Article

Optimal Land Use Regulation for Human–Coyote Conflicts in the Denver Metropolitan Area

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Abstract: While human–wildlife conflicts are an emerging problem in urban areas, wildlife conservation is needed to sustain human life. Because the degree of conflict depends on land cover types and housing density classes, land-use policies intended to influence both resident and wildlife behavior are needed. This paper numerically simulates the optimal urban boundary regulation to reduce human–coyote conflicts and conserve the ecosystem. Given the parameters of the Denver Metropolitan Area, the optimal location of the urban boundary is estimated as 1 km farther away from the market city boundary. As a result of the optimization more coyotes emerge in urban areas, while fewer herbivores and plants emerge in natural habitats. Because of a “cascade effect”, that is, secondary-and-later effects on the number of certain species through a food chain, the optimal result sees the number of plants increase with a smaller natural habitat than the market size. This indicates that because both direct and cascade effects are affected by the degree of land-use policies, it is necessary to consider the cascade effect when designing these policies.

Keywords: urban boundary regulation; human–wildlife conflict; food chain; ecosystem conservation; numerical simulation

1. Introduction

Human–wildlife conflicts are an emerging problem around the world, as some wildlife creatures encroach into cities. Conflicts with wildlife can cause direct material and economic damage to crops, livestock, and property, and sometimes threaten human life when residents are attacked by creatures such as bears in Japan, foxes in London, coyotes in the United States and Canada, or elephants in Africa. Wild creatures can transmit zoonotic diseases, including those transmitted by parasites such as bloodsucking mosquitoes (e.g., [1–3]). According to [4], malaria-carrying mosquitoes kill 830,000 humans, including children, each year, making them the deadliest animal on the planet. While indirect impacts of human–wildlife conflicts are difficult to measure, they include the costs to farmers of protecting their crops and livestock, reduced psychosocial well-being, disruption of livelihoods, and food shortages [3]. Because the animals and organisms in question are often important for the stability of ecosystem services to humans [5], it is important to resolve these conflicts and conserve the related ecosystems.

Human–wildlife coexistence refers to a sustainable and dynamic state in which human–wildlife interactions are effectively managed and wildlife populations can persist in a socially legitimate way and at an acceptable level of risk [6]. To make progress towards human–wildlife coexistence we need to better understand the causes of wildlife damage from various perspectives, including wildlife ecology and human perception and behavior, and require a new governance model to balance shared land use between humans and wildlife [7].

This paper examines how to manage the trade-offs between biodiversity conservation and human–wildlife conflicts through land-use regulations that control city size. Technically,
we estimate the welfare effects of these land-use regulations on biodiversity and the degree of the conflict. We use the model of [8], which considers spatial densities of land use for humans, carnivores, herbivores, and plants in cities and natural habitats. This model can consider the way in which spatially dependent interactions between humans and wildlife creatures within a city affect overall biodiversity.

Papers that focus on resident–coyote conflicts in North America [9–13] collect newspapers, research papers, and records from wildlife agencies that report coyote attacks on humans in the United States and Canada in order to classify the attacks by category (investigative, defensive, predatory, etc.); their results state that the frequency of coyote attacks on residents has gradually increased in recent years across North America.

To develop and optimize the management effort, information on where coyotes appear and how long they remain there and interact with residents is needed. In an investigation of the temporal and spatial patterns of conflicts between humans and coyotes particularly as they relate to land cover types and housing density classes in the Denver Metropolitan Area (DMA), hot spots of conflict with coyotes were primarily found in the southern part of the DMA with coyotes accessing developed areas and interacting with residents via natural areas [14]. In their study of inter-species dynamics in urban areas, colonies of prey species have an important role in the distance between humans and coyotes through changes in predator species behavior and human behavior near colonies [13].

These observations require spatially-dependent land-use policies intended to influence animal behavior and human behavior in cities, such as zoning. To design such policies effectively requires a theory of land use that can consider spatial interactions between humans and wildlife in residential areas.

