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

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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 overall 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 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 heterogenous 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.

Keywords Cityscape · Net displacement · Mesopredators · Coyotes · Zoochory · Carnivore · Seed dispersal · Cities

Introduction

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

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seed dispersers for a wider range of plant species within the urban environment, and may be key in determining the composition of plant communities in urban forests, as they do in other environments (Melo et al. 2010).

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

In this study we used coyotes (*Canis latrans*) as a model species, given their wide movement ranges (Gehrt et al. 2009), and their remarkable adaptation to both urban and rural areas. Coyotes have been identified as an effective seed disperser for several plant species, via both primary ingestion of wild and farmed fruits (Rubalcava-Castillo et al. 2020), secondary ingestion of seeds through prey (Sarasola et al. 2016; Hämäläinen et al. 2017), and through 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 (Fig. 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 (Fig. 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 (Fig. 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) (Fig. 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, while identifying intraspecific differences in their seed dispersal contributions in both urban and rural landscapes.

Methods

Study area

Our study area included the Greater Toronto Area (GTA), a metropolitan region, and the surrounding rural areas within southern Ontario (Fig. 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 km^2 or a minimum of 50% share of built-up land, totaling a minimum of 50,000

Fig. 1 Flow chart illustrating the 4 hypotheses tested (a-d) and the associated predictions
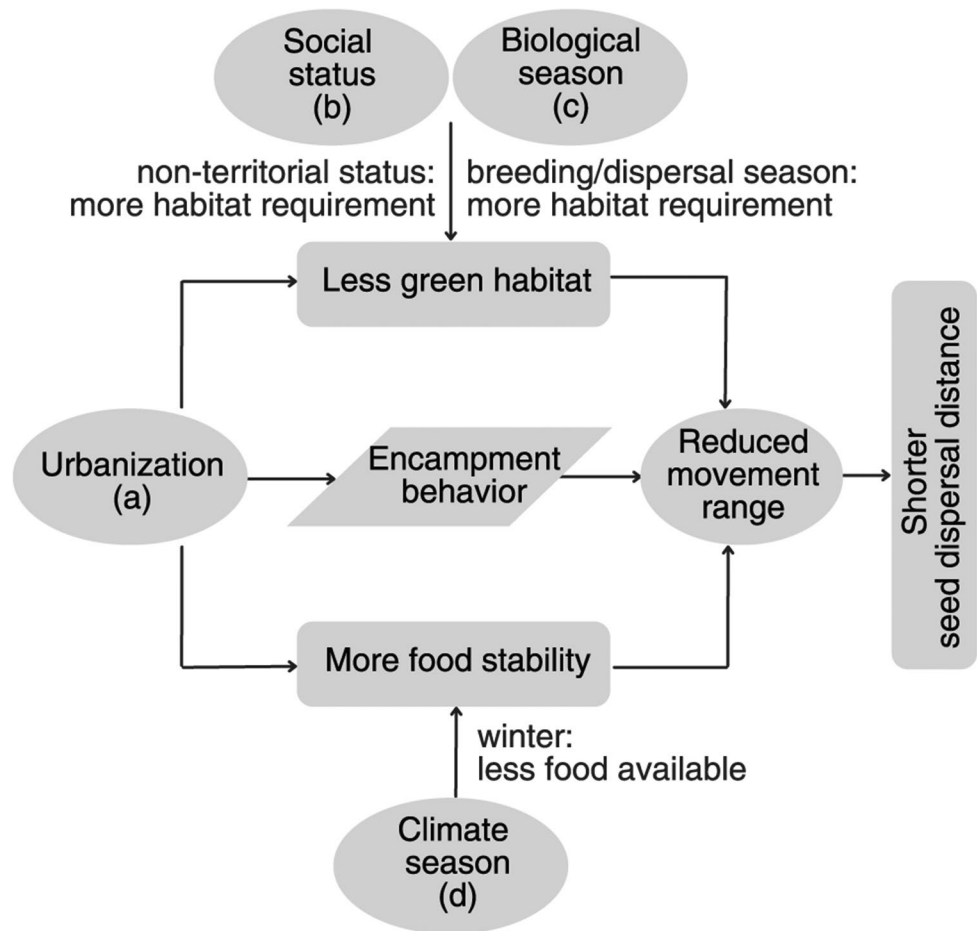
inhabitants. Following this definition, all areas outside urban centers were considered rural, which included the following landcover classes: agricultural land, small towns, and low-density human settlements.

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, most 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 may 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.

