BLACK-TAILED DEER POPULATION AND SPATIAL RESPONSES TO AN IMMUNOCONTRACEPTION TRIAL IN ESQUIMALT, BRITISH COLUMBIA

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Dr. Adam Hering led all deer captures and treatments, with the support of dozens of volunteers from University of Victoria. Dr. Lynette Brown, veterinarian, also spent substantial volunteer efforts on this project. Brianna Brandon, Katie Baillie-David, and then Isabel Giguére took turns coordinating the project, with contributions from Emerald Arthurs. Camera image tagging was shared among many people, but much ultimately led by Isabel Giguére and Emerald Arthurs. Isabel conducted the research and created chapters two and four of this report, managed the Esquimalt Deer Project from 2023-2025, and contributed extensively to field work in both Esquimalt and Oak Bay. Dr. Andrew Barnas led the density estimation and provided statistical oversight and great mentorship. Dr. Jason T Fisher led the scientific aspects of the program and is responsible for the reporting. Thanks to all property owners, private businesses, and clubs across Esquimalt who hosted cameras who granted access to their property to locate and dart deer to administer immunocontraception. Our deepest gratitude to the countless volunteers who spent hundreds of hours cataloguing deer images and assisted with locating and capturing deer for immunocontraception treatment.

CHAPTER ONE: INTRODUCTION TO URBAN DEER POPULATION RESEARCH

Isabel Giguére and Jason T Fisher

As the human-wildlife interface grows with urbanization, so does the societal pressure for effective, evidence-based wildlife management[1]. Effective management of wildlife populations requires understanding processes that drive population dynamics, which often result from interacting intrinsic and extrinsic factors. For long-lived mammals like deer, population fluctuations have ecological and social consequences that extend across ecosystems and communities. Columbian black-tailed deer (*Odocoileus hemionus columbianus*; hereafter BTD) hold significant ecological, cultural, and economic importance in North America [2]. BTD function as keystone browsers, regulating plant communities and serving as prey for carnivores. They are also culturally significant within Indigenous knowledge systems and contribute to food security and local economies through hunter harvest [3,4]. Maintaining these ecological and social benefits requires BTD populations to remain at sustainable levels. However, many deer populations have fluctuated dramatically—from near extirpation in the 18th and 19th centuries through subsequent expansion in the 20th. Today some wild populations are declining, whereas some urban populations are “overabundant”. Understanding the causes of these population trends is key to sustainable management of deer.

The persistence of deer populations is largely driven by reproduction, as adult survival is typically stable while fawn and juvenile survival are more variable [5]. In urban areas, female deer ("does") often experience high reproductive success due to reduced predation and abundant nutritional resources [6,7]. Urban deer are considered "overabundant" when their numbers exceed ecological or social carrying capacity [5,8-10]. When populations surpass ecological carrying capacity, over-browsing of understory vegetation alters plant community structure and composition, ultimately leading to declines in biodiversity and ecosystem function [3,4,6,11]. These cascading effects disrupt ecological integrity, reducing habitat quality for species dependent on this vegetation, such as pollinators and migratory songbirds [6,12-14]. When deer exceed social carrying capacity, human tolerance and acceptance to deer decreases, often related to increased human-wildlife conflicts such as vehicle collisions and property damage [5,15,16]. When deer populations are maintained slightly below these capacities, they function as keystone browsers that support ecosystem processes, provide economic benefits and food security as a primary game species and reduced human-wildlife conflicts [3,4,17,18].

With BTD populations increasing in suburban and urban areas, various human-deer coexistence challenges may arise. Urban deer can be perceived as "pests" when foraging on gardens or agricultural crops[19], may act as vectors of disease[20], and lead to increased traffic accidents[21,22], although human perceptions of wildlife impacts vary[23,24]. To address these challenges, some municipalities have implemented culling programs to directly reduce the number of deer present in communities[25]. Unfortunately, these culls have thus far been based on little scientific data and results are highly variable[26]. Moreover, the culling of wildlife can be a contentious and politicized issue, leading to divided communities and even legal battles[27,28].

One alternative urban deer management strategy that is growing in popularity is the use of immunocontraceptive (IC) treatments to reduce reproductive output[29-31].

Immunocontraceptive vaccines trigger an animal's immune system to prevent fertilization of the egg[32], and vaccines such as porcine zona pellucida (PZP) have been applied to various urban deer populations as means of non-lethal deer population control[30,33-35]. Prior to the fall reproductive season (the "rut"), IC vaccines can be delivered remotely to adult female deer to suppress pregnancy. As time reduces populations through natural mortality, without new reproduction populations decline.

To estimate the effectiveness of any wildlife population management strategy, it is necessary to estimate population density before and after treatment. However, collecting precise estimates for deer population density in urban environments comes with challenges. Traditional surveys are based on herd counts – which provide useful distribution information but generally provide low-precision results with wide confidence limits [36] – or aerial surveys which are nearly impossible in suburban areas. Citizen-based herd count surveys engage the public but can lack the statistical rigor to justify management actions scientifically or legally. Collecting precise estimates of urban BTD population density requires the application of rigorous surveying approaches using a combination of remote cameras, individual tagging, and novel statistical techniques.

Remote cameras are rapidly becoming a popular wildlife research tool because they produce large volumes of data at low cost[37,38]. Their reliability in surveying wildlife species can be quantified [39] and cameras have been shown to have very high accuracy at detecting deer[40,41]. Remote camera surveys are an increasingly common approach for surveying ungulate occurrence[42-44], and they have been used to monitor deer in urban areas but previously without the statistical ability to estimate density from the data[45]. The recent advent of novel statistical techniques has allowed for the comparison of urban deer population response before and after management actions.

Changes to population size is only one aspect of the possible outcomes of IC treatment. Deer, like all animals, distribute in space by selecting high-value resources and avoiding perceived risk[46,47]. Part of that decision-making is accounting for the other deer in the landscape, who are competitors for resources, and which can defend territories, excluding outsiders[48,49]. Space-use therefore changes with the number of animals competing in a landscape[50-52]. Understanding how deer reproductive success affects space-use is also key to wildlife management.

In this research we show how the structure of an urban landscape affects deer movement into and out of that landscape, how deer density responds to reduced reproduction, and how the distribution of risks and resources affects where deer live and reproduce.

CHAPTER TWO: INFLUENCE OF LANDSCAPE PERMEABILITY ON EFFECTIVENESS OF IMMUNOCONTRACEPTIVE POPULATION CONTROL OF URBAN BLACK-TAILED DEER

Isabel Giguére, Andrew F. Barnas, Adam Hering, and Jason T Fisher

2.1 Abstract

Population regulation varies with landscape permeability: closed (insular) populations are shaped primarily by births and deaths within their boundaries, whereas permeable (open) landscape are also subject to immigration and emigration. For urban Columbian black-tailed deer (BTD), reproductive success is a key driver of population persistence, as abundant forage and lack of predators often keep mortality rates low. Immunocontraception (IC) offers a non-lethal and safe approach to managing abundant deer in human-dominated areas, but its success in free-ranging populations remains constrained by limited data on how immigration may offset reductions in reproduction. We evaluated the effectiveness of IC in two urban populations of BTD on southern Vancouver Island, British Columbia. One system was more permeable, bordered by municipalities containing deer populations free to disperse, whereas the other was insular, on a peninsula surrounded by ocean that restricted movement. We marked and treated most adult females with IC and used multi-year camera-trap data to monitor fawns and does, including marked residents and unmarked immigrants, across both systems. We observed temporal variation in population response to IC. Initially, reproduction declined in both systems. In the permeable system, unmarked does and fawns increased after treatment, suggesting immigration from adjacent areas contributed to increases in the population. In contrast, the insular system maintained low counts of unmarked does and

fawns, sustaining population reduction. These findings demonstrate that extrinsic factors such as landscape permeability can drive intrinsic processes like reproductive success and shape population dynamics, underscoring the need to account for landscape-dependent processes when implementing management interventions like fertility control.

2.2 INTRODUCTION

The mechanisms driving wildlife population variability remain unclear in many cases, due to limited data on the relative role of births, deaths, immigration, and emigration in driving population change. Persistent logistical challenges remain to physically tracking immigration and emigration [53,54]. Deer management often emphasizes demographic processes (e.g. births and deaths) but can overlook how dispersal barriers interact with reproduction to shape population growth or decline. This lack of understanding can therefore limit management effectiveness of wildlife birth control.

Whereas immunocontraception is effective in captive populations, it can be less so in free-ranging wildlife, where dispersal also influences population dynamics beyond the birth and death rates that primarily drive captive systems [55]. In free-ranging populations, births, deaths, immigration, and emigration collectively shape population dynamics and must be considered to achieve effective long-term population control [56]. Most inference about population dynamics in large terrestrial mammals like deer is derived from simulation studies [54,57-59]. Research shows that IC can be an effective management tool if there is either no immigration or minimal immigration, with most resident females (~ 60% - 80%) treated [33,58-60]. BTD populations reduced through IC may be more susceptible to immigration than emigration because urban landscapes retain sufficient forage and minimal predation; with open territories, immigration may offset reproductive losses to sustain populations near pre-treatment densities [59].

Here we evaluate how landscape permeability influences immigration and, in turn, intrinsic processes of reproduction. To do so, we compared population responses of two urban populations of Columbian black-tailed deer on Vancouver Island, British Columbia, residing in landscapes that differed in the degree of dispersal barriers present.

2.3 Methods

2.3.1 Study area

Our study was conducted in two urban municipalities on southern Vancouver Island, British Columbia, where BTD are abundant and considered by some residents to be above social carrying capacity. Both study areas lie within the coastal rainforest ecoregion, characterized by mild, dry summers and cool, wet winters, with annual temperatures ranging from approximately 5 °C to 26 °C [61]. BTD in this area are not considered as heavily regulated by extreme weather like droughts and dense snowpack compared to BTD further north [61].

The insular landscape is the township of Esquimalt; a municipality located on a peninsula within the greater Capital Regional District (CRD) on the southern tip of Vancouver Island (Figure 1). The township holds approximately 17,500 people and is 7.08 km^2 in size [62]. Esquimalt is characterized by a combination of open green space and forest patches and is primarily residential except for the west side where the Canadian Pacific Navy Base and Saxe Point Park are located. Surrounding ocean and major roadways present dispersal barriers that likely limit deer from easily moving into and out of the landscape. The majority of Esquimalt borders the Pacific Ocean and contains a single land connection to the rest of the island as a narrow isthmus where a multilane roadway intersection exists. All other land connections between the peninsula and island are roadway bridges (Figure 1).

The permeable landscape is the District of Oak Bay, another municipality within the greater CRD (Figure 1). Oak Bay lacks major physical barriers on three of its four boundaries, allowing relatively free deer movement between adjacent areas. Its eastern boundary lies along the Strait of Juan de Fuca, while the remaining periphery borders the municipalities of Saanich and Victoria, both supporting abundant deer populations. Oak Bay covers 10.5 km², with a population of approximately 17,900 [62]. The area is an affluent, primarily residential community characterized by large lots and extensive green space throughout [7].

2.3.2 Sampling design

We used camera traps to gather information on deer demographics. Remote infrared trail cameras are a common method used by researchers to non-invasively monitor animal populations to generate spatial and temporal estimates of relative abundance, presence-absence, density, and occupancy [37,61]. Compared to other survey techniques, camera trapping offers a relatively low cost to survey effort, enabling the collection of extensive long-term wildlife monitoring data [37,63].

We used a systemic random sampling design and deployed camera trap arrays in Oak Bay and Esquimalt, fully operational in August 2018 and November 2021, respectively. We deployed a total of 80 cameras; Esquimalt consisted of 41 Reconyx Hyperfire 2™ (Wisconsin, USA) and Oak Bay consisted of 39 Bushnell™ (Overland Park, USA) infra-red remote digital cameras.

