ORIGINAL ARTICLE

Decadal trends in a population of urban white-tailed jackrabbits at the northern edge of its range

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Abstract

The urbanization of environments is a major land use change across the globe that is expected to continue. While the urban environment typically presents wildlife with lethal challenges, it may also present new opportunities for species able to behaviourally adapt. White-tailed jackrabbits are a quintessential prairie adapted species, which are understudied and are suggested to be in decline across their range. In the first urban study for this species, we surveyed the white-tailed jackrabbit population in Edmonton, Alberta, Canada. This population is at the northern edge of the distribution for this species. Using surveys conducted over a 24-year period across different land use strata, we show that the current average population density of white-tailed jackrabbits (8.0 hares/km^2) is very similar to densities in their southern range and significantly higher than local rural populations. Our models suggest that the population is relatively stable and exhibits approximately 7-year cycles. We discuss the importance of upland city park habitats for this species and suggest further research to determine the spatial dynamics of the species in an urban setting. Given the dynamics of climate change, we highlight the importance of studying species at the leading edge of possible range expansion.

Keywords Urban ecology · Population trends · White-tailed jackrabbits · Lepus townsendii

Introduction

Urbanization is one of the hallmarks of the proposed Anthropocene, and the expansion of urban environments is expected to continue (Grimm et al. 2008). Historically, and despite this trend, we know considerably less about the biology of urban ecosystems than rural or exurban ones. For many species, the habitat modification, loss, and fragmentation due to urbanization result in negative effects including population declines and local extirpation (McKinney 2002; Shochat et al. 2006). However, for other species who are urban adaptable (sensu Blair 1996), the proximity to human habitation offers up opportunities for establishment

and adaption (McKinney 2002; Ditchkoff et al. 2006) in a process called "synurbanization" (Luniak 2004). Organisms that are predisposed to synurbanization tend to be generalists that exhibit behavioural shifts in activity patterns to avoid humans, have varied diets, take advantage of novel and abundant urban food sources, and have increased reproductive output (Ditchkoff et al. 2006; Beaudoin and Beaudoin 2012; Lowry et al. 2013; Ritzel and Gallo 2020). Further, prey species that are urban adaptable may also take advantage of the fact that predators may avoid areas of human habitation resulting in an urban "predator shield" (Hebblewhite et al. 2005; Berger 2007), although some predators may become established in urban environments (Bateman and Fleming 2012).

In addition to urbanization, organisms also contend with adapting to a changing climate. Climate change may potentially cause range shifts in wildlife species as warming and/or moisture regimes induce vegetation and habitat distributions to contract, change in elevation, or even to move poleward. This phenomenon has been observed in many birds and forest mammals (Hitch and Leberg 2007; Deb et al. 2020). While portions of a range may contract, other populations at the leading edge of range expansion

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hold particular value for conservation in a changing climate (Gibson et al. 2009; Rehm et al. 2015). Likewise, variation in climate may also influence populations and contribute to observed declines (McCarty 2001) and has been implicated in the reduction in population cycles (Yan et al. 2013). Less is known about the effects of climate change in urban environments, which may buffer its effect, further complicating our understanding of urban ecology (Parris and Hazell 2005; Shochat et al. 2006; Wilby and Perry 2006).

White-tailed jackrabbits (*Lepus townsendii*) are nocturnally active large hares of the open plains, found throughout central and western North America (Beever et al. 2018; Rogowitz 1997; Simes et al. 2015), although their range appears to be contracting on its southern edge (Easterla 2003; Brown et al. 2020). Current range maps generally place the northern edge of the species distribution approximately along the latitude of the North Saskatchewan River (www.mol.org; Lim 1987; Brown et al. 2020), with the earliest record for these hares in this region being a sighting in 1920 from New Sarepta, a village 50 km southeast of Edmonton, and is reflective of early twentieth century land use changes in the Aspen Parkland transition zone between the prairie grasslands and the boreal forest to the north (Wood et al. 2006). White-tailed jackrabbits are prey for a wide variety of species (Simes et al. 2015), and their foraging primarily shift from grazing on grasses and forbs in spring until fall to browsing on shrubs during winter months (Simes et al. 2015) including non-native ornamental plants in urban settings (Beaudoin and Beaudoin 2012). In spring, white-tailed jackrabbits produce approximately three or four precocial young per breeding event and under good conditions have the capacity for up to 4 L/year (Simes et al. 2015). While across their range periodic population irruptions or aggregations have been noted (Mohr and Mohr 1936; Brunton 1981), it is unknown if white-tailed jackrabbits undergo the typical 10-year population cycles noted in some other Leporids (Keith 1983). There has been little research conducted on white-tailed jackrabbit populations, and trends suggest that they are declining across their range (Easterla 2003; Wood et al. 2006; Simes et al. 2015; Brown et al. 2020; Schlater et al. 2021). Finally, we are unaware of any research that has been conducted on an urban hare population in North America and there are a very limited number of studies globally (see Mayer and Sunde 2020).