Most existing studies about the interaction between humans and wildlife focus on land-use competition between humans and wildlife, showing how the sizes of both natural habitats and urban land are endogenously determined [15–18]. However, these studies consider only the effects of the respective area sizes of humans and wildlife, not the interaction between humans and wildlife which takes place spatially. [8] developed a theoretical model explicitly considering the human population density, where and how long carnivores stay in the urban areas, where and how long herbivores stay in natural habitats, and plant density in order to understand spatially dependent interactions between humans and wildlife in a closed monocentric city, i.e., a city with an exogenous human population and one Central Business District (CBD). Using this model, they theoretically derived the second-best optimal conditions for land-use policies that protect human lives while preserving the ecosystem.

While [8] developed a theoretical model for land use regulation considering the ecosystem, this paper quantitatively obtains the optimal land use regulation for the conflict situation between humans and coyotes in the DMA. Technically, we apply their [8] model to human–coyote conflicts in the DMA in order to measure the overall welfare effect of the urban boundary regulation through decrease in human–coyote conflicts and change in the populations of both coyotes and the herbivores which are coyotes’ primary diet, as well as of plants.

This paper contributes to ecosystem management through land-use policy. Regarding optimal land use regulation, see [19–23]. However, these studies do not consider the effect of land-use changes on ecosystems. Previous studies [16–18] all state that the optimal city size is always smaller than the equilibrium size to conserve the natural habitats. [24] proposes a simple framework in which urban expansion reduces the amount of open space available, and thus equilibrium cities are too large. To conserve ecosystems, it is important to reduce human demand for land and change land-use patterns to minimize habitat fragmentation [25]. Land use planning that maximizes the value of ecosystem services [26,27]. However, the effects of land use regulation on wildlife preservation through changes in the spatial land use of animals and the change in the situation of human–wildlife conflicts have not been numerically measured by previous papers.
Setting the parameters of our model based on real data, we obtain two different results from the previous studies: (i) when the city size expands, the number of top predator animals (coyotes) increases; and (ii) the optimum city size can be larger than the current (equilibrium) city size. We numerically obtain that the optimal location of the urban boundary in the southern part of DMA is 15 km away from the CBD.

The urban boundary regulation immediately affects the number of plants because it converts natural habitats into urban areas. Additionally, in our numerical simulation we observe the “cascade effect”, that is, secondary-and-later indirect effects on the number of certain species through a food web. Because of the cascade effect, we obtain an interesting result: the number of plants increases despite the smaller size of the natural habitat. When the natural habitats are converted into urban areas by urban boundary regulations, the number of deer decreases because the number of coyotes becomes greater. Thus, fewer plants are consumed by deer (i.e., the number of plants increases due to the urban boundary regulation). The negative direct effect of the urban boundary regulation on the number of plants is smaller than the positive cascade effect on the number of plants, which is why the number of plants increases. Hence, it is necessary to design land-use policies considering both the direct and the cascade effects.

The rest of the paper is organized as follows: Section 2 introduces the model; Section 3 shows the effect of urban boundary regulation on the population of animals; Section 4 shows the numerical simulation for the Denver Metropolitan Area; and the final section concludes the paper.

2. The Model

We use the urban–ecosystem model for a closed monocentric city surrounded by natural habitat proposed by [8], the geographical pattern of which is depicted in Figure 1. In the model, land is divided into the following three zones: (i) central business district (CBD) \( (x = 0) \); (ii) housing zone \( (x \in [0, Z^{H}]) \); and (iii) natural habitat \( (x \in [Z^{H}, Z^{A}]) \), where \( Z^{H} \) is the urban boundary and \( Z^{A} \) is an exogenous boundary of the natural habitat. In this paper, we use (1)–(8) as shown in [8]. Superscripts \( H \) and \( A \) indicate the housing zone and the natural habitat, respectively, and subscripts 1, 2 and 3 indicate the plants, herbivores, and carnivores, respectively, throughout the paper.

