Cities and biodiversity: Spatial efficiency of land use

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Cities and biodiversity:
Spatial efficiency of land use*

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Abstract. Biologically important but dangerous wildlife creatures encroach into cities, which causes human-wildlife conflicts. To explore the effect of the encroachment of wildlife into cities on equilibrium land use and its efficiency, we develop an equilibrium theory of land used for humans and wildlife by combining an ecosystem model with urban economics model. Humans choose their housing location and size in response to the risk of encountering wildlife in cities, and animals optimize their food intake by spreading out in response to heterogeneous feeding grounds in both urban areas and natural habitats, which determines the spatial heterogeneous distribution of both agents. We first prove the existence and uniqueness of the spatial equilibrium in a linear city adjacent to natural habitats. Next, our theory provides new insights for the wildlife conservation: (i) this spatial heterogeneity generates inefficient predator-prey interactions, leading to an inefficient steady state population equilibrium of animals; (ii) With the spatial inefficiency, the equilibrium city size is not always too big. We numerically demonstrate how both the equilibrium and the optimal solution are affected by the scale of conflicts and the value of wildlife.

JEL classification: R11; R14; Q28

Keywords: Land use, location-dependent externality, human-wildlife conflicts, biodiversity.

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1. Introduction

While wild animals constitute biodiversity and thus bring a positive externality that has public goods charactristics, they bring about negative externalities when they approach people. For example, some wildlife—large carnivores, mosquitoes, and so on—encroach into cities and harm humans or pets through injury, infectious deseases, and, in extreme cases, loss of life (Penteriani et al., 2016).[1] Indeed, in many cities worldwide, conflicts between people and urban beasts are reported. For example, Rome has a problem with wild boars; wolves mingle with suburban Gemans; mountain lions frequent Los Angeles (The Guardian, 2017).[2] Therefore, a certain distance between humans and wildlife is important to resolve human–wildlife conflicts and conserve biological resources efficiently.[3]

This paper develops a novel model considering spatial density of land use of humans and an ecosystem, and studies the existence and uniqueness of an equilibrium where wildlife interacts with humans within cities. In addition, we investigate how animal behavior, residents' location choice, and city size deviate from the first-best social optimum where the social planner controls all endogenous variables including animal behavior. This exploration is indispensable for making ecological and urban policies such as land use regulations.[4]

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[1] According to World's Deadliest Animals (reporting the number of people killed by animals per year) mosquitoes carrying malaria kill 830,000 humans every year and are the deadliest animal on earth. See https://www.gatesnotes.com/Health/Most-Deadly-Animal-Mosquito-Week-2016 (accessed November 29, 2017)

[2] The Guardian (May 2017) further reports "All around the world, city life seems to be increasingly conducive to wildlife. Urban nature is no longer unglamorous feral pigeons or urban foxes. Wolves have taken up residence in parts of suburban Germany as densely populated as Cambridge or Newcastle. The highest density of peregrine falcons anywhere in the world is New York; the second highest is London, and these spectacular birds of prey now breed in almost every major British city. And all kinds of wild deer are rampaging through London, while also taking up residence everywhere from Nara in Japan to the Twin Cities of the US."

[3] The WWF report identifies basic list of available and tested solutions for human–wildlife conflicts. One solution is land-use planning that ensures that both humans and animals have the space they need is possible. For example, protecting key areas for wildlife, creating buffer zones and investing in alternative land uses are some of the solutions. See https://wwf.panda.org/our_work/wildlife/human_wildlife_conflict/ (accessed Jaunuary 25, 2019)

[4] In reality, we cannot effectively allocate all natural resources including animals' behavior. However, it may

It is recognized that biodiverisity provides humans with important benefits.[5] However, nations worldwide have experienced urban land expansion, reducing the size of the natural habitats, which leads to biodiversity loss (e.g. Pidgeon et al., 2007; Radeloff et al., 2010; Seto et al., 2012). Weitzman (1992) and Solow et al. (1993) attempt to value the biodiversity based on the genetic distance. Brock and Xepapadeas (2003) develop a conceptual framework for valuing biodiversity in terms of ecosystem services. Moreover, some studies analyze what size of habitat must remain to sustain the ecosystem service (e.g. Walker, 2001; Eppink et al., 2004). On the other hand, protection or extermination of certain species by humans might have unexpected results such as an extinction of other species. To optimally control biological resources, we need to integrate an economic model and an ecosystem having predator-prey interactions.

The work of integrating the micro-founded ecosystem model with the economic model was initiated by Eichner and Pethig (2006, 2009). They apply the ecosystem model that has been developed in the ecological literature (e.g. Hannon, 1976; Crocker and Tschirhart, 1992; Tschirhart, 2000). Eichner and Pethig (2006, 2009) focus on land use competition between wildlife and humans, implying that the sizes of both natural habitat and land used

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be possible for humans to change the animals' behavior at least to some extent by using some policies such as fences and food traps to attract the animals. If we take some concrete second-best measures, we can evaluate how useful these are. Yoshida and Kono (in press) analyze how close the social welfare approaches the ideal first best optimum by adopting the second-best land use policies. Environmental management through land use policy has been widely studied. The effects of urban land use and transportation policies on the energy footprint have been explored by Larson, Liu, and Yezer (2012), Larson and Yezer (2015), and Borck (2016). The optimal energy taxation and its effect on urban spatial structure has been studied by Borck and Brueckner (2018). Brueckner (2000) presents a simple framework in which urban expansion reduces the amount of open space available, so that equilibrium cities are too large. The externality in his paper is driven by the amenity value of undeveloped land. So, it is interpreted as benefits from wildlife preservation. The effects of land use regulation on the wildlife preservation through changes in the spatial land use of animals have not been considered by the previous papers.

[5] The Millennium Ecosystem Assessment (2005) reports that ecosystem services can be classified into four categories: provisioning services (e.g. food and fresh water), regulating services (e.g. climate regulation and disease control), cultural services (e.g. landscape esthetics and recreation), and supporting services (e.g. nutrient cycling and soil formation).

by humans are endogenously determined. They show that the optimal city size is smaller than the laissez-faire equilibrium city size because an increase in natural habitats can maintain the supply of ecosystem services to humans.[6]

The externalities identified in these previous papers are independent of spatial land use of humans and wild animals. But in a real city, they influence each other, and the degrees of their influences depend on their spatial land use. For example, some species inhabit not only suburban areas but also developed areas (Woodroffe et al., 2005). For example, foxes in London and coyotes in Chicago and California sometimes attack domestic animals and residents, and bloodsucking mosquitoes and mites infect humans. These are negative externalities which must be reduced by keeping some distance between humans and wildlife.

We summarize the arguments as follows. The value of a species depends on its distance from humans. When humans and wildlife are close to each other, a negative externality such as injury and loss of life may occur. The amount of the externality depends on the duration of their coexisttence in the same place, the number of species entering urban areas, and human population density. To solve the human-wildlife conflict, a distance dimension, which has been absent in previous models, is required.

This paper focuses on modeling the above-mentioned mechanisms to identify location-dependent market failures in urban areas and natural habitats. Technically, we add a continuous distance dimension to the urban-habitat-allocation model of Eichner and Pethig (2006, 2009), extending the traditional urban economic model (e.g. Alonso, 1964) to have natural habitats with animals.[7] To explicitly model the spatial distribution of wild animals, we introduce *a time density* as the population density of wildlife at each location. This

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[6] In the study of Eichner and Pethig (2006), the social planner solves her maximization problem by taking the individual organism's behavior as given.

[7] In Eichner and Pethig (2006, 2009), the urban area is used only for production of composite goods. However, to handle the human-wildlife conflict, we consider residential districts. So, we use the urban economics model.

indicates the total amount of time that an animal spends at each point in one year.

To take the effects of the interaction between certain species and humans on other species into account, we consider a food chain of three species: plants as a producer, herbivores feeding on plants, and carnivores feeding on herbivores. All of the animals behave so as to maximize their net offspring, as in Eichner and Pethig (2006, 2009). To generate the offspring, the animal searches the habitat for prey species, while trying to avoid encountering predators. In other words, the animal chooses its favorable time density so as to maximize its net offspring, taking the other species' time densities as given, subject to a time constraint.[8] Carnivores search the city for human-related sources of food such as garbage.[9] Then, humans have disutility of a risk of encountering carnivores. On the other hand, they benefit from ecosystem services depending on the numbers of all species.

To consider of the dynamic population of wildlife in the simplest possible way, we employ a traditional dynamic population growth model called the Lotka-Volterra model, and we put the wildlife behavior into the model. This enables us to focus on a steady-state population equilibrium, and to show how the complex human-wildlife interactions affect the population equilibrium through the food chain.

Finally, we explore characteristics of market failures in terms of the time density of animals at each location by comparing the first-best optimum with the equilibrium. We find that i) there exists a unique equilibrium in the model; ii) unless the plant densities are spatially uniform, the animals' behavior deviates from the first-best optimum at each location within not only cities but also the natural habitat; iii) the first-best optimal city size

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[8] In Eichner and Pethig (2006, 2009), the animal is assumed to trade his/her own biomass in a virtual competitive market. But, we do not follow this idea because the time constraint is more natural for animals.

[9] The geographic distribution of coyotes has expanded dramatically across North and central America (Hody and Kays, 2018), and their presence in urban areas has often elicited concern from the public (Gehrt, 2009, Baker and Timm 2017). Fedriani et al. (2001) found human-related foods in as much as 25% of coyote diets in areas of high human population densities in southern California.

can be larger or smaller than the equilibrium city size.

The paper is organized as follows. Section 2 combines a closed monocentric city with an ecosystem model. Section 3 shows the existence and uniqueness of equilibrium allocation. Section 4 defines the first-best optimum, then derives the values of species and their components, and it shows how the animals' and humans' behavior bring about market failures. Section 5 shows numerical simulations. The final section concludes the paper.

2. The Model

2.1 City and natural habitat

Consider a closed monocentric city adjacent to a natural habitat. There are $2\overline{N}_h$ identical households in the city and land is equally owned by the city residents.[10] For simplicity, the city population equals the number of households. The city is linear with the width of one unity, and the size is defined by $x \in [-Z^H, Z^H]$, where x denotes a distance from the city center, and Z^H is an urban boundary. The city is symmetric, and the right hand side (RHS, hereafter) has $\overline{N}_h$ population. We ignore the production of housing and assume that land is directly used by residents. Households do not enter the habitat.

There is an ecosystem in the habitat. In order to represent the ecosystem in the simplest possible framework, we suppose a food-chain of three species indexed by *i*: carnivores (*i* = 3) feed on herbivores (*i* = 2), herbivores feed on plants (*i* = 1), and plants take up nutrients from the land. The populations are denoted by $\mathbf{N} = \{N_1, N_2, N_3\}$. All animals or organisms belonging to the same species are assumed to be identical.

Carnivores and herbivores search the habitat for prey species, and eat prey species when

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[10] This is a typical urban economics model, which is referred to as the closed-city model under public landownership (CCP) by Fujita (1989).

meeting them. Suppose that only carnivores leave the habitat up to location $X \in [0, Z^H]$ in the residential area to seek human-origin food such as garbage. X is endogenously determined. Closer to the CBD, the availability of garbage to carnivores increases because of an increase in human population density, whereas the risk of being killed by people increases with time spent in the city. Carnivores determine their search boundary X by equalizing the marginal benefit with respect to distance to the marginal cost.

