Comparison of beaver density and foraging preferences between urban and rural riparian forests along the South Saskatchewan River, Canada

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Abstract

Beavers have recolonized much of their historic range throughout the northern hemisphere and numerous studies have documented their habitat preferences and foraging behavior in rural riparian areas. Beavers, however, are also recolonizing waterways in cities, yet there has been little study of habitat use and foraging practices in these managed, urban systems. We studied beaver lodge distribution and riparian foraging preferences along the South Saskatchewan River, Canada, comparing a reach (24 km) passing through the City of Saskatoon where beavers and trees are managed with an upstream reach (29 km) passing through a conservation area where neither beavers nor trees are managed. In a canoe-based census at low flow, we found that beaver density in the conservation area was twice that in the city. Lodges were dispersed in the city with longer water-based distances between them. We found both differences and similarities in beaver foraging behavior. Riparian tree sampling along transects revealed that while diversity in the city and conservation area is markedly different, beavers preferentially cut green ash, Manitoba maple, paper birch and three poplars in both places. Beavers also cut six other tree species in the city, including three that are introduced, but the diversity was higher. A least-squares general linear model showed greater probability of cutting of trees further from the river in the city than conservation area, but of smaller diameter. Study results will be useful to urban planners in managing urban riparian forests and in developing beaver management plans.

Key words: beaver lodge, Castor canadensis, riparian areas, tree cutting, large rivers

Introduction

Riparian forests in cities may superficially appear similar to their natural counterparts, but they differ in the way they are formed, defined and maintained (Blood et al. 2016). An urban riparian forest includes all naturally occurring and planted trees (Rowntree 1988). While easy to delineate, understanding urban riparian forest dynamics is difficult owing to the interplay between natural and anthropogenic drivers of change (Groppman et al. 2003). Cities across much of the arid and semi-arid North American prairies were established on wide, navigable rivers during the fur trade (Vandiveer 1929). The riparian forests originally found on the floodplains of these rivers were often the only deciduous forests on the prairie landscape (Merritt and Cooper 2000), primarily composed of Populus spp. (Rood and Mahoney 1990) and Salix spp. (González et al. 2018). Regeneration occurred mainly by major flood events (Politti et al. 2018). As cities grew, the riparian forests within them...
changed. They became increasingly disturbed, fragmented and isolated (Moffat et al. 2004) in part because of flow alteration that minimized natural disturbance (Poff et al. 2011), but also because of management (Ordóñez and Duinker 2013). While possible to manage riparian forests in cities with knowledge of common ecological principles and how they operate over space and time (Dale et al. 2000), successful management is challenged by multiple stakeholders with different interests (Gaston, Ávila-Jiménez, and Edmondson 2013). Adding to this complexity is the idea that management and conservation of riparian forests, especially those in cities, requires the inclusion of natural ecological disturbances that occur during the long-term history of the specific forest (Lorimer 2001). One such natural agent of ecological disturbance in riparian forests is the beaver, Castor canadensis in North America and C. fiber in Eurasia (Naiman, Johnston, and Kelley 1988; Nummi and Kuuluvainen 2013).

Beavers have recovered much of their pre-fur trade range in North America (Naiman et al. 1988), and are still expanding into urban waterways where historically there has been low social tolerance for them (Siemer et al. 2013). Although public perceptions of beaver are continuing to shift in North American cities toward a growing acceptance of coexistence, conflicts do occur and need to be managed (Bailey, Dittbrenner, and Yocom 2019). In waterways too large to dam, conflicts arise over the cutting of trees planted or protected by cities to enhance riparian esthetics (Rosell et al. 2005; Loeb, King, and Helton 2014). Tree cutting can be a considerable loss of living woody biomass from the overall canopy of the riparian forest (Boczo, Bróbel, and Synisiev 2009). While some beaver damage to trees is publically tolerable, the degree tolerated depends on personal experience (Siemer et al. 2013). When people experience problems with beavers, most notably property damage, they tend to view them as a nuisance and seek population or forage control (Schulte and Müller-Schwarz 1999).

To protect riparian trees from being felled by beavers, cities will employ lethal and non-lethal management (Nolte et al. 2003). Lethal management typically involves killing trap (Novak 1987; Nolet and Rosell 1998) and is most commonly practiced in areas where beavers are abundant, unwanted and considered a nuisance (Mozzillo and Needham 2015). But, lethal control is becoming less publically acceptable and cities are turning toward non-lethal management options and focusing on coexisting with beavers (Bailey et al. 2019). The most invasive non-lethal option is live-trapping and relocation (Pollock et al. 2015). Other non-lethal options include regulation of undesired beaver actions, including forage control attained via access barriers and behavior manipulation (Severud et al. 2011; Pollock et al. 2015).

