonally resident on our trapping grids (eight voles were resident in both summer and autumn). We documented 314 captures of 48 seasonal residents in the summer breeding season and 316 captures of 55 seasonal residents in the autumn non-breeding season (Figure S1). An additional 20 animals were captured at least five times, but the captures were split between the breeding and non-breeding seasons, so they were not included as seasonal residents. In summer and autumn, seasonal residents were both males and females (Figure S2). The breeding status of seasonal residents generally matched that expected in the season (i.e. majority reproductive in summer, non-reproductive in autumn) and this was consistent between treatments (Figure S3). The age class of seasonal residents suggested most were adults (>17 g) in summer and sub-adults (≤17 g) in autumn, and this was similar across treatments (Supporting Information: Age classes of seasonal residents; Figure S4).

3.1.1 Space use was greatest in males during the breeding season

Space use of seasonal residents varied by sex and season but did not differ by treatment. In the summer breeding season, male and female space use differed (Mann-Whitney U test, $p<0.001$) and male space use was greater and more variable than that of females (male mean area=0.18±0.12 hectares ([range: 0.02-0.60 ha]; female mean area=0.04±0.04 hectares [range: 0.00-0.15 ha]; Figure 2A; Table S1). Summer space use did not differ between treatments for

males or females (Kruskal-Wallis test, males p=0.77; females p=0.29). In the autumn non-breeding season, male and female space use did not differ (Mann-Whitney U test, p=0.22; male mean area = 0.04±0.04 [range: 0.00-0.20]; female mean area=0.03±0.04 [range: 0.00-0.17]; Figure 2A; Table S1). Autumn space use did not differ between treatments for either sex (Kruskal-Wallis test, males p=0.16; females p=0.51). Male space use differed between summer and autumn with mean summer space use over four times greater than autumn space use (Mann-Whitney U test, p<0.001). Female space use was not different between summer and autumn (Mann-Whitney U test, p=0.72).

3.1.2 Food addition increased female-female shared space use in the non-breeding season

The number of capture polygon overlaps per seasonal resident (indicating shared space use between pairs of voles) differed by season for males and was higher in summer (Mann-Whitney U test, p<0.001; summer mean overlaps=2.16±1.61 [range: 0-5]; autumn mean overlaps=0.59±0.78 [range: 0-2]; Table S2). Females had a similar number of overlaps in summer and autumn (Mann-Whitney U test, p=0.64). In summer, males had more overlaps than females whereas the two sexes had a similar number in autumn (Mann-Whitney U test, summer p<0.001; autumn p=0.91).

The proportion of capture polygon overlap between seasonal residents did not differ by treatment in summer or fall (Kruskal-Wallis test, summer p=0.50; fall p=0.13). In the summer, the proportion of capture polygon overlap was low to moderate in most treatments and was only observed for male-male pairings or male-female pairings (Figure 2B). In the autumn, the proportion of overlap was higher than in summer in all treatments except unfed-deworm where it was similar (Figure 2B). Female-female overlap was observed in fed treatments in autumn and the mean proportion of overlap was high (F-C mean=0.54±0.51 [range: 0.18-0.90]; F-D mean=0.50±0.24 [range: 0.33-0.67]), while low female-female overlap was observed in unfed-

deworm treatments (U-D mean=0.16±0.13 [range: 0.06-0.25]; Table S3). There was no male-male overlap in fed treatments in autumn.

