

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/374693215>

The effect of urbanization and behavioral factors on coyote net displacement and its implications for seed dispersal

Preprint · March 2023

DOI: 10.21203/rs.3.rs-2743672/v2

CITATIONS

0

READS

74

4 authors, including:



Tiziana A. Gelmi Candusso

University of Toronto

13 PUBLICATIONS 118 CITATIONS

SEE PROFILE



Brent Patterson

Trent University

142 PUBLICATIONS 3,571 CITATIONS

SEE PROFILE



Marie-Josée Fortin

University of Toronto

452 PUBLICATIONS 29,155 CITATIONS

SEE PROFILE

The effect of urbanization and behavioral factors on coyote net displacement and its implications for seed dispersal

Tiziana A. Gelmi-Candusso (✉ tiziana.gelmicandusso@utoronto.ca)

University of Toronto

Tyler J. Wheeldon

Ontario Ministry of Natural Resources and Forestry

Brent R. Patterson

Ontario Ministry of Natural Resources and Forestry

Marie-Josée Fortin

University of Toronto

Research Article

Keywords:

Posted Date: October 12th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2743672/v2>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

The effect of urbanization and behavioral factors on coyote net displacement and its implications
for seed dispersal

Tiziana A. Gelmi-Candusso^{1*}, Tyler J. Wheeldon², Brent R. Patterson², Marie-Josée Fortin¹

¹Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

²Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, Canada

*** Correspondence:**

Tiziana A. Gelmi Candusso. tiziana.gelmicandusso@utoronto.ca . Orcid: 0000-0003-0990-5255

Keywords: cityscape, net displacement, mesopredators, coyotes, zoochory, carnivore, seed dispersal, cities

Acknowledgements

We acknowledge the contribution of all employees at the Ontario Ministry of Natural Resources and Forestry and the Toronto Wildlife Centre involved in collaring and tracking coyotes in the GTA, including Ashley McLaren and Andrew Wight. We acknowledge the German Research Foundation (DFG) for supporting this project through the research fellowship GE 3103/1-1 and Marie-Josée Fortin NSERC Canada Research Chair in Spatial Ecology.

Abstract

Coyotes (*Canis latrans*) may be important seed dispersal vectors in urban areas, given their omnivorous diet and wide-ranging movement patterns potentially able to bypass fragmentation. Yet, fragmentation itself, anthropogenic food sources, and human activity can limit their natural movement patterns. Previous research has found urbanization limits movement range across mammals; however, it remains unclear the degree to which this may cascade into seed dispersal as seed retention time also plays an important role in seed dispersal distance. Additionally, social and temporal changes in behavior influence coyote movement patterns, likely interacting with the effect of urbanization on net displacement and, consequently, seed dispersal. We used GPS telemetry data to analyze the effect of urbanization on coyote net displacement ($n=94$ individuals), in interaction with social and temporal factors, for a series of seed retention timeframes. We found that urbanization led to shorter net displacement in comparison to rural areas. The effect of urbanization increased with increasing seed retention timeframe and disproportionately affected long-distance seed dispersal. Seasonality influenced the effect of urbanization to a smaller extent than social status. Social status had a strong interaction effect, as urbanization negatively impacted the net displacement of transient and dispersing coyotes but had a negligible influence on resident coyotes. Territoriality was likely the main limiting factor for the latter, whereas the former, which were wider ranging, were likely most affected by the landscape configuration. In terms of seasonality, climate seasons explained variability in the data better than biological seasons, where net displacement remained more stable across climate seasons in urban areas, as opposed to rural areas, where net displacement increased during winter and decreased during summer. Interestingly, despite the urban effect, coyote net displacement varied across social statuses and seasons in both landscape types, suggesting coyotes can provide a heterogeneous seed dispersal contribution within and across plant species. Future research on fine-scale movement patterns and scat analysis is needed to better understand the cascading effects of decreased long-distance net displacements on urban plant populations.

38 1. Introduction

39 Urban areas are characterized by isolated remnants of vegetation patches scattered across a developed matrix
40 composed of varying degrees of built infrastructure and human activity. The presence of animals with large movement
41 capabilities and the ability to bypass the inhospitable developed landscape found in urban areas is key for maintaining
42 seed dispersal between remnant vegetation patches. While birds are effective seed dispersers in urban areas and can
43 travel for long distances using small patches as stepping stones (Han and Keeffe 2019), their gape size and shape
44 limits the range of fruits ingested (Mazer and Wheelwright 1993). In contrast, mammals can ingest larger seed species
45 in greater quantities and retain them for longer periods of time, given their body size and digestive tracts (Willson
46 1993). Mammals can also disperse seeds that attach to their fur (Hovstad et al. 2009) and those acting as predators can
47 also disperse seeds previously eaten by their prey (Hämäläinen et al. 2017). Hence, mammals are potential seed
48 dispersers for a wider range of plant species within the urban environment, and may be key in determining the
49 composition of plant communities in urban forests, as in other environments (Melo et al. 2010).

50 Nonetheless, anthropogenic footprint and built infrastructure have been found to shorten movement ranges
51 of mammals in urban landscapes, in comparison to those in rural and forested landscapes. These shorter movement
52 ranges caused by the anthropogenic footprint and built infrastructure have been suggested to have implications for
53 seed dispersal distance (Tucker et al. 2018). However, seed dispersal distance is not only the direct result of movement
54 range, but the combined result of animal movement and seed retention time (Nield et al. 2020). In addition, the
55 movement range of mammals that are socially complex and subject to seasonality, may be further altered by behavior
56 changes associated with social dynamics, breeding and pup-rearing requirements and resource availability
57 (Franckowiak et al. 2019; Larson et al. 2020; Ellington et al. 2020). Therefore, a more in-depth analysis of how
58 urbanization alters movement ranges of mammals, considering their behavioral complexity, and the retention time of
59 the seeds they transport, is needed to further understand the ecological implications of urbanization on seed dispersal.

60 In this study we used coyotes (*Canis latrans*) as a model species, given their wide movement ranges (Gehrt
61 et al. 2009), and their remarkable adaptation to both urban and rural areas. Coyotes have been identified as an effective
62 seed disperser for several plant species, via both primary ingestion of wild and farmed fruits (Rubalcava-Castillo et
63 al. 2020), secondary ingestion of seeds through prey (Sarasola et al. 2016; Hämäläinen et al. 2017), and through
64 epizoochory, including diaspores of grass and bushes (Quick et al. 2017). Furthermore, coyote movement patterns are

strongly influenced by their social dynamics, whereby group-living resident coyotes partition the landscape through territoriality, while solitary transient and dispersing coyotes traverse the landscape between territories (Kamler and Gipson 2000; Mitchell et al. 2015). Temporal dynamics also influence coyote movement patterns, following breeding, pup-rearing, and dispersal activity, and climate-driven changes in resource and shelter availability (Sasmal et al. 2019).