Including beavers in riparian forests in urban systems, even at a lower than historic density, requires a holistic view of urban planning. Seattle and New York City, for example, have transitioned to more ecologically-based design practices that encourage the integration of keystone species and ecosystem engineers, including beavers, to increase the level of ecosystem function of urban ecosystems (Bailey et al. 2019). While exciting, the problem is that there is much we do not yet know about habitat use and foraging practices of beavers in managed, urban systems, knowledge crucial for beaver–human coexistence in cities and the development of beaver management and riparian forest management plans. To address this shortcoming, we asked how beaver density and foraging differed between an urban, managed riparian forest (city) and a rural, non-managed riparian forest (conservation area) along the same river. The first hypothesis we tested was that beaver lodge and population density would be lower along the river reach flowing through the city vs. conservation area. The riparian system is managed in the city (both beaver numbers and tree availability) and this is expected to reduce the beaver population density (Boyce 1981). The second hypothesis we tested was that beavers will forage closer to shore in the city vs. conservation area due to human activity. The third hypothesis we tested is that beavers will be less selective in foraging choices in the city vs. conservation area. In the city, we expect them to cut the most available species since this will reduce forage time and thus potential exposure to human interference (Loeb et al. 2014; Vorel et al. 2015). In the conservation area, we expect beavers to be more selective.

Methods
Study site

We studied the riparian forest of a reach of the South Saskatchewan River, Saskatchewan, Canada known as Meewasin Valley. The Meewasin Valley river reach flows through the City of Saskatoon (52.1332° N, 106.6700° W) and an adjacent, upstream conservation area (Fig. 1). The South Saskatchewan River is a braided, sand-bed system with wide meanders, large permanent islands as well as transient sand islands. Through the study reach, the river has a sinuosity of 1.7 and a width of 300–450 m. The drainage area for the river at Saskatoon (Water Survey of Canada gauge 05HG001) is 1.41 × 10^5 km^2. The South Saskatchewan River flows northward. Gardiner Dam, located ~100 km upstream of Saskatoon, has modified the runoff regime of the river since 1967, with the monthly mean discharge now peaking in January at 301 m^3/s and again in June at 220 m^3/s (Pomeroy, de Boer, and Martz 2005). Statistics Canada reports the population of Saskatoon as 246,376 in the 2016 census.

The study site is located within the moist mixed grassland ecoregion within the prairie ecozone of the Central Plains of Western Canada. The geomorphology of much of the ecoregion is a broad plain interrupted by glacially cut deep valleys and subdued hilly uplands. The South Saskatchewan River valley is sunken up to 100 m or more into the plain. Much of the characteristic vegetation is grass assemblages with riparian areas supporting forest communities. The riparian forest composition in the study area was described by Lineman (2000). Woody species near the river include mountain alder (Alnus tenuifolia) sandbar willow (Salix exigua) and red-osier dogwood (Cornus stolonifera) with some cottonwood (Populus deltoides). Further upslope balsam poplar (Populus balsamifera) interspersed by Manitoba maple (Acer negundo), trembling aspen (Populus tremuloides), Saskatoon berry (Amelanchier alnifolia) and chokecherry (Prunus virginiana) were common. Lineman (2000) reports that introduced species comprised 22% of the City of Saskatoon’s riparian forest.

A unique conservation strategy exists for Meewasin Valley. It is managed through a multi-agency partnership known as the Meewasin Valley Authority. While primarily a cultural and natural resource conservation organization, Meewasin Valley Authority has legal authority over the Meewasin Valley. In the portion of the valley that lies within the City of Saskatoon, there is ~90 km of walking trails along both sides of the river connecting several river parks and natural areas. Trails use is high, with >200 people using the trails per hour on bikes (43%) or foot (57%) between 4 and 6 pm daily (Stein 2014). Native introduced
and invasive woody plants are managed in the riparian forest. Select trees, particularly those in parks along the South Saskatchewan River that the city considers to be of high value, are protected from beaver foraging by wire cage enclosures. As well, beavers are managed in the portion of the Meewasin Valley within city limits. The city regularly employs a trapper to kill and sometimes relocate problem beaver. The portion of Meewasin Valley that lies upstream of Saskatoon is located in the Rural Municipality of Corman Park. This portion of the valley is a conservation area in which there is no management of beaver or woody vegetation other than the occasional removal of a tree that has fallen over one of the few walking paths. There is no commercial trapping of beaver in the study area. A Hudson Bay fur trading post, however, was located on the South Saskatchewan River within the Meewasin Valley circa 1863.