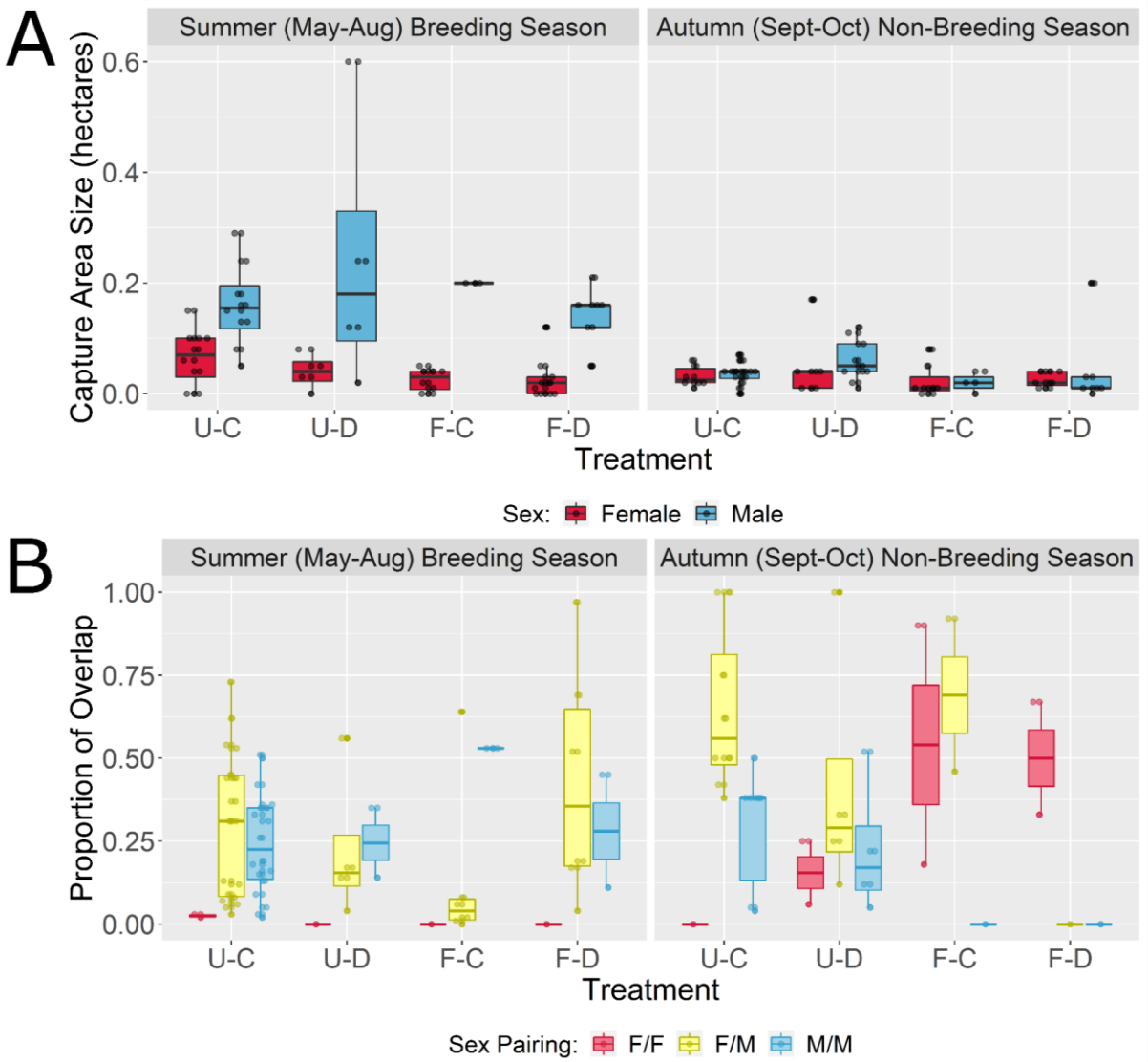

Figure 2. Summary boxplots of space use and shared space use of seasonal residents by sex and season, jittered points overlaid to show actual data values. (A) Space use (capture area size in hectares) in the summer (left panel) and autumn (right panel). Males (blue) show greater space use compared to females (red) in summer (Kruskal-Wallis test, $p<0.001$). (B) Shared space use (proportion of capture polygon overlap) in summer (left panel) and autumn (right panel). Female-female shared space use (red) is rarely observed in summer but is high in fed

treatments in autumn.

3.2 Spatial overlap networks

The June-October data used for this analysis comprised 2052 captures of 759 unique voles. All sites had at least two animals captured in each of the months in which networks were constructed, however, two sites had no edges in the June network. Networks frequently had disconnected nodes and often had multiple components. Generally, we only observed networks with all edges in a single component in the months of highest population density (Figure S5).