![Figure 1. The model city adjacent to a natural habitat.](image)

Figure 2 shows the DMA map with the density of coyote conflicts reported for 2003–2010 and the four land-use patterns (the map is from [14]; we plotted the location of the central business district on the map). From the DMA map, it can be seen that there are conflicts between coyotes and humans in the southern part of the urban areas, and that the urban areas are surrounded by the natural habitat. Thus, the urban–ecosystem model we use in this paper corresponds to the situation in the DMA.
The overview of the model developed by [8] is as follows. The natural habitat has three kinds of species forming a food chain: a carnivore species, a herbivore species, and a plant species. All animals or plants belonging to the same species are identical. An individual animal behaves in such a way as to maximize net offspring, which is essential for the continued existence of a species. An individual animal consumes prey species to take in nutrients to produce offspring while trying to avoid encountering predator species as much as possible. The carnivores feed on the herbivores in the natural habitat and leave the natural habitat, up to location $X \in [0, Z^H]$ in the residential area, in order to seek human-related foods such as garbage, even though they may encounter humans and be killed by them. The herbivores feed on plants and encounter carnivores in the natural habitat, by whom they might be eaten. The plants take up nutrients from the soil. The number of plants, herbivores, and carnivores is denoted by $N_1$, $N_2$, and $N_3$, respectively.

To capture the spatial aspect of human–wildlife conflict in the city, [8] use the idea of the time density that indicates how long the animal will stay at each location. The individual animal chooses how long it spends feeding on prey species and avoiding predators at each location to maximize the net offspring subject to a time constraint, taking both prey and predator species’ time density as given.

Identical households live in the housing zone, and land is equally owned by city residents. Each household residing at location $x \in [0, Z^H]$ commutes to the CBD and earns an exogenous wage. As carnivores search the housing zone for human-generated food such as garbage, households may encounter carnivores. They feel afraid of encountering...
carnivores and being attacked by them, which decreases their utility. On the other hand, the household’s utility increases with the quality of ecosystem services determined by the populations of all species. This utility explains the positive externality for humans, which includes the existence value of animals and plants. The marginal increase in the quality with respect to any element of \( N = \{ N_1, N_2, N_3 \} \) is positive, while the marginal benefit of each component is diminishing. We did not consider the utility derived from a sense of security by preparing guns and alert systems in households; thus, we dropped the third term \((g_3(\beta_3(x)))\) from the utility function in (8) in [8].

The market-clearing conditions and the population dynamics of animals are the same here as (9)–(20) in [8]. The numbers of animals and plants are determined by the predator-prey interaction formulated by the Lotka–Volterra equations, as shown in (10) and (11) in [8]. The steady-state populations of animals and plants are obtained by (13) and (14) in [8].

The laissez-faire equilibrium can be obtained using the same procedure as Section 3 in [8]. The human population density is determined as a result of competition for housing locations among residents. The equilibrium condition with respect to the time density of each animal is obtained from (24) in [8]; they found that in the housing zone, the time density of carnivores first continuously increases, then decreases as it approaches the CBD before finally reaching zero. In short, the degree of conflicts shows a bell-shaped curve analogous to the observation of the density of coyote conflicts in the Denver Metropolitan Area by [14].

### 3. The Impact of Urban Boundary Regulation on an Ecosystem

In this section, we investigate the impact of the urban boundary regulation on the population of animals in the equilibrium and compare the results with [18]. In this way it is possible to capture the population change in a static model without following the route of population change. Even in such a case, different results were obtained from [18]. They captured the dynamic pathway of wildlife population change by changing the size of natural habitats through an external shock. This setting is not suitable for the present situation, where carnivores can leave the natural habitat. We therefore investigated the local stability analysis of the equilibrium point. Let \( N^* = (N_3^*, N_2^*) \) be the steady-state population equilibrium of carnivores and herbivores. In the situation where carnivores encroach into a city, if neither \( N_3^* \) nor \( N_2^* \) is extinct, then \( N^* \) is locally asymptotically stable.

As shown in (10) and (11) in [8], the dynamic system of predator–prey interaction is

\[
\frac{dN_3}{dT} = N_3 b_3 = N_3 [a_3 (Q_2^A + Q_3^H) - \beta_3 M_3 - m_3],
\]

\[
\frac{dN_2}{dT} = N_2 b_2 = N_2 [a_2 Q_2 - \beta_2 M_2 - m_2],
\]

where \( b_i (i = 2, 3) \) is net offspring of an individual animal in species \( i \), \( Q_2^A \) is the carnivore’s intake of herbivores, \( Q_3^H \) is the carnivore’s intake of human-generated food waste, \( Q_2 \) is the herbivore’s intake of plants, \( M_3 \) is the carnivore’s expected number of encounters with humans, \( M_2 \) is the herbivore’s expected number of encounters with its predator species, \( a_i > 0 \) is the reproduction efficiency of an individual animal in specie \( i \) per prey eaten, \( \beta_i > 0 \) is the reproduction loss of an individual animal in specie \( i \) per encounter with a predator species, and \( m_i \) is an exogenous positive parameter representing the loss rate of offspring of an individual animal in specie \( i \) due to natural death. Using \( Q_3^A = PN_2 \) and \( M_2 = PN_3 \), the steady-state population equilibrium is derived from \( dN_3/dT = dN_2/dT = 0 \):