Management of beaver activity in the city limits (city), and lack thereof upstream of the city (conservation area), served as the two treatments for this research. The most southerly portion of Meewasin Valley was the upstream boundary for the reach of the South Saskatchewan River studied. The intersection of the South Saskatchewan River with the City of Saskatoon northern municipal boundary was planned as the northernmost extent of the study area. However, there was a water diversion structure at the northern bridge that prevented river access to the lower reaches of the river within the city limits during the study. The construction made the river here inaccessible; thus, 1.7 km of the river and riparian area in the city was excluded from the study. Other than the bridge, there was negligible development of the excluded section of the river valley at the time of the study.

Density and distribution of beaver lodges

A beaver lodge census was carried out along the city and conservation area river reaches between 10 August and 22 September 2017. The lodge census included the river banks, islands and side channels. It was purposely conducted coincident with a period of very low river flow. Performing the census then meant that the likelihood of finding all active and inactive beaver lodges and lodge complexes was high, where higher flow might conceal some. The census was also coincident with the start of the period beavers are most active in stocking winter food caches (August–October). The survey was mainly conducted via canoe, but since beavers live in the South Saskatchewan River at all levels of river flow, on-foot surveys were used over the islands and oxbows. Beaver lodge census protocols from other jurisdictions (Novak 1987; Parker and Rosell 2003) were adapted for use here. Observation of a principal bank lodge, defined as a bank burrow with a fortified wooden structure atop, along with an active food cache, and fresh castoreum deposits (territorial scent mounds) was confirmation of an active beaver lodge complex used by a single beaver colony (family). The presence of a principal bank lodge without the other two factors indicated an inactive lodge complex. With the intent of recording the location, type and habitation status for each beaver lodge complex, each primary bank

Figure 1: Map of the study area, known as Meewasin Valley, showing the City of Saskatoon municipal boundary (red outline). The study treatments were a reach of the South Saskatchewan River passing through the City of Saskatoon (medium blue) where beavers and trees are managed and an upstream reach passing through a conservation area (light blue) where neither beavers nor trees are managed.
lodge structure was identified and photographed; observations were recorded in the field using an app (Fulcrum, Spatial Networks Inc.). Secondary bank lodges, as well as other indicators of beaver activity, were also recorded. Lodge sites were considered to be separate territories if they were at least 0.5 km in distance.

**Riparian trees and beaver foraging preferences**

Transects perpendicular to the river were established in the city and conservation area. Beavers are central place foragers and return to their lodge after foraging excursions (Jenkins 1980). We used active beaver lodges as the place at which to start the process of establishing vegetation transects. First, we surveyed the riverbanks and adjacent riverine forests within 150 m of an active lodge (or primary lodge if there were several) for evidence of the most recent and abundant beaver foraging activity. Next, we selected the beaver foraging path that appeared both well-established and recently active, as evidenced by observations of recent beaver tracks and maintained bank slides into the river. A vegetation transect was established in alignment with this beaver foraging path into the riparian forest. To create a balanced tree sampling design, we selected an equal number of active beaver lodges in the city and conservation area. Since there were only 11 active beaver lodges in the city, we selected all of them. During the vegetation sampling, however, we noticed that two of these beaver lodges were not active, owing to either recent trapping (we saw one beaver carcass in a trap) or site abandonment, reducing the sample size to 9. In the conservation area, we randomly selected 11 of the 25 active beaver lodge complexes at which to establish vegetation transects. We conducted one vegetation transect per active site sampled (9 in the city and 11 in the conservation area).

The transects were 10 m wide, extending 5 m on either side of the beaver foraging path. The transects started at an active lodge complex, ran along a main foraging path and ended at the maximum extent of the riparian forest. At each transect we recorded all the living trees and the stumps of beaver cut trees >0.5 cm diameter at breast height (DBH) or stump height (DSH) if the tree was cut, their species, their distance from the shore, transect length and presence of wire cage enclosures. In order to have comparable diameters for cut and uncut trees, we measured the DBH and DSH of 50 randomly selected, intact, beaver preferred trees in the study area in November 2020. The two variables were linearly correlated ($r^2 = 0.972$); the relationship was used to estimate the DBH of cut trees (DBH = 0.9073 (DSH) – 0.6803). Taxonomy and classification of each tree were reported as per Budd, Looman, and Best (1987) and Argus et al. (2016). The conservation status of each tree was determined via the online taxon list for vascular plants (Saskatchewan Conservation Data Centre 2020).