3.2.1 Network size was greatest in fed treatments

Network size was highly variable across months and treatments (range: 2-52 voles). Network size increased through the year in all treatments. Networks were smallest in June, peaked in August (unfed treatments) or September (fed treatments), and then decreased slightly though October (Figure 3A). Network size was moderately affected by food treatment (β=0.50, p=0.013) and by month (β=0.31, p<0.001; Table S4) with fed treatments and months later in the year having larger networks. At peak size in September, mean network size in fed treatments was 1.6-3.1x larger than unfed treatments (Table S5). Deworming treatment had a negligible effect on network size (β=-0.17, p=0.340; Table S4).

3.2.2 Network clustering metrics were similar between treatments

Network clustering metrics were visualized as a mean and standard deviation per treatment (for a description of the network metrics and their biological relevance, see Table 1). Modularity increased and became less variable within treatment from June to October (mean across treatments: June: 0.27±0.27; Oct: 0.62±0.08, Figure 3B; Table S6), indicating voles overlapped with more distinct groups of other voles as the year progressed. Mean modularity was similar between treatments in each month (Kruskal-Wallis test, p>0.12). Betweenness centralization

was low (annual mean across treatments: 0.13±0.11; Figure 3C; Table S7) and similar between treatments in all months (Kruskal-Wallis test, p>0.22), indicating overlap occurred between many unique pairs of voles and was not focused at a hub individual.