In this paper, we report on the first systematic surveys of white-tailed jackrabbits conducted in an urban environment over a 24-year period in Edmonton, Canada, where they are year-round residents. Using a stratified survey approach, we model population trends through time to determine if the population is in decline, as has been reported elsewhere (Simes et al. 2015; Brown et al. 2020). Further, we determine, for this data deficient species, if this population has any evidence of cyclical population fluctuations.

Methods

Study area

Edmonton, in Alberta, Canada (53.54624° N, − 113.49037° E) is a large metropolitan city with a 2021 population of 1,491,000 people; it is situated in the central parkland ecoregion naturally characterized by aspen dominated grasslands, but most of which has been converted for agricultural or urban purposes. The city itself is bisected by the North Saskatchewan River valley, which constitutes one of the largest connected urban parkland systems in North America (www.edmonton.ca). Observation transects were established starting in 1992 across representative land use survey strata in Edmonton, including residential neighbourhoods, industrial areas, isolated city parks, and generally contiguous river valley parks. High-density office/commercial areas in the urban core were not systematically sampled. Residential neighbourhoods consisted of single and multifamily dwellings along one or two laned streets and may contain tree lined boulevard or small "pocket parks" well under a hectare in size. Industrial areas included manufacturing, refining, storage, railway, or minimal retail space and generally had little pedestrian foot traffic and light vehicle traffic after dark. River valley parks were part of the connected park system adjacent to the North Saskatchewan River; these locations were generally large and contained mowed (including golf courses) and unmowed areas, natural, and cultivated shrubbery as well as a wooded edge immediately adjacent to the river. Upland city parks were generally isolated from one another and from the river valley and often contained mowed grass (including school and athletic fields) and scattered trees. Coyotes have become increasingly common in the city of Edmonton through the duration of the study and probably comprise the main natural predator in this urban setting (Murray et al. 2015; Murray and St. Clair 2017; Sugden et al. 2021). A total of 19 transects were established in the four survey strata, residential (5 transects), industrial (3 transects), city parks (10 transects), and river valley parks (2 transects). For comparison, we also conducted surveys in outlying rural areas (3 transects) across most years. Rural transects consisted of a mix of small "hobby farms" as well as extensive farming consisting of grazing pastures typical of the human impacted aspen parkland ecosystem and associated residences.

We used a spotlight line transect modified for urban use (Anonymous 1989; Smith and Nydegger 1985). From October through April, transects were driven at slow and consistent speeds or walked (in the case of parks) to standardize sampling effort. The survey season corresponds approximately with when snow can be expected in

Edmonton and when nights were long enough to facilitate surveys. The surveys were conducted by multiple volunteers after sunset, from 2000 to 0300 h, and the number of white-tailed jackrabbits was recorded. The timing of surveys was selected to correspond to when individual daily activity was most likely based on observation and activity studies of this species in Edmonton and literature on white-tailed jackrabbit activity (Rogowitz 1997; Wood, unpublished data). The area surveyed for each transect was determined using a GIS. For residential and industrial transects, it was assumed that observers could only see until the façade of the buildings on either side along the length of the road being used to survey the area. City parks were surveyed in their entirety, and a representative portion of the river valley parks were surveyed, and the area was estimated based on the visual area that could be scanned along the transect. Further information on survey methods can be found in Wood et al. (2006), and the noninvasive survey methods were approved by The King's University Research Ethics committee.