\[
N_3 = \frac{a_2 Q_2 - m_2}{\beta_2 P},
\]

\[
N_2 = \frac{\beta_3 M_3 - a_3 Q_3^H + m_3}{a_3 P},
\]
where \( P \) is the probability of an encounter between an individual carnivore and an individual herbivore in the whole habitat.

Using the envelope theorem for comparative static analysis, we can obtain the following proposition.

**Proposition 1.** (Comparative static of population of animals with respect to the urban boundary).

(i) Herbivores: When \( \frac{\partial P}{\partial Z_H} > 0 \), then \( \frac{dN_2}{dZ_H} < 0 \). When \( \frac{\partial P}{\partial Z_H} < 0 \), if \( \alpha_3 \frac{\partial Q_H}{\partial Z_H} - \beta_3 \frac{\partial M_3}{\partial Z_H} > 0 \), then \( \frac{dN_2}{dZ_H} < 0 \).

(ii) Carnivores: If either \( \frac{\partial Q_H}{\partial Z_H} \gg (\ll) 0 \) or \( \frac{\partial Q_H}{\partial Z_H} \gg (\ll) 0 \) (i.e., either the increase (decrease) in the herbivore’s net offspring or the increase (decrease) in the carnivore’s net offspring with respect to the urban boundary is large enough), then \( \frac{dN_3}{dZ_H} > (\ll) 0 \).

**Proof of Proposition 1.** See Appendix A. □

An intuitive explanation for result (i) is given as follows. When natural habitats convert into urban areas, which implies that plants disappear at \( Z_H \), herbivores will spend more time at every location to compensate for plants that cannot be eaten at \( Z_H \). At the same time, carnivores cannot encounter herbivores at \( Z_H \). Thus, the probability of an encounter between a herbivore and a carnivore across the habitat, \( P \), becomes either higher or lower. If the probability becomes higher, then the carnivore’s amount of predation in the habitat increases, which leads to a decrease in the number of herbivores. In contrast, if the probability becomes lower (that is, the carnivore’s amount of predation in the habitat decreases), then the change in the number of herbivores depends on the carnivore’s amount of predation in urban areas. If total changes in the amount of the carnivore’s predation in both urban areas and natural habitats are positive (i.e., the increase in the amount of the carnivore’s predation in urban areas is larger than the decrease in that in the natural habitat), then the number of herbivores decreases, and vice versa.

An intuitive explanation for result (ii) depends on the changes in net offspring of both animals; \( \frac{\partial b_3}{\partial Z_H} \gg 0 \) means a case in which carnivores can eat a lot of food in the urban area and the residents or city government do not substantially eliminate carnivores. If this is the case, the number of carnivores increases; \( \frac{\partial b_3}{\partial Z_H} \ll 0 \) means a case in which there are plentiful plants (which are important food supply sources for herbivores) next to the urban boundary that are destroyed by urban development. Thus, herbivores will spend more time seeking food in the natural habitat, which leads to an increase in the risk of encountering carnivores. Consequently, the net offspring of herbivores is greatly reduced, and the number of carnivores is reduced as well due to the loss of a food source.

**Corollary 1.** Suppose that the number of plants that grow naturally without being planted by humans \( F(x) \) is uniform across the natural habitat. If \( \frac{\partial b_2}{\partial Z_H} > 0 \), then \( \frac{dN_3}{dZ_H} > 0 \).

**Proof of Corollary 1.** See Appendix A. □

This assertion implies that if the number of plants that grows naturally before being eaten by herbivores (which is \( F(x) \) in [8]) is uniform across the habitat, the change in the number of carnivores depends only on the change in the herbivores’ offspring. When \( F(x) \) is uniform across the habitat, the time density of both carnivores and herbivores is uniform across the habitat. Then, regardless of the size of the natural habitats the carnivore’s amount of predation does not change in the habitat, while it increases in the urban area. Thus, the carnivore’s net offspring always increases. In contrast, the change in the herbivore’s net offspring is ambiguous. If the herbivore’s amount of foods available in the rest of the habitat is larger than the loss of plants in ecosystem areas converted into urban areas, then
the herbivore’s net offspring increases, which in turn leads to an increase in the number of carnivores.