Movement analysis

We used telemetry data from 94 coyotes that were captured, radio-collared, and released within southern Ontario (Fig. 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 h. We estimated net displacement at each timepoint by measuring the Euclidean distance between contiguous GPS datapoints (Fig. 3).
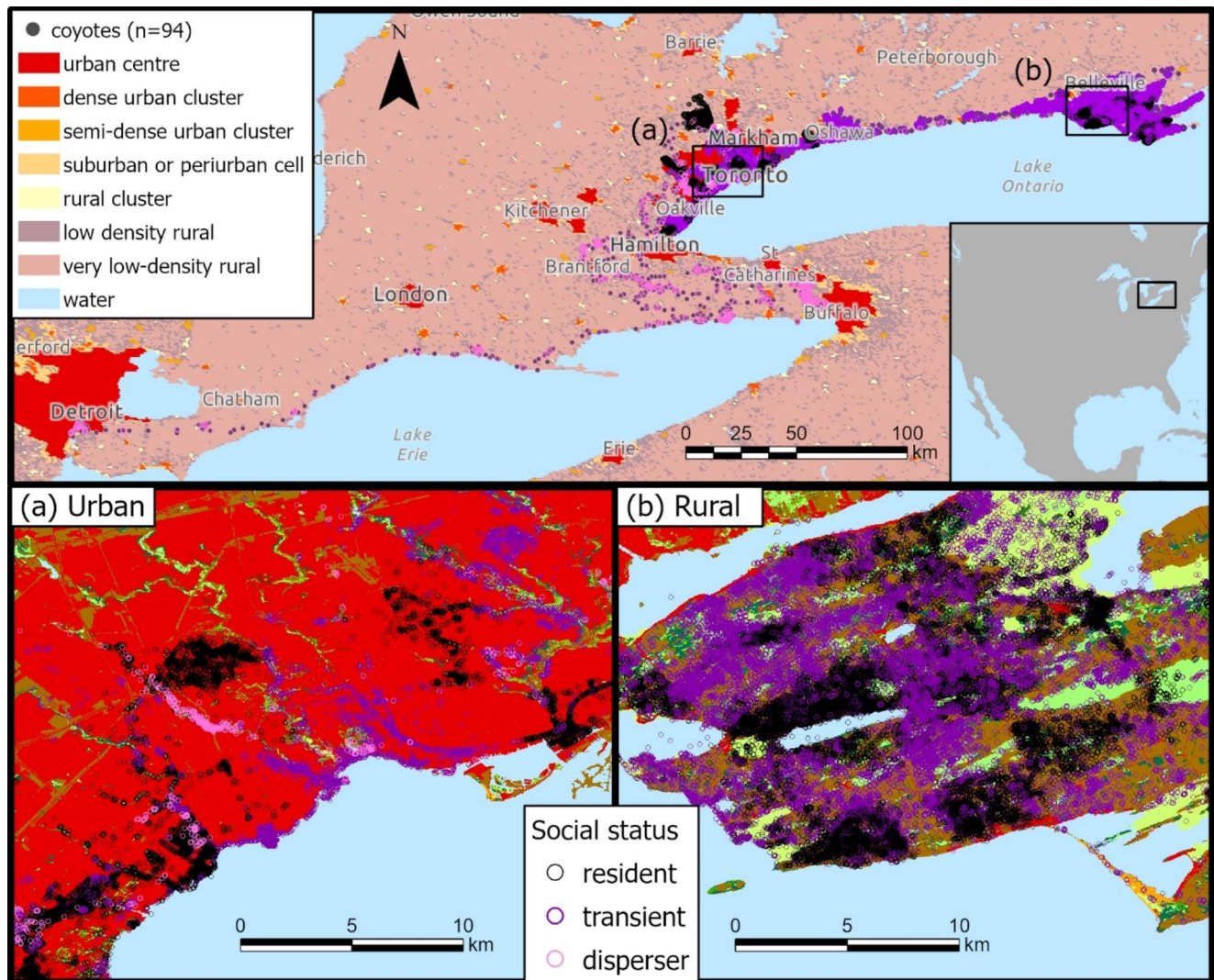
Fig. 2 Top map: GPS telemetry data for 94 GPS-collared coyotes included in this study, over the urbanization degree following the global human settlement project definition (Florczyk et al. 2019). Areas (**a**) and (**b**) in top map represent dense areas of points in urban and rural landscape and are enlarged in Fig. 2a and b, respectively. Landcover map for Fig. 1a and b sourced from the Ontario government (OMNRF 2023), representing urban areas (red), agricultural areas (brown) and vegetated 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