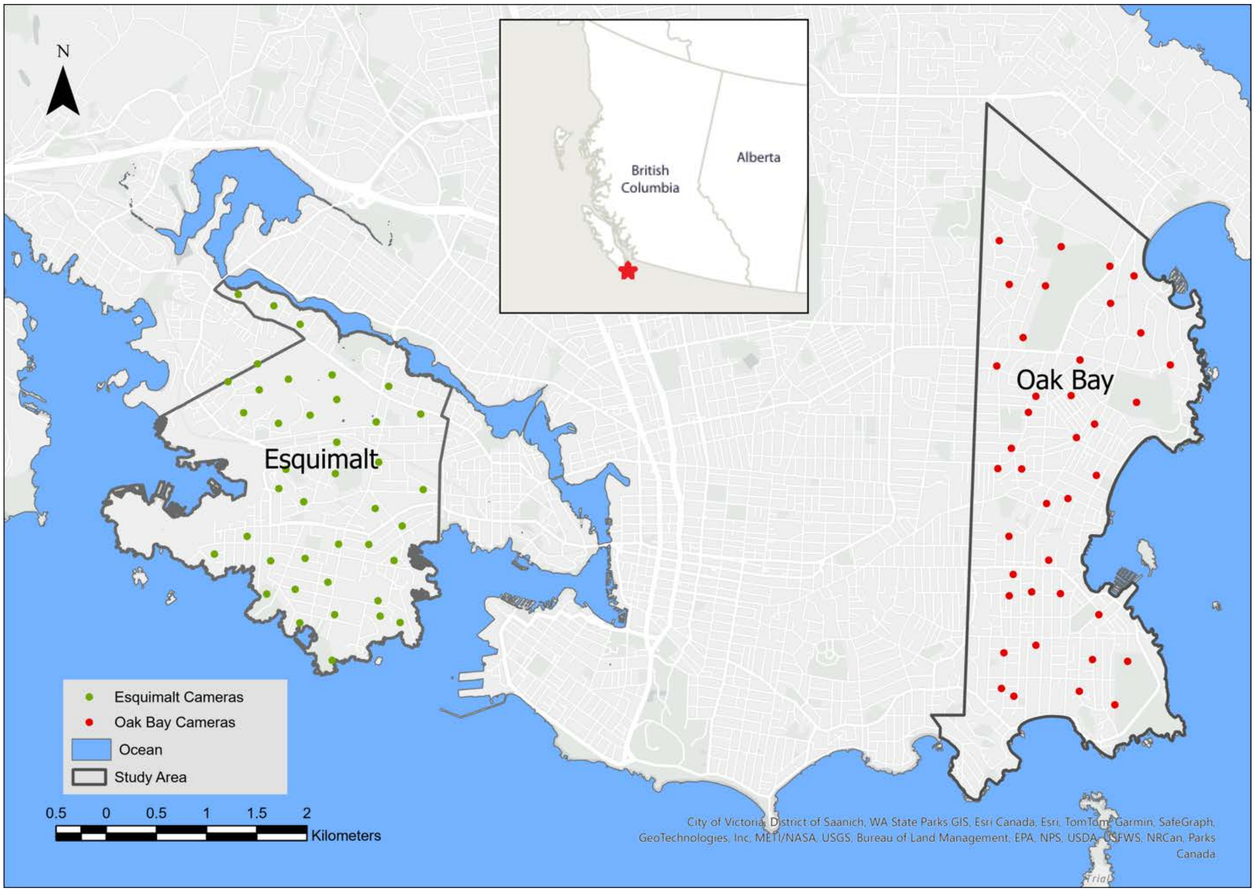


Figure 1. Systematic camera trap array used to monitor black-tailed deer in Esquimalt and Oak Bay, British Columbia Canada from 2021 – 2024 in Esquimalt, and 2018-2023 in Oak Bay. Municipal boundaries are defined by black outlines for each study areas.

Each study area was divided into 400-m hexagonal grid cells, and a camera was deployed within each cell. Precise camera locations were highly dependent on landowner permissions, so cameras were not placed at the center of the cell in all cases. This grid cell size aligns with the average home range size of female BTD in Oak Bay reported by Fisher, et al. [7]: this camera spacing allows individual doe to be detected on multiple cameras across the study area– a prerequisite for estimating population density [64]. Cameras were often fixed to a tree, approximately 0.5m – 1.5 m from ground level, which allows the camera's field of view to capture the full body of an average-sized

BTD. Cameras were strategically placed within cells where there was evidence of deer activity such as a game trail, abundant forage or known bedding sites [65,66]. Camera batteries and SD cards were collected and replaced at the end of summer and autumn each year.

Images collected from cameras were manually processed using Timelapse 2.0 software [67] based on a custom protocol that classified deer into demographic groups. Autumn sampling was chosen as the sampling period, as adults are most mobile and detectable on cameras, and conditions are optimal for camera-trap based density estimation [7]. September images were sampled for Oak Bay and October images were sampled for Esquimalt, but due to logistic constraints and camera theft in Oak Bay, October images were used for 2019 and 2020. Further, due to camera failures in Esquimalt, much of October data was lost for 2023. To correct for this, both October and November data were sampled for 2022, 2023 and 2024. Unfortunately, COVID-19 restrictions delayed camera array deployment in Esquimalt during 2021, which was originally scheduled for September deployment to mirror the sampling period for Oak Bay. Due to this, only November data were available for all cameras in the array for 2021. In November, it is more challenging to discern between adult females and female fawns, especially without October imagery for comparisons, resulting in many individuals classified as “unknown” rather than “fawn”. Therefore, due to lower sample size for 2021, fawn estimates were omitted for 2021.

2.3.3 Deer captures and treatments

To assess population responses to fertility control and movement within urban environments, we selected adult female deer for capture and marking. Females were prioritized because they represent the reproductive component of the population and are most responsive to both fertility treatment and resource availability [68,69]. Deer were located using systematic road-based searches covering the entire municipal area, as described by Fisher, et al. [7]. Searches were conducted multiple times per week during peak morning activity (sunrise – 11 h), allowing equal capture opportunity across neighborhoods. Individuals were opportunistically captured where deer naturally occurred, with preference given to adult females in good condition and representative of the local population density and distribution.

A total of 140 deer were captured in Oak Bay and 80 were captured in Esquimalt (Table 1). PZP vaccine was used as the contraceptive treatment in both municipalities. In both areas, 20 control animals were given unique identification tags and not given immunocontraception (Table 1). Based on municipal permissions, Oak Bay deer were given Zonastat-D vaccine (Science and Conservation Center, Montana) that achieved maximum fertility control for 12 months, decreasing in effectiveness slowly thereafter. Esquimalt deer were given PZP-22 (University of Toledo, Ohio) that maintained maximum fertility control for 22 months. In both cases animals were given booster vaccines to maintain fertility control in the years following.

Female does were captured via chemical immobilization by a qualified wildlife veterinarian, Dr. Adam Hering (University of Victoria Animal Care Protocols 2022-013, FL-001, FL002-, FL003, and FL-004), aided by a capture crew. Deer were immobilized with a mixture of Butorphanol (27.3 mg), Azaperone (9.1mg), and Medetomidine (10.9 mg), commonly referred to as BAM. BAM was loaded into a 1cc type C dart with a 1” length barbed needle and a tri-port release mechanism. Darts also contained a miniature radio frequency transmitter so crew could locate deer using radio telemetry if needed. The dart was delivered using a Pneu-Dart – Model 389 rifle intramuscularly in either the fore or hindlimb of the animal.

After the animal was sedated, the field crew blindfolded and positioned them in sternal recumbency and monitored vitals every 5 minutes, keeping supplemental oxygen in proximity if necessary. Per provincial regulations, all animals received a RAPP (Report All Poachers and Polluters) ID tag. Blood, hair, and biopsy samples were collected and submitted to the provincial wildlife veterinarian. The immobilization dart was carefully removed and an initial dose of PZP (0.5-0.7mg) was given intramuscularly to IC does. After receiving an injection of Lidocaine at the base of the ear to help with pain control, IC animals were given ID tags; in Oak Bay, IC does were given numbered ear tags and in Esquimalt IC does were given numbered collar tags (Figure 2). Control does were not given IC and fitted with identification collars; in Oak Bay control BTD were fitted with a GPS collar displaying unique colour combination/patterns and in Esquimalt control does were fitted with collars displaying unique tag shapes (Figure 3). Animals were reversed with Atipamazole (50 mg), and Naltrexone (25 mg) delivered intramuscularly. Crew monitored animals as they recovered to full consciousness.

All collared deer from the project reported deceased by authorities or residents were recorded by lead wildlife veterinarian Dr. Adam Hering. If deer died withing 6 months of capturing or darting, they were necropsied by Dr. Hering to ensure deaths were not related to any captures.

Table 1. Immunocontraception treatments [no.] administered to black-tailed deer in Oak Bay and Esquimalt, British Columbia, Canada.

Location	Year	Controls	IC Treatments	Boosters
Oak Bay	2018	20	N/A	N/A
	2019	N/A	60	55
	2020	N/A	60	104
	2021	N/A	N/A	71
Esquimalt	2021	20	41	N/A
	2022	N/A	14	N/A
	2023	N/A	3	36
	2024	N/A	N/A	12

2.3.4 Measuring doe and fawn occurrences

From camera images, age class was estimated using morphological characteristics including the presence of white fawn spots, body size relative to known adults (e.g., marked does or antlered males), presence of antler buttons or small spikes, facial roundness, interocular distance, and neck girth. These criteria allowed differentiation between adults ≥1.5 years old and fawns <1 year. Adult sex was determined from the presence of antlers, identification tags, and body size and composition.

We considered camera detections of deer to be temporally independent when separated by a threshold of 30 minutes [37]. We categorized detections into two demographic groups – does and fawns – and further categorized doe detections into "marked" or "unmarked" does. Considering the majority of resident does were tagged within the first 2 years of each study, we reasoned that increases in unmarked deer past this point inferred immigration and informed to what degree each group (marked/unmarked) is contributing to recruitment.

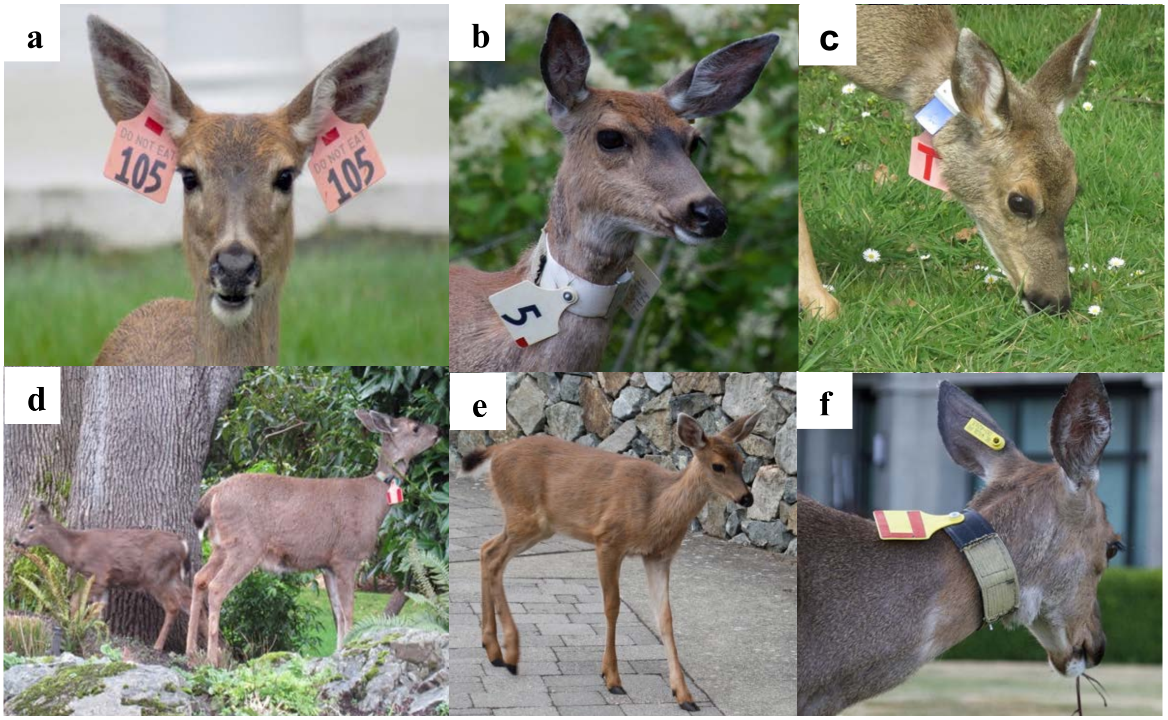


Figure 2. Imagery illustrating does and fawns in the study area a) PZP-treated doe in Oak Bay displaying ear tag ID #105 b) PZP-treated doe in Esquimalt displaying collar tag ID #5 c) Control doe "T" in Oak Bay d) Control doe in Esquimalt displaying unique collar shape ID "| |" with fawn in Esquimalt e) Fawn in Oak Bay f) Control doe ID backwards "C" displaying RAPP tag in left ear.

2.3.5 Modelling and statistical analysis

For each study area, independent detections of does, fawns, unmarked does and marked does were summed for each site and year (site-year pair) and used as the response variable for models. Generalized linear models (GLMs)[70,71] were used to model temporal trends in each response variable (e.g. demographic group) for each landscape, generating a total of 8 models. Models were structured with a Poisson distribution, with offset function to account for site-specific camera trapping effort, by including the number of days each camera was active. Year was set as a fixed effect and site ID was set as a random effect[72] to account for repeat sampling at the same site across years. For the global model below, let i index camera sites and j years; Y_{ij} is total number of independent detections of the response variable (does, fawns, unmarked or marked does) at site i in year j, and μ_{ij} is the corresponding expected count. Response variables were modelled with a Poisson distribution with mean μ_{ij}, and the linear predictor was specified as:

$$\log(\mu_{ij}) = \beta_0 + \beta_1 \times \mathrm{Year}_1 + \beta_2 \times \mathrm{Year}_2 + \beta_3 \times \mathrm{Year}_3 + \beta_4 \times \mathrm{Year}_4 + \beta_5 \times \mathrm{Year}_5 + \beta_6 + \log(\mathrm{effort}_{ij}) + u_i$$

with

$$Y_{ij} \sim \mathrm{Poisson}(\mu_{ij}),\ u_i \sim N\,(0, \sigma^2_{\mathrm{site}})$$

...where β_0 is the intercept, $\beta_1 – \beta_6$ are fixed effect coefficients representing temporal trends (relative to baseline years of 2018 for Oak Bay and 2021 for Esquimalt), $\log(\mathrm{effort}_{ij})$ is an offset to adjust for variation in active camera-days among sites, and u_i is a normally distributed site-level random intercept to account for repeated measurements among sites. The term $N\,(0, \sigma^2_{\mathrm{site}})$ specifies that the random site effects (u_i) are assumed to follow a normal distribution with a mean of zero and variance σ^2_site, representing unexplained variation among sites after accounting for fixed effects.