The land is divided into the following three zones: (i) a point central business district (a point CBD) ($x = 0$), (ii) housing zone (called the human zone) ($x \in [0, Z^H]$), and (iii) the natural habitat (called the animal zone) ($x \in [Z^H, Z^A]$), where Z^A is the boundary of the natural habitat. Superscript H indicates the human zone, and A indicates the animal zone throughout the paper. Following a real land use pattern, the geographical pattern is assumed as depicted in Figure 1, which shows only the right hand side of the land.[11] We model each agent's behavior for one year in a steady state.

[Figure 1 here]

2.2 Ecosystem model

An individual animal or organism of species *i*, called individual *i* for short, behaves so as to maximize its net offspring, as set in some papers including Eichner and Pethig (2006, 2009). This behavior is supposed to be essential for continuation of a species. To produce offspring, individual *i* feeds on prey species to take in nutrients, while trying to avoid encountering its predator species as much as possible. For simple analysis, we express such instinctive behavior by the traditional Lotka-Volterra-type equation:

$$b_i = \alpha_i Q_i - \beta_i M_i - m_i, \tag{1}$$

where b_i is individual *i*'s offspring, Q_i is individual *i*'s intake of prey, M_i is the number of

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[11] To focus on the case where carnivores enter residential areas, this model omits the land used for agriculture.

predators that individual *i* encounter, and m_i is a positive parameter representing individual *i*'s loss rates due to natural death. $\alpha_i > 0$ is individual *i*'s reproduction efficiency per prey eaten, and $\beta_i > 0$ is individual *i*'s reproduction loss per encounter with predators.

Based on the common behavior of organisms, we develop a model that can capture the spatial aspect of the behavior of organisms. The following model can apply to any mobile organisms. In the paper, it applies to herbivores and carnivores ($i = 2, 3$).

The individual *i* spends time to search zone *j* for prey species and consumes them when encountering them. So, $Q_i = \sum_j Q_i^j$, where Q_i^j is individual *i*'s intake of prey species in zone *j*. The individual *i*'s expected intake of prey species at location *x* depends on the time density of individual *i* in zone *j* and the density of individual *i*'s prey species in zone *j*. The time density is formally defined as follows.

Definition 1. Individual *i*'s *time density* within zone *j* (i = 2, 3 and j = H, A), $t_i^j(x)$, indicates the total length of time that individual *i* spends at location *x* within zone *j* for eating in certain time periods.

The time density, $t_i^j(x)$, which maximizes the net offspring, depends on the location. Actually, some empirical ecological studies (e.g., Yoda et al., 2012; Pyke, 2015) show that animals optimize their food intake by spreading out in response to the current heterogeneity of each feeding ground.

The sum of intake of prey species per individual *i* in zone *j* is expressed by integrating the expected intake of prey species at location *x* over the search range:

$$Q_i^j = \int_{D_i^j} t_i^j(x) n_{i,prey}^j(x) dx , \tag{2}$$

where $n_{i,prey}^j(x)$ is the density of individual *i*'s prey species at location *x* in zone *j* and D_i^j

is individual *i*'s search range in zone *j*, that is, $D_3^H = [X, Z^H]$ and $D_3^A = D_2^A =$ $[Z^H, Z^A]$.[12] The individual carnivore (*i* = 3) eats herbivores (*i* = 2) in the animal zone and human-origin food such as garbage in the human zone. So, $Q_3 = Q_3^A + Q_3^H$. $n_{3,prey}^A(x) = t_2^A(x)N_2$, where $t_2^A(x)N_2$ is the density of harbivores at location *x*. $n_{3,prey}^H(x) = \rho_3(t_3^H(x))n_h(x)$, where $n_h(x)$ is human population density and $\rho_3(t_3^H(x))$ expresses the availability of garbage.[13] The representative herbivore (*i* = 2) searches the animal zone for plants. So, $Q_2 = Q_2^A$ and $n_{2,prey}^A(x) = \rho_2(t_2^A(x))n_1(x)$, where $n_1(x)$ is the density of plants and $\rho_2(t_2^A(x))$ expresses the availability of plants.

Similarly, $M_i = \sum_j M_i^j$, where M_i^j is the number of predators that individual *i* may encounter in zone *j*. M_i^j is expressed by integrating $t_i^j(x)$ multiplied by the density of predators at location *x* $n_{i,predator}^j(x)$ over its search range:

$$M_i^j = \int_{D_i^j} t_i^j(x) n_{i,predator}^j(x) dx. \tag{3}$$

In the human zone, the carnivore may encounter humans and might be killed by them. So, $M_3 = M_3^H$ and $n_{3,predator}^H(x) = k(x)n_h(x)$, where $k(x)$ is a parameter that explains humans' chance of encountering carnivores.[14] The herbivores may encounter carnivores in the animal zone. So, $M_2 = M_2^A$ and $n_{2,predator}^A(x) = t_3^A(x)N_3$, which is the density of carnivores at location *x*. The time constraint for individual *i* is

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[12] We do not have to divide $t_i^j(x)$ by N_i because $t_i^j(x)$ is the individual *i*'s time density and $t_i^j(x)n_{i,prey}^j(x)$ is the food consumption per individual *i* at location *x*.

[13] We assume that $\rho_i(\cdot) > 0$ in $t_i^j(x) \in [0,\ 1]$ to avoid a case in which individual *i*'s intake of food is negative and that $\rho'_i(\cdot) < 0$, and $\rho''_i(\cdot) < 0$, implying that the more food individual *i* eats, the more difficult it is to find new food at location *x*. For example, the availability of foof waste in garbage to carnivores in the city depends on the garbage cans, and the availability of plants to herbivores in the habitat depends on height of trees and topological situation. A carnivore eats food waste in garbage at one location. Then, if the carnivore wants more food waste at the same location, it tries to find the new trash container and break it open. However, in order to obtain more food, it is easier to move to a different location and find new garbage than to stay and search for food at the same location. In this way, function $\rho_i(\cdot)$ is exogenously given and is used for the situation where animals have foods that are not moving objects. It is not applicable to carnivores' food, "herbivores", because herbivores can avoid encountering predators by themselves, and thus $n_{3,prey}^A(x) = t_2^A(x)N_2$ is enough to express such a situation.

[14] The value of the parameter increases with *x* (i.e. $k'(x) < 0$). It implies that the closer to the CBD they are, the more chances they have of meeting humans.

$$\bar{T} = \sum_j \int_{D_i^j} t_i^j(x)dx, \tag{4}$$

where $\bar{T}$ is one year, $\int_{D_i^j} t_i^j(x)dx$ is the time spent searching in zone *j*.[15]

Individual *i* maximizes function (1) by controlling Q_i^j, M_i^j, $t_i^j(x)$ subject to (2)–(4), taking the prey and predator's densities as given. In addition to these variables, the boundary of search range *X* is also endogenous in the case of carnivores. The Lagrangian function for the maximization problem of each animal and its first order conditions are found in Appendix A.[16]

2.3 Household behavior

Each household resides at location $x \in [0, Z^H]$. They commute to the CBD where all firms are located and earn exogenous wage *w*. As carnivores search the human zone for food, households may encounter carnivores. The number of carnivores that each household may encounter is denoted by $M_h(x)$, which implies the risk of being injured by carnivores:

$$M_h(x) = t_3^H(x)N_3. \tag{5}$$

To reduce the time density of carnivores, households try to put more risk to the carnivores directly by using the risk-increase-measure such as guns or alert or monitoring systems that can immediately repel or exterminate carnivores. Thus, the longer the carnivores spend at a given location, the more risk of being killed by humans the carnivore faces. The degree of risk the carnivore faces is denoted by $\beta_3(x)$, which indicates the probability of extermination per unit time the carnivore spends at location *x* within the city.

The household spends money on commuting, housing, composite goods, and preparing the risk-increase-measure. By installing the risk-increase-measure, the household have a

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[15] In previous papers (e.g. Eichner and Pethig, 2009), the animal is assumed to trade its own biomass in a virtual competitive market. We do not use this idea because the time constraint is more natural for ecosystems.

[16] This model considers the spatial dimension and we want to solve the spatial path of time density of both animals. In that case, the effect of increasing the time density at each location on social welfare or net offspring can be different across locations (that is, the Lagrange multiplier of the time density can be different across locations). So, we have to use the optimal control theory to solve the model. For example, see Brueckner (2007). By using the theory, we can find that the Lagrange multipliers are constant across locations. In the paper, we omit the procedure of the theory for simplicity.

sense of security when encountering carnivores at the home. The household's utility increases with the quality of ecosystem services. The quality is determined by the population of all species according to the function $e = E(\mathbf{N})$. We assume that the partial derivative of e with respect to **N** is positive but diminishing marginal benefits. The utility function is

$$v(x) = u\big(C(x), f(x)\big) - g_1(M_h(x)) + g_2(\beta_3(x)) + E(\mathbf{N}), \tag{6}$$

where $C(x)$ is the consumption of numeraire composite goods, $f(x)$ is the housing lot size, $g_1(M_h(x))$ is the disutility from a fear of encountering carnivores, and $g_2(\beta_3(x))$ is the utility gained from a sense of security by installing the risk-increase-measure for carnivores. We assume that marginal utilities with respect to $C(x), f(x)$, and $\beta_3(x)$ are positive, and diminishing marginal utility with respect to them. The income constraint is given by

$$w + \Omega = C(x) + r(x)f(x) + \tau(x) + p_3\beta_3(x), \tag{7}$$

where Ω is the per-resident revenue from land ownership, $r(x)$ is the land rent at location x, $\tau(x)$ is the commuting cost depending on distance from the CBD, and p_3 is the cost of preparing the risk-increase-measure. Ω should equal or less than per-capita land rent revenue.[17]

$$\bar{N}_h\Omega \le \int_0^{Z^H} [r(x) - r_H]dx, \tag{8}$$

where r_H is the cost of housing land development, that is, the cost of land conversion from natural habitats to residential areas.

Endogenous and exogenous variables for each agent are summarized in Table 1.

[Table 1 here]

2.4 Market clearing conditions and definition

The populations of carnivores and herbivores are determined by predator-prey interactions.

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[17] Inequality implies that residents can refuse the receipt of the land revenue. However, as long as per-capita land revenue has a positive utility, equality holds in (8). This inequality is useful to derive the sign of the Lagrange multiplier for this constraint, simply using the Kuhn-Tucker condition. The same treatment with the same objective is shown in Kono and Kawaguchi (2016) and Kono and Joshi (2017).