We investigated differences in coyote net displacement over four seed retention timeframes, reflecting their diverse seed dispersal modes. To quantify net displacement, we used telemetry data from GPS-collared coyotes ($n=94$ individuals) in urban and rural landscapes in southern Ontario, Canada. We integrated into the analysis the effect of social status (i.e., resident, transient, dispersing), biological season (i.e., breeding, pup-rearing, dispersal), and climate season (i.e., spring, summer, autumn, winter). We hypothesized that (1) reduced habitat availability, increased anthropogenic food availability, and increased encampment behavior (Ellington and Gehrt 2019) would increase movement tortuosity in urban areas, leading to shorter net displacement over time, affecting longer-retained seeds the most (Figure 1a). (2) Non-territorial coyotes, given their larger movement ranges and predominantly linear movements (Webster et al. 2022), would be more affected by urbanization, leading to increased differences in net displacement between landscape types for all seed retention timeframes (Figure 1b). (3) Seasonal changes resulting in biological constraints on coyote movement (i.e., pup-rearing season) (Kitchen et al. 1999) would decrease differences in net displacement between landscape types, and those biological seasons resulting in greater movement requirements (i.e., dispersal and breeding season) would increase differences in net displacement between landscape types (Figure 1c.). (4) Harsher climate seasons would lead to increased differences in net displacement between landscape types, given more stable resource and shelter availability in urban areas (Sugden et al. 2021) (Figure 1d).

Ultimately, this study aims to explore the effect of urbanization on the scale of seed dispersal by coyotes for seed species with different retention time ranges, considering their social and temporal behavioral complexity, and identify intraspecific differences in their seed dispersal contributions in both urban and rural landscapes.

2. Methods

2.1. Study area

Our study area included the Greater Toronto Area (GTA), a metropolitan region, and the surrounding rural areas within southern Ontario (Figure 2). The largest urban landscape in the study area, the GTA, contains forested river

valleys crossing transversally over high-density and medium-density residential areas. These forested river valleys are well-suited habitats for coyotes and connect the lakeshore with the green belt, a large protected natural area surrounding the GTA. Coyotes also utilize other green areas in the GTA, such as parks, cemeteries, golf courses, and backyards, similar to other mesopredators in the area (Rosatte and Allan 2009). The rural landscape in the study area is composed mainly of plantations, agricultural fields, orchards, densely wooded vegetation, and scattered small towns.

To distinguish between urban and rural landscapes, we defined urbanization degree following the Global Human Settlement project (Florczyk et al. 2019), whereby an urban area was characterized by contiguous grid cells containing a minimum of 1,500 people per km² or a minimum of 50% share of built-up land, totaling a minimum of 50,000 inhabitants. Following this definition, all areas outside urban centers were considered rural, which included the following landcover classes: agricultural land, small towns, and low-density human settlements.

2.2 Model species

Coyotes have adapted well to cities by fine-tuning their space-use to the presence of humans while making use of the large availability of resources within. In general, diurnally, coyotes encamp in forested or enclosed urban green areas (Ellington and Gehrt 2019), while nocturnally, they make use of residential areas (Thompson et al. 2021) and vegetated areas (Murray and St Clair 2017; Wurth et al. 2020), potentially moving daily between source areas of non-native plant species and forested land, where they deposit scats.

Coyotes have been found to have important contributions to seed dispersal of native species in temperate regions, e.g., Bearberries (*Arctostaphylos glauca*), a native species to the Canadian Pacific coast, and Prickly cactus (*Opuntia* spp.) (Silverstein 2005), potentially including the Eastern prickly-pear cactus (*Opuntia humifusa*), an endangered species of prickly pear endemic to southern Ontario. They can also be important in the spread of invasive species such as Rose hip (*Rosa rugosa*), for which seeds have been consistently found in their scats (Garbary et al. 2013). Nonetheless, with opportunistic omnivorous diets, and high germination rates of the seeds they deposit (Silverstein 2005), the plant species effectively dispersed by coyotes are possibly numerous.

2.3 Movement analysis

We used telemetry data from 94 coyotes that were captured, radio-collared, and released within southern Ontario (Figure 2, Table S1). The coyotes were fitted with GPS collars by the Ontario Ministry of Natural Resources and Forestry and the Toronto Wildlife Centre between 2010 and 2021, following methods described by Wheeldon (2020) and Thompson et al. (2021). GPS collars (Wildcell SG, Lotek Wireless Inc., Newmarket, Ontario) recorded locations at variable fix rates, but location data were rarefied to a constant fix rate of 3 hours. We estimated net displacement at each timepoint by measuring the Euclidean distance between contiguous GPS datapoints (Figure 3).

2.4 Behavioral factors

We included the interaction of factors influencing coyote behavior: social status, biological season, and climate season. (1) Social status distinguished coyotes following their movement patterns, i.e., (i) resident, if coyote used the same area continuously for ≥ 3 months; (ii) transient, if coyote did not use the same habitat fragments continuously; and (iii) dispersing, if the coyote was traveling in a unidirectional mode. Coyotes with different social statuses were evenly distributed across urban and rural landscapes. (2) Biological seasons included time periods when coyotes are known to breed (January to April), rear pups (May to August), or disperse (September to December); these may not be applicable for every coyote, but they serve to account for anticipated behavioral changes throughout the biological year that might affect net displacement (Sasmal et al. 2019). (3) Climate seasons included time periods defining temperature changes affecting fruit production, resource availability, and foliage acting as shelter: spring (April to June), summer (July to September), autumn (October to December), and winter (January to March). For this, we noted the characteristics at the start point of the movement trajectory and discarded any potential seed dispersal events with differing characteristics between the start point and endpoint.

2.5 Seed dispersal analysis

To understand the implications of changes in net displacement on seed dispersal, we analyzed coyote net displacement over time within four seed retention timeframes (Gelmi-Candusso et al. 2019). For this, we assumed that coyote net displacement within a seed retention timeframe is a potential seed dispersal event, with the start point of each step being a potential seed ingestion/attachment event, and the endpoint of each step being a potential seed

deposition/release event (Figure 3). To reduce autocorrelation between estimates obtained from one movement trajectory, we averaged the net displacements occurring within an equal timeframe for each trajectory.

The seed retention timeframes analyzed herein considered that coyotes can disperse seeds through both epizoochory, whereby seeds may stay attached to coyote fur for up to two days, and endozoochory, whereby seeds reside in the gastrointestinal tract for up to three days in canids (i.e., gut-passage time) (Graae et al. 2004; Hernot et al. 2005; Varela and Bucher 2006; Quick et al. 2017; Draper et al. 2021). Thus, the range of seed retention timeframes included (i) 0–6 hrs, (ii) 6–24 hrs, (iii) 24–48 hrs, and (iv) 48–72 hrs. Steps beyond the 72 hrs time range from a start point were not included in the analysis, as these go beyond seed retention time ranges found in the literature for carnivore seed dispersal.