Estimated marginal means (least-squares means) were calculated from model outputs to obtain annual estimates of doe (marked/unmarked) and fawn independent detections, averaged across all sites. Pairwise contrasts between estimates of sequential years were tested for significance to yield year-to-year differences in doe (marked/unmarked) and fawn occurrences, rather than to a single baseline year.

Diagnostic plots were generated and visually inspected for each model to assess overall fit and model validity, along with tests of overdispersion. All statistical analyses, model predictions, and validations were conducted in R-Studio v4.4.1 [73]. The glmmTMB package was used for model construction [74], *eemeans* package was used to estimate and statistically compare marginal means [75], *dplyr* for data management [76], ggplot2 for data visualization [77], *DHARMa* for model validation [78], and *ggpredict* for model predictions [79].

2.4 Results

2.4.1 Permeable system: Oak Bay

The temporal models indicate a more widely fluctuating and less predictable population in the permeable system (Oak Bay; Figures 3a and 3b). Estimated marginal means revealed a 35% increase in doe counts from 2020-2021 (M = 1.35, 95% CI = 1.23-1.50, p <0.0001) (Table 2), pushing estimated daily doe count from 17.32 (95% CI: 13.46 - 22.30) in 2020 to 23.50 (95% CI = 18.25 - 30.25) in 2021 (Figure 3a). The highest doe count occurred in 2021, which is higher than pre-treatment doe counts in 2018 (Figure 3a). Trends in overall estimates in doe and unmarked does closely mirror one another in 2021 (Figures 3a and 3b). A 36% (M = 1.62, 95% CI =1.41-1.85, p <0.0001) increase in unmarked does occurred in 2021 (Table 2). In 2021, the majority of does were unmarked (Figure 3b), and in 2020 and 2021 fawn numbers were the lowest throughout the study period (Figure 3a). Daily fawn counts were 4.30 (95% CI = 2.87-6.43) and 4.41 (95% CI = 2.93- 6.64) in 2020 and 2021 respectively (Figure 3a). Prior to the significant rise in unmarked deer, fawn counts experienced a 40% decrease from 2019-2020 following IC application (M = 0.60, 95% CI = 0.510-0.696, p <0.0001; Table 2). Fawn counts significantly increased by 48% in 2022 (M = 1.476, 95% CI = 1.25-1.75, p <0.0001), following the rise in unmarked/immigrant deer (Table 2).

After this significant increase of does in the landscape, the composition of the population changed and unmarked doe counts remained much higher than marked doe counts (Figure 3b). In 2022 and 2023, predicted marked doe counts lowered to 6.51 (95% CI = 4.38-9.68) and 6.36 (95% CI = 4.28-9.46), respectively (Figure 4b). Conversely, estimated daily doe counts were almost double this in these same years and were 11.57 (95% CI = 8.86-15.12) in 2022 and 11.11 (95% CI = 8.50-14.54) in 2023 (Figure 4b).

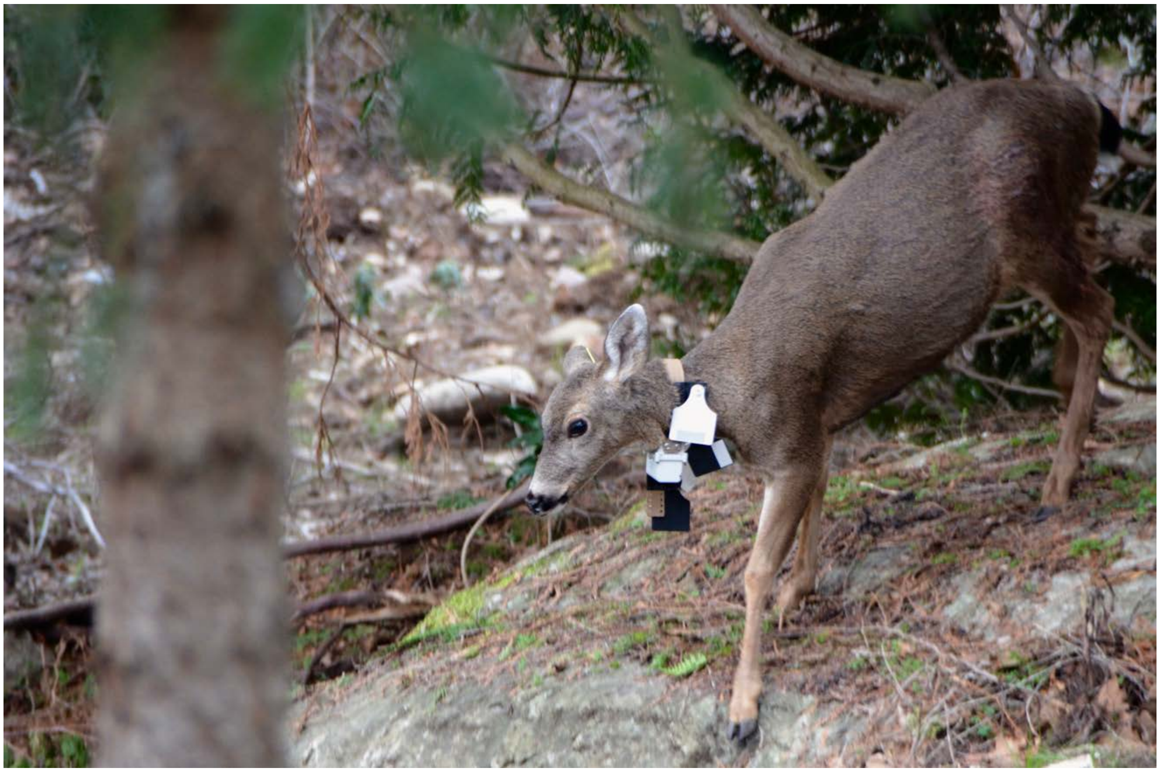
2.4.2 Insular system: Esquimalt

The insular landscape (Esquimalt) showed more stable, predictable, and gradual population trends relative to the permeable system (Figures 3c and 3d). Estimated marginal means revealed a 15 % decrease (M = 0.851, 95% CI = 0.781-0.928, $p < 0.0001$) in does, and 28% decrease in fawns in 2022 (M = 0.727, 95% CI = 0.635-0.831, $p < 0.0001$; Table 3). This is expected following high IC efforts. Fawn detections remained consistent from 2023 to 2024 (M = 0.955, 95% CI = 0.831-1.098, $p = 0.520$), with estimated daily fawn counts at 4.62 (95% CI = 2.66 - 8.01) and 4.41 (95% CI = 2.55 - 7.61) (Figure 3c).

Doe detections increased slightly from 2023 to 2024 (M = 1.24, 95% CI = 1.14–1.35, $p < 0.001$) (Table 3). However, there were consistently low counts of unmarked deer from 2021–2024 (Figure 3d). Unmarked does declined by 14% in 2024 (M = 0.76, 95% CI = 0.60–0.95, $p = 0.0179$) (Table 3). Marked doe counts were consistently higher – in the range of 7-11 times higher – than unmarked doe counts across the study period (Figure 3d). Unmarked doe counts never exceeded 2.3 in any year, reaching the lowest count of 1.67 in 2024 (95% CI = 1.03–2.71; Figure 3d).

2.4.3 Mortalities

A total of 47 marked does were reported deceased in Oak Bay from 2018-2025, constituting 33% of the marked population, with most of these mortalities occurring in 2021 and 2022. A total of 9 marked deer were reported deceased in Esquimalt from 2021-2025, constituting 11% of the marked population, and most mortalities occurring in 2022. Both study areas experienced 2 mortalities related to the capture process; the remaining mortalities of marked does in the study were determined to be predominantly from vehicle-collision related injuries. Although mortality data from unmarked does is limited, it is likely unmarked individuals experience similar rates and causes of mortality.



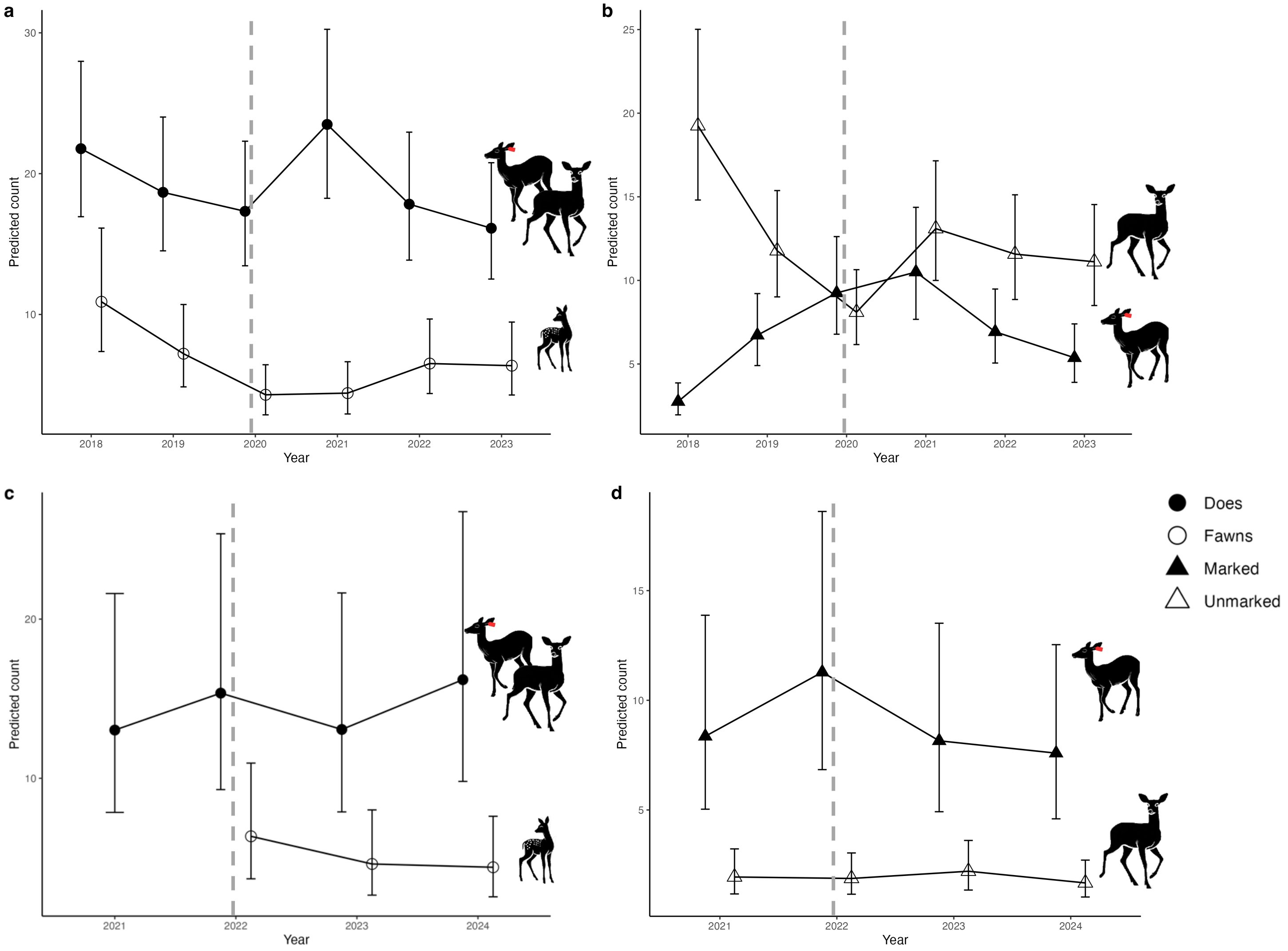


Figure 3. Estimated counts of a) does and fawns in the permeable system; b) marked and unmarked does in the permeable system; c) does and fawns in the insular system; and d) marked and unmarked does in the insular system located in British Columbia, Canada. Dotted grey line indicates the year in which most females were treated in each system.

Table 2. Year-to-year estimates (coefficient ± 95% CI; exponentiated values in parentheses) of annual variation in response variables tested in the generalized linear mixed model framework, derived using the *emmeans* function. Based on camera trap data collected in the permeable system, Oak Bay, British Columbia, Canada, 2018–2023.