4. Numerical Simulation

4.1. Resident–Coyote Conflicts in the Denver Metropolitan Area

Ref. [14] researched the spatial patterns of human–coyote conflicts in the DMA using media reports for the period 2003–2010 from sixteen municipalities, five county governments, and Colorado Parks and Wildlife (which manages 42 state parks, all of Colorado’s wildlife, more than 300 state wildlife areas and a host of recreational programs). The reports provide information on coyote observations (signs, sightings, and encounters) and conflicts (incidents, pet attacks, and human attacks). An incident means a conflict where coyotes exhibited unsafe behavior for humans, such as baring teeth as if to attack a human immediately. Human attacks involve physical contact such as a human being injured or killed by a coyote. From the DMA map in Figure 2, it is apparent that the density of conflicts is low near the urban boundary, while it becomes higher approaching the city center before becoming lower again in the city center proper.

4.2. Parameter Calibration

As shown in Figure 2, the development (residential) area of the DMA spreads concentrically outwards from the CBD. The development area is contiguous to natural habitats from the North West to the South East, and is contiguous to agricultural areas in the North East. Our focus here is on the half-circle of the DMA with a natural habitat. The boundaries of the development area and the natural habitat are set as 14 km and 34 km distant from the CBD, respectively. The boundary of carnivore foraging behavior toward the CBD, $X$, is located about 6 km away from the CBD. The total number of households in the development area is set at 563,859, obtained from the total number of households in Denver County including the cities of Lakewood, Littleton, Aurora, Englewood, Centennial, and Thornton in 2012, with the city divided into discrete areas with 2 km widths.

The parameters relate to the ecosystem (that is, $\alpha_i$, $\beta_i$, $m_i$, $i \in \{2, 3\}$ along with the parameter that explains a carnivore’s chance of encountering humans (denoted by $k(x)$ in [8]) were calibrated in order to obtain the real situation in DMA as expressed by the dynamic system of population growth (1) and (2). Coyotes usually prey on small mammals, domestic pets, and livestock, and they may eat garbage. Their diet primarily consists of meat such as rodents (squirrels, mice, rats, etc.), rabbits, birds, and deer. Here, we focus on the coyote–deer–plants food chain.

Coyotes usually give birth to an average of six offspring, of which only 20% survive each year. Thus, we set $\alpha_3(Q_A^3 + Q_H^3) = 1.2$. Per [28], 56 coyotes were exterminated to tackle the resident–coyote conflict within the development area of DMA during the five years 2009–2014. Thus, we set $\beta_3 M_3 N_3 = 56/5$, where $k(x) = 1000(14 - x)^3$. Per the data on small game statistics by Colorado Park and Wildlife, on average 2404.5 coyotes were killed by hunters in the DMA during the two years 2012–2013. Thus, we set $m_3 N_3 = 2404.5$.

Deer hunt statistics from Colorado Park and Wildlife provide the number of harvests and post-hunted population of deer according to the Deer Data Analysis Unit. We selected three units (D-17, D-27, and D-49) from the Deer Data Analysis Unit and calculated the total number of deer and the total number of harvests in these units during 2012–2013. The total average number of harvests was 2333.5; thus, we set $m_2 N_2 = 2333.5$. The total average pre-hunted population of deer was 22,433.5. According to the deer hunt statistics from Colorado Park and Wildlife, a deer usually gives birth to one offspring per year, and 70% of the population is female; Thus, we set $\alpha_2 Q_2 = 0.7$.