2.6 Statistical analysis

We analyzed the effect of urbanization (i.e., landscape type) on net displacement within each seed retention timeframe, with individual variation as a random effect, using a generalized linear mixed model (GLMM). We log-transformed the response variable, and followed a gamma distribution using the `glmer()` function from the *lme4* package (Bates et al. 2015) in R (R Core Team 2013).

We integrated the effect of factors influencing behavior (i.e., social status, biological season, and climate season) by analyzing net displacement differences within each factor level in interaction with landscape type using a GLMM. To avoid double interaction factors, we ran the models for each seed retention timeframe. The GLMMs followed a gamma regression with log-transformed data and accounted for individual variation as a random effect. Given the partial temporal overlap between biological and climate seasons, we ran these separately and compared both models, along with the social status model, using the Akaike information criterion (AIC) to evaluate which seasonal scale better explained the variability seen in our data (Akaike 1974) using `aictab()` from the *AICcmodavg* package (Mazerolle 2020) in R (R Core Team 2013).

To understand the potential seed dispersal kernels (i.e., probability density of seed dispersal with increasing distance from source), including how far most seeds would be dispersed in the different landscapes and how far those rare long-distance seed dispersal events would reach, we quantified coyote net displacement in terms of quantiles (5%, 50%, 95%). We considered net displacements in the top 95% as potential long-distance seed dispersal events (Cain et

al. 2000). We used the `ggpredict()` function from the *ggeffects* package (Lüdtke 2018), in R (R Core Team 2013), which computes predicted values for all possible levels and values from the models' predictors, to predict net displacement across all our conditions analyzed and thus determine potential seed dispersal distance. While the relationship between net displacement and seed dispersal distance may also be influenced by the complex number of factors determining where a seed will be deposited after being retained, these predictions are meant for comparing the potential seed dispersal distance across all the conditions tested under a constant setting. Future research using scat analysis and seed tracking should further analyze effective seed dispersal distance (Schupp et al. 2010; Gelmi-Candusso et al. 2019) and any potential seed aggregation patterns following coyote scent-marking behavior (Barrette and Messier 1980).

3. Results

As expected, the difference in net displacement between urban and rural landscapes was significant for all seed retention timeframes and increased with increasing seed retention timeframe. Based on the GLMM output, coyotes in urban landscapes had a greater decrease in net displacement with increasing seed retention timeframe than coyotes in rural landscapes (Table S2). Interestingly, the main urban-rural difference on all seed retention timeframes was seen for net displacements in the top 95%, i.e., the potential long-distance seed dispersal events. For these, the difference between urban and rural landscapes increased exponentially with increasing seed retention timeframe (orange lines, Figure 4), in comparison to net displacements in the lower 50%, which increased linearly with increasing seed retention timeframe (purple and green lines, Figure 4). For long-distance seed dispersal events, the difference between urban and rural environments doubled for >24 hours seed retention timeframes, as seed dispersal distance in urban landscape reached a plateau at 4–4.5km after 24-hour seed retention, while seed dispersal distance in rural environment kept increasing with seed retention timeframe, reaching 7.5km at the 24–48 hour retention timeframe and almost 10km at the 72-hour retention timeframe.

Our statistical analysis including an interaction component showed the effect of urbanization on net displacement was strongly influenced by social status. Dispersing coyotes ($n=4$ individuals) were the most affected by urbanization, whereby they exhibited a significant 56–69% decrease in net displacement in urban areas (Figure 5, Table S2.1), and they were also the main drivers of potential long-distance seed dispersal events in both landscape types (Table 1). Transient coyotes ($n=16–43$ individuals) were also affected by urbanization, whereby they exhibited

a significant 15–19% decrease in net displacement in urban areas (Figure 5, Table S2.1). The urban-rural difference in net displacement increased linearly with seed retention timeframe for transient coyotes and increased exponentially for dispersing coyotes (Figure 5). As a result, dispersing coyotes had comparable net displacement to transient coyotes in urban areas, including for longer seed retention timeframes, leading to similar maximum potential seed dispersal distance. In contrast, resident coyotes ($n=23\text{--}43$ individuals) did not have significant differences in net displacement between landscape types, and this was the case for all seed retention timeframes, whereby they exhibited a 0–8% decrease in net displacement in urban areas (Figure 5, Table S2.1).

Biological seasons influenced net displacement on all seed retention timeframes but did not influence the difference in net displacement between urban and rural landscapes, as the decrease in urban areas ranged between 24–39%, comparable to that found in the landscape-only model. The shortest net displacement was observed during the pup-rearing season, in both landscape types and on all retention timeframes (Table S3). In terms of urbanization effect, the largest and smallest differences in net displacement between urban and rural landscapes were seen during breeding season (38–39% decrease in urban areas) and pup-rearing season (24–29% decrease in urban areas), respectively (Table S2.1). As with the landscape-only model, the difference in net displacement between urban and rural landscapes increased with increasing seed retention timeframe for all biological seasons, albeit at a lower rate for pup-rearing season (Figure 5, Table S3).

In terms of climate seasons, coyotes in rural areas had the greatest net displacement during winter and the shortest during summer, while in urban areas, net displacement remained stable across climate seasons (Figure 5). Therefore, the largest and smallest differences in net displacement between urban and rural landscapes were seen during winter (39–42% decrease in urban areas) and summer (18–26% decrease in urban areas), respectively (Table S2.1). This difference in net displacement between urban and rural landscapes increased with increasing seed retention timeframe (Figure 5, Table S3). Biological and climate seasons partially overlapped temporally, and both had a strong effect on net displacement across seed retention timeframes; however, AIC differences between the models (Table S2.2) suggest climate seasonality better explained the variability in our data for all seed retention timeframes.

4. Discussion

Our results confirm our main hypothesis, as we found a reduction in the net displacement of coyotes in urban areas, whereby this reduction became stronger with increasing time scale, in line with previous global findings on terrestrial mammal movement (Tucker et al. 2018). The reduction in net displacement in urban landscapes, as our hypothesis predicted, resulted in a reduction in seed dispersal distance, particularly for long-distance seed dispersal events (top 95% distance quantile), halving the overall potential of coyotes as long-distance seed dispersal vectors. Furthermore, we found the impact of urbanization on seed dispersal distance increased as seeds were retained for longer, as would be the case for seeds with longer gut passage times or epizoochorous seeds. Our subsequent hypothesis regarding the interaction effect of social status and urbanization on net displacement was confirmed. Urbanization disproportionately affected the seed dispersal potential of transients and dispersing coyotes (i.e. non-territorial coyotes), which were the main drivers of long-distance movements, while urbanization did not affect at all the seed dispersal potential of resident coyotes which remained at a maximum of ~4 km in both landscape types. Biological and climate season both influenced net displacement across landscapes, however, our hypothesis on whether these factors interacted with the urbanization effect was confirmed for climate season but not biological season, as while the difference between urban and rural landscapes moderately increased during winter and decreased during summer, it remained constant across biological seasons.