RESPONSE	YEAR	ESTIMATE (EXP)	95% CI (EXP)	P-VALUE
DOE	2018 - 2019	0.858	[0.782, 0.940]	1.08e-03 **
DOE	2019 - 2020	0.928	[0.841, 1.024]	1.36e-01
DOE	2020 - 2021	1.356	[1.228, 1.497]	1.59e-09 ***
DOE	2021 - 2022	0.759	[0.687, 0.838]	5.31e-08 ***
DOE	2022 - 2023	0.904	[0.818, 0.999]	4.77e-02 *
FAWN	2018 - 2019	0.661	[0.587, 0.746]	1.42e-11 ***
FAWN	2019 - 2020	0.596	[0.510, 0.696]	6.01e-11 ***
FAWN	2020 - 2021	1.027	[0.854, 1.236]	7.74e-01
FAWN	2021 - 2022	1.476	[1.245, 1.749]	6.96e-06 ***
FAWN	2022 - 2023	0.977	[0.854, 1.118]	7.33e-01
MARKED	2018 - 2019	2.441	[2.006, 2.971]	4.87e-19 ***
MARKED	2019 - 2020	1.376	[1.196, 1.583]	7.94e-06 ***
MARKED	2020 - 2021	1.135	[0.992, 1.299]	6.62e-02
MARKED	2021 - 2022	0.660	[0.570, 0.763]	1.99e-08 ***
MARKED	2022 - 2023	0.776	[0.664, 0.906]	1.34e-03 **
UNMARKED	2018 - 2019	0.612	[0.549, 0.681]	2.38e-19 ***
UNMARKED	2019 - 2020	0.688	[0.602, 0.787]	4.40e-08 ***
UNMARKED	2020 - 2021	1.617	[1.410, 1.854]	5.66e-12 ***
UNMARKED	2021 - 2022	0.884	[0.778, 1.004]	5.79e-02
UNMARKED	2022 - 2023	0.960	[0.850, 1.086]	5.18e-01

Table 3. Year-to-year estimates (coefficient ± 95% CI; exponentiated values in parentheses) of annual variation in response variables tested in the generalized linear mixed model framework, derived using the *emmeans* function. Based on camera trap data collected in the insular system in Esquimalt, British Columbia, Canada, 2021-2023.

RESPONSE	YEAR	ESTIMATE (EXP)	95% CI (EXP)	P-VALUE
DOE	2021 - 2022	1.178	[1.075, 1.291]	4.65e-04 ***
DOE	2022 - 2023	0.851	[0.781, 0.928]	2.42e-04 ***
DOE	2023 - 2024	1.239	[1.139, 1.349]	6.70e-07 ***
FAWN	2022 - 2023	0.727	[0.635, 0.831]	3.10e-06 ***
FAWN	2023 - 2024	0.955	[0.831, 1.098]	5.20e-01
MARKED	2021 - 2022	1.350	[1.205, 1.512]	2.25e-07 ***
MARKED	2022 - 2023	0.723	[0.649, 0.804]	2.79e-09 ***
MARKED	2023 - 2024	0.931	[0.832, 1.042]	2.13e-01
UNMARKED	2021 - 2022	0.966	[0.751, 1.242]	7.85e-01
UNMARKED	2022 - 2023	1.175	[0.938, 1.473]	1.61e-01
UNMARKED	2023 - 2024	0.759	[0.603, 0.954]	1.79e-02 *

2.5 Discussion

Reproduction and immigration drive population growth in urban BTD, but the relative contribution of each varies with landscape permeability. Experimentally reducing reproduction across systems differing by the degree of immigration potential (e.g. permeability) reveals that dispersal into these systems can substantially influence population dynamics, thus mediating the effectiveness of population control. We examined temporal trends in fawns, marked (resident), and unmarked (immigrant) does to infer immigration potential and identify which groups drove population-level reproductive success. Consistent with our hypothesis, IC initially reduced reproduction in both populations, as indicated by declines in fawning following treatment. However, these reductions were not sustained in the permeable system, where detections of unmarked females rose sharply, suggesting immigration of reproductive females and a subsequent rebound in reproduction. In contrast, the insular population, buffered by dispersal barriers, exhibited minimal immigration, and sustained low reproductive output.

2.5.1 Dispersal

Trends in relative occurrence of marked and unmarked does fluctuated much more widely in the permeable landscape, indicating possible immigration following the reduction in fawns. After the influx of unmarked deer in the permeable landscape, unmarked deer counts remained higher than marked deer counts, suggesting that many of these deer immigrated. It is possible that some unmarked deer could have temporarily entered the system during the sampling period. Regardless, fertile unmarked does and accompanying fawns entered the permeable landscape, and based on the rise in fawn counts, many immigrant fawns remained and recruited, likely driving later population rebounds. We speculate that the initial reduction in fawns created a "sink" population, where unmarked deer entered from adjacent source populations in neighbouring Victoria and Saanich municipalities [68,80,81] to take advantage of abundant resources with less competition. In contrast, the more insular system exhibited more consistent population declines after IC application. We observed low unmarked deer throughout the entire study period, suggesting a lack of movement of fertile females entering the system. The ocean and major roads bordering the insular landscape played a major role in limiting potential immigration, contributing to a more stable population response after maximum IC efforts were made [68,82,83].

The insular Esquimalt system more closely meets key criteria identified in simulations for effective immunocontraception: a small female breeding-age population size, a semi-isolated or isolated landscape, and limited dispersal [60,84]. For IC to be effective, the number of breeding-age females must be small to be treated reliably within a single year. Rudolph (1999) modelled an optimal threshold of approximately 100 breeding females—balancing treatment effort, efficiency, and encounter rates in suburban environments. Above this threshold, annual treatment becomes logistically difficult; below it, the probability of encounter rates declines, so effort increases [85]. Based on Rudolph [85]'s findings, our insular population was an ideal size, as pre-treatment density estimates indicated an adult female breeding age size of around 74-100 female deer. Additionally, the field crew was able to treat most adult females in the first year (it became extremely difficult to located unmarked females in the years following), falling within the recommended range of 60% - 80% for maximum IC effectiveness [33]. Like the trends found in our insular system, other small insular urban IC studies with minimal immigration reported population reductions within 1–2 years of treatment, followed by modest gradual declines thereafter [34,86]. Rutberg and Naugle [34] documented an average annual decrease of approximately 7%, whereas Rutberg, et al. [86] observed a decline of about 11% per year. Consistent with modelling, with minimal immigration, these insular systems respond to IC quickly and exhibit modest but stable population declines afterwards [58,84]. Due to the small initial population size, and minimal immigration, the insular landscape in this study achieved infertility in most residents much more quickly than in the permeable landscape, leading to quicker reduction times with less IC effort.

Oak Bay is permeable to adjacent municipalities and is therefore more open to immigration. We conclude permeability facilitated the influx of unmarked does and then the rise in fawns in the following year. After IC treatment in the permeable system, Frey, et al. [87] reported a 57% and 23% decrease in relative fawn abundance in 2019 and 2020, respectively, with lowest deer densities in 2020. Therefore, the reduced densities in the permeable landscape likely turned the landscape into a sink, with source animals free to move in from adjacent municipalities to take advantage of high-quality habitat [88]. Although we did not directly measure immigration rates an immigration event clearly occurred as evidenced by the influx of unmarked does, and even modest dispersal can significantly alter population dynamics and the success of population control [54,58,59,83,89]. For example, simulations show that immigration rate as low as 8%, contraception efforts would need to double to compensate [59]. Without accounting for even small immigration events, it exacerbates the time to reduction. In past studies time to reduction took 5 years with just an estimated 8 immigrants per year [34,90].

The more permeable the system, the higher the immigration potential, which generally results in longer reduction times but shorter rebound times after fertility controls cease [34,91]. Here, highly fluctuating trends in the permeable system were largely driven by dispersal, but the population contained almost double the number of breeding-age females than the insular system, which likely further contributed to more variable trends [87]. Our team treated 140 females over two years, meaning roughly half the population was treated and half untreated initially, with staggered booster eligibility thereafter. This makes it difficult to maintain the recommended annual coverage of contracepted females, especially when new individuals are consistently being introduced into the system [33,58-60]. However, our permeable system was still relatively small, by definition < 200 females, which is likely why we saw reductions the year following IC [60]. However, as predicted, since the system was not isolated, an immigration event occurred that caused the population to rebound [34,83,91].

2.5.2 Deer accessibility and booster success

Accessibility to adult female deer, as well as the vaccine type used, can influence the effectiveness of population control via IC [85,86,90,92]. Longer-lasting vaccines reduce booster requirements and coupled with high deer accessibility typically yield greater population control success [55,93,94]. PZP-22 was used in the insular system and requires boosters 2 years after initial dose. Zonastat D was used in the permeable system requires a booster 3 weeks to 1 year after the initial dose, making PZP-22 initial dose longer lasting [92]. However, if deer are easily accessible for boosters, shorter-acting vaccines can be just as effective as longer-acting vaccines [92]. Boosters can sustain antibody levels to maintain fertility suppression for 1-2 years in ungulates [56,95]. For example, Kirkpatrick, et al. [55] maintained infertility in feral horses with boosters for up to 8 years. In our insular system deer accessibility was lower due to denser housing, but we used a longer-acting vaccine which minimized population-level impacts of any missed boosters that had to be administered in following years. While in our permeable system, we used a shorter-acting vaccine but had higher booster success as deer were easier to locate. Therefore, differences in vaccine durations and deer accessibility likely did not cause any notable differences in population responses observed in this study.

2.6 Management Implications

In small populations (e.g. N <200), IC has the potential to reduce deer populations, but sustaining reductions in permeable landscapes will require more effort due to higher immigration potential [60]. Isolated or semi-isolated populations—those bounded by highways, oceans, or other dispersal barriers—are better candidates for IC programs because comparatively fewer resources are needed to compensate for annual immigration. Unless, of course, IC programs are implemented across the CRD and so reduce the possibility of immigration from one municipality to another.

In any case, managers should also aim to acquire reliable pre-treatment densities estimates to ensure most animals can be treated within the first year. Where resighting rates are low, we recommend using longer-acting contraceptives to extend booster opportunities, and missed individuals should be prioritized in subsequent years. Successful population control via IC requires treating most females in the population quickly and maintaining population-level infertility. Most importantly, collaboration among neighboring municipalities in coordinated IC programs is essential to overcoming the logical issues from immigration. Although management is limited by jurisdictional boundaries, deer movements are not. IC programs would be far more effective if adjacent municipalities coordinated their efforts with a common goal, preventing immigration from replenishing populations in permeable landscapes.

CHAPTER THREE: BLACK-TAILED DEER POPULATION DENSITY ESTIMATE AND RESPONSE TO IMMUNOCONTRACEPTION IN ESQUIMALT, BC

Andrew F. Barnas, Isabel Giguére, Adam Hering, and Jason T Fisher

3.1 Introduction

Anthropogenic disturbance is a driver of global terrestrial biodiversity loss, but ensuing landscape change stemming from development can impact species in both negative and positive ways[96-99]. Some anthrophilic species, or human commensals [100] can benefit from anthropogenic activity which can create predator refuges [101,102] or provide increased resource availability[103-105]. Typically, the outcome of anthropogenic commensalism is population growth for those wildlife populations in developed environments[100]. Although in anthropogenic commensal relationships where there is no loss to human populations, the increased population growth of commensals species can be perceived as threatening and translate to human-wildlife conflicts[23,106,107]. Conflicts are pronounced in urban and suburban areas of intermediate human population density when residences are proximal to wildlife habitats[108]. The global urban population is expected to increase by 2.5 billion people over the next 30 years [109] and urban landscapes have doubled in the last few decades[110]. As such, there is a growing need to understand the population dynamics of anthropogenic commensals and explore strategies for mitigating human-wildlife conflict.

Population growth is the outcome of births, deaths, immigration and emigration, and substantial literature has been devoted to the primary mode of experimental wildlife population reduction[111], specifically increased mortality through harvest [112] or culls[113]. Less studied are the population outcomes of reducing populations through non-lethal means, such as suppressing reproductive output through fertility control. The paucity of such research is in part owing to fertility control being used often as a management tool without a solid ecological research framework[29,114-116]. Even less research has focused on monitoring population response when management intervention actions such as fertility control are paused or ceased entirely, allowing for a potential population rebound through immigration or increased births.

Here, we examine applied reproductive control and density estimation methods to evaluate population outcomes of Columbian black-tailed deer (BTD). In British Columbia's suburban environments, deer have been shown to select for areas with high vegetation greenness, a high proportion of large-sized residential lots, and proximity to parks and golf courses [117] suggesting that human-driven changes to the landscape are key to maintaining urban deer populations. As BTD populations are sensitive to factors affecting recruitment[69,118], the lack of natural predation coupled with the abundance of high-quality food resources on urban and suburban landscapes has likely contributed to greater reproductive output and subsequent population growth for BTD.

Culling deer is the most direct and immediate method of reducing deer population density, including in urban and suburban environments[25,119]. However, the culling of wildlife can be a contentious and politicized issue[120], leading to divided communities and even legal battles[27,28]. Fertility control may be used as a non-lethal strategy for reducing population size and immuno-contraceptive (IC) treatments are used on free-ranging ungulates to reduce reproductive output[29-31]. Immuno-contraceptive vaccines trigger the female immune system to prevent fertilization of the egg[32], and vaccines such as porcine zona pellucida (PZP) have been applied to various urban deer populations as means of non-lethal deer population management[30,33-35]. Prior to the fall rut, IC vaccines can be delivered remotely to adult does to suppress her ability to produce young the following spring, thus eliminating the need for lethally removing individuals in a growing population. While fertility control is suggested to be a socially acceptable and effective method for wildlife population management compared to culls, the effectiveness of IC treatment to suppress population growth in BTD in urban environments has not yet been examined. The rarity of such research has likely partly been due to the past inherent difficulties in estimating population size and density for free-ranging populations[121].

Here, we apply IC to a free-ranging population of urban BTD and monitor via remote cameras[122] the population response over a course of four years to understand the demographic and population outcomes of reduced reproduction in a population with few opportunities for compensatory immigration.