By using the above equations with the population equilibrium of carnivores and herbivores, $N_3 = \frac{\alpha_3 Q_3^3 - m_3}{\beta_3}$ and $N_2 = \frac{\beta_3 M_3 - \alpha_2 Q_2^{H1} + m_3}{\alpha_2}$, we find that the equilibrium number of coyotes in this area is 2013. Then, we substitute these parameters into the equilibrium conditions and calculate the endogenous variables. As a result, we find that $\alpha_3 = 0.0186$, $\beta_3 = 2.96 \times 10^{-10}$, $\alpha_2 = 0.0290$, $\beta_2 = 0.547$, $m_3 = 1.19$, and $m_2 = 0.104$. 
Deer herbivory greatly reduces the seed production and seedling recruitment of wild plants. [29] investigated the effects of the deer herbivory on plants in the Elk Mountains of western Colorado. They state that plants exposed to deer were on average 30% less productive than the same number of plants when caged to exclude deer. Thus, we set \( F(x) - \beta_1 (Z^2) N_2 \) = 0.7, where \( \beta_1 = 1 \).

Finally, we specify the utility function as \( v(x) = C \left( x + b \ln f(x) - c_1 M_0(x) + \sum_{i=1}^{3} \theta_i N_i \right) \), where \( b, c, \) and \( \theta_i, i \in \{1, 2, 3\} \) are positive parameters. The parameter \( c \) is set such that the willingness to pay per month per household for completely removing coyotes from the residential area is USD 150. Parameters \( \theta_i, i \in \{1, 2, 3\} \) are set such that when carnivores, herbivores, and plants are close to extinction in the DMA, the value of each species is USD 100, 60, and 20, respectively.

4.3. Results and Discussions

4.3.1. Numerical Results

Here, we calculate how the number of animals and plants, human fear of encroachment by carnivores, and the value of the ecosystem change when the urban boundary is spread outward by 0.5 km. We then obtain the optimal location of the boundary in the DMA given the above parameters. The numerical results are shown in Tables 1 and 2. There are two main results: (i) when the city size expands, the number of top predator animals (coyotes) increases; (ii) under the above parameter settings, the optimal city boundary is located 15 km away from the city center. In other words, the optimum city size is larger than the current (equilibrium) city size.

Table 1. The population of wildlife and the welfare effect of urban boundary regulation.

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4.3.2. Change in The Population Equilibrium

Result (i) is a different result from [18], who state that when the expansion of city size results in the extinction of the top predator species, a new population equilibrium is reached in which herbivores and plants coexist. The reason this paper has a new result is expressed by Corollary 1 in Section 3: in contrast, the number of herbivores is decreased by urban expansion.

Another interesting result is that the number of plants increases when expanding the city size from \( 14^2 \times (\pi/2) \) \( \text{km}^2 \) to \( 14.5^2 \times (\pi/2) \) \( \text{km}^2 \), whereas it decreases as the city size expands over \( 14.5^2 \times (\pi/2) \) \( \text{km}^2 \). This is due to a “cascade effect”, which is an indirect effect through a food web. When city size expands, the number of carnivores increases because they can eat more food in the city. Thus, the number of deer decreases and the number of plants increases temporarily. As the city size expands, the direct effect of the urban expansion on the number of plants (that is, by cutting trees directly) is greater than the cascade effect, and the number of plants decreases.

4.3.3. Overall Welfare Effects

When expanding the city size from \( 14^2 \times (\pi/2) \) \( \text{km}^2 \) to \( 14.5^2 \times (\pi/2) \) \( \text{km}^2 \), the value of the ecosystem increases because the numbers of both carnivores and plants increase. As the city size expands over \( 14.5^2 \times (\pi/2) \) \( \text{km}^2 \), the number of carnivores increases, while the number of plants begins to decline. The value of biodiversity increases, while the rate
of increase decreases. At the same time, overall welfare starts to decline as the fear of encroachment by carnivores increases. Under the above parameter settings, the optimal city boundary is located 15 km away from the city center.

Table 2. Human population density and time densities of wildlife in DMA.

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<thead>
<tr>
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<th>UGB = 14.5 km</th>
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</tbody>
</table>

This result indicates that even if human fear of carnivores increases, the value of the ecosystem may rise. Furthermore, the number of plants is sensitively changed by the urban expansion. In other words, the number of plants depends on which of two effects is dominant: the direct effects of urban expansion on plants, or indirect effects on plants through a decrease in the number of deer. Hence, it is necessary to consider these effects when designing land use regulations.

5. Conclusions

This paper uses the urban–ecosystem model developed by [8] to measure the effect of urban boundary regulation on the population of animals and numerically optimize city size, given the parameters for the Denver Metropolitan Area.

