

# Black-tailed deer resource selection reveals some mechanisms behind the ‘luxury effect’ in urban wildlife

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## Abstract

The global urban population is expected to increase by 2.5 billion people over the next 30 years. Yet the doubling of urban landscapes in the last decades have already led to habitat loss and concomitant impacts to biodiversity. Nonetheless urban landscapes remain important for wildlife, and global syntheses have revealed that wealthy urban areas house more biodiversity, a ‘luxury effect’. We researched some of the mechanisms for the luxury effect for urban black-tailed deer, a species of increasing concern in urban landscapes across the northwestern Nearctic. We satellite collared twenty deer in an urban landscape in British Columbia, Canada, with high-resolution fix rates. We used generalized models in an information-theoretic framework to weigh evidence for competing hypotheses about the role of tree cover, productivity, public green spaces, and wealth in explaining deer selection. Wealth, manifesting as housing lot size, emerged as the dominant predictor of deer space-use, which is highly concentrated into very small home-ranges. Other landscape elements stemming from affluence, including golf courses and parklands, were also strongly selected by deer. We show post-colonization landscape conversion from dry semi-arid savannah to well-watered high-productivity landscapes is supporting deer, with ramifications for the rest of the biotic community. With urban landscapes becoming an increasingly important for biodiversity conservation, understanding these mechanisms can help to promote wildlife-human coexistence.

## Introduction

The global urban population is expected to increase by 2.5 billion people over the next 30 years (Seto, Güneralp and Hutya 2012), following decades of continued urban growth (Seto, Fragkias, Güneralp and Reilly 2011). Consequently, urban landscapes have doubled in the last few decades leading to direct and indirect forest loss (van Vliet 2019). By 2030, global urban land cover is projected to increase between 430,000 km<sup>2</sup> and 12,568,000 km<sup>2</sup> (Seto, Güneralp and Hutya 2012). With urbanization comes a loss of natural habitats – especially tree cover – and increase in impervious surfaces, of low value to biodiversity (Nowak and Greenfield 2020). Thus urbanization generally correlates to losses in biodiversity (McDonald, Güneralp, Huang, Seto and You 2018, van Vliet 2019). However, many anthrophilic species continue to coexist with humans in urban environments (Magle, Hunt, Vernon and Crooks 2012, Møller 2012) and there is sustained advocacy, research, and planning for urban areas that promote wildlife-human coexistence (Apfelbeck, Snep, Hauck, Ferguson, Holy, Jakoby, Scott MacIvor, Schär, Taylor and Weisser 2020, Larson, Lerman, Nelson, Narango, Wheeler, Groffman, Hall and Grove 2022).

Although urban wildlife ecology as a discipline was advocated by Aldo Leopold in the 1930s it remains markedly understudied in academia (Adams 2005). The biodiversity outcomes of urban development have been varied, from local extirpation of undesirable species such as predators (McCance, Decker, Colturi, Baydack, Siemer, Curtis and Eason 2017) to multi-taxic rapid phenotypic changes in urban centers, implicating urbanization as a mode of evolutionary change (Alberti, Correa, Marzluff, Hendry, Palkovacs, Gotanda, Hunt, Apgar and Zhou 2017). In summary species’ responses vary within and among cities and contextualizing

the mechanisms behind responses remains a key endeavor (Magle, Hunt, Vernon and Crooks 2012, McDonald, Mansur, Ascensão, Crossman, Elmqvist, Gonzalez, Güneralp, Haase, Hamann and Hillel 2020, Seto, Güneralp and Hutrya 2012).

We know that globally, large carnivores are one of the first groups extirpated, as we seek to “make safe” urban places for humans. One of the outcomes of extirpating large carnivores from urban environments is providing prey species with refugia from predation (Gallo, Fidino, Lehrer and Magle 2019, Møller 2012), often combined with substantial foraging subsidies for browsing and grazing herbivores (DeStefano and DeGraaf 2003). These anthropogenic changes to landscapes and wildlife communities have led to the perception of an “urban deer (*Odocoileus spp.*) problem” (Bowman 2011, Conover 1995, Rondeau and Conrad 2003) in wildlife management. Fifty-four percent of the world’s population lives in urban areas and is expected to increase to 66% by 2050 (Soulsbury & White 2019). Within cities, low-medium density housing areas the highest likelihood of urban wildlife interactions due to high species richness and low species extinction rates (Magle et al. 2016) and the greatest areas of greenspace and diversity of landcover (Loram et al. 2007). Yet people living within these low-medium density housing tend to react most negatively to human-wildlife conflict (Wine et al. 2015).

More than a problem however, urban wildlife is an unplanned scientific experiment that allows us to examine the roles of different forms of landscape heterogeneity on species’ space-use and resource selection. Urban areas are complex mosaics of impervious surfaces (buildings, roads, parking lots), natural or semi-natural greenspaces (parks), and heavily modified greenspaces (yards, gardens, golf courses), each offering different resources and risks for different species. Those resources are the outcome of social and economic drivers within the human population (Belaire, Westphal and Minor 2016).