Since b_i is individual i's offspring produced in one year, the dynamics of population change is described by the following differential equations:

$$\frac{dN_i}{dT} = N_i b_i, \qquad i = 2,\ 3 \tag{9}$$

where T is time. The current paper assumes that neither species is extinct. N_3 and N_2 in a steady state are straightforwardly derived from (9) with $dN_3/dt = dN_2/dt = 0$ and (1):

$$N_3 = \frac{\alpha_2 Q_2 - m_2}{\beta_2 P}, \tag{10}$$

$$N_2 = \frac{\beta_3 M_3 - \alpha_3 Q_3^H + m_3}{\alpha_3 P}, \tag{11}$$

where

$$P = \int_{Z^H}^{Z^A} t_2^A(x) t_3^A(x) dx, \tag{12}$$

which implies the probability of an encounter between a carnivore and a herbivore.[18]

In the steady state, the plant density at location $x \in [Z^H,\ Z^A]$ is

$$n_1(x) = F(x) - \beta_1 t_2^A(x) N_2, \tag{13}$$

where $F(x)$ is the plant density that grows naturally before being eaten by herbivores and β_1 is a parameter indicating the herbivore's intake of plants per unit of time. We assume that $F(x)$ is continuous on $x \in [Z^H,\ Z^A]$. The total number of plants is obtained by integrating the plant density over the habitat:

$$\int_{Z^H}^{Z^A} n_1(x) dx = N_1. \tag{14}$$

Next, (15) implies that household's utility will be common across locations because households can migrate for free:

$$v(x) = V,\ \forall x \in [0,\ Z^H]. \tag{15}$$

Households at location x consume $f(x)$ area of lot; therefore, total lot consumed at each location equals the unit land area supplied:

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[18] Since N_2 and N_3 are independent of x, $Q_3^A = PN_2$ and $M_2 = PN_3$.

$$n_h(x) f(x) = 1. \tag{16}$$

(17) indicates that the total city population $\bar{N}_h$ equals households' population:

$$\bar{N}_h = \int_0^{Z^H} n_h(x) dx. \tag{17}$$

At the equilibrium, the urban boundary is determined at which the land rent equals the cost of housing development:

$$r(Z^H) = r_H.^{19} \tag{18}$$

In this setting, an allocation will mean a collection of continuous functions ($f(x)$, $n_h(x)$, $r(x)$, $M_h(x)$, $t_3^H(x)$, $\beta_3(x)$) on [0, Z^H], continuous functions ($t_3^A(x)$, $t_2^A(x)$) on [Z^H, Z^A], and (endogenous) variables (Q_3^H, Q_3^A, M_3, M_2, Q_2, N_3, N_2, N_1, V, Ω, Z^H).

3. Laissez-faire equilibrium

3.1 Equilibrium conditions

At the equilibrium, human population density is determined as a result of competition for housing location among residents. $r(x)$ equals the maximum bid rent as a result of competition among residents. Mathematically, such bid-rent behavior is formalized as

$$\max_{C(x), f(x), \beta_3(x)} r(x) = \frac{w + \Omega - \tau(x) - C(x) - p_3 \beta_3(x)}{f(x)} \quad \text{s.t. (6)} \tag{19}$$

Solving (6) for $C(x)$ yields $C(G(x) - g_2(\beta_3(x)), f(x))$, where $G(x) = v(x) + g_1(M_h(x)) - E(\mathbf{N})$. We substitute this into the objective function. Then, the first order condition with respect to $\beta_3(x)$ is

$$\frac{\partial C}{\partial \left(G(x) - g_2(\beta_3(x)) \right)} g_2'(\beta_3(x)) = p_3. \tag{20}$$

Assuming that the size of the risk to carnivores from the households does not affect the choice of housing lot size $f(x)$, the maximization problem yields

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[19] This model does not consider the agricultural area, so that the land rent at the city boundary equals the cost of housing development in the market equilibrium.

$$f(x) = f\left(G(x), I(x)\right), \tag{21}$$

where $I(x) = w + \Omega - \tau(x)$.

Next, we show the time density of animals at the equilibrium. From Appendix A, the equilibrium condition with respect to $t_3^H(x)$ at any $x \in [X, Z^H]$ and that with respect to $t_3^A(x)$ at any $x \in [Z^H, Z^A]$, taking other species' behavior $n_h(x)$ and $t_2^A(x)$ as given, are

$$\frac{\partial b_3}{\partial t_3^H(x)} \equiv \alpha_3 \rho_3(t_3^H(x)) n_h(x) + \alpha_3 \rho_3'(t_3^H(x)) n_h(x) - \beta_3(x) k(x) n_h(x) - \lambda_3 = 0, \tag{22}$$

$$\frac{\partial b_3}{\partial t_3^A(x)} \equiv \alpha_3 t_2^A(x) N_2 - \lambda_3 = 0. \tag{23}$$

The equilibrium condition with respect to $t_2^A(x)$ at any $x \in [Z^H, Z^A]$, taking other species' time density $t_3^A(x)$ as given, is

$$\frac{\partial b_2}{\partial t_2^A(x)} \equiv \alpha_2 n_1(x) \rho_2(t_2^A(x)) + \alpha_2 n_1(x) t_2^A(x) \rho_2'(t_2^A(x)) - \beta_2 t_3^A(x) N_3 - \lambda_2 = 0. \tag{24}$$

(20)–(24) indicates that the equilibrium land use of humans and animals in both urban area and natural habitat. (22)–(24) equations intuitively reflect the animal behavior at each location. For example, in (22), it reflects that when the carnivore stays longer at one location, it could obtain more foods (the first term), but it could decrease marginal returns of foods (the second term) and increase the number of humans the carnivores may encounter, that is, face more risk of extermination (the third term) and lose the chance to obtain foods at the other locations (the fourth term).

3.2 Existence and uniqueness of equilibrium allocation

This subsection shows that there exists a unique equilibrium allocation that satisfies the market clearing conditions and definitions defined in Section 2. We first show that there exists a unique equilibrium land use where carnivores enter the city and interact with residents. All other endogenous variables are uniquely determined by the unique equilibrium land use, even if any equilibrium land use is determined, using market cleaning conditions and definitions. This conclusion is stated at the end of this subsection as Theorem 1.

We have three steps to prove the uniqueness of equilibrium land use that satisfies equilibrium conditions (20)–(24). First, we show that given the equilibrium utility level V, and the land use at all other locations, there is a unique equilibrium of housing size and the carnivore's time density at any x in the city. Second, we show that given V, there is a unique equilibrium path of housing size, the carnivore's time density on $[0, Z^H]$ and there is a unique equilibrium path of both the carnivore's and the herbivore's time density in the habitat. Finally, we show that V is uniquely determined. Proofs of Lemmas can be found in Appendix B.

Under the assumption that the choice of $\beta_3(x)$ does not depend on the choice of $f(x)$, there exists one inner solution $\beta_3(x)$ satisfying (20) at any x in the city. Next, substituting the obtained $\beta_3(x)$ into the system of (21) and (22), we can show the uniqueness of housing lot size and the carnivore's time density at any x in the city.

Lemma 1. *Housing lot size which is the residents' best response function of the carnivores' time density,* $f(x) = R_{res}(t_3^H(x))$, *monotonically increases with* $t_3^H(x)$ *on* [0, 1]. *Carnivores' time density which is the carnivores' best response function of the housing lot size,* $t_3^H(x) = R_{car}(f(x))$, *monotonically decreases with* $f(x)$.

We illustrate the best response functions of carnivores and residents as Figure 2. At any location $x \in [X, Z^H]$, there exists one inner solution except for the following two kinds of corner solutions: (i) Point A is smaller than point B; (ii) point C is lower than point D.[20]

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[20] Case (i) may occur if humans are eager to exterminate the harmful carnivores and/or the carnivores' availability of food is quite low because the carnivore do not want to stay even if the human population density

Each solution is uniquely determined.

[Figure 2 here]

Next, given the utility level *V*, we show $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ are continuous in $[X, Z^H]$. To prove this, we apply the implicit function theorem to a system of the equilibrium conditions with respect to $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ for all $x \in [X, Z^H]$. We also investigate whether the equilibrium path of both carnivore's and herbivore's time density, $t_3^A(x)$ and $t_2^A(x)$, are continuous in the habitat $[Z^H, Z^A]$. We obtain Lemma 2.

Lemma 2. *Given the utility level V, there is a unique equilibrium path of* $f(x)$, $t_3^H(x)$, *and* $\beta_3(x)$ *in* $[X, Z^H]$ *and* $t_3^A(x)$ *and* $t_2^A(x)$ *in* $[Z^H, Z^A]$ *such that* (20)–(24) *are satisfied.*

Finally, we have to investigate the uniqueness of the equilibrium utility level *V*. *V* is determined such that (17), $\overline{N}_h = \int_0^{Z^H(V)} n_h(V, x)dx$, is satisfied. To show the uniqueness of *V*, it is sufficient to prove that the RHS of (17), $\int_0^{Z^H(V)} n_h(V, x)dx$, monotonically changes in *V*. Let $\Psi(V)$ be the RHS of (17), $\int_0^{Z^H(V)} n_h(V, x)dx$. We can obtain the following.

Lemma 3. $\Psi(V)$ *monotonically decreases with V.*

Hence, as shown in Lemmas 1-3, we can obtain that there exists the equilibrium land use. In addition, the unique equilibrium paths of $f(x)$, $t_3^H(x)$, $t_3^A(x)$, $t_2^A(x)$, and $\beta_3(x)$ uniquely determine all other endogenous variables using associated market cleaning conditions and definitions.[21] We sum up the above analysis in Theorem 1.

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becomes larger. Case (ii) may occur when wildlife are less dangerous to humans because the housing size is not affected by the time density of carnivores.

[21] Lucus and Rossi-Hansberg (2002) also demonstrate that a uniquely determined wage path determines associated endogenous variables uniquely.

Theorem 1. *There is an allocation where all endogenous variables are determined such that* (2)–(8), (10)–(18), *and* (20)–(24) *are satisfied. Any such allocation is uniquely determined by the unique equilibrium land use* ($f(x)$, $t_3^H(x)$, $t_3^A(x)$, $t_2^A(x)$, $\beta_3(x)$).

3.3 Effect of the encroachment of wildlife into cities on equilibrium land use

From the above analysis, we can obtain the following property about how equilibrium land use of humans and animals ($f(x)$, $\beta_3(x)$, $t_3^H(x)$, $t_3^A(x)$, $t_2^A(x)$) changes with location x.

Property 1

(i) In the residential area, the time density of carnivores $t_3^H(x)$ first continuously increases, then it decreases as it approaches the CBD, and finally it reaches zero.

(ii) Human population density $n_h(x)$ continuously decreases with x (i.e. Lot size $f(x)$ continuously increases with x). The decrease in human population density with respect to x in the area with carnivores is larger than that in the area without carnivores.

(iii) The degree of the risk-increase measure that each household sets for carnivores, $\beta_3(x)$, is independent of the location.

(iv) The time density of herbivores $t_2^A(x)$ is spatially uniform across the habitat regardless of whether the plant density is spatially uniform or not.

(v) In the habitat, the time density of carnivores $t_3^A(x)$ is proportional to the plant density that grows naturally $F(x)$.

First, we focus on Property (i)–(iii). Applying the implicit function theorem to the system of equilibrium conditions with respect to $f(x)$, $t_3^H(x)$, and $\beta_3(x)$, given in Appendix B, we can obtain $\frac{df(x)}{dx} > 0$, $\frac{dt_3^H(x)}{dx} \gtreqless 0$, and $\frac{d\beta_3(x)}{dx} = 0$ at any $x \in [X, Z^H]$. $\frac{df(x)}{dx} > 0$ holds because the commuting cost increases with x. In contrast, $t_3^H(x)$ can either increase or decrease. As carnivores move towards the CBD, both human population density, $n_h(x)$, and the probability of encountering residents, $k(x)$, increase. When the amount of increase in $n_h(x)$ is larger (respectively, smaller) than that in $k(x)$, $t_3^H(x)$ increases with x because carnivores can obtain more (respectively, less) food with less (respectively, more) risk of encountering residents by moving towards the CBD. Thus the welfare impacts on residents differs in size across space. Reflecting the residents' fear of encountering carnivores, the land rent at location with carnivores is lower than that at locations without carnivores.

Next, we focus on Property (iv)–(v). Combining (23) and (4) at which i = 2 yields $t_2^A(x) = \overline{T} / (Z^A - Z^H)$; thus we can obtain Property (iv). Combining $t_2^A(x) = \overline{T} / (Z^A - Z^H)$ with (13) and (24) yields Property (v). The reason why we obtain Property (iv) and (v) is given as follows. Suppose an equilibrium where $t_3^A(x)$ is smaller in places with high $F(x)$. Then, herbivores spend more time there because they are able to eat more plants with less risk of encountering carnivores. Hence, there is an incentive for carnivores to deviate from this equilibrium. As a result, carnivores choose higher $t_3^A(x)$ in place with high $F(x)$ so that herbivores are evenly distributed across the habitat. If $F(x)$ is spatially uniform across the habitat, then both $t_3^A(x)$ and $t_2^A(x)$ are uniform because herbivores can eat the same amount of plants everywhere, and carnivores do not have to spend more time in a specific location.