Data analysis

Count number of white-tailed jackrabbits were standardized to density (hares/km^2) as the dependent variable for further analysis and divided by the number counted in the area surveyed along each transect. To estimate trends in population densities, we employed a two-step approach to model building and selection. In the first step, we built to predict density as a function of survey strata, year of the survey, local weather conditions (snow accumulation, and air temperature during the survey), and measures of interannual climatic variability (accumulated rainfall and growing degree days in the previous year). Snow accumulation and temperature were included because they may impact the activity of white-tailed jackrabbits and impact the number counted at a transect (Rogowitz 1997), while climatic variables were included to determine (Langvatn et al. 1996; Witter et al. 2012). Local weather climatic variables were extracted from records of a local weather station (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html). We also modelled the potential interaction between strata and year to determine if the rate of population change might differ between strata. We included models with a cosine function, in particular, to determine if there was any evidence for a cyclical population trend (Schmidt et al. 2018). We then determined what periodicity fit the data best. We did this by fitting periodicities representing cycles from 1 to 20 years and selected the model with the best fit. We used the profile-likelihood of models fit to the different periodicities and to estimate the 95% confidence interval (values within 1.92 log likelihood units of the best model) around the periodicity with the best fit. In both steps, we compared models

using Akaike information Criterion for small sample sizes (Burnham and Anderson 2002). In all cases, we employed a general linearized model with random-effects framework to account for repeated sampling of a particular transect and a gamma distribution with a log link to ensure that model estimates for density (hares/km^2) did not go below zero (Zuur et al. 2009). The gamma distribution required that we add 0.001 to all the densities to avoid initialization issues associated with zero values. All analysis was conducted using R (R Core Team 2021). We calculated density estimates from rural transects but did not include them in the model which was specifically focused on modelling the urban population.

This model was then used to estimate the most recent mid-cycle (year 2013) population size of white-tailed jackrabbits in Edmonton. This was done by determining the area within the city limits that comprised each of the surveyed strata, multiplying the density by the total area for each stratum, and summing up the area weighted population sizes for all strata to a total estimate. We exclude agricultural area within the city limits and use the average of the two lowest density strata to apply to business and commercial areas, for which we have no estimates of density. We used the City of Edmonton online GIS data to conduct this analysis based on a reclassification of their land use layer (City of Edmonton, www.data.edmonton.ca).

Results

A subset of focal transects within each of the four urban strata were visited in 12 years from 1992 to 2016. Some focal transects were selected to be revisited within years and were revisited, on average, 2.8 times. In total, there were 321 transect specific observations of urban white-tailed jackrabbits (Fig. 1). We found that, averaged across years, white-tailed jackrabbit densities were highest in upland city parks (14.50 hares/km$^2 \pm 14.73$ SD), followed by residential areas (5.62 hares/km$^2 \pm 6.00$ SD), river valley parks (3.41 hares/km$^2 \pm 4.33$ SD), industrial areas (3.31 hares/km$^2 \pm 3.15$ SD), and rural (0.10 hares//km$^2 \pm 0.11$ SD).

Model selection indicated that there was considerable evidence for the top model ($w_i = 0.69$), which included a positive association with accumulated growing degree days in the previous year ($p < 0.001$) and a negative association with accumulated snow on the date of the survey (($p < 0.001$), sampling strata, year, and their interaction (Table 1). This model also included a cosine function of year, with a periodicity of 7.33 years (95% CI ranged from 6.46 to 8.02 years). Model diagnostics suggested that the top model (Loglikelihood = -691.31, AIC$_c$ = 1409.80, $w_i = 0.69$) fit the data reasonably well (conditional $r^2 = 0.60$, marginal $r^2 = 0.46$). We found less evidence that the inclusion of temperature on the day of the survey or