One interesting outcome observed in urban ecology is the “luxury effect” wherein differences in affluence among neighborhoods generates differences in biodiversity. Evidence for a luxury effect dates back thousands of years, arising from Egyptian archaeological records, and continue through the Anthropocene (Leong, Dunn and Trautwein 2018). The luxury effect spans spatial scales, occurring both within and among cities (Magle, Lehrer and Fidino 2016), albeit inconsistently. Among 20 North American cities studied (Magle, Fidino, Lehrer, Gallo, Mulligan, Ríos, Ahlers, Angstmann, Belaïre and Dugelby 2019) per capita income played a role in explaining vertebrate diversity in half; instead species richness was highly (negatively) correlated with urban intensity (Magle, Fidino, Sander, Rohnke, Larson, Gallo, Kay, Lehrer, Murray and Adalsteinsson 2021). Affluence is thus a proxy measure for biological properties associated with rich neighborhoods (Magle, Fidino, Sander, Rohnke, Larson, Gallo, Kay, Lehrer, Murray and Adalsteinsson 2021): low human density, energy subsidy, and especially greenness. Indeed the luxury effect is generally amplified in arid environments (Leong, Dunn and Trautwein 2018).

Most research on luxury effect uses species richness of plant or animal assemblages as the metric. For large mammals, individual behavior is a key mechanism explaining response to urban development (Honda, Iijima, Tsuboi and Uchida 2018), so we examine luxury effect from this different angle. We examine resource selection by highly abundant urban black-tailed deer (*Odocoileus hemionus columbianus*; deer), a native to the western Nearctic including the Canadian province of British Columbia (BC). They are important prey for BC’s diverse carnivore population (Ballard, Lutz, Keegan, Carpenter and deVos Jr 2001) but the changing landscape has led to abundant urban deer populations. Predator persecution is an obvious culprit, but we suspect landscape change is an important driver. Deer select high-energy and high-nutrient plants as forage (Weckerly 1994) and are very sensitive to factors affecting the recruitment of young deer into the breeding population (Forrester and Wittmer 2013, Gilbert and Raedeke 2004). The abundant backyard gardens of urban and suburban areas in affluent neighborhoods (Larson, Lerman, Nelson, Narango, Wheeler, Groffman, Hall and Grove 2022) provide ample deer food, potentially allowing deer to breed more often and more successfully than in ‘natural’ (non-urban) landscapes.

However, even in natural systems the trade-off between security from predation and food resources is not well understood (Bowyer, Kie and Van Ballenberghe 1998), so how deer perceive risk in urban areas – and how they capitalize upon potential resource subsidies – remains unknown. Urban environments have

been shown to impact wildlife behaviour, resulting in unique adaptations that differ from their non-urban counterparts (Schell, Stanton, Young, Angeloni, Lambert, Breck and Murray 2021, Wright, Adams, Stent and Ford 2020). Similarly animal behaviour and personalities influence the efficacy of behavioural tools for urban wildlife management such as hazing deterrents and culls (Honda, Iijima, Tsuboi and Uchida 2018). A better understanding of urban deer resource selection, avoidance, and spatial landscape use would help determine if the luxury effect is impacting individual deer behavioural, and if so, what are some of the proximal mechanisms for this effect. This information is also an important tool for suburban deer management, both in terms of minimizing the impacts on wildlife population processes as well as negative human-wildlife interactions (Klees van Bommel et al. 2020).

We quantified deer locations via satellite telemetry collars and estimated home-range sizes to better understand urban deer habitat selection. To evaluate our hypotheses about the luxury effect, we used resource selection function (RSF) analyses to make inferences about how deer use different landcover features (Boyce and McDonald 1999, Seidel, Dougherty, Carlson and Getz 2018). RSFs have been used extensively to assess animal movement patterns, response to novel anthropogenic features, and identify movement pathways (Abrahms, Sawyer, Jordan, McNutt, Wilson and Brashares 2017, Anderson, Turner, Forester, Zhu, Boyce, Beyer and Stowell 2005, Chetkiewicz and Boyce 2009, Darlington, Ladle, Burton, Volpe and Fisher 2022, Laforge, Brook, van Beest, Bayne and McLoughlin 2016, Stewart, Darlington, Volpe, McAdie and Fisher 2019). We examined the role of (1) vegetation productivity and tree cover, (2) residential lot size, (3) road density, (4) golf courses and public green spaces, and combinations thereof. We included variables measuring these features in a generalized linear model and examined effect sizes ( $\beta$  coefficients). We hypothesized that if the luxury effect was apparent, then residential lot size would show the significantly positive effect size. We also predicted that road density was a risk deer avoided, and that native (parks) and non-native (golf courses) forage sources would be selected, but with smaller effect sizes.