In closing this section, we illustrate one possible example of the equilibrium land use of humans and an ecosystem on [0, Z^A] as Figure 3 under the case where plant densities that grows naturally linearly increases with x.

[Figure 3 here]

4. First-best optimum

The purpose of this section is to understand how the equilibrium deviates from a social optimum due to two externalities: the absence of markets in the ecosystem and human–wildlife conflicts. The first best or practically unconstrained optimum requires complete regulation of time density of animals at every location in both city and habitat. We first formally define the social welfare maximization problem. Then, we explore the sign of the marginal social value or shadow price of carnivore S_3, herbivore S_2, and plant at location x $s_1(x)$ because it is important to determine how each variable deviates from the social optimum. In addition, we clarify how much more knowledge is needed to measure the value of each species in the location-dependent setting than in the location-independent setting as in Eichner and Pethig (2009). Proof of the following propositions are found in Appendix D.

4.1 Social welfare function

The social welfare function W is composed of the total utility of households:[22]

$$W = \bar{N}_h V . \tag{25}$$

A social planner maximizes the social welfare by controlling all endogenous variables including variables related with animal behavior. We define this as the first best optimum.

$$\max_{C(x), f(x), r(x), n_h(x), \Omega, V, Q_3^H, M_3, P, t_3^A(x), t_3^H(x), t_2^A(x), n_1(x), Z^H, X, \mathbf{N}} \bar{N}_h V \quad \text{s.t. (2)–(8), and (10)–(17).}$$

We obtain the social optimal solution using the following Lagrangian function:

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[22] We also analyzed the case where people are concerned about animal welfare in terms of the awareness of animal protection. There are some animal protection organizations on a worldwide scale such as the International Fund for Animal Welfare (IFAW). In this case we should consider the animals' utility. The following utility function of individual animal in species i is assumed: $u_i = U_i(Q_i, M_i)$. The social welfare is composed of total utility of households, carnivores and herbivores: $W = \bar{N}_h V + \beta N_3 u_3 + \gamma N_2 u_2$. Alternatively, this can be regarded as an altruistic utility function of humans by regarding $\beta \geq 0$ and $\gamma \geq 0$ as weights.

$$
\begin{aligned}
L = {} & \frac{\bar{N}_h V}{\mu} \\
& + \int_0^{Z^H} \frac{\lambda_h(x)}{f(x)} [w + \Omega - C(x) - f(x)r(x) - p_3\beta_3(x) - \tau(x)]dx + \int_0^{Z^H} \theta(x)\left[\frac{1}{f(x)} - n_h(x)\right]dx \\
& + \left\{\int_0^{Z^H} [r(x) - r_H]dx - \bar{N}_h\Omega\right\} + \int_0^{Z^H} \sigma(x)\left[M_h(x) - t_3{}^H(x)N_3\right]dx + \sum_{i=2}^{3} \lambda_i^O[\bar{T} - \sum_j \int_{D_i^j} t_i^j(x)dx] \\
& + \int_0^{Z^H} \eta(x)[U_h\left(C(x), f(x)\right) - g_1\left(M_h(x)\right) + g_2\left(\beta_3(x)\right) + E(\mathbf{N}) - V]dx + S_1[\int_{Z^H}^{Z^A} n_1(x)dx - N_1] \\
& + \int_{Z^H}^{Z^A} s_1(x)[F(x) - \beta_1 t_2^A(x)N_2 - n_1(x)]dx + S_3\left[\frac{\alpha_2\int_{Z^H}^{Z^A} t_2^A(x)\rho_2(t_2^A(x))n_1(x)dx - m_2}{\beta_2\int_{Z^H}^{Z^A} t_2^A(x)t_3^A(x)dx} - N_3\right] \\
& + S_2\left[\frac{\int_X^{Z^H} \beta_3(x)t_3^H(x)k(x)n_h(x)dx - \alpha_3\int_X^{Z^H} t_3^H(x)\rho_3(t_3^H(x))n_h(x)dx + m_3}{\alpha_3\int_{Z^H}^{Z^A} t_3^A(x)t_2^A(x)dx} - N_2\right], \qquad (26)
\end{aligned}
$$

where $\lambda_h(x)$, $\theta(x)$, μ, $\sigma(x)$, $\eta(x)$, $s_1(x)$, λ_3^O, λ_2^O, and S_i $i \in \{1,2,3\}$ are shadow prices.[23] The boundary condition is $t_3^H(X) = 0$. We divide the original Lagrangian function by the Lagrangian multiplier with respect to (8), μ, to represent it in monetary terms. The first order conditions are found in Appendix C.

4.2 Marginal social value of species

We can obtain Proposition 1 from the Lagrange multipliers of Eq. (26).

Proposition 1. *The marginal social value of carnivores, herbivores, and plants at location x, or Lagrange multipliers S_3, S_2, and $s_1(x)$ are given by, respectively,*

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[23] In the literature of urban economics, the optimal control theory has been applied to distance dimension instead of time dimension to obtain optimal solutions at each location (e.g. Pines and Sadka 1985; Arnot, Pines and Sadka 1986). This Lagrangian includes distance from the CBD *x,* and it has three heterogenous regions: residential area without carnivores' entering, residential area with carnivores' entering, and natural habitat. The boundary conditions between heterogenous regions are endogenously determined. A similar type of Lagrangian is employed in Kono and Kawaguchi (2016) to explore transport policies in a city with heterogenous regions and in Kono and Joshi (2017) to explore land use regulation in multiple heterogenous zones.

$$S_3 = \underbrace{\int_0^{Z^H} n_h(x)\frac{\partial E/\partial N_3}{\partial U_h/\partial C}dx}_{\text{[1] Ecosystem services of carnivores}} - \underbrace{\int_0^{Z^H} n_h(x)\frac{\partial g/\partial M_h}{\partial U_h/\partial C}t_3^H(x)dx}_{\text{[2] Humans' aggregate disutility of carnivores}} , \tag{27}$$

$$S_2 = \underbrace{\int_0^{Z^H} n_h(x)\frac{\partial E/\partial N_2}{\partial U_h/\partial C}dx}_{\text{[3]Ecosystem services of herbivores}} + \underbrace{\beta_1\int_{Z^H}^{Z^A} s_1(x)t_2^A(x)dx}_{\substack{\text{[4] Benefit or cost of a decrease in plants}\\ \text{due to being hervested by a herbivore}}} , \tag{28}$$

$$s_1(x) = \underbrace{\int_0^{Z^H} n_h(x)\frac{\partial E/\partial N_1}{\partial U_h/\partial C}dx}_{\text{[5] Ecosystem services of plants}} + \underbrace{S_3\frac{\alpha_2}{\beta_2 P}t_2^A(x)\rho_2(t_2^A(x))}_{\text{[6] Benefit or cost of an increase in carnivores}} \quad \forall x \in [Z^H, Z^A]. \tag{29}$$

Considering the location dependent externalities caused by the encroachment of carnivores into the urban areas, some novel components are observed in the value of species: i) the humans' aggregate marginal disutility with respect to the risk of being killed by carnivores, which is represented by term [2]; ii) the social benefits or damages of changes in the steady-state population of the other species, which are represented by terms [4] and [5].[24] Terms [1], [3], and [5] represent the humans' aggregate marginal benefits of enhancing the provision of ecosystem services by a marginal increase in each species.

These equations imply that the first terms on the right hand side are positive but the second terms can be either positive or negative. Thus, these animals and plants are biologically important, but their shadow prices can be negative. In addition, the sign of one species depends on the sign of other species through the food-chain. It is intuitive that S_3 can be negative because of the humans' aggregate disutility of the entrance of carnivores, and S_2 can be negative because of decrease in the number of plants. However, it is not so intuitive that $s_1(x)$ can be also negative because of the increase in the number of carnivores that can

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[24] In the current paper the value of species *i*'s biomass consumed by humans and the opportunity cost of urban land use, which are observed in Eichner and Pethig (2009), do not appear in (27)–(29). The former is regarded as a part of ecosystem services. Thus this component corresponds with term [1], [3] or [5]. The latter is not observed because the current paper does not consider habitat resources such as the territory of animals.

give the risk to humans.

5. Distance-dependent market failures

This section is devoted to comparing the equilibrium with the first best optimum in terms of time density of animals, $t_3^H(x)$, $t_3^A(x)$, and $t_2^A(x)$, human population density $n_h(x)$, and city size Z^H. We begin with the time density of animals.

5.1 The time density of animals

The optimal condition with respect to the time density of carnivores in the city, $t_3^H(x)$, is

$$-\frac{S_2}{\alpha_3 P}\left[\frac{\partial b_3}{\partial t_3^H(x)}\right] = \underbrace{n_h(x)\frac{\partial g/\partial M_h}{\partial U_h/\partial C}N_3}_{\text{[7] Humans' disutility of carnivores}} \quad \underbrace{-S_3\frac{N_3}{P}t_2^A(x)}_{\text{[8] Benefit or cost of an increase in carnivores}} \quad , \tag{30}$$

where $\frac{\partial b_3}{\partial t_3^H(x)} = 0$ at the equilibrium as shown in (22). The LHS indicates the benefit or cost of changes in herbivores when the time density of carnivores marginally increases at $x \in [X,\, Z^H]$ within the city. The first term on the RHS of (30) represents the humans' aggregate marginal disutility of encountering carnivores. Since the carnivores stay longer in the urban area, the herbivore's risk of encountering carnivores decreases. From (10), this leads to increasing the steady state population of carnivores, which is represented by the second term on the RHS of (30). Since S_3 and S_2 can be either positive or negative as shown in Proposition 1, we can obtain the following proposition by comparing the equilibrium condition (22) with the optimal condition (30).

Proposition 2. *The optimal time density of carnivores within the city,* $t_3^H(x)$, *at any* $x \in [X,\, Z^H]$ *can be either larger or smaller than the equilibrium* $t_3^H(x)$. *If the increase in humans' disutility associated with the risk of encountering carnivores is larger than the increase in the utility associated with the ecosystem services when the steady state* *population of carnivores increases* (*that is*, S_3 *is negative*) *and if* S_2 *is positive (negative), then the optimal* $t_3^H(x)$ *is larger (smaller) than the equilibrium* $t_3^H(x)$.

This result may appear counter-intuitive because Proposition 3 says that even if the humans' disutility of encountering carnivores is larger, when the value of herbivores is positive, the carnivore should spend more time in the city at optimum. This result tells us that when carnivores encroach into a city, we should not only try to drive carnivores out of the city, but also simultaneously take account of the effects of a change in the number of herbivores on the social welfare. The intuitive reason for this counter-intuitive result is as follows. When S_3 is negative, an increase in the number of carnivores indicates a social cost; so, the RHS is positive. To satisfy (30), the LHS should be positive, that is, a marginal social benefit. When S_2 is positive, an increase in the number of herbivores is socially beneficial. If carnivores stay longer in the city, they can eat more garbage, but face a higher risk of mortality. A longer $t_3^H(x)$ than the equilibrium increases the carnivore's risk, and the increased risk is larger than the benefit of eating garbage. As shown in (11), this situation leads to an increase in the steady state population of herbivores, which is socially beneficial.