We obtained the following two different results from the previous studies: (i) when city size expands, the number of top predator animals (coyotes) increases; and (ii) the second-best optimum city size is larger than the current (equilibrium) city size. We obtained result (i) because, with our parameters, carnivores can eat food in the urban area and the residents and city government do not sufficiently eliminate carnivores. The optimal city size is determined by the trade-off between the benefit of ecosystem conservation and the fear of coyote attacks in urban areas. As in result (i), with our parameters the number of carnivores increases as the city size expands. As the value of carnivores is high, the benefit of conservation of the ecosystem increases, while the fear of encroachment by carnivores increases as well. As a result, given the parameters used here, the optimal location of the urban boundary in the southern part of the Denver Metropolitan Area is 15 km away from the CBD.

In addition, both the direct effect of urban boundary regulation on plants and the cascade effect, that is, secondary-and-later effects on the number of certain species through a food web, were numerically confirmed. Because the direct and cascade effects depend
on the degree of regulation, it is necessary to consider the cascade effect when designing land-use policies.

As we used a basic ecosystem model composed of coyotes, deer, and plants to form a food chain, and there are some reports that coyotes feed on a variety of other food sources, analysis of more complex food chains may be a promising future subject.

**Author Contributions:** Conceptualization, J.Y. and T.K.; methodology, J.Y. and T.K.; formal analysis, J.Y. and T.K.; data curation, J.Y.; writing—original draft preparation, J.Y.; writing—review and editing, T.K.; supervision, T.K. All authors have read and agreed to the published version of the manuscript.

**Funding:** JSPS KAKENHI Grant Number JP21420010 and the Environment Research and Technology Development Fund (JPMERF20 S11821) of the Environmental Restoration and Conservation Agency of Japan.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest.

**Appendix A. Proofs of Proposition 1 and Corollary 1**

**Proof of Proposition 1.** Using (12) in [8] and

\[
Q_2 = \int_{Z_H}^\beta t_2^A(x)\rho_2(t_2^A(x))n_1(x)dx
= t_2^A(Z_H)^2\rho_2(t_2^A(Z_H))\int_{Z_H}^\beta [a_1(x) + a(x) - \beta_1t_2^A(Z_H)N_2]dx
= \tilde{Q}_2(Z_H)[\int_{Z_H}^\beta [a_1(x) + a(x)]dx - \beta_1\frac{N_2}{Z_H}Z_H^\beta \int_{Z_H}^\beta dx]
= \tilde{Q}_2(Z_H)[a_1(Z_H) - \beta_1N_2],
\]

we can write the dynamic system of two animals as

\[
\begin{align*}
\alpha_3N_2t_2^A(Z_H)\int_{Z_H}^\beta t_3^A(x)dx + \alpha_3Q_3^H(Z_H) - \beta_3M_3(Z_H) - m_3 &= 0, \\
\alpha_2\tilde{Q}_2(Z_H)(a_1(Z_H) - \beta_1N_2) - \beta_2N_3t_2^A(Z_H)\int_{Z_H}^\beta t_3^A(x)dx - m_2 &= 0.
\end{align*}
\]

(Totally differentiating (A2) with respect to \(N_2, N_3\), and policy variable \(Z^H\) yields

\[
\begin{pmatrix}
\alpha_3t_2^A(Z_H)\int_{Z_H}^\beta t_3^A(x)dx \\
-\alpha_2\tilde{Q}_2(Z_H)\beta_1
\end{pmatrix}
\begin{pmatrix}
0 \\
-\beta_2t_2^A(Z_H)\int_{Z_H}^\beta t_3^A(x)dx \equiv A
\end{pmatrix}
\begin{pmatrix}
dN_2 \\
dN_3
\end{pmatrix}
= -\left(\frac{\partial H}{\partial Z^H}\right)\frac{dH}{dZ^H},
\]
where
\[
\frac{\partial h}{\partial z_H^x} = a_3 \frac{\partial P}{\partial z_H^x} N_2 + a_3 \frac{\partial Q_3^H}{\partial z_H^x} - \beta_2 \frac{\partial M_3}{\partial z_H^x}
\]
\[
= a_3 \left[ \frac{\partial t_2^A}{\partial z_H^x} \int_{Z_H^x} t_3^A(x)dx - t_2^A(Z_H^x) t_3^A(Z_H^x) \right] > 0
\]
\[
+ t_3^H(Z_H^x) n_h(Z_H^x) [a_3 \rho_3(t_3^H(Z_H^x)) - \beta_3 k(Z_H^x)] > 0
\]  \hspace{1cm} (A4)