## METHODS

### *Study Area*

Our sampling frame is the western distribution of the Columbia black-tailed deer (*Odocoileus hemionus columbianus*) on the Nearctic Pacific coastline, within the dry Garry Oak (*Quercus garryana*) savannah (Barlow 2017, GOERT 2021, McCune, Pellatt and Vellend 2013, Pellatt and Gedalof 2014). This savannah's Canadian distribution includes the District of Oak Bay on Vancouver Island, British Columbia, characterized by small- and large-lot residential areas, urban development, golf courses, as well as managed and natural parks throughout. The district is bordered by the Salish Sea to the east and south (Fig. 1).

### *Deer Locations*

We deployed 20 LOTEK Lifecycle GPS collars (Newmarket, ON, CAN) collars on female black-tailed deer in Oak Bay. We opted for female deer as the reproductive component of the population is expected to be most susceptible both to risk and to available forage. Through February - March 2018 we conducted road-based surveys every morning from sunrise to 11.00 hrs (when deer were most active). We systematically searched the entire OB period multiple times over this span, ensuring that animals throughout the study areas had the opportunity for capture. However, captures are necessarily constrained to where deer occur (Fig. 2). Female deer were captured using chemical immobilization *viadarting* with a Pneu-Dart - Model 389 Rifle with cartridge fired projector, 1cc Type C darts with a 1" needle, a wire barb, and a tri-port. Deer were immobilized by the wildlife veterinarian (AH) using 1ml of Wildpharm's BAM II Premix (27.3mg of Butorphanol, 9.1mg of Azaperone, and 10.9mg of Medetomidine) and reversed with 2ml of Atipamazole (50mg) administered intramuscularly (IM), and 0.5ml of Naltrexone (25mg) IM. Animals were moved to safety and blindfolded. Vital parameters including heart rate, respiratory rate, mucus membrane colour, and body temperature were monitored. Supplemental oxygen was administered via nasal cannula when needed. Collars were applied with unique coloured tags to allow field identification.



Fig. 1.

Fig. 1. We researched black-tailed deer resource selection in the District of Oak Bay, Vancouver Island, British Columbia, Canada. Oak Bay is bounded by the ocean (dark blue) to the south and east and by Greater Victoria to the north and west. Housing is depicted in grey, golf courses and private and public green spaces in green.

#### *Deer home-range size*

Space use by individual deer is an important parameter and we used kernel density estimation (KDE) to estimate home-range size. We applied a smoothed “kernel” of equal-sized grid cells in a systematic pattern across a study region weighted by the density of observations and their locations (Hooten, Johnson, McClintock and Morales 2017). We calculated the 97.5% *isopleth* – the largest area used by the animal

(within the chosen timeframe), excluding the extreme 2.5% of movements. Home range analyses were executed using ArcGIS v10.6 (ESRI, Redlands, CA, USA), using the Geospatial Modelling Environment package and the KDE tool.

### Landscape Quantification :

We extracted residential zoned lots from zoning maps for the municipalities of Oak Bay, Saanich, and Victoria. We used a BC provincial dataset (<https://catalogue.data.gov.bc.ca/dataset/bc-parks-ecological-reserves-and-protected-areas>) to quantify parkland and manually digitized golf courses. We discretized residential lots into three area classes – small, medium, and large – using the *Natural Breaks (Jenks) classification* algorithm in ArcMap. We used a publicly available BC roads dataset (<https://catalogue.data.gov.bc.ca/dataset/digital-road-atlas-dra-master-partially-attributed-roads>) to quantify roads, and a 100-m resolution impervious surfaces percent-cover dataset from Habitat Acquisition Trust (Blyth 2013) to quantify non-road urban features.

### Deer resource selection analysis

We evaluated  $\beta$  coefficients from a single global model containing all selected landscape features. We chose not to do model selection as our goal was not to find the most parsimonious (reduced) model with a small subset of component variables, but rather to ascertain the selection strength of multiple variables (Burnham and Anderson 2002). We used a logistic regression in a generalized linear model (GLM with binomial errors and a logit link) with used locations (1's) and randomly selected available locations (0's) regressed against landscape covariates. We examined the second order of selection (Johnson 1980) which examines use within a group of animals: in this case the population of Oak Bay. Third-order selection – selection of resources by individuals within their home-range – is a useful analysis when considering individual-specific behaviours or when resources are not available to all members of a population (Manly, McDonald, Thomas, McDonald and

Erickson 2007), but given our small study area and the movement of individuals across that area (making all resources accessible), the second-order analysis was of interest here. We used k-fold cross-validation (Roberts, Bahn, Ciuti, Boyce, Elith, Guillera-Arroita, Hauenstein, Lahoz-Monfort, Schröder, Thuiller, Warton, Wintle, Hartig and Dormann 2017) to examine model fit and calculated odds ratios (OR) from  $\beta$  coefficients as  $e^{\beta}$ .