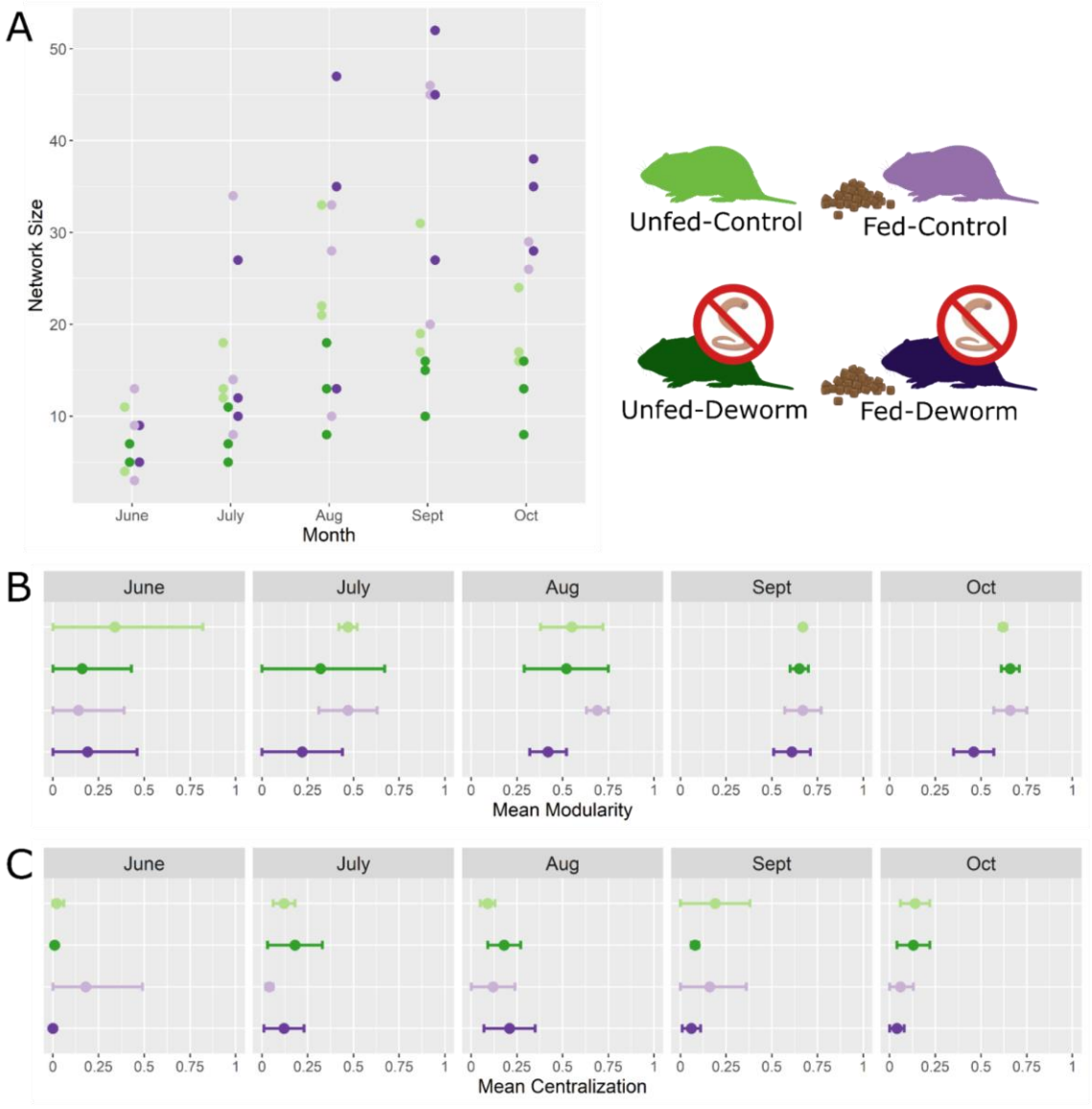

Figure 3. Network size by site and mean values of network clustering metrics by treatment: (A) Network size (number of voles) by month increased more dramatically in fed treatments (purple) compared to unfed treatments (green) and fed treatments reached a larger maximum network size. (B) Mean modularity (the clustering of nodes into highly connected groups) increased from

June to October and became less variable. (C) Mean betweenness centralization (whether the network is linear or focused at a hub) was low throughout the year. Network metrics shown per treatment: unfed-control (light green), unfed-deworm (dark green), fed-control (light purple), fed-deworm (dark purple). Error bars show standard deviation around the mean.

3.2.3 Number of spatial overlaps per vole was greater and more heterogeneous in fed treatments

Unweighted degree (the number of unique spatial overlaps between a focal vole and its neighbors) per site and month was visualized as density distributions. In these, the x-axis indicates the value of interest, and the height of the curve suggests the frequency of occurrence of that value in the population. Bimodal or multimodal distributions indicate that multiple values occur in the population at a similar frequency. Narrow distributions suggest low variation in the population values while wide distributions indicate greater variation.

Mean unweighted degree was similar between treatments in July and August (Kruskal-Wallis test, July p=0.086; August p=0.056; Figure 4; Table S8). In June, mean degree in the unfed-control treatments was different from all other treatments (Kruskal-Wallis test p<0.001; Dunn test p<0.018) but there was no difference between the other treatments (Dunn test p>0.08). Mean degree differed by treatment in September and October (Kruskal-Wallis test, Sept p<0.001; Oct p<0.001) where fed treatments had higher degree than unfed (Dunn test, Sept p<0.0013; Oct p<0.013; Figure 4; Table S8). The distribution of degree values per site varied by treatment and month. Fed treatments tended to have longer tails of degree (i.e. a few voles had a large number of overlaps) in August-October (Figure 4).