Fig. 1 Survey transects location within the administrative boundaries of city of Edmonton divided by neighbourhoods. Transect locations are coloured by survey strata, and the size indicates the number of overall visits made to a transect (min = 3 and max = 35 visits) between the years of 1992 and 2016. Location of the city of Edmonton within the province of Alberta is given in the inset
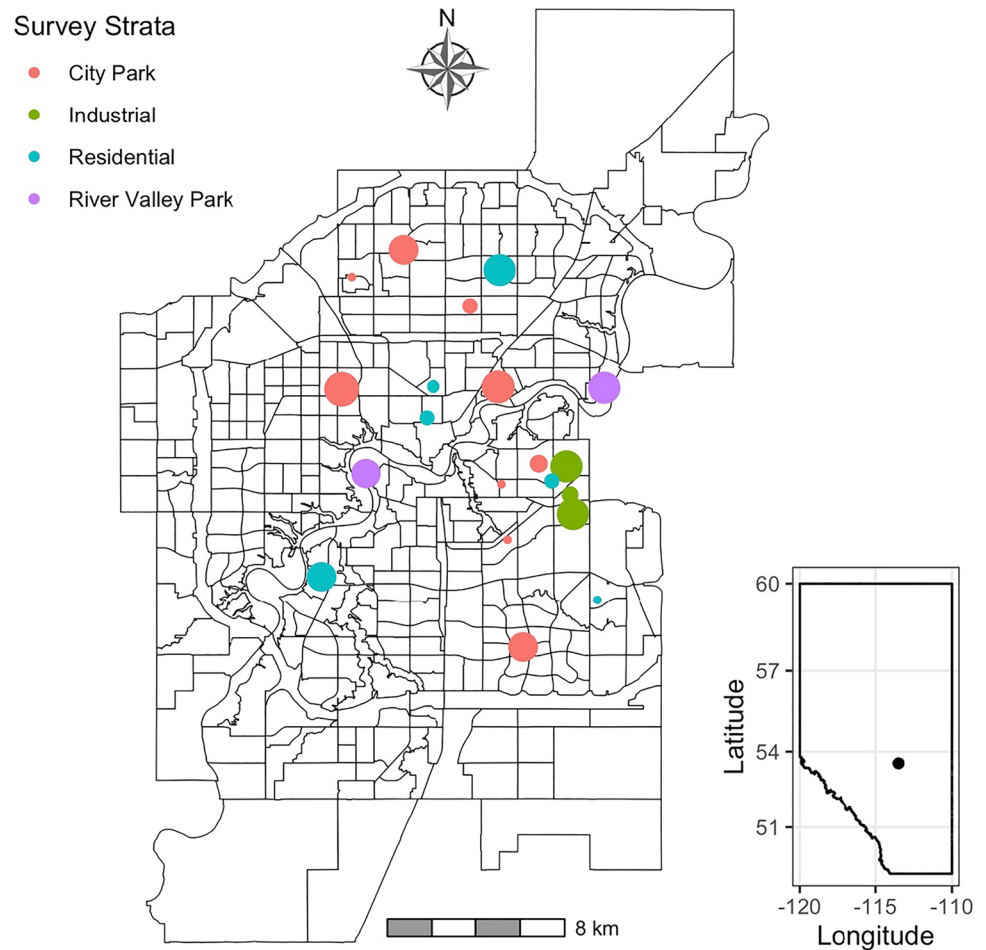

Table 1 Model selection to determine the covariates and their potential interaction (x) included in the model of white-tailed jackrabbits density (D) and whether or not there was evidence of cyclical population trends. The periodicity identified by profile likelihood as the best fit to the data was also included in the candidate set. Covariates included survey strata (strata), the year of the survey (year), the presence of a cycle as a function of year (cos(year)), local conditions (snow accumulation (cm) and temperature (temp) on the day of the survey), and measures of seasonal conditions (accumulated precipitation (precip) and growing degree days (GDD) in the year previous to the survey). Where K is the number of estimate parameters, LL is the log likelihood, AIC_c is the Akaike information criterion corrected for small samples sizes, and w_i is the AIC weight of evidence for a particular model

Model	K	LL	AIC_c	w_i
$D \sim year \times strata + cos((2 \times pi)/7.33) \times year) + snow + GDD$	13	−691.31	1409.80	0.69
$D \sim year \times strata + cos((2 \times pi)/7.33) \times year) + precip + GDD$	13	−693.10	1413.39	0.11
$D \sim year \times strata + cos((2 \times pi)/7.33) \times year) + snow + temp$	13	−693.24	1413.66	0.10
$D \sim year \times strata + cos((2 \times pi)/7.33) \times year) + temp + snow + precip + GDD$	15	−691.15	1413.88	0.09
$D \sim year + strata$	7	−703.20	1420.77	<0.01
$D \sim year + strata + cos(year)$	8	−703.04	1422.54	<0.01
$D \sim year \times strata + cos(year)$	11	−700.84	1424.53	<0.01
$D \sim strata$	6	−708.45	1429.17	<0.01

total precipitation in the previous year improved the model in terms of parsimony ($w_i < 0.12$); indeed, further inspection of the p-values indicated they were not significant. The coefficients for the top model are given in Table 2.