## RESULTS

### *Space-use*

Urban black-tailed deer occupied very small home ranges. Mean core home range size (50% isopleth) for the 20 collared does was 0.14 km<sup>2</sup> (14 ha) (SD=0.07), and the mean outer home range size (95% isopleth) was 0.64 km<sup>2</sup> (64 ha) (SD=0.31). Female deer displayed high site fidelity over the two-year period, staying centralized during that time (Fig. 2).

### *Deer resource selection analysis*

Urban deer strongly selected large residential lots and areas of high vegetation productivity (or greenness; NDVI). Model validation did not indicate any model misspecification (Dsq = 10.21; overdispersion = 0.98; K-fold  $\Delta$  = 0.17). Deer were more than twice as likely to use an area with each unit increase in residential lot size ( $\beta$  = 0.89, s.d. = 0.04, OR = 2.44) and NDVI ( $\beta$  = 0.80, s.d. = 0.06, OR = 2.21) (Fig. 3). Deer also selected areas closer to public parks ( $\beta$  = 0.68, s.d. = 0.04, OR = 1.97) and golf courses ( $\beta$  = 0.68, s.d. = 0.05, OR = 1.97) (Fig. 3). Deer showed a weaker selection for small ( $\beta$  = 0.35, s.d. = 0.05, OR = 1.41) and medium-sized residential lots ( $\beta$  = 0.21, s.d. = 0.04, OR = 1.23). Deer strongly avoid areas with high road densities ( $\beta$  = -0.03, s.d. = 0.04, OR = 0.74). Deer did not select or avoid area of treed cover ( $\beta$  = 0.01, s.d. = 0.05, OR = 1.01). Effect sizes varied among landscape features, and error was small (Fig. 4). Extrapolation of observed deer responses (i.e.,  $\beta$  coefficients) to natural and urban landcover covariates across our study area highlights affluent neighbourhoods in Oak Bay are most strongly selected by urban black-tailed deer, along with golf courses, followed by parks (Fig. 5).