**Data analysis**

The similarity in lodge density between the city and conservation area river reaches was assessed using the chi-squared ($\chi^2$) test with one degree of freedom. To assess whether lodge complexes were randomly distributed in the city and conservation area, the nearest neighbor ratio was calculated in ArcGIS. Since beavers are semi-aquatic rodents and prefer water-based over land-based travel to protect them from predators, a least-cost path analysis (Adriaensen et al. 2003) was used to determine the water-based travel path distance between lodges. Resulting median travel distance among lodges was compared between the city and conservation area using a Mann–Whitney U-test. For trees, we first verified completeness of the sampling effort by ensuring a species-area curve reached an asymptote using PC-Ord version 4.14 (Wild Blueberry Media). We then computed standard indices of biodiversity (richness, Shannon–Weiner diversity and evenness) for each transect. Biodiversity indices, transect lengths and tree density were compared between the city and conservation area using a Mann–Whitney U-test. Variation in biodiversity indices, transect lengths and tree density was expressed as interquartile range, IQR, the difference between the third and first quartiles. To test the selectivity of beavers toward different tree species, the procedure outlined by Salandre et al. (2017) was used. In brief, the procedure employs a $\chi^2$ goodness-of-fit test to determine a difference between expected and observed use of tree species along with Bonferroni confidence intervals to determine which species are preferred. Tree species for which <4 individual trunks were recorded (<1% of the total number) were excluded from the analysis, as the method is more robust for larger sample sizes. We further analyzed forage preferences using a least squares GLM to model probability of tree cutting as a function of tree location (binary: city, conservation area), distance from river (m), and size (DBH, cm), with transect as a random effect. All statistical analyses were carried out using JMP version 5.0.1 (SAS Institute Inc., USA).

**Results**

**Density and distribution of beaver lodges**

Of the 144 sites found during our census, 34 (24%) were active (Table 1). Some active sites (15/34, 44%) had multiple principal bank lodges and one or more secondary bank dens (lodge complexes), while the majority (19/34, 56%) consisted of a single bank lodge. Most lodge sites (115/144, 80%) were on the river banks; the rest (29/144, 20%) were found on large, permanent islands within the channel. There were two active lodge sites on islands. Of note, Yorath Island, a large permanent island in the most downstream part of the conservation area (Fig. 1), appeared to be long-utilized habitat with 72% (21/29) of the lodge sites occurring on islands found along its shores.

Lodge occupancy rate in the city (24.3%) and conservation area (23.4%) was similar, but active lodge density was 56% higher in the conservation area than city ($I^2 = 7.529$, $P = 0.0061$; Table 1). Active lodge sites had a dispersed distribution in the city (nearest neighbor ratio = 1.88, $P < 0.0001$) and a clustered distribution in the conservation area (nearest neighbor ratio = 0.628, $P = 0.0004$). The water-based travel distance between active lodge sites was greater in the city (median = 1162 m) than in the conservation area (median = 992 m), U = 88, $P = 0.049$.

**Riparian trees and beaver foraging preferences**

Riparian forest width (transect length) ranged from 50 to 110 m in the city and from 30 to 180 m in the conservation area, with a median of 70 m in each (IQR = 10 m (city) and 40 m (conservation area)). Riparian forest width was similar in the city and conservation area, z-score = 0.152, $P = 0.881$. Similarly, median tree density along the transects was similar in the city (400 trees/ha, IQR = 338) and conservation area (194 trees/ha, IQR = 687), z-score = 0.674, $P = 0.502$.

A total of 470 trees from 14 unique genera and 20 unique, confirmed species were recorded in the transects (Table 2). There were 277 trees in the city transects from 20 different species, significantly higher than 293 trees in the conservation area transects from 14 species, z-score = 2.548, $P = 0.011$. The city transects contained a wider range of species, with a maximum of 12 species, whereas the conservation area transects contained a maximum of 6 species. Density of individual species varied across transects, with 58 individual trees of Sitka Spruce (Picea sitchensis) recorded in the city transects, and 26 individual trees of Paper Birch (Betula papyrifera) recorded in the conservation area transects. Taxonomy and classification of each tree were reported as per Budd, Looman, and Best (1987) and Argus et al. (2016). The conservation status of each tree was determined via the online taxon list for vascular plants (Saskatchewan Conservation Data Centre 2020).
species. The four most abundant species were Manitoba maple, green ash, hybrid poplar and paper birch. There were 193 trees in the conservation area transects from 8 species. The four most abundant tree species were green ash, Manitoba maple, trembling aspen and paper birch. Richness ($z$-score = 1.69, $P = 0.091$), diversity ($z$-score = 0.85, $P = 0.395$) and evenness ($z$-score = −1.24, $P = 0.215$) of the riparian tree community, however, were similar in the city and conservation area transects (Table 2). Wire cage enclosures were found on 6.1% (17) of the trees occurring in the city transects, on 8 different species (Table 2).