Decreased forest cover and increased spatial aggregation of vegetation created by fragmentation has led to shorter mean seed dispersal distance by mesopredators in other landscapes (Herrera et al. 2016), and these are landscape characteristics also found in urban areas, likely explaining our findings. Furthermore, in urban landscapes, the availability of anthropogenic food sources and rodent populations in residential areas may also reduce the foraging travel distance to areas surrounding the habitat patches, potentially reducing the need to travel between habitat fragments. In non-urban fragmented landscapes, the presence of movement corridors can reduce the difference in seed dispersal distance between fragmented and continuous habitats (Herrmann et al. 2016), as these create a directed form of movement between green patches, bypassing landscape fragmentation. Similarly, improving landscape connectivity by maintaining coyote movement corridors within cities (Gelmi-Candusso et al. in press) may help bypass the inhospitable landscape in urban areas, thereby alleviating the effect of urbanization on coyote net displacement and its cascading effect on seed dispersal (Uroy et al. 2019).

Interestingly, our analysis found that urbanization had little effect on the difference in net displacement of resident coyotes between urban and rural landscapes. These results suggest that, in our study area, the main limiting

factor for urban and rural resident coyotes' net displacement was their territory, rather than landscape fragmentation and configuration. However, this might not be the case for resident coyotes living in cities with fewer or smaller green spaces. The reason is that, in our study area the forested river valleys travelling across the urban matrix provide large areas where resident coyotes can thrive (Figure 2a and Figure S2a, Thompson et al. 2021) and the network of railways and power lines provide corridors facilitating their movement between habitat patches (Gelmi-Candusso et al. in press). These factors potentially reduce the difference in net displacement between urban and rural landscapes for resident coyotes in our study area. In contrast to resident coyotes, urbanization had a strong effect on the net displacement of transient and dispersing coyotes (i.e., non-territorial coyotes), suggesting landscape configuration in urban areas to be a main constraining factor for their net displacement, as these coyotes have wider movement ranges and utilize more inhospitable land, such as smaller suboptimal urban green fragments and residential areas (Newsome et al. 2015; Mitchell et al. 2015; Thompson et al. 2021). This decrease in net displacement strongly reduced the long-distance seed dispersal potential of both groups of non-territorial coyotes in urban areas, in particular of those actively dispersing individuals. Albeit with a low sample number of four individuals actively dispersing across both urban and rural landscapes, given the intrinsic low probability of collaring dispersing individuals, our results suggest that urbanization hinders the movement of a key demographic of mammals involved in long-distance seed dispersal. These findings also suggest that intraspecific differences in wide movement ranges observed in non-urban settings do not automatically translate into urban settings as urbanization may limit the maximum net displacement of individuals, regardless of their movement disposition. A reduction in long distance seed dispersal can lead to negative implications for plant adaptation to climate change and the restoration of anthropogenically disturbed areas (Cain et al. 2000; Nathan et al. 2008; Mokany et al. 2014).

We found temporal changes in coyote net displacement following biological and climate seasonality. In both landscape types, net displacement decreased during summer and pup-rearing seasons in comparison to the other seasons. Because there is a partial overlap between biological and climate seasons, in particular between summer and pup-rearing seasons, it is unclear whether the reduced net displacement observed was due to movement restrictions while caring for dependent pups or an abundance of available resources (Mueller et al. 2011). However, given the model comparison results (Table S2.1), our findings suggest climate seasons might be a more important factor for coyote net displacement. While the urban-rural difference in coyote net displacement was considerably less affected by seasonality than when considering coyote social status, the difference in net displacement between urban and rural

landscapes was twice as large during the harshest season (i.e., winter), than during summer. These findings likely reflect the more constant availability and widespread abundance of resources in urban areas throughout the year, the ability of coyotes to exploit anthropogenic food sources and yard fruit availability, and a higher abundance and richness of prey species exploiting urban greenspace, leading to a wider dietary breadth in urban coyotes (Murray et al. 2015; Hansen et al. 2020; Sugden et al. 2021).

Coyote heterogeneous contribution to seed dispersal

Our results showed differences in coyote net displacement across seasons and social statuses in both landscape types, albeit to a lesser extent within urban areas. The seasonal differences in coyote net displacement increase the plant specificity in their seed dispersal contribution, providing different seed dispersal range to different plants following their specific phenology and seasonality in fruit production, suggesting future studies should focus on plant species-specific seed dispersal, especially in rural areas. Most importantly, the intraspecific and seasonal diversity in coyote movement patterns, habitat use (Kamler and Gipson 2000), and food consumption (Bartel and Orrock 2022) create functional differences in the seed dispersal kernels coyotes create. A heterogeneous array of seed dispersal kernels provide plant species with different movement pathways and diverse microhabitats for deposition, and have been found to be key in habitat regeneration (Gonzalez-Varo et al. 2013; Escribano-Avila et al. 2014), suggesting an important role of coyotes and likely other wide-ranging omnivore predators in urban habitat renaturalization.

5. Conclusion

Urbanization limited the net displacement of non-territorial coyotes, had a stronger effect for seeds with longer retention times, and predominantly affected long-distance seed dispersal events. Maintaining animal movement between vegetated fragments by enhancing connectivity is a crucial factor in supporting seed dispersal by terrestrial wildlife in urban areas. Our study also suggests coyotes have a high likelihood of providing an intraspecific heterogeneous contribution to seed dispersal, given their complex social dynamics and biological/climate-driven seasonality in their movement patterns, indicating the potential species-specific effect of seed dispersal by coyotes. Future research identifying seed species dispersed in temperate climates through scat analysis, tracking seeds to quantify effective seed dispersal distance, and defining urban foraging areas through behavioral state analysis, is needed to further understand the ecological implications of seed dispersal by coyotes, their impact in terms of spread of invasive species and their contribution to urban forest biodiversity.

6. Declarations

Author Contributions

T.A.G.C. conceived the study, designed the model and the computational framework, implemented the model, analyzed the data, drafted the manuscript, and designed the figures. T.J.W. and B.R.P. collected and curated the coyote tracking data and provided comments and edits on the manuscript. M-J.F. supervised the development and findings of this work and contributed to the writing of the manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethics approval

Ethics approval was obtained to conduct live-trapping and collaring.

Availability of data and code

The net displacement data will be deposited in Dryad upon acceptance of the manuscript.

Code availability

Code available on the corresponding author's Github.