Next, we focus on the time density of animals in the habitat.

Proposition 3. *The optimal time density of herbivores is spatially uniform across the habitat:*

$$t_2^A(x) = \frac{\bar{T}_2}{Z^A - Z^H}. \tag{31}$$

This assertion says that even at the optimum as well as in the market equilibrium, herbivores spend time spatially uniformly in the natutal habitat. But the optimal time density is different from that at the equilibrium because city sizes are different so that $Z^A - Z^H$ is different.

Next, we focus on the carnivore's one in the habitat $t_3^A(x)$. The optimal condition is

$$\frac{S_3}{\beta_2}\left[\frac{\partial b_2}{\partial t_2^A(x)}\right] = \underbrace{S_2N_2[t_3^A(x)}_{\substack{\text{[9] Benefit or cost of} \\ \text{decreasing herbivores}}} - \underbrace{\frac{\int_{Z^H}^{Z^A} t_3^A(x)dx}{Z^A - Z^H}}_{\substack{\text{[10] Benefit or cost of} \\ \text{increasing herbivores}}}], \tag{32}$$

where $\frac{\partial b_2}{\partial t_2^A(x)} = 0$ at the equilibrium as shown in (24). The LHS indicates the benefit or cost of changes in the number of carnivores when the time density of herbivores marginally increases at $x \in [Z^H, Z^A]$ within the habitat. The interpretation of the RHS is as follows. $\int_{Z^H}^{Z^A} t_3^A(x)dx \Big/ (Z^A - Z^H)$ implies the average time density of carnivores in the habitat. When increasing $t_2^A(x)$ at any $x \in [Z^H, Z^A]$, the herbivore's probability of meeting carnivores increases, which causes a reduction in the number of herbivores. This is represented by term [9]. At the same time, the herbivore's time density in any other locations decreases. So, the herbivore's probability of meeting carnivores decreases at that locations, which leads to an increase in herbivores. This is represented by term [10].

Using the fact that the herbivore's optimal time density is equal throughout the habitat, we can obtain that the optimal $t_3^A(x)$ varies (is constant) among locations when the density of wild plants, $F(a(x))$, varies (is constant) among locations. Comparing the equilibrium condition (24) with the optimal condition (32), while keeping this relation in mind, we can obtain how the equilibrium $t_3^A(x)$ deviates from the optimum at any location.

Proposition 4 (optimal time density of carnivores (*i* =3) in natural habitats).

(i) *When the density of wild plants,* $F(x)$, *equal among locations, the optimum* $t_3^A(x)$ *corresponds with the equilibrium* $t_3^A(x)$ *at any* $x \in [Z^H, Z^A]$.

(ii) *When the density of wild plants,* $F(x)$, *varies among location, the optimal* $t_3^A(x)$ *at any* $x \in [Z^H, Z^A]$ *can be either larger or smaller than the equilibrium* $t_3^A(x)$ *except for the location where the optimum* $t_3^A(x)$ *is equal to its average.*

This assertion says that predator-prey interactions (that is, the probability of encountering between prey and predator species depending on the time density) are inefficient at each location unless the plant density is uniformly distributed. In view of some observation-based studies conducted by ecological researchers (e.g., Yoda et al., 2012; Pyke, 2015) reporting that animals optimize their food intake by spreading out in response to the current heterogeneity of each feeding ground, our results suggests that the current situation is inefficient.

To clearly understand result (ii), suppose that $F(x)$ linearly increases with x, and that $S_3 < 0$ and $S_2 > 0$. Then, if $F(x)$ is larger (smaller) than its average, then the sign of the RHS of (32) is positive. Thus, the optimal $t_3^A(x)$ is larger (smaller) than the equilibrium $t_3^A(x)$. This means that in places with higher $F(x)$, the equilibrium herbivore's risk of encountering predators is smaller than the optimum level. When increasing $t_3^A(x)$ beyond the equilibrium level, in the steady state, there is a decrease in not only the number of herbivores but also the number of carnivores, resulting from the decrease in their prey species. To achieve the optimum, $t_3^A(x)$ is increased so that the social marginal benefit of a decline in carnivores equals the social marginal cost of a decline in the number of herbivores. In places with lower $F(x)$, vice versa.

5.2 Human population density

According to (16), $n_h(x)$ is the reciprocal of housing lot size $f(x)$. The social optimum condition with respect to $f(x)$ at any $x \in [X,\ Z^H]$ is

$$\frac{\partial U_h}{\partial f(x)} - \frac{\partial U_h}{\partial C(x)} r(x) = \underbrace{-S_2 \frac{n_h(x) t_3^H(x)}{\alpha_3 P} \alpha_3 \rho_3(t_3^H(x))}_{\text{[11] Benefit or cost of increasing herbivores}} + \underbrace{S_2 \frac{n_h(x) t_3^H(x)}{\alpha_3 P} \beta_3 k(x)}_{\text{[12] Benefit or cost of decreasing herbivores}} \quad . \quad (33)$$

Since the RHS should equal zero at the equilibrium, we can obtain the following result.

Proposition 5. *If* $\beta_3(x)k(x) - \alpha_3\rho_3(t_3^H(x)) > 0\ (< 0)$ *then the optimal human population density* $n_h(x)$ *is larger (smaller) than the market equilibrium at any* $x \in [X,\ Z^H]$.

The interpretation of (33) is given as follows. When the human population density decreases, the carnivores will feed on less food. So, from (11), the population of herbivores will increase. The first term in the RHS of (33) represents the externality of an increase in the population of herbivores. On the other hand, the carnivores face less risk of being killed by humans. From (11), this makes the number of herbivores decrease. The second term in the RHS of (33) represents the externality of decreasing the population of herbivores.

In Proposition 5, $\beta_3(x)k(x)$ reflects the humans' response to harmful carnivores: if the response is large, they try to exterminate them even if the harmful carnivores stay in the urban areas for a short time. $\rho_3(t_3^H(x))$ indicates the carnivores' availability of food. The intuition behind this assertion is that if humans are eager to exterminate the harmful carnivores and/or the carnivores' availability of food is quite low, then the optimal human density is larger than the equilibrium.

5.3 Risk-increase measures against carnivores

The social optimum condition with respect to $\beta_3(x)$ at any $x \in [X,\ Z^H]$ is

$$\frac{\partial g_2 / \partial \beta_3(x)}{\partial U_h / \partial C} - p_3 = -\underbrace{S_2 \frac{t_3^H(x)k(x)}{\alpha_3 P}}_{\substack{\text{[13]Benefit or cost of} \\ \text{increasing herbivores}}} \tag{34}$$

An interpretation of (34) is as follows. When giving more risk to carnivores such as preparing more sensitive alert system, then the carnivore's net offspring decreases. From (11), this leads to an increase in the number of herbivores in the steady state equilibrium. However, the number of carnivores does not increase at equilibrium because carnivores can eat more heribivores in the habitat instead of eating human-related sources of foods.

The left hand side of (34) equaling zero is the equilibrium condition, and the sign of S_2 can be positive or negative from Proposition 1. Thus, we can obtain the following proposition.

Proposition 6. *The first-best optimal probability of extermination per time the carnivore spends within the city* $\beta_3(x)$ *is larger or smaller than the equilibrium one at any* $x \in [X, Z^H]$.

5.4 City size

The equilibrium condition with respect to Z^H is given by (18). However, this condition does not hold in the social optimum because of the externality of changes in the number of animals and plants. In addition, S_2 and S_3 can be either positive or negative depending on the situation, as in Proposition 1.

Proposition 7. *The first best optimal city size can be larger or smaller than the market equilibrium city size.*

6. Numerical examples

The purpose of numerical simulations is to understand how human–ecosystem interactions, such as the degree of human's disutility to the encroachment of carnivores and the value of ecosystem services, would affect the first-best optimal city size.

Suppose the total length of an area consisting of a city plus a natural habitat is 60 km with a width of 1 km. We divide the city into four discrete areas and the natural habitat into five discrete areas. The total number of humans is normalized as $\bar{N}_h = 20$ (thousands of humans).[25] We specify the utility function as $v(x) = C(x) + b \ln f(x) - c_1 M_h(x) + c_2 \ln \beta_3(x) + \sum_{i=1}^{3} \theta_i N_i$, where b, c_1, c_2, and θ_i ($i \in \{1,\ 2,\ 3\}$) are positive parameters. The parameters used in this simulation are collected from previous studies or real situations as much as possible. As in Kono and Kawaguchi (2015), the income per household per year is set at US\$40,000. The housing parameter in the utility function b is set at 8,000, which results in 20 percent of the income of US\$40,000. We set the number of trips to the CBD as 225 round trips per year per person, average speed as 30 km/hour, travel cost including travel time as US\$30/hour. Further, we set the cost of housing land development r_H as US\$20,000.

Next, we set some ecosystem parameters in the Lotka-Volterra equations: α_i, β_i, m_i $i \in \{2,\ 3\}$, and $k(x)$, and we specify some functions in the ecosystem model such as availability of food and plant density: $k(x)$, $\rho_3(t_3^H(x))$, $\rho_2(t_2^A(x))$, and $n_1(x)$. Although these parameters and functions vary according to species, the number of carnivores is smaller than the number of the herbivores as long as these animals are in the same food chain. So, we set the ecosystem parameters so as to satisfy the food chain: $\alpha_3 = 0.889$, $\alpha_2 = 0.604$, $\beta_2 = 1.43$, $m_3 = 0.244$, $m_2 = 0.193$, $\beta_1 = 1$, $k(x) = 1000$, $\rho_2(t_2^A(x)) = -2(t_2^A(x))^2 + 0.5$, and $\rho_3(t_3^H(x)) = -\exp(0.5 t_3^H(x)) + 1.32$. We set the cost of the plant density control and the risk-increase-measure as $p_1 = 1$ and $p_3 = 1$.

Finally, we set some parameters representing the human-ecosystem interactions: θ_i, c_1, and c_2. θ_i indicates the welfare effect of abundance of organism in species i, and c_1

---

[25] Any unit of total number of households will do, as long as it is positive. For example, Eichner and Pethig (2006) used 100 as the total number of households.

represents the humans' fear of encroaching carnivores. Therefore, c_1/θ_i represents the trade-off between them. We set $\theta_1 = \theta_2 = \theta_3 \equiv \theta$ and $c_2 = 0.000117$. Since these values vary according to the situation surrounding humans and ecosystems, we explore whether optimal city size is larger or smaller than the equilibrium city size according to c_1/θ. To conduct sensitivity analyses, we set the following combination of c_1 and θ: $c_1 = 2000, 5000, 8000$, and $\theta = 400, 500, 600$.

[Table 2 here]

[Figure 4 here]

Table 2 and Figure 4 present the results of how human-ecosystem interactions would affect the first-best optimal city size, number of species, and time density of carnivores within the city. Figure 4 shows that regardless of parameter c_1 (see the solied lines), as parameter θ decreases, the relationship between the equilibrium city size Z_H^E and optimal city size Z_H^O changes from $Z_H^E > Z_H^O$ to $Z_H^E < Z_H^O$. In other words, the optimal city size tends to be larger than the equilibrium city size as the value of ecosystem services θ decreases. Next, we focus on the changes in parameter c, taking parameter θ as constant (see the dashed lines). Figure 4 shows that the larger c is, the smaller $Z_H^E - Z_H^O$ is. This implies that the optimal city size tends to be larger than the equilibrium city size as the human's fear of encroaching carnivores increases. Table 2 shows that regardless of parameter c, the optimal numbers of the three species are greater than those at the equilibrium, and the optimal number increases with θ. In addition, regardless of c_1, the optimal time density of carnivores in the residential area is smaller than the equilibrium one, and it decreases as θ decreases.