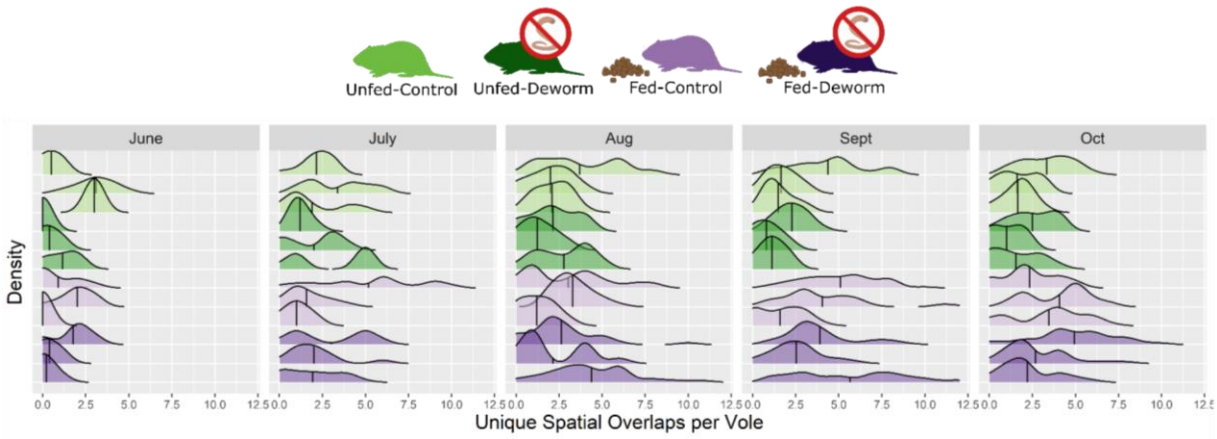

Figure 4. Density distributions of unweighted degree for each of the 12 study sites from June-October (colored by treatment, means indicated by vertical lines). Fed treatments (purple) had longer tails of degree distribution in August-October compared to unfed treatments (green).

We also explored weighted degree (edges weighted by the number of overlaps between each unique pair of voles), but trends were similar to those of unweighted degree (Supporting Information: Weighted degree; Table S9; Figure S6).

3.2.4 Super-overlappers were most numerous in fed-deworm treatments

Based on unweighted degree values, we identified 31 super-overlappers (i.e. voles that disproportionately overlapped with other voles) representing 28 unique voles (three voles were super-overlappers in two separate months) across the 12 sites from June-October (Supporting Information: Super-overlappers). Super-overlappers were not observed in unfed-control treatments and only one was observed in unfed-deworm treatments. All other super-overlappers were observed in fed treatments with 5 times as many super-overlappers in fed-deworm compared to fed-control (Figure S7). Super-overlappers were present in all months but months with the largest network sizes had the most super-overlappers (i.e. 14 super-overlappers were from September and 8 were from August, Figure S8A). Both males and females and reproductive and non-reproductive voles were super-overlappers. The number of males versus

females and reproductive versus non-reproductive voles that were considered super-overlappers were similar between fed-control and fed-deworm treatments (Fisher's exact test, male:female two-tailed p=0.34; reproductive:non-reproductive two-tailed p=0.64; Figure S8B,C; Table S10).

4 DISCUSSION

Food abundance and macroparasite infection can alter individual space use and intraspecific interactions in ways that influence pathogen transmission. By experimentally manipulating food abundance and helminth infection in voles, we quantified drivers of variation in space use and spatial overlap, and how these were modulated by season and sex. Spatial overlap frequency and heterogeneity were affected by food addition but not deworming treatment. However, the population-level clustering of overlaps was similar between treatments. Space use was influenced by season and sex, but not by food addition or deworming treatment. However, sex-based, seasonal changes in shared space use were most apparent with food addition. These findings suggest that while food abundance generally increases transmission opportunities, sex and season are important factors to determine the "who" and "when" of greatest transmission potential.

Seasonal resident vole space use was not affected by food addition or helminth removal in either summer or autumn, which may indicate similar transmission opportunities across a wide range of habitat conditions. The similarity in space use across treatments is surprising as supplemental food is generally thought to influence home range size of bank voles (Bondrup-Nielsen & Karlsson, 1985; Mazurkiewicz, 1983) though studies in other rodents have not found food to be a major factor determining home range size (Sulok et al., 2004; Wolff, 1985). However, space use did differ by sex. During the summer breeding season (May-August), resident male voles had much greater space use than resident females and male space use

was shared with both other males and females. This suggests mature males have a high potential to contribute to transmission with both male and female conspecifics during the breeding season: their large space use provides a greater potential to spread infectious material (urine, feces) across an area that is frequented by other voles. Further, this space use overlap coincides with the breeding season when activity is naturally high in the population where direct and indirect interactions with high transmission potential (e.g. mating or fighting, territory marking - respectively) are more likely to occur. In the autumn non-breeding season (September-October), both male and female space use was limited - potentially decreasing transmission opportunities - however, female-female shared space use was high in fed treatments. High population density associated with abundant food may be an important factor influencing increased shared space use among females, particularly in the non-breeding season when mature females are less territorial (Stenseth et al., 1988). This increased overlap could provide increased transmission opportunities among females. Thus, while we observed males were important to transmission opportunities during the breeding season regardless of food abundance, when food abundance is high, females may become more important for transmission in the non-breeding season. Taken together, our space use findings suggest that seasonal and sex-based differences in animal space use and shared space use may contribute to variable patterns of transmission such as seasonal peaks in transmission or changes in which individuals contribute most to transmission opportunities (Altizer et al., 2006; Hirsch et al., 2016).