7. References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Barrette C, Messier F (1980) Scent-marking in free-ranging coyotes, *Canis latrans*. *Animal Behaviour* 28:814–819. [https://doi.org/10.1016/S0003-3472\(80\)80141-2](https://doi.org/10.1016/S0003-3472(80)80141-2)
- Bartel SL, Orrock JL (2022) The important role of animal social status in vertebrate seed dispersal. *Ecology Letters* 00:1–16. <https://doi.org/10.1111/ele.13988>

326 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using
327 **lme4**. J Stat Soft 67:. <https://doi.org/10.18637/jss.v067.i01>

328 Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations.
329 American Journal of Botany 87:1217–1227. <https://doi.org/10.2307/2656714>

330 Draper JP, Atwood TB, Beckman NG, et al (2021) Mesopredator frugivory has no effect on seed
331 viability and emergence under experimental conditions. Ecosphere 12:e03702.
332 <https://doi.org/10.1002/ecs2.3702>

333 Ellington EH, Gehrt SD (2019) Behavioral responses by an apex predator to urbanization. Behav
334 Ecol 30:821–829. <https://doi.org/10.1093/beheco/arz019>

335 Ellington EH, Muntz EM, Gehrt SD (2020) Seasonal and daily shifts in behavior and resource
336 selection: how a carnivore navigates costly landscapes. Oecologia 194:87–100.
337 <https://doi.org/10.1007/s00442-020-04754-1>

338 Escribano-Avila G, Calvino-Cancela M, Pias B, et al (2014) Diverse guilds provide
339 complementary dispersal services in a woodland expansion process after land
340 abandonment. J Appl Ecol 51:1701–1711. <https://doi.org/10.1111/1365-2664.12340>

341 Florczyk A, Corbane C, Schiavina M, et al (2019) GHS-UCDB R2019A - GHS Urban Centre
342 Database 2015, multitemporal and multidimensional attributes

343 Franckowiak GA, Perdicas M, Smith GA (2019) Spatial ecology of coyotes in the urbanizing
344 landscape of the Cuyahoga Valley, Ohio. PLOS ONE 14:e0227028.
345 <https://doi.org/10.1371/journal.pone.0227028>

346 Garbary DJ, Hill NM, Miller AG (2013) Invasion of *Rosa rugosa* (Rugosa Rose)
347 into coastal plant communities of Brier Island, Nova Scotia. The Canadian Field-
348 Naturalist 127:319–331. <https://doi.org/10.22621/cfn.v127i4.1513>

349 Gehrt SD, Anchor C, White LA (2009) Home Range and Landscape Use of Coyotes in a
350 Metropolitan Landscape: Conflict or Coexistence? Journal of Mammalogy 90:1045–
351 1057. <https://doi.org/10.1644/08-MAMM-A-277.1>

352 Gelmi-Candusso TA, Bialozyt R, Slana D, et al (2019) Estimating seed dispersal distance: A
353 comparison of methods using animal movement and plant genetic data on two primate-
354 dispersed Neotropical plant species. Ecology and Evolution 9:8965–8977.
355 <https://doi.org/10.1002/ece3.5422>

356 Gelmi-Candusso TA, Chin A, Thompson C, et al (in press) Dynamic connectivity assessment for
357 a terrestrial predator in a metropolitan region. Frontiers in Ecology and the Environment.
358 <https://doi.org/10.1002/fee.2633>

359 Gonzalez-Varo JP, Lopez-Bao JV, Guitian J (2013) Functional diversity among seed dispersal
360 kernels generated by carnivorous mammals. J Anim Ecol 82:562–571.
361 <https://doi.org/10.1111/1365-2656.12024>

362 Graae BJ, Pagh S, Bruun HH (2004) An Experimental Evaluation of the Arctic Fox (*Alopex*
 363 *lagopus*) as a Seed Disperser. Arctic, Antarctic, and Alpine Research 36:468–473.
 364 [https://doi.org/10.1657/1523-0430\(2004\)036\[0468:AEEOTA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2004)036[0468:AEEOTA]2.0.CO;2)

365 Hämäläinen A, Broadley K, Droghini A, et al (2017) The ecological significance of secondary
 366 seed dispersal by carnivores. Ecosphere 8:e01685. <https://doi.org/10.1002/ecs2.1685>

367 Han Q, Keeffe G (2019) Stepping stones: Assessing the permeability of urban greenspaces to
 368 climate-driven migration of trees. SASBE 9:246–257. [https://doi.org/10.1108/SASBE-](https://doi.org/10.1108/SASBE-12-2018-0065)
 369 12-2018-0065

370 Hansen CP, Parsons AW, Kays R, Millsbaugh JJ (2020) Does Use of Backyard Resources
 371 Explain the Abundance of Urban Wildlife? Frontiers in Ecology and Evolution 8:

372 Hernot DC, Biourge VC, Martin LJ, et al (2005) Relationship between total transit time and
 373 faecal quality in adult dogs differing in body size. Journal of Animal Physiology and
 374 Animal Nutrition 89:189–193. <https://doi.org/10.1111/j.1439-0396.2005.00544.x>

375 Herrera JM, Teixeira I de S, Rodriguez-Perez J, Mira A (2016) Landscape structure shapes
 376 carnivore-mediated seed dispersal kernels. Landsc Ecol 31:731–743.
 377 <https://doi.org/10.1007/s10980-015-0283-4>

378 Herrmann JD, Carlo TA, Brudvig LA, et al (2016) Connectivity from a different perspective:
 379 comparing seed dispersal kernels in connected vs. unfragmented landscapes. Ecology
 380 97:1274–1282. <https://doi.org/10.1890/15-0734.1>

381 Hovstad KA, Borvik S, Ohlson M (2009) Epizoochorous seed dispersal in relation to seed
 382 availability - an experiment with a red fox dummy. J Veg Sci 20:455–464.
 383 <https://doi.org/10.1111/j.1654-1103.2009.01049.x>

384 Kamler JF, Gipson PS (2000) Space and habitat use by resident and transient coyotes. Can J Zool
 385 78:2106–2111. <https://doi.org/10.1139/z00-153>

386 Kitchen AM, Gese EM, Schauster ER (1999) Resource partitioning between coyotes and swift
 387 foxes: space, time, and diet. Can J Zool 77:1645–1656. <https://doi.org/10.1139/z99-143>

388 Larson RN, Brown JL, Karels T, Riley SPD (2020) Effects of urbanization on resource use and
 389 individual specialization in coyotes (*Canis latrans*) in southern California. PLOS ONE
 390 15:e0228881. <https://doi.org/10.1371/journal.pone.0228881>

391 Lüdecke D (2018) ggeffects: Tidy Data Frames of Marginal Effects from Regression Models.
 392 JOSS 3:772. <https://doi.org/10.21105/joss.00772>

393 Mazer SJ, Wheelwright NT (1993) Fruit size and shape: Allometry at different taxonomic levels
 394 in bird-dispersed plants. Evol Ecol 7:556–575. <https://doi.org/10.1007/BF01237821>

395 Mazerolle MJ (2020) Model selection and multimodel inference using the AICcmodavg package.
 396 22

397 Melo FPL, Martinez-Salas E, Benitez-Malvido J, Ceballos G (2010) Forest fragmentation
398 reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of
399 southern Mexico. *J Trop Ecol* 26:35–43. <https://doi.org/10.1017/S0266467409990435>

400 Mitchell N, Strohbach MW, Pratt R, et al (2015) Space use by resident and transient coyotes in
401 an urban–rural landscape mosaic. *Wildl Res* 42:461–469.
402 <https://doi.org/10.1071/WR15020>