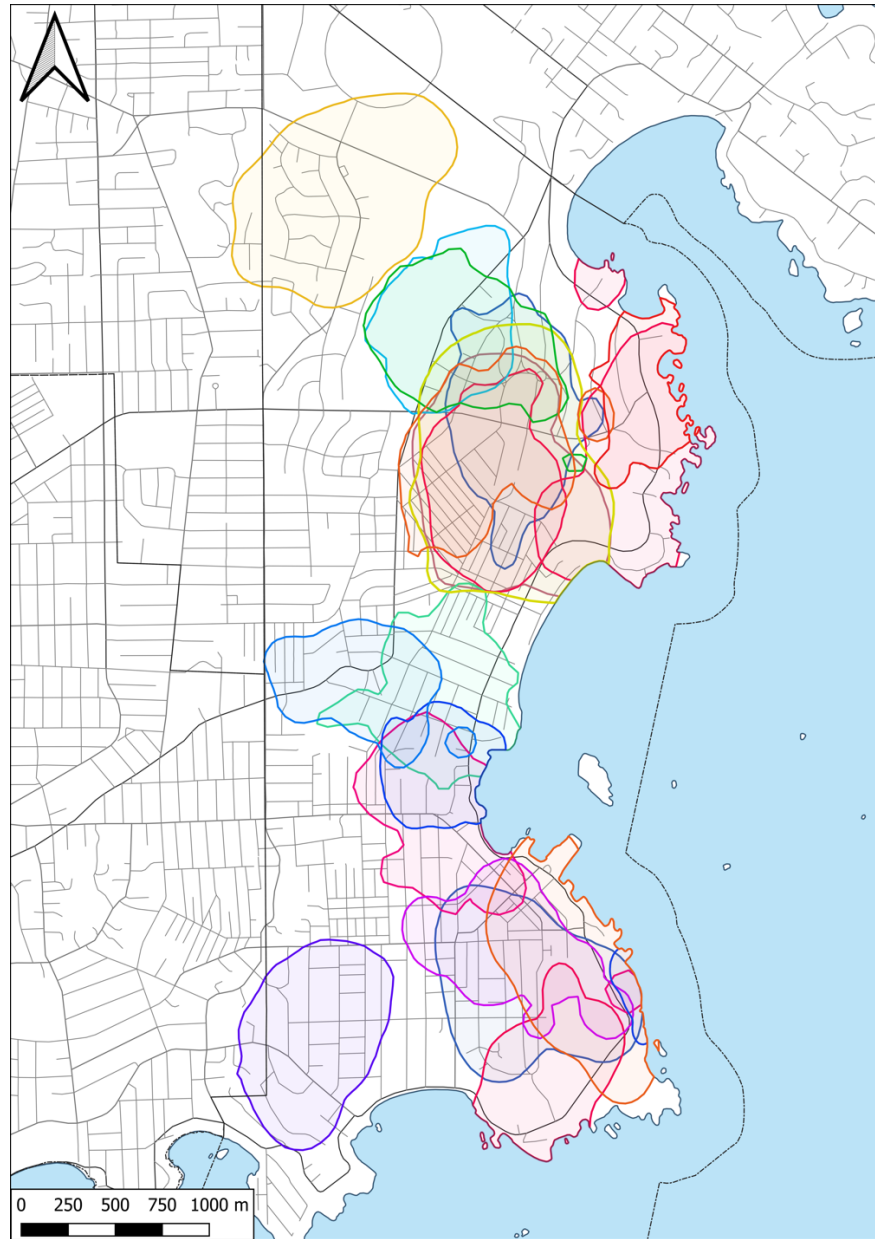


Fig. 2. Home ranges of satellite-collared female black-tailed deer in the urban landscape of Oak Bay, British Columbia. Polygons are 97.5% kernel density estimates. Each individual deer is represented by a unique colour. Home ranges are based on satellite telemetry location fixes collected from February 2018 - March 2020. Main roads (black), residential roads (grey), and ocean (blue) are depicted. Roadless areas are golf courses and public parks.

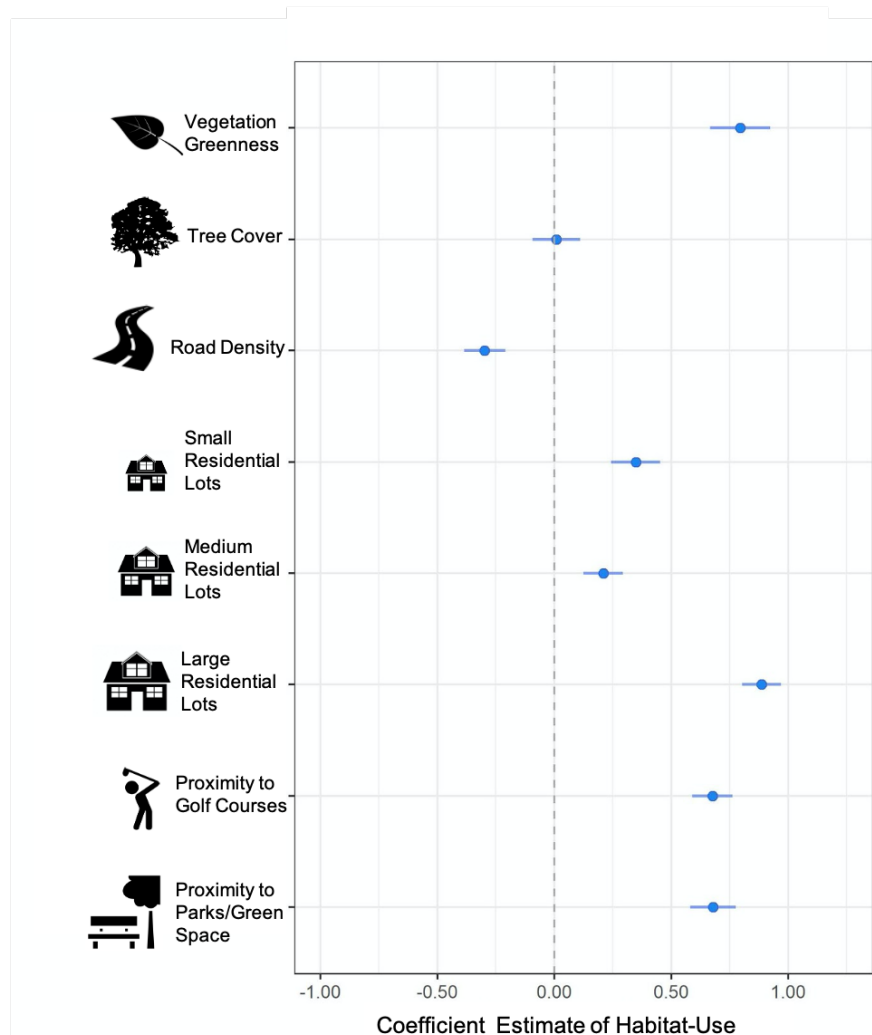


Fig. 3. The probability of black-tailed deer selecting (or avoiding) natural and urban landscape features across Oak Bay, BC. Values greater than 0 represent selection for these features by deer (e.g., vegetation greenness, large residential lots) while values less than 0 indicate avoidance (e.g., roads). Values overlapping zero indicate neither avoidance nor selection (e.g., tree cover).