Our top model suggests that densities of urban white-tailed jackrabbits are increasing year over year in city parks and in residential areas (Fig. 2). Densities in river valley parks appear to be essentially stable (aside from the cyclical
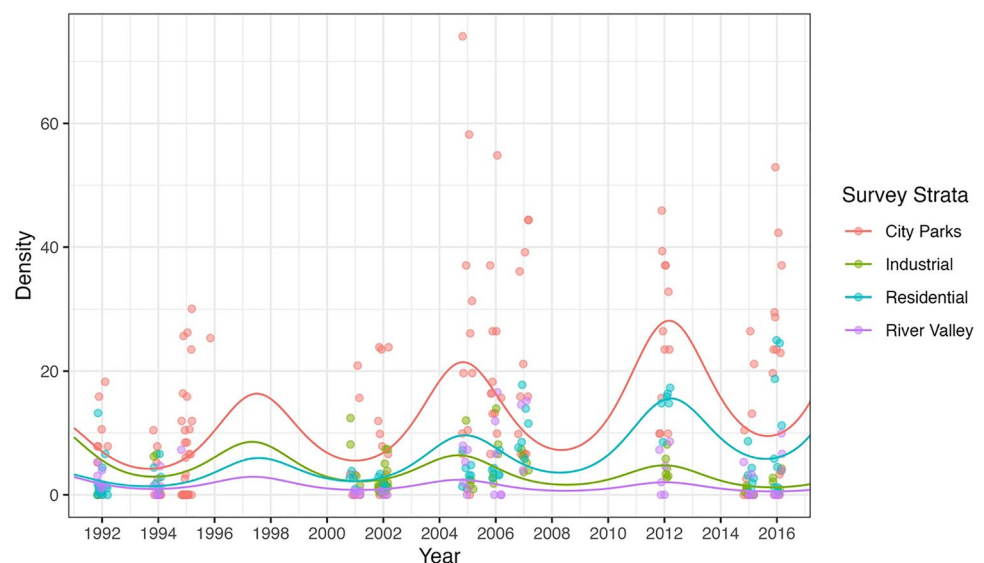
Table 2 The coefficients of the top model as identified by the model selection procedure. Where year is the year of the survey, snow is the accumulated snowfall (cm) on the day of the survey, GDD is the accumulated growing degree days in the previous year, and strata is the land use strata surveyed. Where upland city parks are the reference category for the survey strata. The random effect of transect had a variance of 0.327 (0.572 SD), while the residual variance was 0.894 (0.945 SD). Note that the best fit periodicity (7.33-year cycles) was fit by iteratively maximizing the profile likelihood of values and has an estimated 95% CI of 6.46–8.02 years. Model diagnostics suggested that the model (LL = −691.31, AIC$_c$ = 1409.80, w_i = 0.69) had the most evidence from within the candidate set (Table 1) and fit the data reasonably well (conditional r^2 = 0.60, marginal r^2 = 0.46)

Variable	Coefficient	Std. error	p-value
Intercept	−74.24	0.001	<0.0001
Year	0.037	0.0003	<0.0001
Snow	−0.020	0.001	<0.0001
GDD	0.002	0.0003	<0.0001
Strata = Industrial	153.40	1.891	<0.0001
Strata = Residential	−58.14	0.001	<0.0001
Strata = River Valley Park	122.20	0.001	<0.0001
Cos((2 × pi/7.33) × Year)	−0.609	0.001	<0.0001
Year × Strata = Industrial	−0.077	0.0009	<0.0001
Year × Strata = Residential	0.029	0.0002	<0.0001
Year × Strata = River Valley Park	−0.062	0.0003	<0.0001

trends), while densities in industrial areas appear to be in decline.

Using the model estimates from our top model and the area of land cover strata in the city for which we have density estimates, we estimate that the city-wide white-tailed jackrabbit population in the most recent mid-cycle year of our survey (2013) to have been 2491.81 white-tailed jackrabbits, which amounts to an overall density of 8.02 hares/km^2.