The intuitive interpretation is as follows. Since the value of ecosystem services is high, the city government should expand the natural habitat to enrich the quality of ecosystem services. On the other hand, when the value of ecosystem services is small, the humans' fear of encountering carnivores is more influential on the welfare. Therefore, the government should expand the city to lower the length of time carnivores stay in the residential area.

7. Conclusions

This paper developed a new model that considers spatial interactions between humans and wildlife in cities and studied the equilibrium and the first-best or practically unconstranted optimal land use where the social planner controls both household and animal behaviors. We summarize what we have learned in this paper. There is a unique land use equilibrium where humans and an ecosystem interacts. At the equilibrium, animals are ununiformly distributed in the city: the density of carnivores is increasing, then decreasing, towards the CBD. In the habitat, only if the plant density varies among locations, the animals are ununiformly distributed. This spatial heterogeneity generates the distortion of predator-prey interactions. Consequently, the steady state population equilibrium of animals is inefficient.

One important question which is unanswered by the current paper is how the social planner should design policies subject to the practical constraint, that is, it is impossible for us to regulate the animal behavior directly. One of the useful policies is land use regulation intended to influence residents and animal behavior indirectly, such as controlling city size and plants densities in natural habitats. The model we have developed in this paper provides the bases for analyzing such location dependent policies which are needed to create society coexsisting with biological resources. Yoshida and Kono (in press) characterizes the second-best land use policies in this framework. Other policies can be explored in a similar framework. For example, if the number of kinds of species is increased, we can explore which species are extinct and how we should handle that situation.

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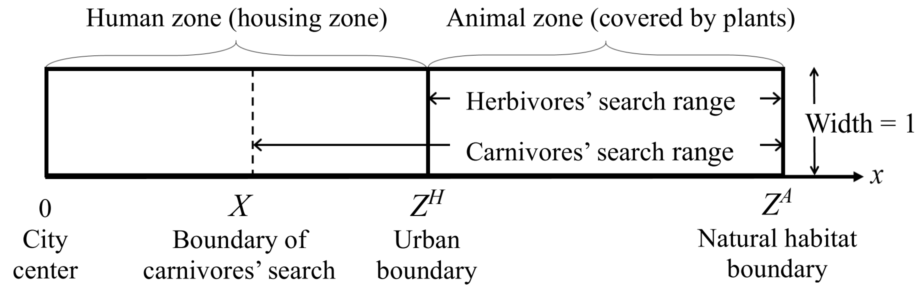

Figure 1. A city adjacent to a natural habitat

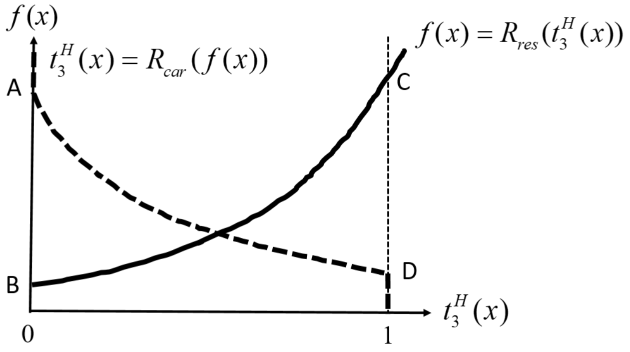

Figure 2. Best response functions of carnivores and humans at any $x \in [0, Z^H]$.

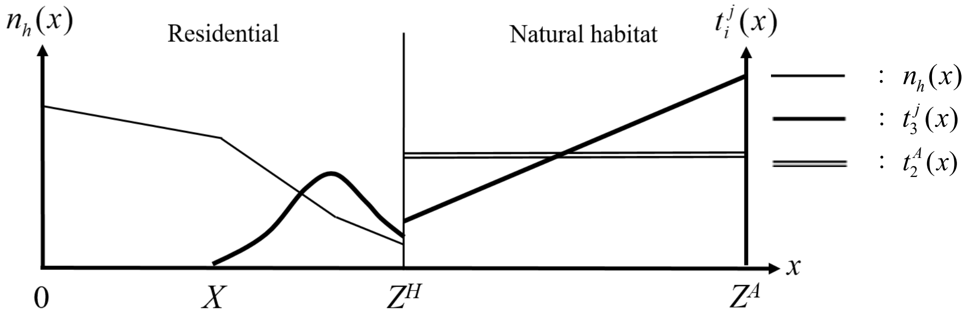

Figure 3. One example of equilibrium land use for humans and wildlife.

Note: The left vertical axis indicates the human population density, the right vertical axis indicates the time density of animals, and the horizontal axis represents the distance from the CBD. The thin line, the bold line, and the double line represent the human population density $n_h(x)$, the time density of carnivores $t_3^H(x)$ on $[X, Z^H]$ and $t_3^A(x)$ on $[Z^H, Z^A]$), and the time density of herbivores $t_2^A(x)$, respectively. The time density of carnivores might be non-continuous at the urban boundary Z^H. In the residential area with carnivores ($x \in [X, Z^H]$), the slope of $n_h(x)$ is steeper than that in the residential area without carnivores ($x \in [0, X]$).

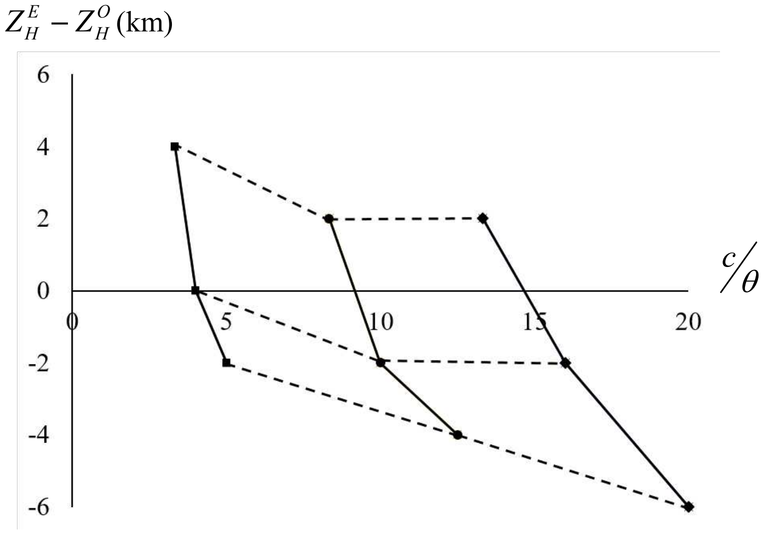

Figure 4. Numerical results: the location of urban boundary at the equilibrium and the first-best optimum

Note*:* Z_H^E and Z_H^O denote the equilibrium and the optimal location of urban boundary, respectively. $Z_H^E - Z_H^O$ in vertical axis is the difference between them. c/θ in horizontal axis is the relation between the value of ecosystem services and the human's fear of carnivores' encroachment. The solied line in left, middle, and right indicate how $Z_H^E - Z_H^O$ changes as θ changes, taking c = 2000, 5000, and 8000 as given, respectively. The dashed line in upper, middle, and lower indicates how $Z_H^E - Z_H^O$ changes as c changes, taking θ = 400, 500, and 600 as given, respectively.

Table 1. Endogenous and exogenous variables for each agent

	External variables for each agent				
	Population	Population Density	Per capita income	Urban boundary	Number of plants that grows naturally
Human	$\bar{N}_h$	$n_h(x)$	W	Z^H	
Plant	N_1	$n_1(x)$			$F(x)$
Animals	N_i				

	Choice variables for each agent						
	Utility / Net offspring	Composite goods / Intake of prey species	Number of predators each agent meets	Lot housing size / Time density	Boundary of search range (carnivores)	Land rent	Strength of the risk increase measure
Humans	$v(x)$	$C(x)$	$M_h(x)$	$f(x)$		$r(x)$	$\beta_3(x)$
Animals	b_i	Q_i^j	M_i	$t_i^j(x)$	X		

Note: Except for $\bar{N}_h$, w, and $F(x)$ all variables are endogenous to the model.

Table 2. Numerical results

(i) $c = 2000$

	Laissez-faire equilibrium					First-best optimum				
	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$
$\theta = 400$	14	36.5	10.6	2.3	0.091	16	39.3	11.6	2.8	0.034
$\theta = 500$	14	36.5	10.6	2.3	0.091	14	42.1	12.0	3.1	0.039
$\theta = 600$	14	36.5	10.6	2.3	0.091	10	46.7	13.2	3.4	0.051

(ii) $c = 5000$

	Laissez-faire equilibrium					First-best optimum				
	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$
$\theta = 400$	12	37.7	11.1	2.1	0.10	16	39.2	11.8	3.0	0.045
$\theta = 500$	12	37.7	11.1	2.1	0.10	14	42.0	12.3	3.2	0.045
$\theta = 600$	12	37.7	11.1	2.1	0.10	10	46.6	13.4	3.4	0.055

(iii) $c = 8000$

	Laissez-faire equilibrium					First-best optimum				
	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$	UGB (km)	N_1	N_2	N_3	$t_3^H(x)$
$\theta = 400$	12	37.7	11.3	2.0	0.095	18	37.2	11.7	2.9	0.044
$\theta = 500$	12	37.7	11.3	2.0	0.095	14	41.9	12.5	3.3	0.051
$\theta = 600$	12	37.7	11.3	2.0	0.095	10	46.5	13.6	3.4	0.057

Note: θ_i and c indicates the positive welfare effect of biodiversity and the humans' fear of encroaching carnivores, respectively. UGB is the location of urban growth boundary Z^H.

Appendix A. First order conditions for the laissez-faire market equilibrium

First, we set the Lagrangian function expressing the carnivore's behavior in the laissez-faire equilibrium:

$$
\begin{aligned}
L = {} & \alpha_3(Q_3^A + Q_3^H) - \beta_3 M_3 - m_3 + \lambda_3\left(\bar{T} - \int_{Z^H}^{Z^A} t_3^A(x)dx - \int_X^{Z^H} t_3^H(x)dx\right) \\
& -\phi_3^A\left[Q_3^A - \int_{Z^H}^{Z^A} t_3^A(x)t_2^A(x)N_2 dx\right] - \phi_3^H\left[Q_3^H - \int_X^{Z^H} t_3^H(x)\rho_3(t_3^H(x))n_h(x)dx\right] \\
& -\varphi_3\left[M_3 - \int_X^{Z^H} t_3^H(x)k(x)n_h(x)dx\right].
\end{aligned}
\tag{A.1}
$$

Differentiating (A.1) with respective variables, we obtain (A.2)–(A.7):

$$\frac{\partial L}{\partial Q_3^A} = 0 : \alpha_3 - \phi_3^A = 0, \tag{A.2}$$

$$\frac{\partial L}{\partial Q_3^H} = 0 : \alpha_3 - \phi_3^H = 0, \tag{A.3}$$

$$\frac{\partial L}{\partial M_3} = 0 : -\beta_3 - \varphi_3 = 0, \tag{A.4}$$

$$\frac{\partial L}{\partial t_3^H(x)} = 0 : \phi_3^H n_h(x)[\rho_3(t_3^H(x)) + t_3^H(x)\rho_3'(t_3^H(x))] + \varphi_3 k(x)n_h(x) - \lambda_3 = 0, \tag{A.5}$$

$$\frac{\partial L}{\partial t_3^A(x)} = 0 : -\lambda_3 + \phi_3^A t_2^A(x)N_2 = 0, \tag{A.6}$$

$$\frac{\partial L}{\partial X} = \lambda_3 t_3^H(X) - \phi_3^H t_3^H(X)\rho(X)n_h(X) - \varphi_3 t_3^H(X)k(X)n_h(X) = 0, \tag{A.7}$$

where we use the boundary condition $t_3^H(X) = 0$.