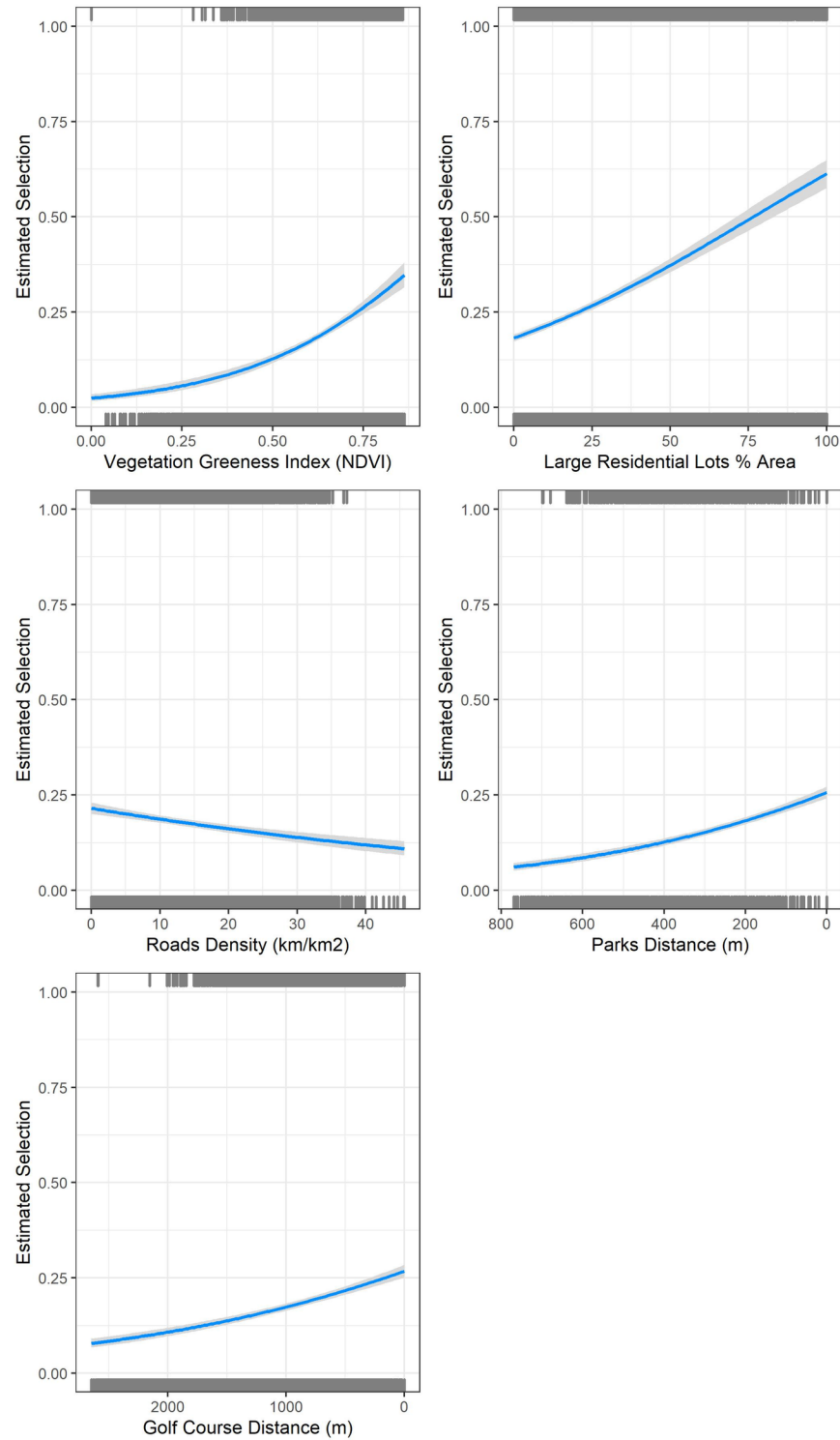


Fig. 4. Deer selection of landscape features in the urban landscape of Oak Bay, British Columbia, 2018-2022. Model  $\beta$  coefficients (“estimated selection”, or effect size) are in blue; grey bands are standard error.