These conclusions about space use were generated from a subset of the vole population that was captured frequently enough to conduct home range analyses. While the interactions of seasonal residents with established home ranges likely account for many of the transmission-relevant interactions in the population (particularly during the breeding season), the role of juveniles or transient individuals may be overlooked. If, for example, juvenile voles have

markedly different space use than mature adults, this could minimize the difference in vole space use between the breeding and non-breeding seasons, potentially providing high and consistent opportunities for environmental transmission throughout the year. Incorporating other monitoring techniques along with capture-mark-recapture methods (e.g. stationary proximity loggers placed on the grid to record the PIT tags of animals that pass within a specified distance) would provide additional locations per individual and would bolster our understanding of the space use of all animals in the population.

Spatial overlap between voles was strongly affected by food addition but there was no clear effect of deworming treatment. Food addition resulted in larger networks with more voles than unfed treatments and voles in fed treatments had more spatial overlaps (higher mean degree) than voles in unfed treatments. Previous studies have attributed short-term increases in rodent populations with food addition to increased immigration rather than recruitment (Prevedello et al., 2017) which aligns with the understanding that abundant food attracts animals to an area. This influx of animals could lead to an increased rate of pathogen introduction to areas of high food abundance. Considering heterogeneous environments as a metapopulation model, areas of high food abundance may play an important role in both concentrating animals, interactions, and pathogens and also being a source of infected dispersers, potentially spreading pathogens more broadly on landscape (Becker et al., 2018). Networks in fed treatments also had a greater number of super-overlappers than unfed treatments, showing that heterogeneity in the number of overlaps increased in populations with abundant food - and the combination of food addition and helminth removal may further increase the number of super-overlappers. Heterogeneity in degree is a common trait of populations and extreme heterogeneity (i.e. the presence of super-spreaders) has been identified as a key feature creating variability in whether diseases spread rapidly or fade out in a population (Lloyd-Smith et al., 2005; Meyers et al., 2005). While the heterogeneity in unweighted degree observed in this study (Supporting Information: Dispersion

parameter (k value) estimates; Table S11) is not as extreme as that of documented superspreader events (Lloyd-Smith et al., 2005), the observed heterogeneity in spatial overlaps per vole does suggest that individual voles do not contribute equally to transmission opportunities and certain individuals could be more important for transmission than others, particularly when food is abundant.

5 CONCLUSIONS

This study has provided empirical evidence of the effects of food abundance and macroparasite infection on space use and spatial overlap in wild rodent populations. Field studies investigating the effects of environmental and individual variation on pathogen transmission are limited, thus this work addresses a gap in our understanding of factors influencing wildlife disease dynamics. Our findings suggest increased transmission opportunities with high food abundance, though which individuals contribute most to transmission may vary by sex and season, particularly when food abundance and population density are high. We have inferred potential consequences for transmission, aiding future research that pairs measures of space use and spatial overlap with infection prevalence to test how these spatial metrics predict transmission opportunities. As such, this research provides necessary, empirical evidence for the effects of environmental and individual variation on animal spatial patterns and suggests associated consequences for pathogen transmission, ultimately helping to better understand and control infectious diseases in animal populations.

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CONFLICT OF INTEREST

The authors claim no conflict of interest.

AUTHOR CONTRIBUTIONS

Kris Forbes and Sarah Budischak (lead), Meggan Craft and Richard Hall (supporting) conceived the ideas, designed methodology, and secured the funding; Shannon Kitchen, Janine Mistrick, Jasmine Veitch, Samuel Clague (lead), and Brent Newman (supporting) collected the data; Janine Mistrick analyzed the data, created visualizations, and led the writing of the manuscript under the mentorship of Meggan Craft. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data will be made available through the Dryad Digital Repository upon manuscript acceptance. Code is available in a GitHub repository (github.com/jmistrick/vole-spatial) which will be archived on Zenodo upon manuscript acceptance.