One-third (157/470) of the trees inventoried in the transects were cut by beavers (Table 2); 92% (144/157) were entirely cut while 8% (13/157) were partially cut. All partially cut trees were still living at the time of the vegetation sampling. Beavers cut trees occurred at approximately the same median density in the city (100 trees/ha, IQR = 257) and conservation area (118 trees/ha, IQR = 409) transects, $z$-score = 0.048, $P = 0.996$. Twelve different tree species were cut in the city transects, three of which were introduced. Six different tree species were cut in the conservation area transects; all of these species were also cut in the city. The tree most commonly cut in both the city and the conservation area transects was green ash (Table 2). Beavers cut 90% (47/52) of green ash trees along city transects and 59% (29/49) along conservation area transects.

### Table 1: Beaver lodge census along the South Saskatchewan River, which passes through the City of Saskatoon, Canada in 2017.

| River reach     | River length (km) | Lodge occupancy status | Beaver lodges |
|-----------------|-------------------|------------------------|---------------|
| City            | 23.7              | Active                 | 9             |
|                 |                   | Inactive               | 28            |
|                 |                   | Total                  | 37            |
| Conservation area | 28.6             | Active                 | 25            |
|                 |                   | Inactive               | 82            |
|                 |                   | Total                  | 107           |
| Total           | 52.3              |                        | 144           |

### Table 2: Trees species sampled within the study site, their conservation status, beaver utilization, number bearing protective wire cages and community ecology summary metrics.

| Tree species                                | Statusa  | City No. trees | City No. cut | City No. with wire cage | Conservation area No. trees | Conservation area No. cut | Total no. trees |
|---------------------------------------------|----------|----------------|--------------|-------------------------|-----------------------------|---------------------------|-----------------|
| Manitoba maple, Acer negundo               | N        | 73             | 6            | 0                       | 46                          | 6                         | 119             |
| Mountain maple, Acer spicatum              | N        | 20             | 4            | 0                       | 0                           | 2                         | 20              |
| Paper birch, Betula papyrifera             | N        | 30             | 3            | 0                       | 28                          | 2                         | 58              |
| Green ash, Fraxinus pennsylvonica          | N        | 52             | 47           | 1                       | 49                          | 29                        | 101             |
| White spruce, Picea glauca                 | N        | 1              | 0            | 1                       | 0                           | 0                         | 1               |
| Blue spruce, Picea pungens                 | N        | 3              | 0            | 0                       | 0                           | 0                         | 3               |
| Jackpine, Pinus banksiana                  | N        | 3              | 0            | 0                       | 0                           | 0                         | 3               |
| Balsam poplar, Populus balsamifera         | N        | 6              | 3            | 0                       | 1                           | 0                         | 7               |
| Eastern cottonwood, Populus deltoides       | N        | 13             | 9            | 3                       | 12                          | 10                        | 25              |
| Trembling aspen, Populus tremuloides       | N        | 4              | 1            | 1                       | 35                          | 11                        | 39              |
| Hybrid poplar, Populus x jackii            | N        | 36             | 15           | 6                       | 15                          | 3                         | 51              |
| American plum, Prunus americana            | N        | 3              | 1            | 0                       | 0                           | 0                         | 3               |
| Bur oak, Quercus macrocarpa                | N        | 2              | 0            | 1                       | 0                           | 0                         | 2               |
| Alternate-leaved dogwood, Cornus alternifolia | I        | 2              | 0            | 0                       | 0                           | 0                         | 2               |
| Russian olive, Elaeagnus angustifolia       | I        | 3              | 0            | 0                       | 0                           | 0                         | 3               |
| Spruce genus, Picea spp.                   | I        | 2              | 0            | 0                       | 0                           | 0                         | 2               |
| Scots pine, Pinus sylvestris               | I        | 3              | 0            | 2                       | 0                           | 0                         | 3               |
| Mountain ash, Sorbus aucuparia             | I        | 3              | 3            | 0                       | 0                           | 0                         | 3               |
| American linden, Tilia americana           | I        | 10             | 0            | 0                       | 1                           | 0                         | 11              |
| English elm, Ulmus procera                 | I        | 4              | 2            | 0                       | 0                           | 0                         | 4               |
| Japanese zelkova, Zelkova serrata          | I        | 2              | 1            | 0                       | 0                           | 0                         | 2               |
| Pine genus, Pinus spp.                     | U        | 2              | 0            | 2                       | 0                           | 0                         | 2               |
| Poplar genus, Populus spp.                 | U        | 0              | 0            | 0                       | 6                           | 1                         | 6               |
| Total                                       |          | 277            | 95           | 17                      | 193                         | 62                        | 470             |