Discussion

While white-tailed jackrabbit populations are reported to be in decline across their range (Brown et al. 2020; Schlater et al. 2021), we found that at the edge of their northern range, and in an urban environment, white-tailed jackrabbit numbers have increased or remained stable since 1992, when our first surveys were completed. Interestingly, both Brown et al. (2020) and Schlater et al. (2021) suggest that habitat alteration and climate change are the biggest drivers of this decline. Our study seems to indicate that at the northern edge of their range, the environmental impact of climate change may lead to increasingly favourable conditions (increased growing degree days; Langvatn et al. 1996; Witter et al. 2012) for white-tailed jackrabbit populations as their preferred habitat shifts northward (Schneider et al. 2009; Levänen et al. 2019). Using our model estimates, our area weighted estimate of overall density in Edmonton at the midpoint of the cycle is 8.0 hares/km^2 or approximately 2500 white-tailed jackrabbits. Our estimate for the city-wide population size is likely a conservative one as it does not include estimates for the agricultural fringe of the city. The urban hare densities that we observed (8.0 hares /km^2) are considerably higher (~80 times) than local rural estimates and similar to, or slightly higher than, estimates from the white-tailed jackrabbits' southern range and very similar to urban populations in Europe (Wood et al. 2006; Simes et al. 2015; Mayer and Sunde 2020).

Models in our candidate set that accounted for cyclical trends via the inclusion of a cosine of year out preformed models which only accounted for linear changes in white-tailed jackrabbit densities. Our top preforming model

Fig. 2 White-tailed jackrabbit density (hares/km^2) through time by survey strata. Data points are jittered horizontally and partially transparent so improve visualization. Model predictions from the best fit random effect model (Table 2) are also given by survey strata. The values of growing degree days in the previous year and snow accumulation at the time of the survey (cm) were set to the mean in the observed data

suggests that there was evidence for a cyclical pattern in hare density and model selection and inspection of the log likelihoods indicated an approximately 7-year cycle. While this is not the 10-year cycle observed in snowshoe hare (*Lepus americanus*) or black-tailed jackrabbits (*Lepus californicus*), and attributed to multiple factors including density dependence, climate, predation, and stress (Keith 1983; Bartel et al. 2008; Krebs 2011), we suggest that further systematic surveys across the range of the cycle (and in particular the rising phase) would be required to determine if this is, in fact, a real difference. Our study was never designed to elucidate the mechanism that gives rise to the cyclical population trends; however, there is evidence that climatic variability, as measured by accumulated growing degree days, may play a role, as may the anecdotal increase in urban coyotes as predators in Edmonton.

Upland city parks, with potentially abundant food, minimal human use after dark, potentially fewer predators than connected river valley parks, and grassy surfaces interspersed with shrubs (not unlike the prairie habitat in which they evolved) appear to provide good habitat for these urban hares (Mayer and Sunde 2020). Our model suggests that hare densities are increasing in city parks and residential areas, while the densities in the other habitat strata (river valley parks and industrial areas) appear only to be cycling. Future surveys may help distinguish between the overall population trend and the cyclical fluctuations present in the population. Similarly, while the residential and upland city park densities have continued to rise for the duration of the study, we suggest that at some point in the future, these locations may become saturated.

Upland city parks in Edmonton are generally isolated from one another within the urban matrix and might be understood as islands of habitat (Fernandez-Juricic and Jokimäki 2001) and facilitate source-sink dynamics between city parks and other areas. However, if the other habitat types cannot support ongoing populations, they may function as ecological traps (Battin 2004). In these traps, increased mortality (or decreased fecundity) could be a result of the additional stress in these more marginal habitats (Sheriff et al. 2009), increased predation rates (Hawlena et al. 2010), or vehicle collisions (Found and Boyce 2011). Urbanization may cause evolutionary impacts on antipredator behaviour that reduces a prey species ability to cope with predation (Geffroy et al. 2020). Interestingly, the large contiguous river valley parks, which are more forested (not the preferred habitat for white-tailed jackrabbits) but included golf courses, had some of the lowest densities of white-tailed jackrabbits and this is likely due to the increasing presence of coyotes at these locations (Murray et al. 2015; Murray and St. Clair 2017; Sugden et al. 2021). Further work is needed on the spatial ecology of urban white-tailed jackrabbits to determine the size and composition of home range areas, connectivity in urban environments, the potential for genetic isolation, and the role urban parks play in mediating these effects (Braaker et al. 2014, 2017; LaPoint et al. 2015; Stillfreid et al. 2017; Van Moorter et al. 2021).