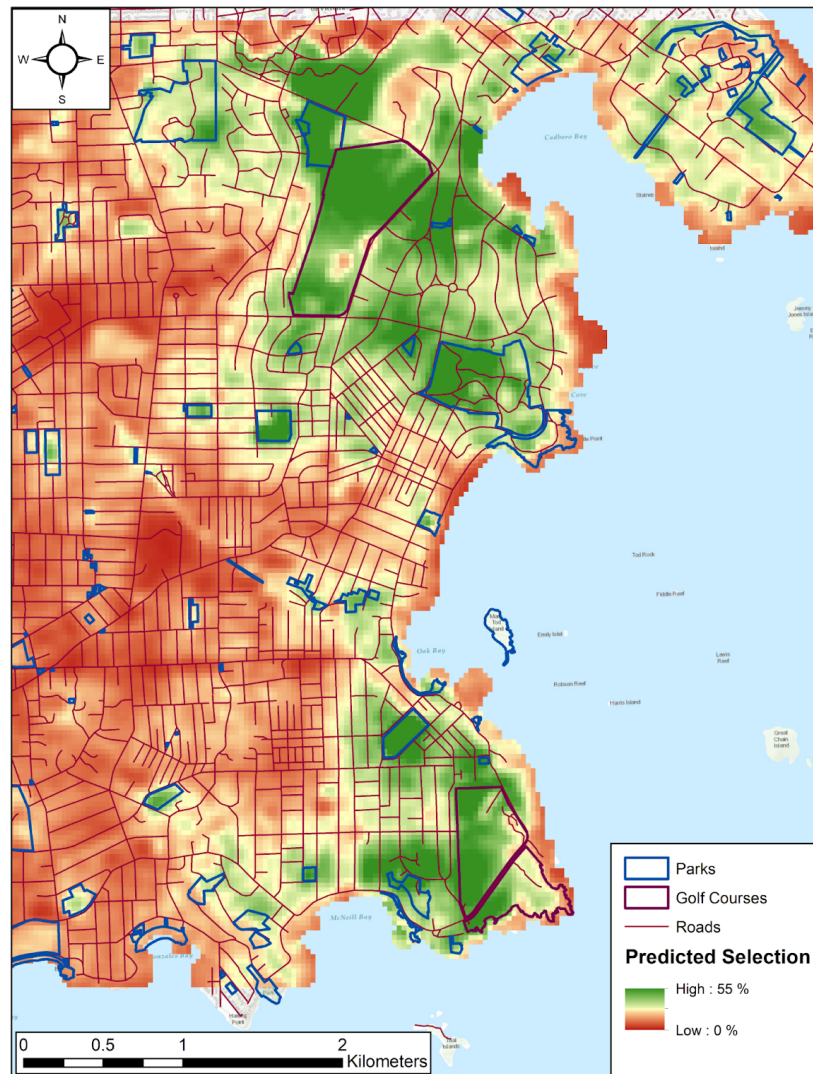


Fig. 5. Predicted black-tailed deer resource selection across the urban landscape of Oak Bay, BC based on extrapolated model  $\beta$  coefficients. Green areas are high use, fading to low use in red. Golf courses (purple) and parks (blue) are outlined. Roads are shown as red lines.

## DISCUSSION

The luxury effect – the relationship between urban biodiversity and human affluence – observed globally (Leong, Dunn and Trautwein 2018, Magle, Fidino, Sander, Rohnke, Larson, Gallo, Kay, Lehrer, Murray and Adalsteinsson 2021) manifests here in the behavioral resource selection by urban black-tailed deer. The greatest drivers of deer selection in this former savannah urban landscape are residential lot size and vegetation greenness (i.e., NDVI). Both are products of wealth. Oak Bay is a highly affluent neighborhood with 2022 house prices ranging from \$1-12 million CAD (mls.ca). Large lots (mean = 3601 m<sup>2</sup>, s.d. = 1609, range 2530-14766) are highly manicured, with gardens offering abundant resource subsidies. Although the

smaller “high density” lots in Oak Bay are not very small (mean = 679 m<sup>2</sup>, s.d. = 176, range 202-1052) and still heavily gardened and watered they are still not as strongly selected as the large lots.

Deer selection for areas with high-productivity vegetation highlights the importance of high-quality forage availability in urban deer resource selection. Higher vegetation greenness is represented in areas with healthy and dense vegetation, and is inversely linked to dry or drought conditions (Drisya and Roshni 2018). We observed a tight correlation with vegetation greenness (measured as NDVI) and the normalized difference moisture index (Supplementary Information, Fig. 1), with higher soil moisture associated with higher vegetation greenness. The unirrigated regions of this landscape experience extended summer drought; Garry Oak meadows provide dry, nutrient-poor vegetation (Barlow 2017, Fuchs 2001, GOERT 2021, Pellatt and Gedalof 2014, Pellatt, McCoy and Mathewes 2015). Parsing apart the effects of urban development is difficult in any system, as pre-development records are typically scant; but historically Cowan (1945) observed “from the standpoint of deer the food potential of a west coast climax forest is so low that over vast areas deer are almost non-existent”. At that time dense deer were only observed in regenerating forestry clearcuts. In the dry summer months, water was noted as particularly in demand, with a strong selection for plants in hygric areas (Cowan 1945). Thus, following European colonization the conversion of historically well-drained, drought-resistant Garry oak savannah ecosystems maintained by Indigenous peoples (Barlow, Pellatt and Kohfeld 2021, McCune, Pellatt and Vellend 2013, Pellatt and Gedalof 2014), to modern watered lawns and high-productivity vegetation is a key contributor to urban black-tailed deer abundance. This supports other research that shows the luxury effect is most commonly observed in arid and semi-arid landscapes, linked to irrigation and diverse plant communities (Leong, Dunn and Trautwein 2018).