3.2 Methods

3.2.1 Statistical Analysis – Adult Population Density Estimation

To estimate population density within Esquimalt, we used the camera array previously described. Using camera images of BTD, we identified independent detections based on a 30-minute threshold, where sequences of images of BTD on the same camera were considered independent if separated by 30 minutes. We also considered images of marked individuals to delineate separate events. Images containing multiple identifiable individuals were recorded as unique events, as we could clearly identify the time and location for everyone. Further, images containing both marked and unmarked individuals were separated into distinct counts of a marked and unmarked detection. For example, an image containing a marked individual and an unmarked individual would count as two distinct events. We did not consider independent events of fawns for density estimation.

We estimated population density of adult BTD using spatially explicit mark-resight (SMR) models with package *secr* v4.6.9 in R Studio 4.4.1[123,124]. SMR models have been developed to estimate density from repeated detections of known individuals in a partially marked population[121,125,126]. SMR models use repeated detections, or "resights", of both unmarked and marked individuals to estimate the density of a population[126,127]. We fit individual models to estimate density separately for each study year. Each study year (session) contained 30 sampling occasions, but varying number of cameras (detectors). Fitting models separately for each year assumes no constant survival across years but assumes that all marked individuals detected within a year were alive across that year's sampling occasions. For all models we specified a half-normal detection function, assuming detections of individuals are maximized closer to activity centers, but decay based on a scale parameter. We treated cameras as "count" detectors which are a class of "proximity" detectors which record animal presence at a point without restricting movement, allowing for >1 detection of animals per sampling occasion. Counts were modelled assuming a Poisson distribution.

We fit models with a 1000m buffer around the study areas, and first fit models assuming no overdispersion to generate initial parameter estimates. We then used those initial estimates to simulate data 10,000 times using the "*nsim*" argument in the "*secr.fit*" function. For each year we obtained a mean density estimate of adult deer ± 95% confidence intervals, converted to estimated deer per km^2.

3.3 Results

In the initial year (2021) we estimated *ca.*13 deer per km^2 (Figure 4). We started IC treatment that fall. The population experienced natural population growth in the following year to approximately 16 deer per km^2; the number of fawns may have been reduced but the natural population die-off had not yet begun to reduce deer populations. This initial growth is the same phenomenon we witnessed in Oak Bay, before that treatment took hold. In 2023 the population fell to 2021 levels and then fell again in 2024 to about 11 deer per km^2 (Figure 4).

3.4 Discussion

Esquimalt experienced a marked increase in adult deer density in the starting year from 2021 to 2022. As we did not monitor previously, we do not know if this was part of an ongoing trend or a unique event. This is an unusually rapid rate of population growth and is unlikely due to reproduction alone; very likely there was some contribution from outside Esquimalt - perhaps Songhees lands or View Royal. In the following year the population returned to the original size, suggesting mortality or emigration was not offset by reproduction, due to the treatment of IC. In the subsequent years as animals died or moved, reproduction also was not sufficient to offset these losses and so the population continued to decline through the final sampling year, 2024. We did not observe any population rebound following the first two intensive years of treatment, due to the use of PZP-22 which lasts almost two years.

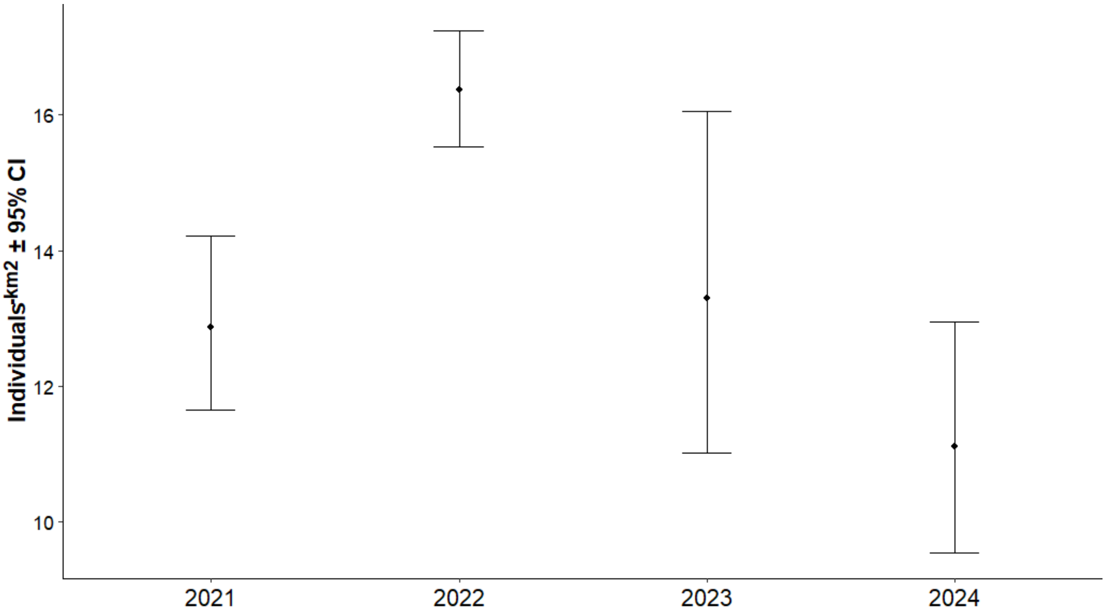


Figure 4. Estimated deer density in Esquimalt from 2021-2024. The average estimated deer density is represented by black dots; the 95% confidence intervals (CI) are represented by the bars around the dots. CI's are interpreted as such: the most likely estimate is around the black dot, with decreasingly likely density estimates moving from the black dot to the ends of the bars, which are only 5% likely.

The effectiveness of IC treatment as a long-term strategy for suppressing urban deer populations likely relies on the use of periodic booster vaccines to maintain the immune response in previously treated animals, as well as primary vaccines to newly recruited or immigrated individuals. Research on closed populations of white-tailed deer (*Odocoileus virginianus*) suggest if 25-50% of females are treated annually, reductions of 30-60% could be achieved over a 4–10-year period[89]. The sharp rebound in reproductive output observed in our study population indicates that a higher proportion (>50%) of females may need to be treated to maintain a suppressed overall population size.

CHAPTER FOUR: THE INFLUENCE OF REPRODUCTIVE STATUS ON HABITAT SELECTION IN URBAN BLACK-TAILED DEER

Isabel Giguére, Andrew Barnas, Adam Hering, and Jason T Fisher

4.0 Abstract

We tested how habitat selection differed between mothers and non-mothers in Columbian black-tailed deer (BTD) populations. In autumn, mothers face high energetic demands for reproductive success. They must balance risk-reward trade-offs between habitats that provide nutrient-rich forage and those that offer safety of protective cover. The most energetically optimal habitats for reproduction supply both, maximizing energy intake from forage while minimizing energetic costs of avoiding mortality of mothers and fawns. We hypothesized 1) mothers select habitats combining nutrient-rich forage and protective cover because it is the most energetically optimal habitat choice for reproduction success; and 2) mothers exhibit stronger selection for these habitats compared to non-mothers because they have higher energy requirements and are more vulnerable to risk. We used multi-year camera-trap data to monitor both landscapes and evaluate how habitat features of various forage quality and cover influence the occurrence of reproductive groups, using an information-theoretic modeling framework. We found a clear difference in habitat preferences between reproductive groups in both landscapes; mothers selected habitats offering both high-quality forage and cover, and avoided open areas that elevated risk, whereas non-mothers selected habitats with low-quality forage in open areas and did not avoid risky features. Habitat influenced the spatial distribution of reproductive groups in BTD, demonstrating that extrinsic factors

such as habitat quality can shape population dynamics by affecting intrinsic drivers like reproductive success.

4.1 Introduction

Urbanization transforms landscapes and alters resource availability for wildlife [7,129,130]. In response to changing habitat, populations will either grow, shrink, or redistribute, driven by shifts in mortality rates or reproduction success [66,81,131,132]. For instance, BTD recruitment rates differ between wild and urban populations within North America [133]. Given that BTD generally have stable adult survival, reproductive success is a primary intrinsic driver of population growth, especially in urban landscapes where the absence of natural predators facilitates high recruitment [134]. In the absence of top-down predator-control, BTD populations are more influenced by bottom-up processes like habitat quality [135-138]. Therefore, habitat quality can function as an extrinsic driver of population dynamics by its influence on intrinsic drivers like reproduction success [139].

To enhance reproduction success, mothers should select habitats that maximize energy intake while minimizing energy expenditure to sustain personal and offspring survival [140-143]. For BTD, this involves consistently making trade-off decisions between their two primary activity states—*foraging and resting*—which together determine daily energy balance [142-144]. These trade-offs should vary among reproductive groups (e.g. reproductively successful mothers and unsuccessful non-mothers) because each has distinct energetic requirements, pressures, and vulnerability to risk [145]. Based on *Optimal Foraging Theory*, *Landscape of Fear*, and *Central Place Foraging Theory*, habitat selection decisions should involve those that maximize net energy gain while also minimizing energetic costs [81,141,146-152]. Within this framework, the concept of an *energetically optimal habitat* reflects one with features that maximize energy acquisition and retention. Therefore, habitat features offering nutrient-rich forage and simultaneous protective cover represents an energetically optimal choice for reproductive females [7,88,131,144,153-155]. Avoiding risk is especially important for mothers because fawns are more susceptible to mortality [145,156,157]. Finally, occupying habitat that satisfies both foraging and resting needs, eliminates the need to expend unnecessary energy travelling between separate forage and resting sites[148]. For mothers, selecting habitats that optimally balance nutrition and safety is especially critical given the added energetic costs of reproduction and parental care; thus, their habitat choices should be fundamental to their reproductive success [143,145,158].

BTD are *income breeders* whereby reproduction success is tightly linked to forage quality and quantity available in the late summer and early fall [131,132,158,159]. At this time of year, mother BTD habitat choices strongly influence their ability to meet the energetic costs of lactation and parental care, thereby affecting fawn survival and recruitment [158,159]. Lactation is the most energetically costly period of a BTD mother's life, raising basal metabolic rates by estimated 4-7 times [132,160,161]. Nutrients offered by BTD milk facilitates rapid fawn growth, gaining ~ 0.5 lbs/day in the first 3 months of life [18]. Attaining large body size quickly is an evolutionary strategy to gain independence quickly to reduce their mortality risks, which increase with decreasing fawn size [162]. Lactation can continue into autumn, but by late summer fawns begin to wean and closely accompany their mothers, gradually adopting similar foraging and resting habitat selection behaviors [163,164]. Pressure for mothers and attendant fawns to select energetically optimal habitat is high because their energetic demands are high. In the late summer and autumn, mothers have undergone lactation, provided maternal care, and must enter to rut and become pregnant again while fawns must grow into independent juveniles large enough to survive their first winter [132,165,166]. To achieve this, mothers must select high-quality habitat in autumn, a time where vegetation quality generally starts to decline in North America [131,159,164,167]. If resource subsidies are scarce at a time when pressure to meet demands is critical, mothers and fawns must occupy most energetically optimal habitat to support reproduction.

The digestibility and concealment vegetation offers plays a critical role in habitat selection in BTD [149,168]. Most of BTD diet is composed of deciduous trees, shrubs and forbs [169-172]. Their gut physiology is specially designed to digest thin cell-walled vegetation types like browse [144]. Comparatively, BTD have more difficulty digesting vegetation with thicker cell walls, such as grasses, so they must consume higher quantities to gain similar nutritional benefits [141,173,174]. It is more difficult for fawns to digest large quantities of fibrous forage like grasses since their gut rumen is still maturing and has lower stomach capacity [18]. Energy gained from forage is retained by resting for most of the day in safe bed sites [130,175]. Canopy cover and low-lying vegetation both provide structural refuge for resting, which reduces thermal stress and offers protection from predation and human disturbance [176]. Fawns are especially vulnerable to these dangers due to their smaller body size and limited experience. Therefore, habitats with vegetation offering both easily digestible energy and concealment would be beneficial for mothers and fawns.

Urban BTD may make similar trade-offs to avoid "human-risks" [177] such as vehicle collisions and conflict with pets and people [16,178,179]. Reproductive groups (mothers and non-mothers) may perceive these "human-risks" differently and prioritize forage-quality and safety differently [180,181]. For instance, it may not be beneficial for mothers to gain nutritional rewards associated with private gardens, if it poses risks associated with being near humans, while it may be worth the trade-off for another reproductive group. Mothers may prefer larger residential properties to take advantage of the associated "luxury effects" because those properties offer both abundant high-quality forage and space segregated from humans [7]. Conversely, large grass-dominated areas like sports fields and school yards are open, lack cover and are nutrient-poor, especially in autumn. Therefore, these habitat features may offer little benefit to mothers but could support non-mothers who have a higher human-risk tolerance and can forage longer on lower-quality vegetation types to meet their energetic demands.

We seek to answer the question: How does reproductive status influence habitat selection in urban BTD? We examined habitat preferences between female BTD with fawns (mothers) and without fawns (non-mothers) for features that offer variable benefits or limitations to reproductive success.

4.2 Methods

We deployed systematic camera trap[37] arrays in Oak Bay and Esquimalt in August 2018 and November 2021, respectively, with a total of 80 cameras. See Chapter 2 for a full accounting of study design.