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.
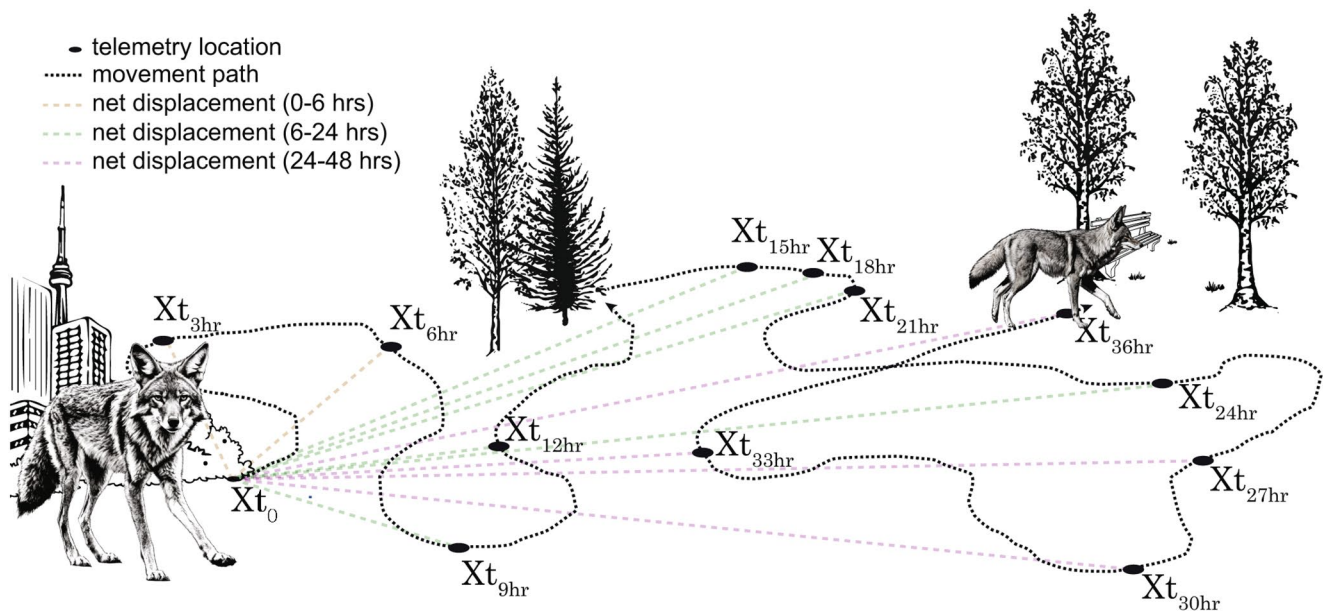
Fig. 3 Methodological representation of the net displacement of GPS-collared coyotes along a movement path following their GPS telemetry locations, and how these were categorized across seed retention timeframes. The start point of the movement path, representing the potential initial seed retention, is marked as X_{t0}. For illustration purposes, the movement path in this example is truncated at 30 h

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 (Fig. 3). To reduce spatial 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 h, (ii) 6–24 h, (iii) 24–48 h, and (iv) 48–72 h. Steps beyond the 72 h 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.

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 separately 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 (Lüdecke 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).

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
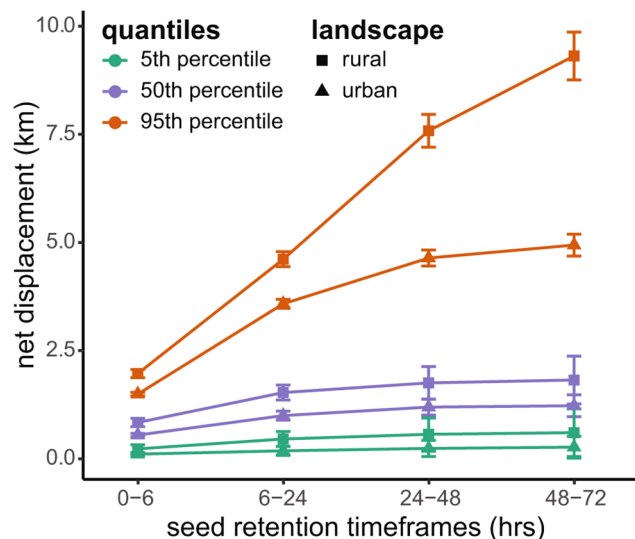

Fig. 4 Difference in coyote net displacement between rural (square) and urban (triangle) landscapes across the four seed retention timeframes analyzed (*x*-axis), subdivided by short-distance net displacements (5th percentile), median distance net displacements (50th percentile) and long-distance net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