Next, we set the Lagrangian function expressing the herbivore's behavior in the laissez-faire equilibrium:

$$
\begin{aligned}
L = {} & \alpha_2 Q_2 - \beta_2 M_2 - m_2 + \lambda_2\left(\bar{T} - \int_{Z^H}^{Z^A} t_2^A(x)dx\right) \\
& -\phi_2\left[Q_2 - \int_{Z^H}^{Z^A} t_2^A(x)\rho_2(t_2^A(x))n_1(x)dx\right] - \varphi_2\left[M_2 - \int_{Z^H}^{Z^A} t_2^A(x)t_3^A(x)N_3 dx\right].
\end{aligned}
\tag{A.8}
$$

Differentiating (A-8) with respective variables, we obtain (A.9)–(A.11):

$$\frac{\partial L}{\partial Q_2} = 0 : \alpha_2 - \phi_2 = 0, \tag{A.9}$$

$$\frac{\partial L}{\partial M_2} = 0 : -\beta_2 - \varphi_2 = 0, \tag{A.10}$$

$$\frac{\partial L}{\partial t_2^A(x)} = 0 : \phi_2 n_1(x)[\rho_2(t_2^A(x)) + t_2^A(x)\rho_2'(t_2^A(x))] + \varphi_2 t_3^A(x) N_3 - \lambda_2 = 0 \,. \tag{A.11}$$

The first order conditions with respect to shadow prices are suppressed because they are obvious.

Appendix B. Proof of Lemma 1, 2, and 3

Proof of Lemma 1. We investigate the sign of the derivative of residents' best response function with respect to the time density of carnivores: the sign of $df(x)/dt_3^H(x)$. The first order condition of the bid rent maximization problem (19) with respect to $f(x)$ at any $x \in [X,\, Z^H]$, taking the carnivore's time density $t_3^H(x)$ as given, is

$$-\frac{w + \Omega - A - \tau(x) - C(V - E(\mathbf{N}) + g_1(M_h(x)) - g_2(\beta_3(x)), f(x))}{f(x)} - \frac{\partial C}{\partial f} = 0 \tag{B.1}$$

Differentiating (B.1) with respect to $f(x)$ and $t_3^H(x)$ yields

$$\begin{aligned} &\left(\frac{w + \Omega - A - \tau(x) - C(\cdot)}{f(x)^2} + \frac{1}{f(x)}\frac{\partial C}{\partial f}\right) df(x) - \frac{\partial^2 C}{\partial f^2} df(x) \\ &\qquad + \frac{1}{f}\frac{\partial C}{\partial (V - E(\mathbf{N}) + g_1(M_h(x)) - g_2(\beta_3(x)))} g'(M_h) M_h{}'(x) dt_3^H(x) = 0, \end{aligned} \tag{B.2}$$

where $\frac{\partial C}{\partial f} = -\frac{U_f}{U_C} < 0$, $\frac{\partial C}{\partial (V - E(\mathbf{N}) + g_1(M_h(x)) - g_2(\beta_3(x)))} = \frac{1}{U_C} > 0$, and $\frac{\partial^2 C}{\partial f^2} = -\frac{U_{ff}}{U_C} + \frac{U_f}{(U_C)^2} U_{Cf}$ (define $U_C = \frac{\partial U_h}{\partial C}$, $U_f = \frac{\partial U_h}{\partial f}$, $U_{ff} = \frac{\partial^2 U_h}{\partial f^2}$, and $U_{Cf} = \frac{\partial^2 U_h}{\partial C \partial f}$).

From the second order condition with respect to the bid rent maximization problem,

$$\frac{\partial^2 r}{\partial f^2} = \frac{w + \Omega - A - \tau(x) - C(\cdot)}{f(x)^2} + \frac{1}{f(x)}\frac{\partial C}{\partial f} - \frac{\partial^2 C}{\partial f^2} < 0 \,. \tag{B.3}$$

Hence we can obtain

$$\frac{df(x)}{dt_3^H(x)} = \frac{1}{\underbrace{\frac{\partial^2 r}{\partial f^2}}_{<0}} \underbrace{\left(-\frac{\partial C}{\partial (V - E(\mathbf{N}) + g_1(M_h(x)) - g_2(\beta_3(x)))}\right)}_{<0} \underbrace{\frac{g'(M_h(x)) N_3}{f(x)}}_{>0} > 0 \,. \tag{B.4}$$

Next, we explore the monotonicity of the best response function $R_{res}(t_3^H)$ at $t_3^H \in [0,\, 1]$. We need to prove that to every t_1 and t_2 in [0, 1] such that $t_1 < t_2 \Rightarrow R_{res}(t_2) > R_{res}(t_1)$. Combining $df(x)/dt_3^H(x) > 0$ and the mean value theorem yields that $R_{res}(t_3^H(x))$ is monotonically increasing in $t_3^H(x)$ on [0, 1].

Next, We investigate the sign of the derivative of the carnivores' best response function with respect to the housing lot size: the sign of $dt_3^H(x)/df(x)$. Substituting (23) into (22) with $t_2^A(x) = \bar{T}/(Z^A - Z^H) \equiv t_2^A(Z^H)$ and (16) yields

$$\alpha_3 \frac{1}{f(x)}[\rho_3(t_3^H(x)) + \alpha_3 t_3^H(x)\rho_3'(t_3^H(x))] - \beta_3(x)k(x)\frac{1}{f(x)} - \alpha_3 t_2^A(Z^H)N_2 = 0 . \tag{B.5}$$

Differentiating (B.5) with respect to $f(x)$ and $t_3^H(x)$ yields

$$-\frac{\alpha_3\left[\rho_3(t_3^H(x)) + t_3^H(x)\rho_3'(t_3^H(x))\right] - \beta_3(x)k(x)}{f(x)^2}df(x) + \frac{\alpha_3\left[2\rho_3'(t_3^H(x)) + t_3^H(x)\rho_3''(t_3^H(x))\right]}{f(x)}dt_3^H(x) = 0 .^{26} \tag{B.6}$$

Then,

$$\frac{dt_3^H(x)}{df(x)} = \underbrace{\frac{1}{\alpha_3\left[2\rho_3'(t_3^H(x)) + t_3^H(x)\rho_3''(t_3^H(x))\right]}}_{<0}\underbrace{\left(\frac{\alpha_3\left[\rho_3(t_3^H(x)) + t_3^H(x)\rho_3'(t_3^H(x))\right] - \beta_3(x)k(x)}{f(x)}\right)}_{>0} < 0. \tag{B.7}$$

Similarly, from the mean value theorem, $R_{car}(f(x))$ is monotonically decreasing in $f(x)$. ||

Proof of Lemma 2. At the carnivores' search boundary within a city *X*, the time density is zero and unique. It is thus sufficient to prove that the determinant of the Jacobian matrix of a system of equilibrium conditions with respect to $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ is different from 0 at all $x \in [X, Z^H]$. Then the system defines $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ at all $x \in [X, Z^H]$ as C^k functions of *x* in some neighborhood of $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ at all $x \in [X, Z^H]$ (from Sydsæter et al., 2005, Chapter 6, 6.3).

The system of equilibrium conditions with respect to $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ is

$$-\frac{[w + \Omega - A - \tau(x) - C(V - E(\mathbf{N}) + g_1(M_h(x)) - g_2(\beta_3(x)), f(x))]}{f(x)} - \frac{\partial C}{\partial f} = 0 \tag{B.7}$$

---

[26] $N_2 = (\beta_3 M_3 - \alpha_3 Q_3^H + m_3)/(\alpha_3 P)$. However, even if you increase $f(x)$ at a certain location *x*, the change in N_2 is zero because there is no width *dx*.

$$\alpha_3\left[\rho_3(t_3^H(x)) + t_3^H(x)\rho_3'(t_3^H(x))\right] - \beta_3(x)k(x) - \alpha_3 t_2^A(Z^H)N_2 f(x) = 0 \tag{B.8}$$

$$g_2'(\beta_3(x)) - p_3 U_C = 0 \tag{B.9}$$

Under the assumption that the choice of $\beta_3(x)$ does not depend on the choice of *f*(*x*), totally differentiating this system with respect to endogenous variables $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ at any location *x* yields

$$\underbrace{\frac{1}{f}\underbrace{\frac{\partial C}{\partial(G(x)-g_2(\beta_3(x)))}}_{=\frac{1}{U_C}>0}\underbrace{g'(M_h)}_{>0}\underbrace{\frac{\partial M_h(x)}{\partial t_3^H(x)}}_{=N_3>0}}_{\equiv\frac{g'(M_h)N_3}{U_C f}} dt_3^H(x) - \frac{1}{f}\underbrace{\frac{\partial C}{\partial(G(x)-g_2(\beta_3(x)))}}_{=\frac{1}{U_C}>0} g_2{}'(\beta_3(x))d\beta_3(x)$$

$$+\underbrace{\left(\frac{w+\Omega-A-\tau(x)-C(\cdot)}{f(x)^2}+\frac{1}{f(x)}\frac{\partial C}{\partial f}-\frac{\partial^2 C}{\partial f^2}\right)}_{=\frac{\partial^2 r}{\partial f^2}<0} df(x) + \underbrace{\tau'(x)}_{>0} dx = 0,$$

$$\underbrace{\alpha_3\left[2\rho_3{}'(t_3^H(x)) + t_3^H(x)\rho_3''(t_3^H(x))\right]}_{<0} dt_3^H(x) - \alpha_3 t_2^A(Z^H)N_2 df(x) - \beta_3(x)\underbrace{k'(x)}_{<0}dx - k(x)d\beta_3(x) = 0.$$

$$\underbrace{g_2''(\beta_3(x))}_{<0} d\beta_3(x) = 0$$

In the matrix form,

$$\underbrace{\begin{pmatrix} \underbrace{\frac{\partial^2 r}{\partial f^2}}_{<0} & \underbrace{\frac{g_1'(M_h)N_3}{U_C f}}_{>0} & \underbrace{-\frac{\partial g_2{}'(\beta_3(x))}{U_C f}}_{<0} \\ \underbrace{-\alpha_3 t_2^A(Z^H)N_2}_{<0} & \underbrace{\alpha_3\left[2\rho_3{}'(t_3^H(x)) + t_3^H(x)\rho_3''(t_3^H(x))\right]}_{<0} & -k(x) \\ 0 & 0 & \underbrace{g_2''(\beta_3(x))}_{<0} \end{pmatrix}}_{\equiv A} \begin{pmatrix} df(x) \\ dt_3^H(x) \\ d\beta_3(x) \end{pmatrix} = \begin{pmatrix} -\tau'(x) \\ \beta_3(x)k'(x) \\ 0 \end{pmatrix} dx.$$

Under the assumption where $\rho_3'(\cdot) < 0$ and $\rho_3''(\cdot) < 0$ on $t_3^H(x) \in [0, 1]$, the determinant of the Jacobian matrix of the system is always negative:

$$|A| = \underbrace{\frac{\partial^2 r}{\partial f^2}}_{<0} \cdot \alpha_3 \underbrace{\left[2\rho_3{}'(t_3^H) + t_3^H\rho_3''(t_3^H)\right]}_{<0} \cdot \underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0} + \underbrace{\frac{g'(M_h)N_3}{U_C}}_{>0} \cdot \underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0} \alpha_3 t_2^A(Z^H)N_2 < 0.$$

Hence, the equilibrium $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ are continuous on $[X, Z^H]$.