While climate change may be making northern regions warmer and potentially more suitable (Schneider et al. 2009), we also cannot discount the effect of the city heat island (Oke 1973) which may be mitigating the ability of white-tailed jackrabbits to survive at the edge of their range (Parris & Hazell 2005). It seems likely that climate change has caused contraction of the southern range for white-tailed jackrabbits (Brown et al. 2020), but it is unknown if there has been a northern shift into suitable habitat for this reason, which while limited, does exist. White-tailed jackrabbits in and around Edmonton may function as a valuable leading-edge population for this expansion (Gibson et al. 2009; Rehm et al. 2015). Indeed, the evolutionary history of North American hares includes genetic introgression at the leading edge of populations which may be linked to adaptive traits (Melo-Ferreira et al. 2014; Levänen et al. 2018). Our results suggest that the white-tailed jackrabbit population appears to respond favourably to increased growing degree days in the year previous, which may be a proxy for foraging opportunities and a generally warming climate (Langvatn et al. 1996; Witter et al. 2012). Additionally, it is likely that, similar to other urban herbivores, increased foraging opportunities are present in the urban environment that include nutritious lawns, shrubs, and ornamental species which may also promote increased population densities (Swihart et al. 1995; Beaudoin and Beaudoin 2012). Increased foraging opportunities in urban spaces may induce increasing acceptance of social interactions and concomitant home range overlap resulting in increased density of individuals (Ims 1987). Similarly, a reduction in predation due to proximity to humans or inability of predators to establish in small habitat patches may further facilitate the population densities we observed (Berger 2007). However, predators may also habituate to humans in an urban setting (Breck et al. 2019; Gamez and Harris 2021) and the urban populations of coyotes in Edmonton appears to be increasing (Murray et al. 2015; Murray and St. Clair 2017).

Mayer and Sunde (2020), in the only other urban hare study published (i.e., European hares; *Lepus europaeus*), found densities of approximately 5.7 hares/km^2 and attributed the colonization of urban centres in Denmark to the intensification of agricultural practices in the surrounding natural habitat for these hares. In their study, as well as ours, the low density of rural hares suggests that movement into the urban centre is not a function of a high population spilling into available habitat (Mayer and Sunde 2020). Rather, this suggests that urban white-tailed jackrabbit adaptation may be the result of bolder individuals

gaining a competitive advantage in the city and subsequent reinforcement of this behavioural shift (Honda et al. 2018; Breck et al. 2019). This may occur via an urban "predator shield" and the development of "preactive" coping styles (Berger 2007; Sadoul et al. 2021).

While we have reported white-tailed jackrabbit density, our estimates are better understood as population indices. Increasingly, the role of detection in studies employing occupancy and abundance estimates has been highlighted (Royle et al. 2005), although assumptions and critiques remain (Newson et al. 2013; Welsh et al. 2013). The practical utility of indices for determining within population trends (Sinclair et al. 2006) and ability to utilize historical and consistent data over long periods (Watkins et al. 2010) suggest that indices, such as our estimates, have a place in ecology (Johnson 2008). Indeed, we found no consistent bias in the detectability of white-tailed jackrabbits, which at worst would have underestimated the density of hares at both upland city and river valley parks (full details can be found in the Supplemental Information).

We have shown that for this data-deficient species, that is undergoing population declines across its southern range, the urban environment of Edmonton appears to function as suitable habitat, particularly in upland urban parks. As urbanization continues, urban-adapted species, as we suggest the white-tailed jackrabbit is, provide unique opportunities to further elucidate how behavioural plasticity contributes to their success. Further, due to their ubiquity and benign nature, white-tailed jackrabbits may have the potential to function as charismatic urban fauna to help promote conservation efforts among citizens (Root-Bernstein, et al. 2013; Egerer and Buchholz 2021). Additional work is needed to fully understand the spatial structuring of this urban population, the role of urban green spaces, and of urban design (Apfelbeck et al. 2020) in maintaining or facilitating its population growth and cycling and interaction with a changing climate.

Declarations

Conflict of interest The authors declare no competing interests.

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