403 Mokany K, Prasad S, Westcott DA (2014) Loss of frugivore seed dispersal services under
404 climate change. *Nat Commun* 5:3971. <https://doi.org/10.1038/ncomms4971>

405 Mueller T, Olson KA, Dressler G, et al (2011) How landscape dynamics link individual- to
406 population-level movement patterns: a multispecies comparison of ungulate relocation
407 data. *Global Ecology and Biogeography* 20:683–694. <https://doi.org/10.1111/j.1466-8238.2010.00638.x>

409 Murray M, Cembrowski A, Latham ADM, et al (2015) Greater consumption of protein-poor
410 anthropogenic food by urban relative to rural coyotes increases diet breadth and potential
411 for human–wildlife conflict. *Ecography* 38:1235–1242.
412 <https://doi.org/10.1111/ecog.01128>

413 Murray MH, St Clair CC (2017) Predictable features attract urban coyotes to residential yards. *J*
414 *Wildl Manage* 81:593–600. <https://doi.org/10.1002/jwmg.21223>

415 Nathan R, Schurr FM, Spiegel O, et al (2008) Mechanisms of long-distance seed dispersal.
416 *Trends in Ecology & Evolution* 23:638–647. <https://doi.org/10.1016/j.tree.2008.08.003>

417 Newsome SD, Garbe HM, Wilson EC, Gehrt SD (2015) Individual variation in anthropogenic
418 resource use in an urban carnivore. *Oecologia* 178:115–128.
419 <https://doi.org/10.1007/s00442-014-3205-2>

420 Nield AP, Nathan R, Enright NJ, et al (2020) The spatial complexity of seed movement: Animal-
421 generated seed dispersal patterns in fragmented landscapes revealed by animal movement
422 models. *Journal of Ecology* 108:687–701. <https://doi.org/10.1111/1365-2745.13287>

423 OMNRF (2023) Ontario land cover compilation v.2.0

424 Quick ZI, Houseman GR, Büyüktaktakin İE (2017) Assessing wind and mammals as seed
425 dispersal vectors in an invasive legume. *Weed Research* 57:35–43.
426 <https://doi.org/10.1111/wre.12232>

427 R Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation
428 for Statistical Computing, Vienna, Austria

429 Rosatte R, Allan M (2009) The Ecology of Red Foxes, *Vulpes vulpes*, in Metropolitan Toronto,
430 Ontario: Disease Management Implications. *Can Field-Nat* 123:215–220

431 Rubalcava-Castillo FA, Sosa-Ramírez J, Luna-Ruíz JJ, et al (2020) Endozoochorous dispersal of
 432 forest seeds by carnivorous mammals in Sierra Fría, Aguascalientes, Mexico. *Ecology*
 433 and Evolution 10:2991–3003. <https://doi.org/10.1002/ece3.6113>

434 Sarasola JH, Zanón-Martínez JI, Costán AS, Ripple WJ (2016) Hypercarnivorous apex predator
 435 could provide ecosystem services by dispersing seeds. *Sci Rep* 6:19647.
 436 <https://doi.org/10.1038/srep19647>

437 Sasmal I, Moorman CE, Swingen MB, et al (2019) Seasonal space use of transient and resident
 438 coyotes (*Canis latrans*) in North Carolina, USA. *Can J Zool* 97:326–331.
 439 <https://doi.org/10.1139/cjz-2018-0209>

440 Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual
 441 review. *New Phytologist* 188:333–353. <https://doi.org/10.1111/j.1469-8137.2010.03402.x>

442 Silverstein RP (2005) Germination of Native and Exotic Plant Seeds Dispersed by Coyotes
 443 (*Canis latrans*) in Southern California. *The Southwestern Naturalist* 50:472–478

444 Sugden S, Murray M, Edwards MA, St. Clair CC (2021) Inter-population differences in coyote
 445 diet and niche width along an urban–suburban–rural gradient. *Journal of Urban Ecology*
 446 7:juab034. <https://doi.org/10.1093/jue/juab034>

447 Thompson CA, Malcolm JR, Patterson BR (2021) Individual and Temporal Variation in Use of
 448 Residential Areas by Urban Coyotes. *FRONTIERS IN ECOLOGY AND EVOLUTION*
 449 9:. <https://doi.org/10.3389/fevo.2021.687504>

450 Tucker MA, Böhning-Gaese K, Fagan WF, et al (2018) Moving in the Anthropocene: Global
 451 reductions in terrestrial mammalian movements. *Science* 359:466–469.
 452 <https://doi.org/10.1126/science.aam9712>

453 Uroy L, Ernoult A, Mony C (2019) Effect of landscape connectivity on plant communities: a
 454 review of response patterns. *Landscape Ecol* 34:203–225.
 455 <https://doi.org/10.1007/s10980-019-00771-5>

456 Varela O, Bucher EH (2006) Passage time, viability, and germination of seeds ingested by foxes.
 457 *Journal of Arid Environments* 67:566–578. <https://doi.org/10.1016/j.jaridenv.2006.03.013>

458 Webster SC, Beasley JC, Hinton JW, Chamberlain MJ (2022) Resident and transient coyotes
 459 exhibit differential patterns of movement behavior across heterogeneous landscapes in
 460 the southeastern United States. *Ecology and Evolution* 12:e8725.
 461 <https://doi.org/10.1002/ece3.8725>

462 Wheeldon T (2020) Population Dynamics of Eastern Coyotes in Southeastern Ontario. Trent
 463 University

464 Willson MF (1993) Mammals as Seed-Dispersal Mutualists in North America. *Oikos* 67:159–
 465 176. <https://doi.org/10.2307/3545106>