*aConservation status: native (N), introduced (I) or unknown (U).
conservation area are given in Table 3. Beavers did not select each species in proportion to its availability in the city transects ($\chi^2 = 84.2, \text{df} = 8, P < 0.001$) or in the conservation area transects ($\chi^2 = 23.0, \text{df} = 6, P = 0.001$). In the city transects, the expected values of utilization of mountain maple, paper birch, green ash, balsam poplar, cottonwood, aspen, hybrid poplar and English elm were below the confidence interval of true utilization, which indicates that these species were selected by the beavers. Manitoba maple was used in proportion to its availability. In the conservation area transects, green ash, cottonwood, aspen, hybrid poplar and Poplar genus were used in proportion to their availability. The majority (58%) of the trees protected with wire cages were species reported in Table 3 as preferred by beavers. Specifically, 17% of the hybrid poplar, 25% of the aspen, 23% of the cottonwood and 2% of the green ash trees occurring along the transects in the city had cages (Table 2).

Cut trees were found 5–174 m from the river, but only one tree was cut farther than 70 m from the river. Overall, 87% of cut trees were <50 m from the river. In the city transects, only 5 cut trees were >50 m from the river while in the conservation area transects, 15 cut trees were >50 m from the river. The median distance of cut trees from the river was significantly further in the city transects (30 m) than in the conservation area transects (19 m), z-score = 2.53, $P = 0.011$. Overall median tree diameter was 5.8 cm. Median diameter of cut trees was smaller in the city (5.4 cm) than that in the conservation area (7.9 cm) transects, z-score = -2.34, $P = 0.019$. The maximum cut tree diameter was 95 cm (cottonwood, conservation area), and the minimum was 1 cm (green ash, city). A least squares general linear model (RMSE = 0.157, F ratio = 13.46; $P < 0.0001$) identified distance from the river (coefficient = -0.0078; $P < 0.0001$) and the interaction of distance and location (city/conservation area; coefficient = 0.0078; $P < 0.0001$) as significant at $\alpha = 0.05$ in influencing whether a tree was cut or not. The interaction of distance and tree size was significant (coefficient = 0.0075; $P = 0.079$) in influencing whether a tree was cut at $\alpha = 0.10$.

The distribution of trees (species and diameter) identified as highly selected by beavers in relation to their distance from the river is presented in Fig. 2. Green ash, with diameters generally <20 cm, occurred from 8 to 69 m along the transects in the city and was only cut from 8 to 49 m from the shore. Green ash occurred from 5 to 29 m in the conservation area and was cut at all distances. Mountain maple, found only in the city transects, had a similar distribution to green ash; however, cut trees were located only <10 m from the river. Trees of the Populus genus, in contrast, occurred across a greater distance from the river than green ash or mountain maple. Cut poplars occurred throughout the riparian forest in the city but only occurred <70 m from the river in the conservation area with the exception of one cottonwood tree that occurred at 174 m. The other preferred tree species—birch—occurred in a narrow band, 35–45 m from the river. All but two of the 17 trees in the city transects with wire cages were located <50 m from the river.

Discussion

Beaver lodge distribution

Our results support the hypothesis that beaver lodge and population density would be lower along the river reach flowing through the city vs. conservation area. Beaver management and riparian forest management practices in the City of Saskatoon are having the intended effect of reducing beaver population density. Active lodge site density of the city is half that in the adjacent conservation area (0.38 vs 0.87 colonies per river km). While beaver avoidance of urban areas could be a factor in driving the lower colony density in the city (Pachinger and Hulik 1999; Zwolicki et al. 2019), this seems less important than the effects of beaver population management, via primarily lethal means, and forage protection via encircling trees with wire cages. Others have shown that the presence of human developments is a minor factor influencing lodge site selection; major determinants of lodge site selection in urban areas, after habitat characteristics, are beaver management practices guided by public acceptance of coexisting with beavers (Mumma et al. 2018). Beaver populations can be density-dependent and handle up to ~40% annual predation without impact (Payne 1989). While the City of Saskatoon does not make public the number of beavers it kills annually, lethal management has traditionally been a preferred practice and we encountered a number of
beaver traps in our census. Saskatoon also uses wire cages to protect trees considered valuable from beaver cutting. While we encountered only 17 trees along the studied transects that were protected with wire cages, most of these were on trees preferred by beavers. The use of protective cages reduces forage availability (Pollock et al. 2015) and this may limit beaver density by forcing beaver colonies to use longer sections of the river to find forage species. Of note, the city uses wire cages most often in riverine parks and along walking/biking paths (J. Boone, pers. comm.).