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, Fig. 4), in comparison to net displacements in the lower 50%, which increased linearly with increasing seed retention timeframe (purple and green lines, Fig. 4). For long-distance seed dispersal events, the difference between urban and rural environments doubled for > 24 h seed retention timeframes, as seed dispersal distance in urban landscape reached a plateau at 4–4.5 km after 24-hour seed retention, while seed dispersal distance in rural environment kept increasing with seed retention timeframe, reaching 7.5 km at the 24–48 h retention timeframe and almost 10 km 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 (Fig. 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 significantly affected by urbanization, whereby they exhibited a 15–19% decrease in net displacement in urban areas (Fig. 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 (Fig. 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 urban areas. In contrast, resident coyotes (n = 23–43 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 (Fig. 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 and 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
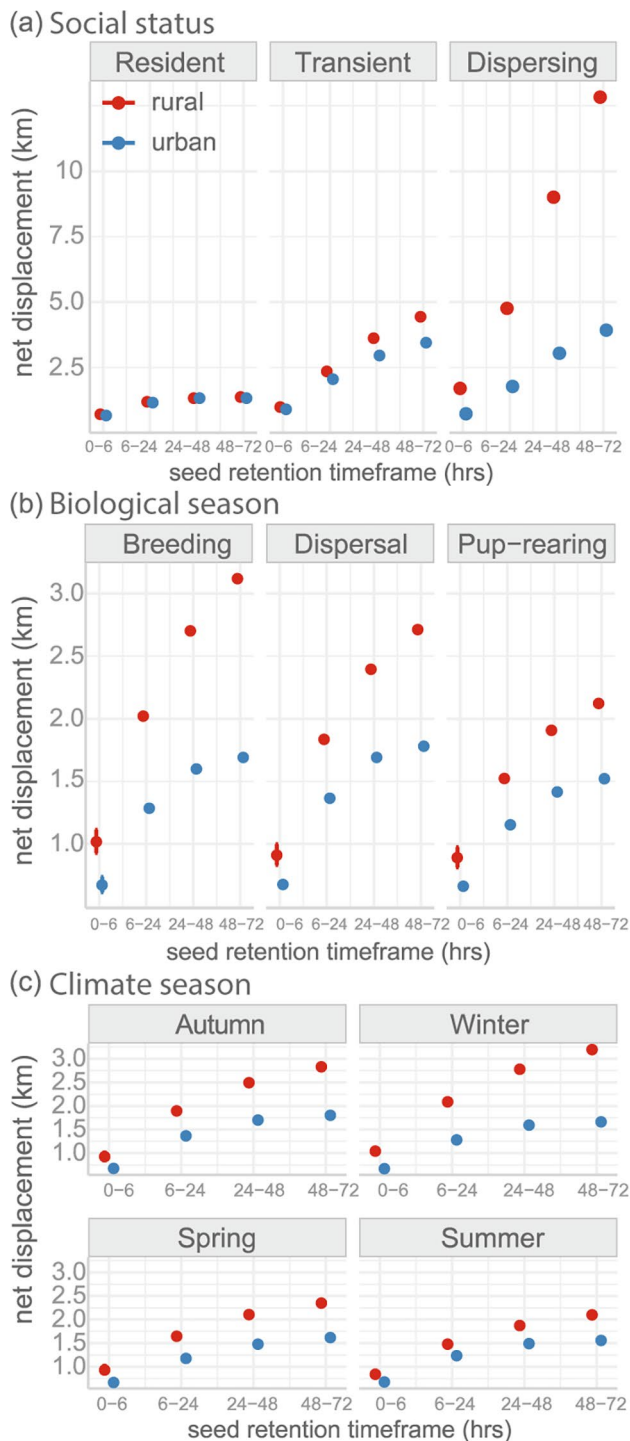
Fig. 5 Net displacement predictions from the best fit generalized linear mixed model (GLMM) with gamma distribution quantifying the effect on mean seed dispersal distance for each seed retention timeframe and landscape type in interaction with (**a**) social status, (**b**) biological season, and (**c**) climate season, with individual variation as a random effect

landscapes increased with increasing seed retention timeframe for all biological seasons, albeit at a lower rate for pup-rearing season (Fig. 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 (Fig. 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 (Fig. 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.

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 seasons 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.

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

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

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 potentially 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 (Fig. 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 species-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, where seasonal variations in potential seed dispersal distance were the strongest. 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 generate, in both landscape types. A heterogenous 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 of other wide-ranging omnivore predators, in urban habitat renaturalization.

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 plant 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.

Declarations

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