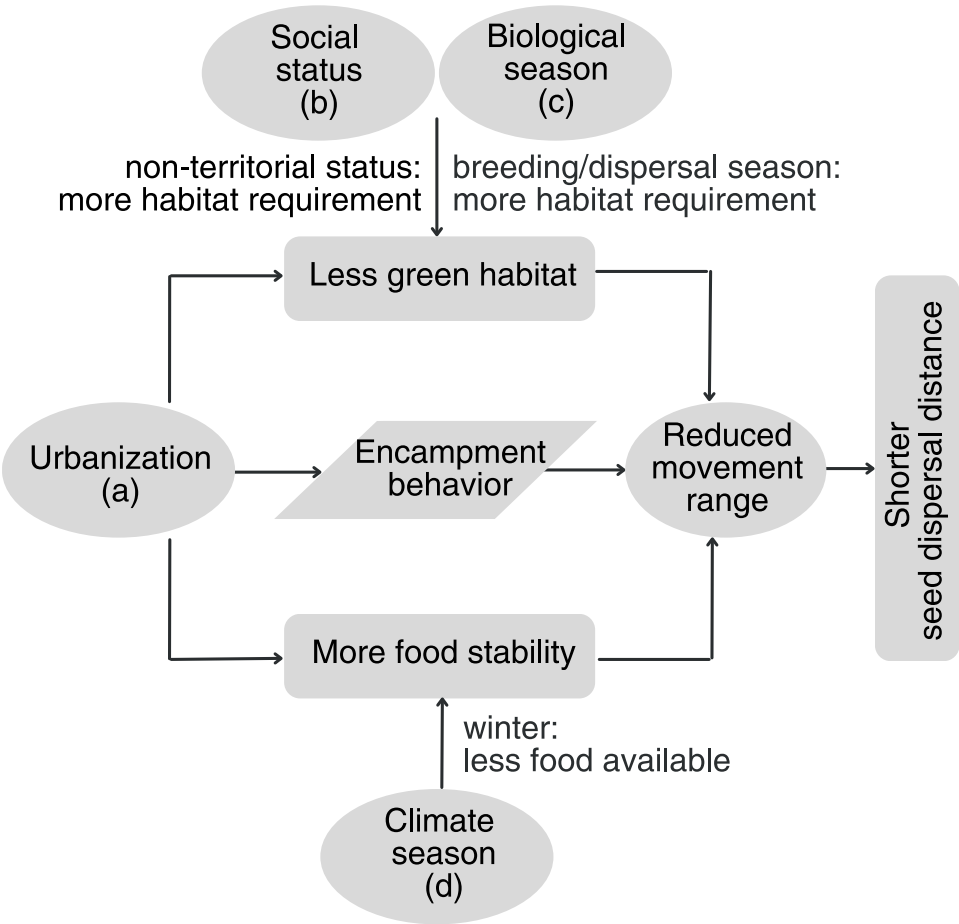
Wurth AM, Ellington EH, Gehrt SD (2020) Golf Courses as Potential Habitat for Urban Coyotes. Wildlife Society Bulletin 44:333–341. <https://doi.org/10.1002/wsb.1081>

Tables

Table 1 Coyote net displacement with respect to social status while moving within urban or rural landscape. Descriptive statistics for movement ranges across seed retention timeframes are given: i) mean daily net displacement across individuals with 95% confidence interval (CI) range, ii) the maximum distance of 50% of their daily net displacements, iii) the maximum distance of 95% of their daily net displacements, and iv) the number of individuals included in each category.

	<i>Landscape</i>	<i>Seed retention timeframe</i>	<i>Mean ± CI (km)</i>	<i>50% (km)</i>	<i>95% (km)</i>	<i>N</i>
Resident coyotes	URBAN	0-6hrs	0.65 ± 0.10	0.56	1.43	23
		6-24hrs	1.17 ± 0.29	0.98	3.39	23
		24-48hrs	1.37 ± 0.37	1.11	4.09	23
		48-72hrs	1.39 ± 0.34	1.11	3.98	23
	RURAL	0-6hrs	0.84 ± 0.81	0.87	1.75	42
		6-24hrs	1.41 ± 0.14	1.44	3.01	43
		24-48hrs	1.63 ± 0.20	1.56	3.88	42
		48-72hrs	1.67 ± 0.22	1.58	4.31	41
Transient coyotes	URBAN	0-6hrs	0.70 ± 0.23	0.52	1.79	15
		6-24hrs	1.70 ± 0.73	1.10	4.16	16
		24-48hrs	2.73 ± 1.51	1.64	5.92	16
		48-72hrs	3.53 ± 2.10	1.86	7.56	16
	RURAL	0-6hrs	1.07 ± 0.29	0.77	2.24	43
		6-24hrs	2.33 ± 0.42	1.74	5.49	41
		24-48hrs	3.86 ± 0.86	2.53	9.27	40
		48-72hrs	4.82 ± 1.25	3.05	11.40	40
Dispersing coyotes	URBAN	0-6hrs	0.72 ± 0.46	0.43	1.36	4
		6-24hrs	1.75 ± 1.17	0.97	3.70	4
		24-48hrs	3.35 ± 2.80	1.61	7.10	4
		48-72hrs	4.46 ± 3.97	1.89	10.77	4
	RURAL	0-6hrs	1.87 ± 1.43	1.03	4.87	4
		6-24hrs	5.41 ± 4.52	2.54	12.39	4
		24-48hrs	10.65 ± 9.67	4.57	26.09	4
		48-72hrs	15.09 ± 13.71	6.47	35.55	4

480



481

482 **Fig. 1** Flow chart illustrating the 4 hypotheses tested (a-d) and the associated predictions.