4.2.1 Measuring mother and non-mother occurrences

For each deer(s) detected in an image, age (fawn or adult), adult sex (male or female), and whether adult females were unmarked or marked were recorded (Figure 5). Age was determined by observation of morphological characteristics; the presence of white fawn spots, relative size to known adults (ID present or 2+ spiked antlered males), presence of antler buttons or small spikes, facial roundness, distance between eyes and neck girth. Adult sex was determined by the presence of antlers, ID tags, body size and composition. Adult females were easily determined to be either marked or unmarked based on the presence of large IDs easily visible on cameras.

We further categorized detections of deer into independent detection events of two reproductive categories: Non-mothers (lone female adults), and mothers (adult females with fawns). We considered detections of the different demographic groups to be independent when separated by a threshold of 30 minutes [37]. If a fawn and doe were detected in the same image, we categorized the independent detection event as "mother", when a doe was detected and a fawn was not, we categorized the independent detection event as "non-mother". If a fawn was detected alone on a camera, we categorized the independent detection event as "mother" because it was assumed that the fawn was born from a mother, who was close by, it just was not in the field of view of the camera [18].

Because deer moved slowly and often with scores of sequential photos, we are confident classifying mothers and non-mothers in this way. For each camera site, we summarized the number of days that each demographic group was detected or not (i.e. present or absent that day). The precise number of active camera days was documented for each site and year to account for uneven sampling effort between camera sites.

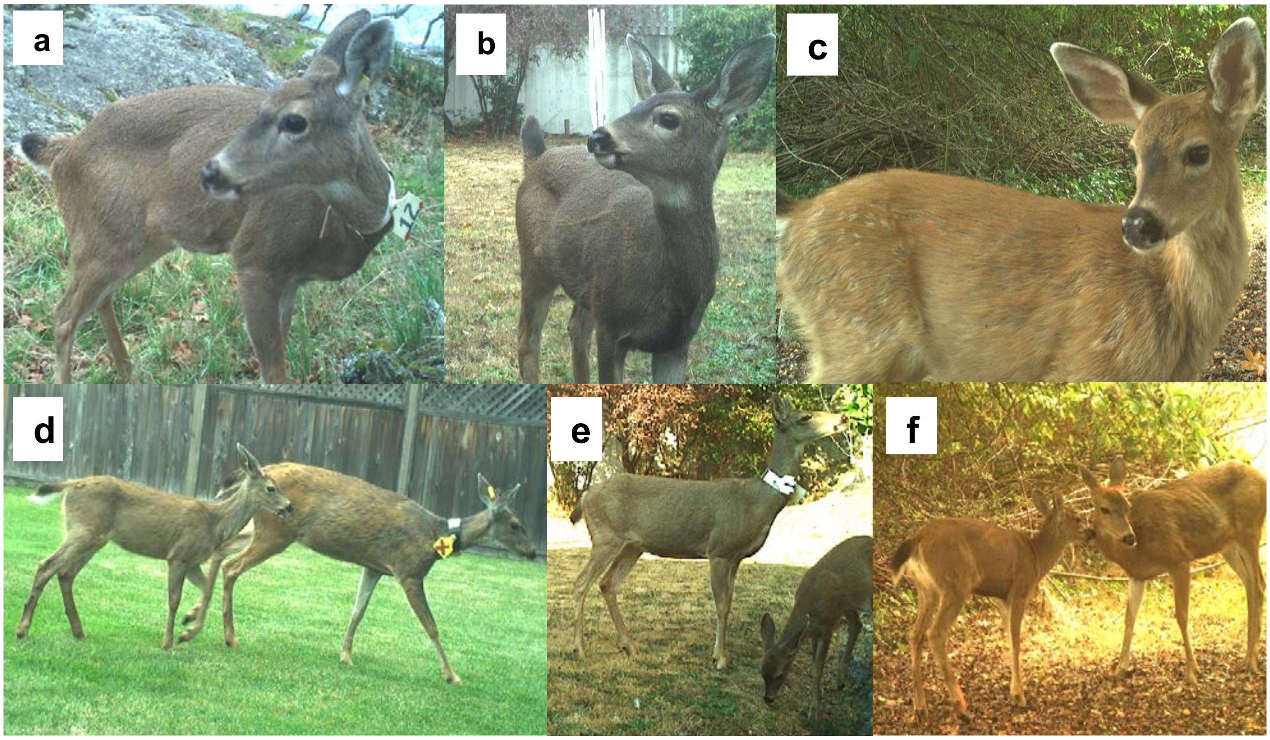


Figure 5. Camera trap imagery of fawns and adults captured throughout the sampling period. a) adult female with elongated snout, b) November fawn with rounded and short snout, c) September fawn with white spots, d) September fawn with button antlers following a marked adult female, e) October fawn foraging with a marked adult female and f) October fawn allogrooming an unmarked adult female

4.2.2 Quantifying habitat features

To evaluate the different habitat types used by deer we collected environmental landscape features surrounding camera traps. We used ARC GIS Pro v 3.2 software to extract habitat features and geospatial statistics [182]. We applied buffers to both the municipal boundaries and individual camera sites to define the spatial extent used for habitat feature extraction. A 400-m buffer was added around each municipal boundary to ensure that habitat features influencing detections were fully represented for cameras near the study area edges, minimizing edge effects and preventing truncation in spatial analyses [183,184]. The 400-m distance corresponds to one grid cell and represents the maximum spacing between cameras, ensuring that habitat data were not excluded for cameras bordering their respective grid cells or municipal boundaries—particularly in Esquimalt. Although cameras in Oak Bay were positioned farther from the boundary, the same buffer was applied to maintain methodological consistency across study areas. A 150-m circular buffer was applied around each camera sites, and habitat variables were extracted from within the area of this buffer radius to characterize camera-specific habitat conditions influencing detections. The 150 m radius represents half the mean inter-camera spacing, providing a biologically meaningful scale for local habitat assessment while minimizing buffer overlap among adjacent camera sites [183,185].

Habitat features with varying degrees of forage quality and protective cover were classified to assess their influence on the presence of demographic groups. Landcover data was collected from a combination of municipal and provincial open-source geospatial databases. We used the Capital Regional District **(***CRD) 2019 LiDAR land cover dataset* (Table 4), chosen for its high-resolution accuracy in capturing current surface features across the study area CRD, [186]. We extracted 10 habitat features: roads, shrub, herbaceous vegetation, coniferous tree, deciduous tree, roads, pavement, bare ground, residential lot density and proximity to green space. All habitat variables, except for residential lot density and proximity to green space were extracted from this dataset and represented as the proportion of surface area (m^2) a given feature covered within the radius of the camera buffer.

Mean residential lot densities were generated by kernel density estimation from residential lot parcel center points [182]. Center points were given to independent living units/dwellings. Civic addresses, satellite imagery, google street view and knowledge of the area were all used to guide decisions around defining a residential unit. For apartments and condos, the number of center points given were based on the number of dwellings on the first floor, that had their own entrance and/or green space. Consequently, every residential address was not assigned a center point to avoid over inflating residential lot density estimates for dwelling types that deer could not utilize. In this way, the ratio of living units and green space within a parcel was consistent among dwelling types. The kernel density tool was applied to residential center points at a cell size of 10 and search radius of 200m. The mean lot density (residential dwelling/m^2) values were calculated for each camera site.

Table 4. Definitions of habitat features hypothesized to influence habitat selection in reproductive groups. Yes/No indicates what resource (cover and/or forage) each habitat feature provides. Definitions of LiDAR variables are extracted from *CRD 2019 LiDAR land cover report (*CRD, 2021)

Predictor variable	**Description**	**Cover**	**Forage**
Bare ground	Areas of exposed soil and bare land falling outside agricultural land uses (e.g., construction sites, cleared areas)	No	No
Grass	Grass land cover falling within residential and urban land uses, including lawns, gardens, playing fields and institutional grounds. These areas represent lands subject to regular maintenance.	No	Yes
Herbaceous	Areas of natural herbaceous vegetation that is not manicured (e.g., grasses, reeds, ferns, flowers and low-lying vegetation).	No	Yes
Shrub	Shrub dominant areas (includes small trees) between 50cm-3m in height. This does not include shrubs such as hedges that are above 3m in height.	Yes	Yes
Deciduous tree	Deciduous trees (and deciduous shrubs) above 3m in height.	Yes	Yes
Coniferous tree	Coniferous trees (and coniferous shrubs) above 3m in height.	Yes	No
Pavement	Paved areas/impervious surfaces excluding buildings (e.g., roads, sidewalks, driveways and parking lots).	No	No
Road	All road networks excluding all other impervious surfaces and paved areas.	No	No
Proximity to green space	The average distance to the closest three green spaces composed of 50% or more green area, excluding residential green lots (e.g., parks, golf courses, cemeteries, schools, regional trails).	Yes	Yes
Residential Lot Density	Mean kernel density of residential lot parcels.	No-High Density Yes-Low Density	

The proximity to green space was generated by calculating Euclidean distance from each camera to the nearest three green spaces. The green space layer was created by including all non-residential parcels that were 50% or more green space. To delineate these areas, an NDVI layer was created to enhance the visualization of vegetation productivity. The NDVI layer was then overlaid with zoning data and satellite imagery to refine polygon placement and define precise boundaries. The resulting green space layer included parks, golf courses, schools, cemeteries, and private water access points. The mean Euclidean distance was calculated for the nearest three polygons to each camera site and referred to as the proximity to green space.

4.3.3 Modelling and statistical analysis

Due to substantial differences in habitat composition, deer density, and study durations between Esquimalt and Oak Bay, we analyzed landscapes separately to avoid obscuring any biologically relevant heterogeneity. To empirically estimate differences in habitat compositions, Wilcoxon rank-sum tests [187] were conducted on all habitat covariates within 150-m buffer around camera sites in both landscapes, which revealed differences in herbaceous vegetation, pavement, deciduous tree, and coniferous tree. This provided empirical support for analyzing landscapes separately. All habitat variables were tested for Pearson correlation ($|r| > 0.6$ threshold) [188]. Variables that exceeded this threshold were not included in the models together to avoid multicollinearity [188].

To analyze the effect of habitat on deer site selection among reproductive groups, candidate model sets were created for “mothers” and “non-mothers” in each landscape. Independent camera trap detections were binned into an annual proportional binomial framework for analysis. For each camera site-year, detections of mothers and non-mothers were summed to generate values for each site-year. Unfortunately, due to camera failures and loss in Esquimalt in 2021, we could not gain reliable fawning estimates for this year, and it was omitted for this analysis.

Generalized linear mixed-effect models (GLMMs)[72] were used to test how reproductive status influenced habitat selection. Response variables were structured as the proportion of daily successes (presence) and failures (absence) throughout the number of active camera traps days for each site-year combination, wherein each day is considered a Bernoulli trial [189]. This structure accounts for camera trapping effort given that the response variables are proportional to the number of camera trapping days unique to each site-year. Candidate models included fixed effects representing varying levels of forage quality and cover, with year included as a random effect. Habitat variables were standardized (mean = 0, SD = 1) prior to modeling to allow comparison of effect sizes across predictors. For the global model below, let i index camera sites and j years; Y_{ij} is the number of days with ≥ 1 detection of either mothers or non-mothers at site i in year j, θ_{ij} is the corresponding daily detection probability, and η_{ij} is the linear predictor such that $\text{logit}(\theta_{ij}) = \eta_{ij}$

$$n_{ij} = \beta_0 + \beta_1 \times \text{road}_{ij} + \beta_2 \times \text{grass}_{ij} + \beta_3 \times \text{herbaceous}_{ij} + \beta_4 \times \text{shrub}_{ij} + \beta_5 \times \text{deciduous tree}_{ij} + \beta_6 \times \text{coniferous tree}_{ij} + \beta_7 \times \text{lot density}_{ij} + \beta_8 \times \text{pavement}_{ij} + \beta_9 \times \text{bareground}_{ij} + \beta_{10} \times \text{proximity}_{ij} + \text{year}_j$$

$$Y_{ij} \sim \text{Binomial}\ (n_{ij}, \theta_{ij}),\ \text{logit}(\theta_{ij}) = n_{ij}$$

$$\text{year}_{ij} \sim N\ (0, \sigma^2)$$

4.3.4 Model evaluation and validation

We used Akaike's Information Criterion corrected for small sample size (AICc) to weigh empirical support for model hypothesis [190]. Top models were defined by those with a ΔAIC = 0 – 2, supported by model diagnostics and validation. Models were fit separately for each reproductive group and landscape. Effect sizes were expressed as odds ratios (OR) by exponentiating model coefficients (e^{β}). Predicted probability plots were generated for all top models to facilitate interpretation and visualization of results.

Diagnostics were performed on candidate models, evaluated for *DHARMa* simulated residual, with overdispersion tests, zero-inflation and residual uniformity [78]. Diagnostic plots were visually inspected for top model for each response variable for validation. All statistical analyses, model predictions, and validations were conducted in R-Studio v4.4.1 [73]. The *glmmTMB* package was used for model construction [74], *dplyr* for data management [76], *ggplot2* for data visualization [77], *DHARMa* for model validation [78], and *ggpredict* for model predictions [79].