and
\[
\frac{\partial b}{\partial z_H^x} = a_2 \frac{\partial Q_2}{\partial z_H^x} N_1 + a_2 \tilde{Q}_2(Z_H^x) \frac{\partial N_1}{\partial z_H^x} - \beta_2 \frac{\partial P}{\partial z_H^x} N_3
\]
\[
= a_2 \frac{\partial \tilde{Q}_2}{\partial z_H^x} (a_1(Z_H^x) - \beta_1 N_2) + a_2 \tilde{Q}_2(Z_H^x) \frac{\partial \tilde{t}_1}{\partial z_H^x} - \beta_2 \frac{N_3}{z_H^x} \int_{z_H^x}^{z_A} t_3^A(x)dx > 0
\]  \hspace{1cm} (A5)

The determinant of matrix $A$ is
\[
|A| = -a_3 \beta_2 \left( t_2^A(Z_H^x) \int_{z_H^x}^{z_A} t_3^A(x)dx \right)^2 < 0.
\]  \hspace{1cm} (A6)

Using Cramer’s rule,
\[
\frac{dN_2}{dZ_H} = \frac{1}{|A|} \left| \begin{array}{cc}
\frac{\partial h}{\partial z_H^x} & 0 \\
-\beta_2 t_2^A(Z_H^x) \int_{z_H^x}^{z_A} t_3^A(x)dx & \frac{\partial P}{\partial z_H^x} + a_3 \frac{\partial Q_3^H}{\partial z_H^x} - \beta_3 \frac{\partial M_3}{\partial z_H^x}
\end{array} \right|
\]  \hspace{1cm} (A7)

Similarly,
\[
\frac{dN_3}{dZ_H} = \frac{1}{|A|} \left| \begin{array}{cc}
a_3 t_2^A(Z_H^x) \int_{z_H^x}^{z_A} t_3^A(x)dx & -\frac{\partial h}{\partial z_H^x} \\
- a_2 \tilde{Q}_2(Z_H^x) \beta_1 & \frac{\partial P}{\partial z_H^x} + a_3 \frac{\partial Q_3^H}{\partial z_H^x} - \beta_3 \frac{\partial M_3}{\partial z_H^x}
\end{array} \right|
\]  \hspace{1cm} (A8)

From these equations, we can obtain Proposition 1. □

**Proof of Corollary 1.** Suppose $F(x)$ is uniform across the natural habitat. Then, from (24) for $i = 3$ in [8], the carnivore’s time density is equal to the habitat. Thus,
\[
\frac{\partial P}{\partial z_H^x} = \frac{1}{Z_A - Z_H^x} \left[ \frac{1}{Z_A - Z_H^x} \int_{Z_H^x}^{Z_A} t_3^A(x)dx - t_3^A(Z_H^x) \right] = 0.
\]  \hspace{1cm} (A9)

Using (A9), we can obtain
\[
\frac{\partial b_3}{\partial z_H^x} = a_3 \frac{\partial Q_3^H}{\partial z_H^x} - \beta_2 \frac{\partial M_3}{\partial z_H^x} = t_3^H(Z_H^x) n_h(Z_H^x) [a_3 \rho_3(t_3^H(Z_H^x)) - \beta_3 k(Z_H^x)] > 0,
\]  \hspace{1cm} (A10)
\[
\frac{\partial b_2}{\partial z_H^x} = a_2 \frac{\partial \tilde{Q}_2}{\partial z_H^x} N_1 + a_2 \tilde{Q}_2(Z_H^x) \frac{\partial N_1}{\partial z_H^x} = a_2 \frac{\partial \tilde{Q}_2}{\partial z_H^x} N_1 - a_2 \tilde{Q}_2(Z_H^x) a_1(Z_H^x) \preceq 0.
\]  \hspace{1cm} (A11)
From (A8), if \( \frac{\partial b}{\partial Z} > 0 \), then \( \frac{\partial N_s}{\partial Z} > 0. \) □

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