The beaver lodge and population density we observed, and its suppression in the city, is similar to that in places in North America where beavers are unexploited and exploited (Boyce 1981; Schulte and Müller-Schwarz 1999; Bloomquist and Neilsen 2010). However, population density in the conservation area was higher than that reported for the similarly sized Yampa River in Colorado where beavers are also bank-dwelling and unexploited (0.35 colonies per river km; Breck, Wilson, and Andersen 2001). Population density in Saskatoon was also similar to that in European cities where beavers are strictly protected by laws prohibiting capturing, killing, or disturbance (Swinnen et al. 2017). The reason for these similarities is unclear. Seattle, Washington has higher beaver population density (2.0 per river km) but lethal management is not used (Bailey et al. 2019). However, direct comparison of beaver lodge and population density in Saskatoon to that in other cities like Seattle is not wise, as river type, climate, flow, vegetation and other factors beyond human tolerance and beaver management differ between the two cities.

Beaver colonies regularly build multiple lodges in this part of the South Saskatchewan River. Our census took place in a time with very low river levels and so we were able to observe lodges that would be fully submerged and/or become fully encased by winter ice in months or years with higher water levels. We also found the occasional abandoned beaver lodge in the few backwater channels that exist along the studied reach; these could only be suitable beaver habitat at high flows. Beaver adaptability to changing bank physical conditions, especially in northern rivers, is not unusual (Fustec, Cormier, and Lodé 2003). On the Yampa River (Colorado), for example, beavers adapt to dynamic annual flows by having a spring den located higher up on the bank and a winter den lower on that bank that is used during baseflow (Breck et al. 2001). Since beavers move from lodge to lodge every few years (Hood and Bayley 2008), some of the inactive lodge sites we observed could just be old lodges used by the same families during different years with different river flow conditions. Thus, the comparison of active sites is the most biologically useful measure of beaver density.

The active lodge sites were closer together in the conservation area than in the city, and lodges had a clustered distribution in the conservation area. This likely results from there being a few places in the conservation area that had particularly high beaver lodge density—20% of the lodges found were located on Wilson and Yorath Islands. Although beaver habitation

![Figure 2: Size of beaver preferred trees utilized and not utilized in relation to their distance from the South Saskatchewan River in the City of Saskatoon and the upstream conservation area. One cottonwood tree occurring at 174 m from the river was excluded from the Poplar panel for visualization purposes.](https://academic.oup.com/jue/article-abstract/7/1/juab021/6344834)
of large rivers is common (Fustec et al. 2003), there are only a few literature examples of river island habitation (e.g. Brown 1988). Side channels of anastomosing rivers are more widely known as preferred beaver habitat (Zadnik et al. 2009). Side channels are uncommon along the studied reach of the South Saskatchewan River owing to the incised river valley (i.e. steep banks). At first glance, islands might seem to be preferred habitat because they provide beavers with greater protection from common terrestrial predators like wolves (Canis lupus), coyotes (Canis latrans) or cougars (Felis concolor). The South Saskatchewan River flowing through the conservation area freezes over in winter, allowing predators overland access to islands; however, beavers are usually in their lodges at this time of year, foraging on their under-ice cache, which limits predator access (Shelton 1966). Beaver colony density may have been high on the islands due to reduced human traffic (Müller-Schwarze 2011) or an abundance of preferred forage; further investigation of beaver habitation of river islands is warranted.

**Riparian tree composition and beaver foraging**

Our data do not support the hypothesis that beavers will forage closer to shore in the city vs. conservation area due to human activity. Our data also do not support the hypothesis that beavers will be less selective in foraging choices in the city vs. conservation area. Beavers were selective in both areas and traveled further from shore in the city than conservation area to cut trees of preferred species, especially green ash.

The riparian forest is not the same in the city and conservation area. Within the city, the riparian forest has a greater overall diversity and density of trees. In part, the higher tree species richness in the city is the result of riparian forest management as there is planting of both native and non-native species, and trees in parks and along paths are protected with enclosures. The City of Saskatoon publicizes that roughly two-thirds of trees planted are English elm, ash (especially Fraxinus mandshurica and F. nigra) spruce and linden. The city also collaborates with the Meewasin Valley Authority to run a memorial ‘plant a tree’ program (R. Grilz, pers. comm.). For a donation of $50–500, citizens can gain a greater sense of ownership of the city’s natural resources by having trees planted on their behalf along the river bank. Although management of urban riparian forests is thought to lead to tree species homogenization (Groffman et al. 2003), we found no evidence in support of this hypothesis in Saskatoon.