4.4 Results

In Oak Bay from 2018-2023 the total number of active cameras in the array for these years were 34, 32, 36, 34, 36 and 34 cameras, respectively, with a mean value of 27 active camera days (*SD = 8.4*, min - max = 1–35). We obtained 1303 independent detections of mothers and 1321 independent detections of non-mothers during the sampling period. In Esquimalt, from 2021-2024 the total number of active cameras in the array for these years were 36, 41, 40, and 40 cameras, respectively, with a mean value of 47 active camera days (SD = 17.8, min – max = 1- 61). We obtained 1044 independent detections of mothers and 1295 independent detections of non-mothers during the sampling period.

4.4.1 Mother habitat selection in Oak Bay

High-quality forage and cover were the most strongly supported model explaining the occurrence of BTD mothers, receiving all the model weight (AICw = 1.00; Table 5). Within this model, mothers showed strong selection for deciduous tree and herbaceous vegetation and avoidance of shrubs (Figure 6). The odds of detecting mothers increased by approximately 29% for every one-standard-deviation increase in the proportion of deciduous trees around the camera site (OR = 1.29, 95% CI = 1.20–1.38) and by about 40% for each one-standard-deviation increase in the proportion of herbaceous vegetation (OR = 1.40, 95% CI = 1.32–1.72), while decreasing by roughly 13% for each one-standard-deviation increase in the proportion of shrub (OR = 0.87, 95% CI = 0.81–0.94; Figure 6).

4.4.2 Non-mother habitat selection in Oak Bay

No habitat feature associated with forage or cover was well supported in explaining the occurrence of non-mothers, the "*no forage" and "cover"* models received essentially all the model weight (AICw = 1.00; Table 5). Within the top model, non-mothers showed strong avoidance of bare ground but little evidence for selection or avoidance of pavement (Figure 6). The odds of detecting non-mothers decreased by approximately 24% for every one-standard-deviation increase in the proportion of bare ground (OR = 0.76, 95% CI = 0.70–0.83), whereas pavement showed little support for an effect on occurrence (OR = 1.03, 95% CI = 0.96–1.11; Figure 6).

4.4.3 Mother habitat selection in Esquimalt

Vegetative cover was the most strongly supported model explaining the occurrence of mothers, receiving all the model weight (AICw = 1.00; Table 6). Model coefficients indicated strong selection for deciduous tree cover and avoidance of coniferous tree cover (Figure 6). The odds of detecting mothers increased by about 68% for every one-standard-deviation increase in the proportion of deciduous tree cover (OR = 1.68, 95% CI = 1.55–1.82) and decreased by roughly 35% for each one-standard-deviation increase in the proportion of coniferous tree cover (OR = 0.65, 95% CI = 0.59–0.72). Shrub cover showed little support for influencing mothers' occurrence (OR = 1.04, 95% CI = 0.95–1.13; Figure 6,7).

4.4.4 Non-mother habitat selection in Esquimalt

Low-quality forage was the most strongly supported model explaining the occurrence of non-mothers, carrying most of the model weight (AICw = 0.95; Table 6). Within this model, non-mothers showed moderate selection for grass and herbaceous vegetation (Figure 6,7). The odds of detecting non-mothers increased by approximately 15% for every one-standard-deviation increase in the proportion of grass cover (OR = 1.15, 95% CI = 1.08–1.23) and by about 24% for each one-standard-deviation increase in the proportion of herbaceous vegetation (OR = 1.24, 95% CI = 1.06–1.44; Figure 6,7).

Table 5. AICc scores of candidate models assessing factors expected to influence occurrence of mothers and non-mothers in the Oak Bay study area, British Columbia, Canada, from 2018–2023. The table includes the number of parameters (K), log-likelihood (logLik), the difference in AICc scores between the best-supported model and all other models (ΔAIC), and model weight (AICw). Top models are bolded for each response variable.

Response	Model	Fixed effects	K	logLik	AICc	Δ AICc	AICw
Oak Bay Mothers	**High-Quality Forage and**	**Shrub + Deciduous Tree +**	**5**	**-1135.33**	**2280.959**	**0**	**1**
	Danger	Road	3	-1165.9	2337.914	56.95438	4.29E-13
	Low-Quality Forage	Herbaceous + Grass	4	-1180.03	2368.26	87.30093	1.1E-19
	Vegetation Cover	Coniferous Tree + Shrub +	5	-1195.31	2400.915	119.9554	8.95E-27
	Forage and Cover	Shrub + Deciduous Tree	4	-1197.5	2403.206	122.2466	2.85E-27
	Residential	Lot Density	3	-1207.21	2420.548	139.5891	4.88E-31
	No Forage or Cover	Bare Ground + Pavement	4	-1207.18	2422.56	141.6004	1.79E-31
	Proximity to Green Space	Nearest 3 Green Patches	3	-1250.95	2508.016	227.0569	4.96E-50
	Null Model	Intercept-only	2	-1253.42	2510.905	229.9453	1.17E-50
Oak Bay Non-	**No Forage or Cover**	**Bare Ground + Pavement**	**4**	**-759.932**	**1528.063**	**0**	**1**
	Low-Quality Forage	Herbaceous + Grass	4	-778.476	1565.151	37.08785	8.84E-09
	Null Model	Intercept-only	2	-785.793	1575.646	47.58222	4.65E-11
	Residential	Lot Density	3	-785.5	1577.119	49.05524	2.23E-11
	Proximity to Green Space	Nearest 3 Green Patches	3	-785.509	1577.137	49.07381	2.21E-11
	High-Quality Forage and	Shrub + Deciduous Tree +	5	-783.557	1577.416	49.35265	1.92E-11
	Danger	Road	3	-785.785	1577.69	49.62689	1.67E-11
	Vegetation Cover	Coniferous Tree + Shrub +	5	-784.275	1578.851	50.78803	9.37E-12
	Forage and Cover	Shrub + Deciduous Tree	4	-785.668	1579.537	51.47341	6.65E-12

Table 6. AICc scores of candidate models assessing factors expected to influence detections of mothers and non-mothers in the Esquimalt study area, British Columbia, Canada, from 2022–2024. The table includes the number of parameters (K), log-likelihood (logLik), the difference in AICc scores between the best-supported model and all other models (ΔAIC), and model weight (AICw). Top models are bolded for each response variable.

Response	Model	Fixed effects	K	logLik	AICc	Δ AICc	AICw
Esquimalt Mothers	**Vegetation Cover**	**Coniferous Tree + Shrub + Deciduous**	**5**	**-**	**1703.093**	**0**	**1**
	Forage and Cover	Shrub + Deciduous Tree	4	-	1787.677	84.58412	4.29E-
	High-Quality Forage and	Shrub + Deciduous Tree + Herbaceous	5	-	1789.859	86.76531	1.44E-
	No Forage or Cover	Bare Ground + Pavement	4	-	1836.557	133.4634	1.04E-
	Low-Quality Forage	Herbaceous + Grass	4	-	1871.04	167.947	3.39E-
	Danger	Road	3	-	1900.517	197.4233	1.35E-
	Null Model	Intercept-only	2	-	1913.077	209.9836	2.53E-
	Residential	Lot Density	3	-	1914.609	211.5156	1.17E-
	Proximity to Green Space	Nearest 3 Green Patches	3	-	1915.086	211.9924	9.26E-
Esquimalt Non-mothers	**Low-Quality Forage**	**Herbaceous + Grass**	**4**	**-**	**1428.841**	**0**	**0.9504**
	Vegetation Cover	Coniferous Tree + Shrub + Deciduous Tree	5	-712.65	1435.836	6.994975	0.0287
	High-Quality Forage and	Shrub + Deciduous Tree + Herbaceous	5	-	1436.488	7.646995	0.0207
	Danger	Road	3	-	1496.907	68.06585	1.58E-
	Residential	Lot Density	3	-747.83	1501.871	73.02975	1.32E-
	No Forage or Cover	Bare Ground + Pavement	4	-	1502.164	73.32301	1.14E-
	Forage and Cover	Shrub + Deciduous Tree	4	-	1506.909	78.06838	1.06E-
	Proximity to Green Space	Nearest 3 Green Patches	3	-	1509.769	80.92769	2.54E-
	Null Model	Intercept-only	2	-	1511.422	82.58072	1.11E-

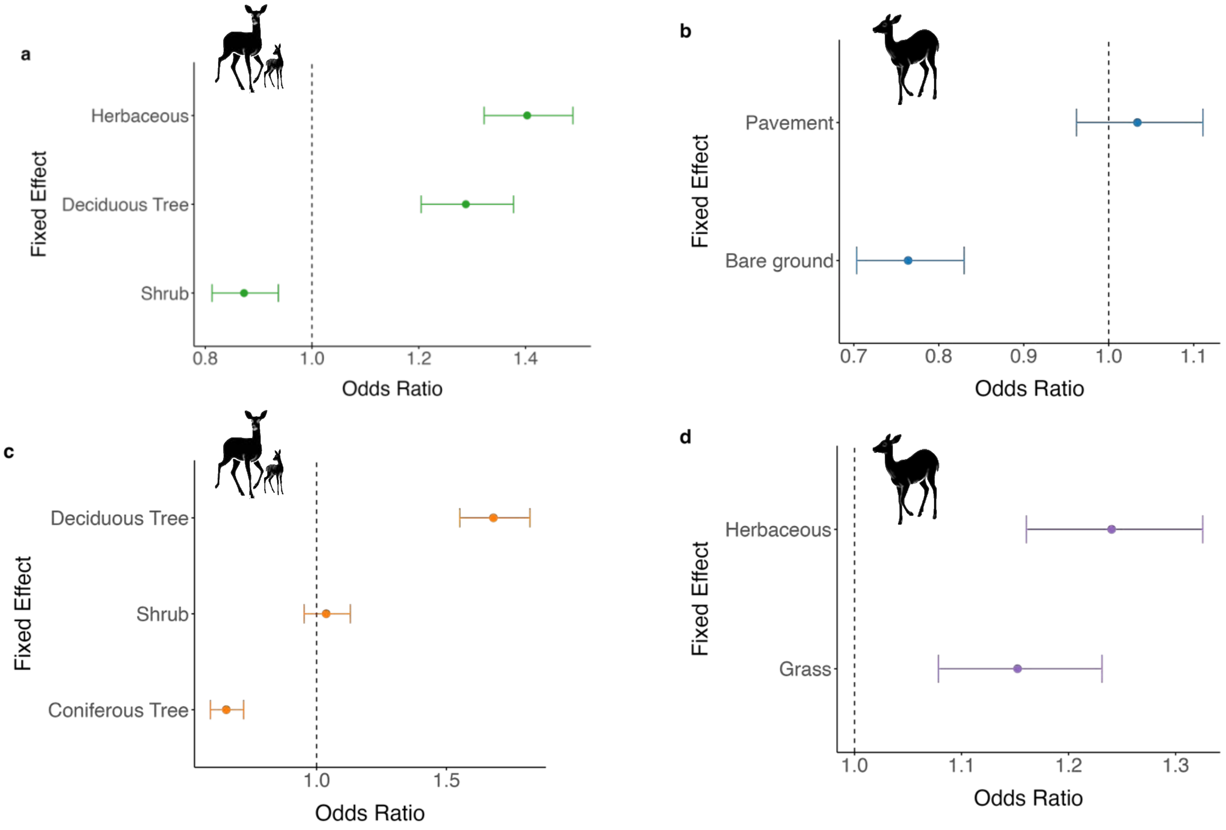


Figure 6. Odds ratio including 95% confidence intervals for fixed effect variables in the top models for each response variable, a) Oak Bay mothers b) Oak Bay non-mothers c) Esquimalt mothers d) Esquimalt non-mothers. The dotted line represents no effect at a value of 1, values above 1 have a positive effect while values below have a negative effect on the response variable. Values further from the red line indicate a stronger effect.