483

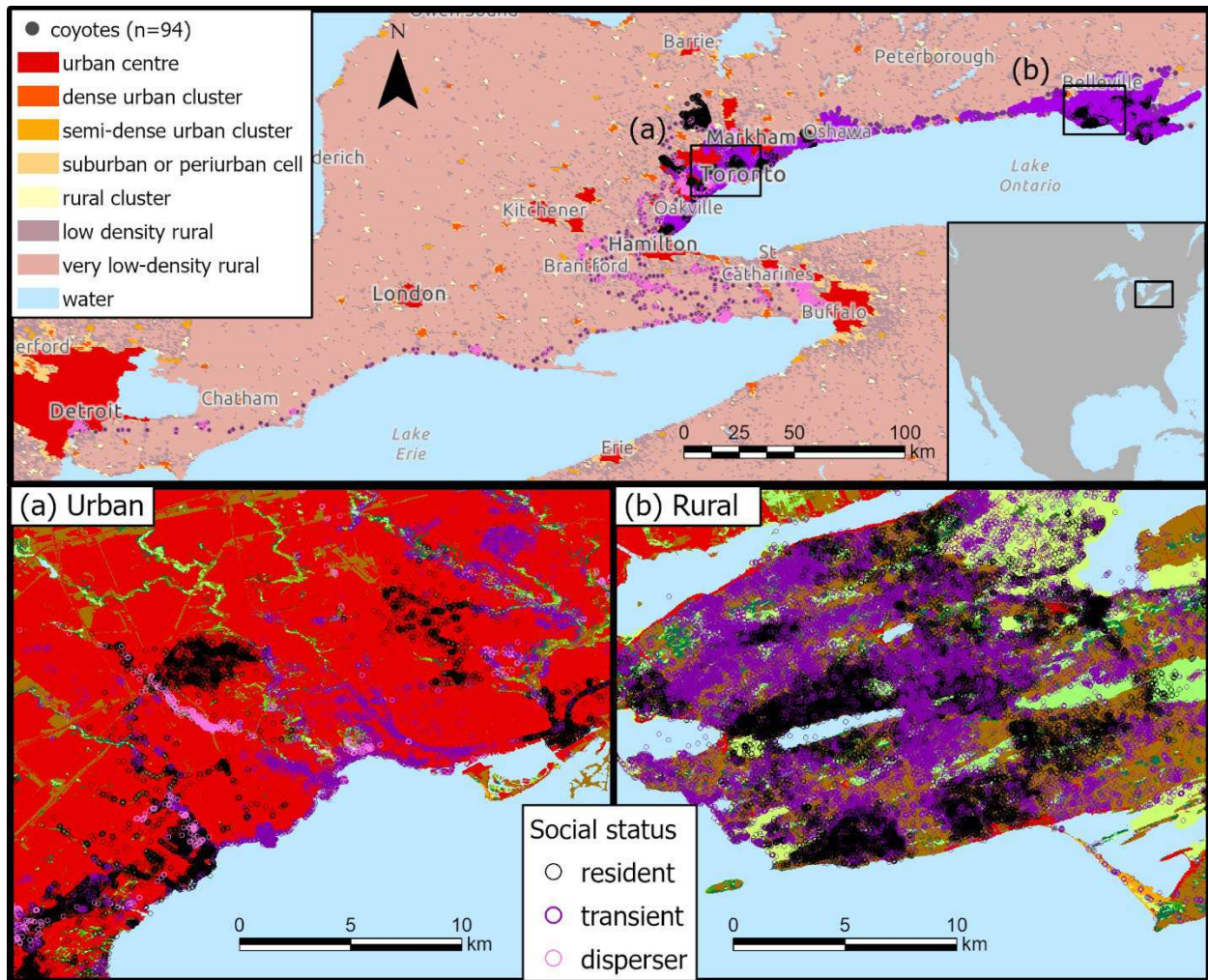


Fig. 2 Top map: GPS telemetry data for 94 GPS-collared coyotes included in this study, over the urbanization degree following the global human settlement project definition (Florczyk et al. 2019). Areas (a) and (b) in top map represent dense areas of points in urban and rural landscape and are enlarged in Fig 2a and 2b, respectively. Landcover map for Fig. 1a and Fig. 1b sourced from the Ontario government (OMNRF 2023), representing developed areas (red), agricultural areas (brown) and green areas (green), detailed landcover type legend given in the supplementary material Fig. S1, along with Fig S2, a replica of Fig 2 omitting GPS telemetry data in order to allow visibility of background landcover types.

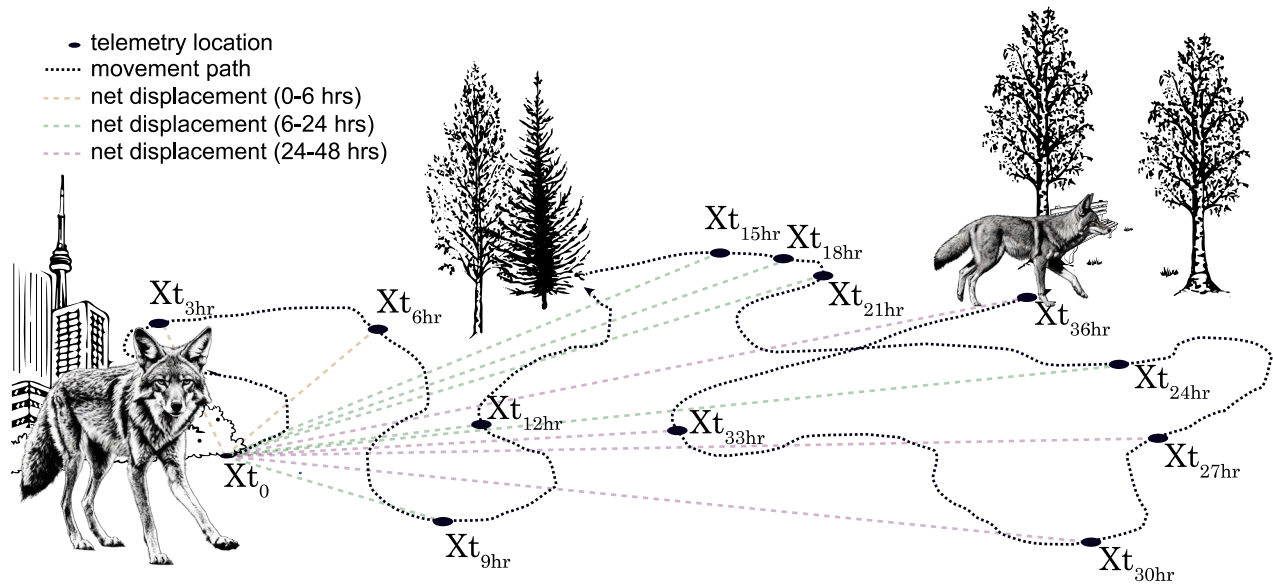


Fig. 3 Methodological representation of the net displacement of GPS-collared coyotes along a movement path following their GPS telemetry locations, and how these were categorized across seed retention timeframes. The start point of the movement path, representing the potential initial seed retention, is marked as X_{t_0} . For illustration purposes, the movement path in this example is truncated at 30 hrs

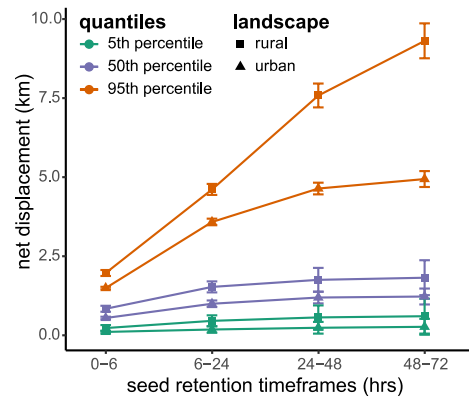


Fig. 4 Difference in coyote net displacement between rural (square) and urban (triangle) landscapes across the four seed retention timeframes analyzed, subdivided by short-distance net displacements (5th percentile), median distance net displacements (50th percentile) and long-distance net displacements (95th percentile).

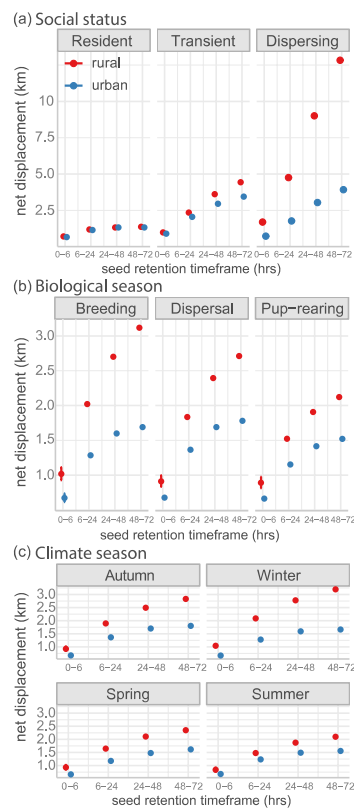


Fig. 5 Net displacement predictions from the best fit generalized linear mixed model (GLMM) with gamma distribution quantifying the effect on mean seed dispersal distance of seed retention timeframe and landscape type in

516 interaction with (a) social status, (b) biological season, and (c) climate season, with individual variation as a random
517 effect

518

519

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [GelmiCandussoSupplementarydata.pdf](#)