Despite the differences in riparian tree species diversity between the city and conservation area, we found that beavers are selective in their choice of trees, utilizing several species more than expected based on their abundance. Beavers in the study area showed preference for green ash and several species of poplars (cottonwood, aspen, hybrid poplar). Green ash may be selected in the study area because they are concentrated close to the river and have a smaller median diameter (4.9 cm), as suggested by Parker and Rosell (2003). Beavers traveled up to 50 m from shore in the city to cut them. Poplars such as cottonwood and aspen are widely reported to be preferred by beavers (Hall 1966; Breck, Wilson, and Andersen 2003; Severud et al. 2013), as is the case in our study site. Although we found about the same number of cottonwood trees in the city and conservation area transects, beaver use of cottonwood was higher in the conservation area. The difference in use is likely partly due to the protection of cottonwood trees in the city with wire cages. As a result, beavers focused their foraging efforts on green ash, cutting 90% of those available in the city transects. As well, beavers in the city cut tree species not present in the conservation area, selecting mountain maple, birch and English elm in greater proportions than which they were available. While it is unclear if these species are consumed, used as construction materials, or cut simply to wear down their continuously growing teeth, beavers have demonstrated a considerable ability to consume woody species with which they did not evolve. In southern South America, for example, invasive beavers have cut huge tracts of three species of Nothofagus which are not woody species available in their native range (Anderson et al. 2009). The simplest explanation for the species we observed cut in the city transects is that while beavers are choosy generalists (Jenkins 1975, 1980), they tend to consume the prevailing genera in the preferred diameters within their travel distance when riparian forests have a diverse composition (Vorel et al. 2015).

Most of the preferred tree species were cut close to the river and the size of the cut trees appeared to be smaller farther from shore, consistent with central place foraging theory (Jenkins 1975). We found that 87% of cut trees were <50 m from the river, which is within the reported distance (95% of foraging occurs within 50 m of shore) for beaver cutting (Stoffyn-Egli and Willison 2011). Beavers forage close to shore to reduce time and energy expenditures associated with cutting down a tree, fractioning it into manageable pieces (if necessary) and dragging it to water where it is consumed or used as building material (Fryxell and Doucet 1991). They also forage close to shore to reduce predator risk (Salandre et al. 2017). To forage further into riparian areas, beavers will often dig a canal network (Hood and Larson 2015) as water-based paths provide safer transit routes and minimizes energy expenditure (Abbott et al. 2013). Beaver canals though are uncommon on this part of the South Saskatchewan River owing to bank steepness. A factor that could be important in influencing beaver foraging distance into the riparian forest is the river’s flow regime, given that it is regulated by Gardiner dam. Flow regulation has been shown to have a positive response on beaver populations via increasing the distribution and availability of some beaver preferred species (Breck et al. 2001). That said, both the city and conservation area riparian forests would be equally affected by flow regulation by Gardiner dam as it is nearly 100 km upstream of the study site. Thus, flow regulation does not explain why beavers traveled farther from the river in the city than conservation area to forage. Most likely, the median travel distance was greater the city than in the conservation area owing to the use of wire cage to protect trees. Tree damage is often the most regularly reported public concern in urban forests (Morzillo and Needham 2015).

Inadvertently, the woody plant species beavers choose to eat or avoid is likely to shape the riparian forest either toward a composition suggested by the natural path of succession or toward a modified woody plant community guided by the intentional management practices of people and unintentional management by beaver. Beavers along this part of the South Saskatchewan River are mostly foraging on native species with smaller stem diameters located within 50 m of the river. Beaver foraging activity may inadvertently support the proliferation of non-native woody plant species, particularly in the city, as has been demonstrated elsewhere (Breck et al. 2003). In particular, their foraging choices might be contributing to the expansion of two non-native woody plant species—Russian olive (Lesica and Miles 2004) and invasive European buckthorn (Rhamnus cathartica) (Archibold, Brooks, and Delanoy 1997).

As beavers are a natural and ecologically important disturbance agent in urban riparian forests that cities are working to...
become more comfortable with (Page 2017), effective beaver management strategies must consider the social and cultural processes in addition to biophysical processes (Duinker et al. 2015). Rather than simply managing beavers in urban environments in the future it may make more ecological and economic sense to integrate their presence as a form of natural habitat restoration and an integral ecosystem process (Severud et al. 2011) and manage some of their less preferred ecological impacts. It is important to recognize that citizen opinions will differ on preferred beaver management strategies. Public education on coexisting with beavers is a must—a strategy used extensively in Europe. It is also critical for managers to develop effective and adaptable beaver management plans (Bailey et al. 2019).

Data availability

Data analyzed during this study that are not already in the manuscript or are in the public domain are available in a public repository within the corresponding author’s Github https://github.com/Ecologyhydrology-westbrook/EnglandWestbrook_MeewasinValley-beavers.

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