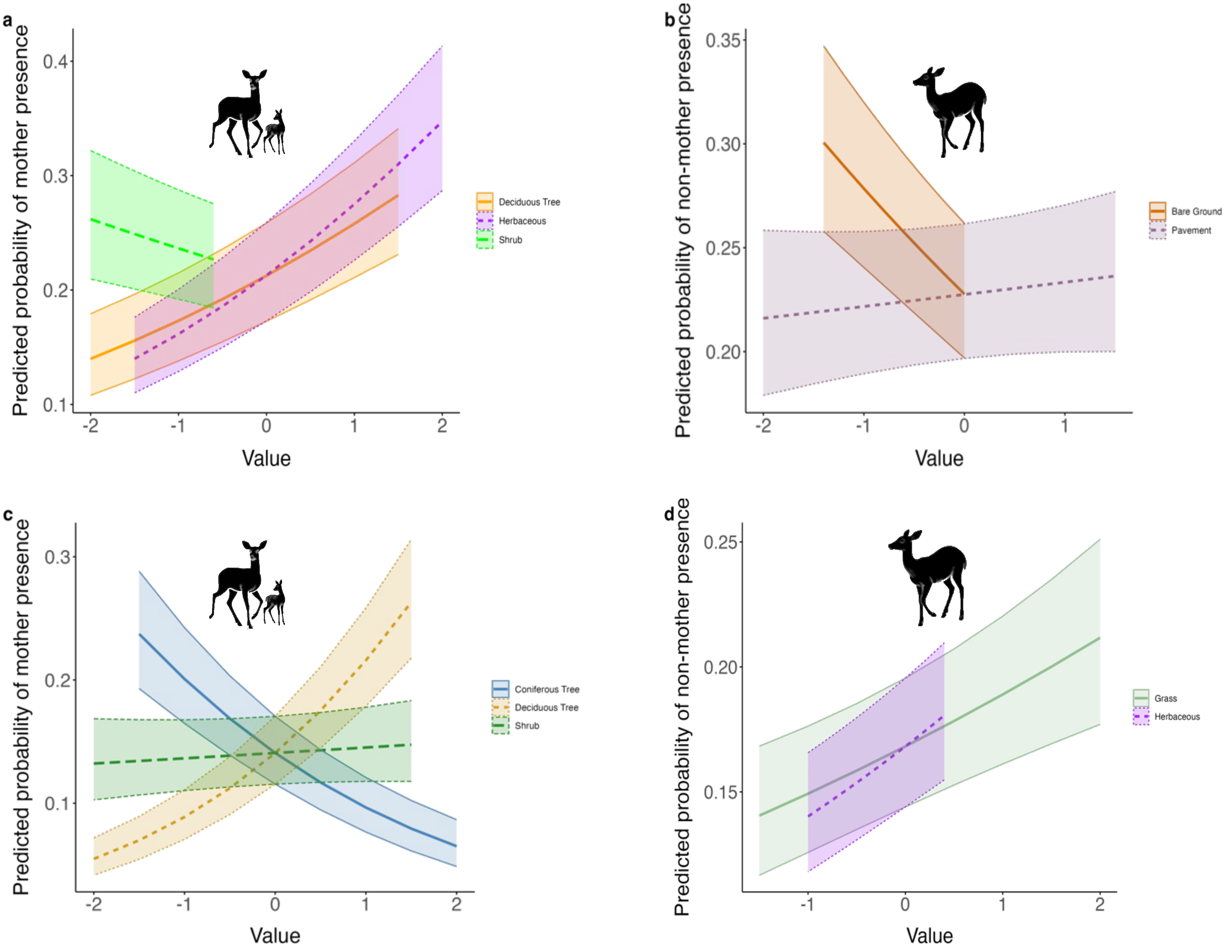


Figure 7. Marginal effects of fixed effects in the top models for a) Oak Bay mothers b) Oak Bay non-mothers c) Esquimalt mothers d) Esquimalt non-mothers representing the predicted probability of daily occurrence of each response variable as a function of each habitat feature. Probabilities of each fixed effect represent those if other variables were held at the mean values.

4.5 Discussion

Reproductively successful and unsuccessful females occupied contrasting habitats. Mothers selected energetically optimal habitat offering both high-quality forage and protective cover, whereas non-mothers used open areas with lower-quality forage and greater exposure to risk. Mothers' strong selection for features that maximize both energy intake and conservation support our hypothesis and aligns with predictions from theory, which posit that individuals balance energy gain against safety when making habitat selection decisions [141,142,148,150]. Elevated energetic demands of mothers at this time likely intensified these risk-reward trade-off decisions, leading mothers to strongly select for nutrient-rich forage for energy acquisition and concurrent cover to reduce energetic costs associated with risk avoidance [142,143,155]. These findings highlight how extrinsic forces like habitat quality can influence intrinsic processes like reproductive success to drive population dynamics. Variation in habitat composition, abundance, and seasonal shifts in deer energy requirements likely influenced these behaviors.

Individuals should select habitats that maximize net energy gain while minimizing risk and energetic costs. Deciduous trees meet these criteria by offering both nutrient-rich forage and structural cover that maximize energy gain and reduces perceived risk. We therefore expected that deciduous-dominated habitats would support reproductive success by providing *energetically optimal conditions* for mothers with fawns. Consistent with this prediction, mothers in both landscapes strongly selected areas with high proportions of deciduous trees, suggesting that these habitats help meet elevated energetic demands during late summer and autumn. The reproductive benefits of occupying deciduous-dominated habitats are well documented and reinforce these theoretical expectations; deciduous browse offers higher digestible energy (DE) for mule deer, relative to other forage types (like grasses), which enhances survival and reproduction [17,131,155]. For example, supplemental feeding experiments offering BTD high DE diets, specifically during late summer and autumn, increased pregnancy rates, milk quality, larger fawn production, higher instances of twinning and overwinter survival compared to BTD fed low and intermediate DE diets [158,159]. Our results are consistent with these studies; reproductively successful females occupied habitats containing deciduous browse with high DE. In Esquimalt, deciduous tree types within this category include plum and cherry (23%), Garry oak (9%) and maple (9%), while in Oak Bay, Garry oak dominate both public (~35%) and private lands [191,192]. Additionally, many nutritious tall shrubs (>3m) such as blackberry, salmonberry, elderberry, salal, and huckleberry are present within the study areas and offer high DE. Similarly, Fisher, et al. [7] found that female (non-contraception-treated) BTD in Oak Bay used areas that mirrored the densest Garry oak distribution in the municipality [191]. Preference for oak-dominated habitats has been consistently linked to higher survival and reproductive success in BTD populations occupying both wild and developed areas [6,130,135,193]. Browse from other deciduous subsidies like fruit-producing trees and shrubs also have high DE content and would also serve nutritional benefits for mothers and juveniles.

Forage quality alone does not fully explain habitat selection, as deer could underuse high-quality forage in areas of elevated risk of predation or human disturbance, instead prioritizing concealment [129,146,150,155,180]. Our results suggest that risk perception varies by reproductive status of females, with deer some using human-dominated areas while others avoid them. Habitat features that enhance concealment or perceived safety appear to promote reproductive success of females [137]. Studies have shown that BTD females generally prefer around 40% canopy cover, which promotes understory forage while maintaining overhead protective cover [176,193], a habitat preference particularly evident among mothers with fawns [193]. This pattern primarily is documented in wild populations and reflects an optimal trade-off between forage benefits and predation risk [135,140,145,194]. In our study, deer appeared to make similar trade-offs but weighed forage benefits against “human-risk” avoidance—selecting habitats that reduce encounters with people, vehicles, or pets. Structural refuge provided by the canopy and understory vegetation likely offers both security for day-bed sites and thermoregulatory benefits [178,193,195,196]. Oak cover has been shown to moderate surface temperatures against both hot and cold ambient temperatures, offering thermal stability for BTD [193,195]. Although continuous forest is limited in our urban landscape, the abundance of oak trees likely provides important thermal benefits and security for bedding sites used by mothers and fawns.

We expected mothers to select both tall deciduous trees/shrubs (>3 m) and smaller shrub (< 3m) because both provide nutritional and concealment benefits [130,193,197]. However, the aerial LiDAR extraction methods likely limited detection of understory shrub beneath tree canopies – a known constraint in remote sensing. Higher LiDAR pulse density (the number of lasers/unit area) improves precision to capture fine details to detect understory vegetation [198]. For instance, Hamraz, et al. [199] found that a pulse density of 170 pt/m² accurately captured sub-canopy vegetation, whereas standard densities (~50 pt/m²) detected only ~60%. Because the LiDAR data used in this study were relatively coarse (~10 pt/m²), understory shrubs were likely underrepresented. As a result, shrub detections may have been biased toward open, roadside vegetation, which mothers might avoid due to elevated risks and human-wildlife conflicts [16]. Additionally, our shrub category included all shrub types (coniferous, evergreen, and deciduous), whereas the deciduous tree class included only deciduous trees and tall shrubs—the vegetation type mothers most strongly selected for. Thus, in this urban landscape, the value of shrub habitat for mothers likely depends on both location and composition, with understory and deciduous shrubs offering greater foraging and concealment benefits than smaller shrubs in open areas containing mixed coniferous, evergreen, and deciduous species.

The preference of Oak Bay mothers and Esquimalt non-mothers for herbaceous vegetation is likely due to differences in the associated ecosystems that made this feature higher quality in Oak Bay and lower quality in Esquimalt. In Oak Bay, mothers likely benefit from herbaceous vegetation associated with Garry Oak ecosystems, which support diverse, nutrient-rich forbs and wildflowers readily consumed by BTD in this area [6]. In contrast, Esquimalt has less Garry Oak, but more herbaceous cover dominated by open, exposed areas where vegetation senesces quickly, becoming fibrous and lower in DE [164]. Thus, herbaceous vegetation likely provides greater nutritional value to mothers in Oak Bay than in Esquimalt. This highlights the importance of identifying forage species when evaluating nutritional quality, as broad categories such as “herbaceous vegetation” encompass flowers, forbs, and grasses that differ markedly in seasonal nutritional value [200]. For example, grasses generally occur in open areas, cure earlier, and have higher bulk density but lower digestibility compared to forbs and shrubs [173,200]. These distinctions help explain why Esquimalt non-mothers selected herbaceous vegetation and grass later in the season (October–November) for nutritional support, while mothers selected herbaceous vegetation earlier (September–October). Without fawns, non-mothers can afford riskier foraging behaviour and graze on fibrous forage subsidies for extended periods to gain the nutritional rewards [129,174]. Conversely, mothers tend to avoid open grassy areas, particularly those near dwellings [129,201], suggesting that the nutritional rewards are outweighed by perceived risk and that concealment remains a stronger driver of habitat selection for mothers than for non-mothers.

Esquimalt mothers' avoidance of conifer trees during autumn suggests that the concealment they provide is not critical for reproductive success at this stage and may even increase exposure to human-related risks. In this landscape, conifers likely function primarily as shelter from UV radiation and precipitation, but not as a valuable forage resource [171,202]. Fecal analyses indicate that conifers are rarely consumed by BTD in any season [179] and mothers use conifer stands only with intermediate canopy cover because of the benefits associated with the understory growth [178,179,195,202]. Within the ecoregion of our study, conifer stands lack understory and develop closed canopies after roughly 25 years [61]. Although wild BTD mothers have been shown to select lower conifer canopy cover during parturition, suggesting potential value at earlier reproductive stages [202], deciduous habitats with understory growth, offer a more energy-efficient alternative for all reproductive stages when available [203]. Avoidance of conifers in Esquimalt may also reflect the prevalence of tall conifer hedges bordering residential properties, which increase human exposure risk to mothers and fawns while offering minimal or no forage benefits in autumn [178,192,202]. Moreover, selecting conifer stands would likely require mothers to forgo higher-quality deciduous habitats, making conifer use an energetically inefficient strategy for meeting reproductive demands.

Habitat selection by Oak Bay non-mothers does not appear driven by optimal forage or risk avoidance. Their lack of avoidance - and even weak selection - for pavement suggests riskier behavior in the absence of fawns, despite paved areas like driveways, parking lots, and sidewalks being associated with high human activity. In contrast, mothers consistently avoid these features, likely because they pose risk to reproductive success [178,204]. For non-mothers, potential nutritional rewards from landscaping near paved areas may outweigh these risks. This discrepancy highlights differing energetic requirements and risk-reward trade-offs between reproductive groups, with Oak Bay non-mothers showing little preference for either forage or cover. Strong avoidance to bare ground, an inhospitable feature offering no nutritional or concealment value, is expected for survival. Overall, non-mothers in Oak Bay exhibited weaker habitat preferences than mothers, reflecting relaxed energetic and risk constraints outside the reproductive period.

4.6 Management implications and future directions

In urban black-tailed deer populations, reproductive groups differ in habitat preferences, with deciduous trees, shrubs, and herbaceous vegetation bolstering reproductive success. Management interventions that restrict deer access to these habitats may aid in urban deer management. Because reproductive success drives population growth in urban BTD [68], the attractiveness of urban habitats as a valuable forage resource to BTD mothers and fawns may be an effective lever for population control. Garry Oak forests are an at-risk ecosystem and protected federally[205], so not much can be done in those ecosystems. However, most of Esquimalt is not in covered in Garry Oak ecosystems. Encouraging residential and commercial landowners to replace nutrient-rich ornamental vegetation with native forbs, shrubs, and herbaceous plants—and to use exclusion fencing—could reduce nutritional availability for deer while simultaneously enhancing biodiversity, a key objective in urban ecosystem management [206,207]. Coordinated efforts to increase native plantings among private and public landowners, can scale yard-level changes into neighborhood networks that protect threatened ecosystems like Garry oak and support declining pollinator and bird populations [6,206-208].

4.7 Conclusion

We show that extrinsic factors like habitat-quality can shape intrinsic drivers of population dynamics like reproduction. Reproductive groups exhibited distinct habitat preferences, reflecting differing energetic requirements and risk-reward trade-offs: mothers selected habitats characterized by nutrient-rich forage with simultaneous cover, while non-mothers used more nutrient-poor forage without cover and showed weak avoidance of human-associated risks. Specific habitat features beneficial for reproduction may be landscape-dependent, as risk-reward trade-offs and the resulting nutritional benefits and risks vary across space and time. Therefore, future work should focus on the function of features to consider whether they offer forage and cover benefits. This will involve improved urban vegetation surveys and human-activity monitoring to fully capture these forage benefits and risk trade-offs. Such efforts will also strengthen the use of urban systems as models for testing ecological concepts across larger scales. This manipulative study provides a reference for identifying habitat predictors of reproductive success in large herbivores like BTD and demonstrates how integrating empirical data from management interventions with ecological theory can fill knowledge gaps in our understanding of drivers in population dynamics and inform effective management, a prerequisite to coexist with wildlife.

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