Beyond the effects of natural vegetation, large residential lots are also a highly significant predictor of urban deer habitat-use in our study area. Large-sized residential lots are embedded in neighborhoods of similar-sized lots, generating low housing density. Deer are therefore likely responding to the decreased human disturbance associated with these neighborhoods, as well as higher densities of high-productivity vegetation associated with larger residential lots, and vegetative cover on lots. Neighborhoods with larger lot sizes and high investment into landscaping – features generated by financial affluence – are therefore more likely to experience higher deer use, and to perceive these interactions negatively (Wine et al. 2015).

Concentrated, high-quality resources mean deer can maintain smaller home ranges, which we observed here. Female urban deer home ranges were a quarter of the size of wild females in nearby Washington State (Bender, Anderson and Lewis 2004). Small home ranges in suburban environments have been noted by Happe (1982) and Bender, Anderson and Lewis (2004). Ideal free distribution theory suggests animals occupy the smallest areas that provide the resources they require (Fretwell 1969, Harestad and Bunnell 1979), and this phenomenon has been noted for other deer species (Said and Servanty 2005). In natural landscapes black-tailed deer strongly select shrubs (as opposed to graminoids or forbs) in early successional conifer stands (14-20 years) (Hanley 1984), and the abundance of hygric shrubs throughout large residential lots offers substantial subsidies that keep home-ranges small. People living in large residential lots tend to have the highest per capita income yet react most negatively to human-wildlife conflict (Wine et al. 2015). Thus, citizen reports of hyperabundant deer stem from peoples’ negativity bias (Jacobs & Vaske 2019; Buijs & Jacobs 2021) and repeated sightings of deer.

Citizen sightings suggested urban deer were strongly associated with golf courses and green spaces and our analysis corroborates this observation. Natural green spaces remain semi-arid oak savannahs but provide abundant escape cover; golf courses offer abundant well-watered grazing opportunities. Both parks and golf courses are elements of wealthy landscapes (Chamberlain, Henry, Reynolds, Caprio and Amar 2019, Schell, Dyson, Fuentes, Des Roches, Harris, Miller, Woelfle-Erskine and Lambert 2020), and the relationship between affluence and negativity bias towards urban wildlife (Wine et al. 2015) are bound to make these citizen sightings noteworthy.

Habitat selection by urban deer occurs on a predator-free backdrop. No wolves (*Canis lupus*), cougars (*Puma concolor*), or black bears (*Ursus americanus*) – primary prey of Columbia black-tailed deer – live in these urban landscapes, as none were ever detected on cameras. Wolves in particular regulate black-tailed deer;

in wild landscapes on northern Vancouver Island wolf control was associated with increased deer numbers; modelling (and mortality observations, (McNay and Voller 1995)) suggested that increased recruitment was the primary mechanism (Hatter and Janz 1994). Therefore, a predator-free urban environment is expected to markedly increase recruitment (and hence abundance) over natural landscapes. However, predator regulation of black-tailed deer populations is mediated by forage availability and proximity to carrying capacity; dense deer populations are less affected by predators (Ballard, Lutz, Keegan, Carpenter and deVos Jr 2001). Even if urban environments did allow predators, the abundant resource subsidies are likely to sustain abundant deer populations.

## Conclusions

The luxury effect for urban wildlife manifests as strong selection by black-tailed deer for landscape features associated with wealth which provide resource subsidies. Large residential lots of the wealthy had the greatest positive effect on urban deer habitat selection, in combination with protected green spaces and golf courses and with a smaller effect of smaller residential lots. Our research illuminates some of the mechanisms of the luxury effect of urban wildlife observed across the globe, which are driven by subsidies of water and vegetation (Chamberlain, Henry, Reynolds, Caprio and Amar 2019, Leong, Dunn and Trautwein 2018, Magle, Fidino, Sander, Rohnke, Larson, Gallo, Kay, Lehrer, Murray and Adalsteinsson 2021). Here, the conversion of historical drought-resistant Garry oak ecosystems into lush and landscaped urban environments have altered deer selection. The consequences for biodiversity more generally remains unknown; we can surmise greater biodiversity with luxury as observed elsewhere (Chamberlain, Henry, Reynolds, Caprio and Amar 2019, Magle, Fidino, Sander, Rohnke, Larson, Gallo, Kay, Lehrer, Murray and Adalsteinsson 2021), but given the negative effects on biodiversity of highly abundant deer (Beckett, Elle, Kremen, Sherwood, McComb and Martin 2022, Côté, Rooney, Tremblay, Dussault and Waller 2004, Martin, Arcese and Scheerder 2011) this is worth close examination. As urbanization continues to expand around the world, thrusting humans into higher densities and radically altering the habitats for millions of species, the mechanisms driving urban biodiversity should be a 21<sup>st</sup> century focus for wildlife ecology, so that future planning can effectively allow for coexistence of urban population and wildlife approximating as much as possible natural conditions.

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