In addition, to investigate how $f(x)$, $t_3^H(x)$, and $\beta_3(x)$ change with *x*, we derive

$$\frac{df(x)}{dx}=\frac{1}{|A|}\left[\underbrace{-\underbrace{\tau'(x)}_{>0}\underbrace{[2\rho_3'(t_3^H(x))+t_3^H(x)\rho_3''(t_3^H(x))]}_{<0}\underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0}}_{>0}-\underbrace{\underbrace{\frac{g'(M_h)N_3}{U_C}}_{>0}\underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0}\underbrace{\beta_3(x)k'(x)}_{<0}}_{>0}\right]>0,$$

$$\frac{dt_3^H(x)}{dx}=\frac{1}{|A|}\left[\underbrace{\underbrace{\frac{\partial^2 r}{\partial f^2}}_{<0}\underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0}\underbrace{\beta_3(x)k'(x)}_{<0}}_{<0}-\underbrace{\underbrace{\tau'(x)}_{<0}\alpha_3 t_2^A(Z^H)N_2\underbrace{\frac{g_2''(\beta_3(x))}{U_C}}_{<0}}_{<0}\right]\overset{>}{\underset{<}{}}0,$$

$$\frac{d\beta_3(x)}{dx}=0.$$

Since $\frac{df(x)}{dx}>0$ at any $x\in[X,Z^H]$, the urban boundary Z^H is uniquely determined. This implies that there is no sub-center and natural habitats within residential districts in a city.

Next, we consider the equilibrium path of the time density of both carnivores and herbivores within habitats: $t_3^A(x)$ and $t_2^A(x)$. Combining (23) and (4) at which i = 2 yields $t_2^A(x)=\overline{T}/(Z^A-Z^H)$, implying that the time density of herbivores is spatially uniform everywhere at the equilibrium. Since $t_2^A(x)=\overline{T}/(Z^A-Z^H)$ and the urban boundary Z^H is uniquely determined, $t_2^A(x)$ is unique at all $x\in[Z^H,Z^A]$. Next, solving (24) for $t_3^A(x)$ after using (13) yields

$$t_3^A(x)=\frac{\alpha_2\left[F(x)-\beta_1 t_2^A(x)N_2\right]\left[\rho_2(t_2^A(x))+t_2^A(x)\rho_2'(t_2^A(x))\right]-\lambda_2}{\beta_2 N_3}\quad\text{at any } x\in[Z^H,Z^A]. \qquad \text{(B.3)}$$

Because of the unique equilibrium path of the carnivore's time density within the city and the uniqueness of Z^H, the carnivore's total time spent in the natural habitat is uniquely determined. In addition, there is one variable depending on the location in (B.3): exogenous variable $F(x)$, and it has a unique path on $[Z^H,Z^A]$ and $F(x)>0$ at all $x\in[Z^H,Z^A]$. Hence, $t_3^A(x)$ is continuous on $[Z^H,Z^A]$. Combining the carnivore's total time spent in the habitat (4) and (B.3) determines $t_3^A(x)$ at all $x\in[Z^H,Z^A]$ uniquely.||

Proof of Lemma 3. V is determined such that (17) is satisfied, that is,

$$\bar{N}_h = \int_0^{Z^H(V)} n_h(V,x)dx\,. \tag{B.4}$$

To show the uniqueness of V, it is sufficient to prove that the RHS of (B.4) monotonically changes in V. Let $\Psi(V)$ be the RHS of (B.4). We can obtain

$$\frac{d\Psi(V)}{dV} = n_h(Z^H(V))\frac{dZ^H(V)}{dV} + \int_0^{Z^H(V)} \frac{dn_h}{dV}dx < 0. \tag{B.5}$$

The proof of (B.5) is given as follows. From the comparative static analysis of the bid rent maximization problem, $df(x)/dV > 0$, given $t_3^H(x)$. This implies that the best response function of $f(x)$, shown as B-C line in Figure 2, shifts upward. So, we can obtain $df(x)/dV > 0$ at all $x \in [0,\ Z^H]$. From (16), $dn_h(V,x)/dV < 0$. The second term on the LHS of (B.5) is thus negative. To satisfy $df(x)/dV > 0$ at all x, the market land rent should decrease at all $x \in [0,\ Z^H]$. This implies that the city size becomes small: $dZ^H(V)/dV < 0$. The first term on the LHS of (B.5) is thus negative. Therefore, the LHS of (B.5) is monotonically decreasing in V. ||

Appendix C. First order conditions for the first-best optimum

The Lagrangian function (26) can be rewritten as

$$
\begin{aligned}
L = {} & \frac{\bar{N}_h V}{\mu} \\
& + \int_0^{Z^H} \frac{\lambda_h(x)}{f(x)} [w + \Omega - C(x) - f(x)r(x) - p_3\beta_3(x) - \tau(x)]dx + \int_0^{Z^H} \theta(x)\left[\frac{1}{f(x)} - n_h(x)\right]dx \\
& + [\int_0^{Z^H} [r(x) - r_h]dx - \bar{N}_h\Omega] + \int_0^{Z^H} \sigma(x)\left[M_h(x) - t_3^H(x)N_3\right]dx \\
& + \int_0^{Z^H} \eta(x)\left[U_h\left(C(x), f(x)\right) - g_1\left(M_h(x)\right) + g_2\left(\beta_3(x)\right) + E(\mathbf{N}) - V\right]dx \\
& + \int_{Z^H}^{Z^A} s_1(x)[F(x) - \beta_1 t_2^A(x)N_2 - n_1(x)]dx \\
& + S_1\left[\int_{Z^H}^{Z^A} n_1(x)dx - N_1\right] + S_3\left[\frac{\alpha_2\int_{Z^H}^{Z^A} t_2^A(x)\rho_2(t_2^A(x))n_1(x)dx - m_2}{\beta_2\int_{Z^H}^{Z^A} t_2^A(x)t_3^A(x)dx} - N_3\right] \\
& + S_2\left[\frac{\int_X^{Z^H} \beta_3(x)t_3^H(x)k(x)n_h(x)dx - \alpha_3\int_X^{Z^H} t_3^H(x)\rho_3(t_3^H(x))n_h(x)dx + m_3}{\alpha_3\int_{Z^H}^{Z^A} t_3^A(x)t_2^A(x)dx} - N_2\right] \\
& + \lambda_3^O[\bar{T} - \int_{Z^H}^{Z^A} t_3^A(x)dx - \int_X^{Z^H} t_3^H(x)dx] + \lambda_2^O[\bar{T} - \int_{Z^H}^{Z^A} t_2^A(x)dx].
\end{aligned}
\tag{C.1}
$$

Differentiating (C.1) with respective variables, we obtain (C.2)–(C.17):

$$\frac{\partial L}{\partial f(x)} = 0 : -\lambda_h(x)\frac{r(x)}{f(x)} - \theta(x)\frac{1}{\left(f(x)\right)^2} + \eta(x)\frac{\partial U_h}{\partial f} = 0\,, \tag{C.2}$$

$$\frac{\partial L}{\partial C(x)} = 0 : -\frac{\lambda_h(x)}{f(x)} + \eta(x)\frac{\partial U_h}{\partial C} = 0\,, \tag{C.3}$$

$$\frac{\partial L}{\partial r(x)} = 0 : -\lambda_h(x) + 1 = 0\,, \tag{C.4}$$

$$\frac{\partial L}{\partial \Omega} = 0 : \int_0^{Z^H} \frac{\lambda_h(x)}{f(x)}dx - \bar{N}_h = 0\,, \tag{C.5}$$

$$\frac{\partial L}{\partial n_h(x)} = 0 : -\theta(x) - \frac{S_2}{P}t_3^H(x)\rho_3(t_3^H(x)) + S_2\frac{\beta_3(x)}{\alpha_3 P}t_3{}^H(x)k(x) = 0\,, \tag{C.6}$$

$$\frac{\partial L}{\partial V} = 0 : \frac{\bar{N}_h}{\mu} - \int_0^{Z^H} \eta(x)dx = 0\,, \tag{C.7}$$

$$\frac{\partial L}{\partial M_h(x)} = 0 : \sigma(x) - \eta(x)\frac{\partial g}{\partial M_h(x)} = 0\,, \tag{C.8}$$

$$\frac{\partial L}{\partial N_3} = 0 : \int_0^{Z^H} \eta(x)\frac{\partial E}{\partial N_3}dx - \int_0^{Z^H} \sigma(x)t_3{}^H(x)dx - S_3 = 0, \tag{C.9}$$

$$\frac{\partial L}{\partial N_2} = 0 : \int_0^{Z^H} \eta(x)\frac{\partial E}{\partial N_2}dx + \beta_1\int_{Z^H}^{Z^A} s_1(x)t_2^A(x)dx - S_2 = 0, \tag{C.10}$$

$$\frac{\partial L}{\partial N_1} = 0 : \int_0^{Z^H} \eta(x) \frac{\partial E}{\partial N_1} dx - S_1 = 0 , \tag{C.11}$$

$$\frac{\partial L}{\partial n_1(x)} = 0 : S_1 - s_1(x) + S_3 \frac{\alpha_2}{\beta_2 P} t_2^A(x) \rho_2(t_2^A(x)) = 0 , \tag{C.12}$$

$$\begin{aligned} \frac{\partial L}{\partial Z^H} = 0 : & r(Z^H) - r_H - S_1 n_1(Z^H) + \lambda_2^O t_2^A(Z^H) \\ & + S_2 \frac{\beta_3(Z^H)}{\alpha_3 P} t_3^H(Z^H) k(Z^H) n_h(Z^H) - \frac{S_2}{P} t_3^H(Z^H) \rho_3(t_3^H(Z^H)) n_h(Z^H) \\ & - S_3 \frac{\alpha_2}{\beta_2 P} t_2^A(Z^H) \rho_2(t_2^H(Z^H)) n_1(Z^H) \\ & + S_2 \frac{N_2}{P} t_3^A(Z^H) t_2^A(Z^H) + S_3 \frac{N_3}{P} t_3^A(Z^H) t_2^A(Z^H) = 0, \end{aligned} \tag{C.13}$$

$$\begin{aligned} \frac{\partial L}{\partial t_3^H(x)} = 0 : & -\sigma(x) N_3 - \lambda_3^O - \frac{S_2 n_h(x)}{P} \left[\rho_3(t_3^H(Z^H)) + t_3^H(x) \rho_3'(t_3^H(x)) \right] \\ & + S_2 \frac{\beta_3(x)}{\alpha_3 P} k(x) n_h(x) = 0, \end{aligned} \tag{C.14}$$

$$\frac{\partial L}{\partial t_3^A(x)} = 0 : -\lambda_3^O - S_2 \frac{N_2}{P} t_2^A(x) - S_3 \frac{N_3}{P} t_2^A(x) = 0 \quad , \tag{C.15}$$

$$\begin{aligned} \frac{\partial L}{\partial t_2^A(x)} = 0 : & s_1(x) \beta_1 N_2 + S_3 \frac{\alpha_2 n_1(x)}{\beta_2 P} \left[\rho_2(t_2^A(x)) + t_2^A(x) \rho_2'(t_2^A(x)) \right] - S_2 \frac{N_2}{P} t_3^A(x) \\ & - S_3 \frac{N_3}{P} t_3^A(x) - \lambda_2^O = 0. \end{aligned} \tag{C.16}$$

$$\frac{\partial L}{\partial X} = \lambda_3^O t_3^H(X) + \frac{S_2}{P} t_3^H(X) \rho_3(X) n_h(X) - S_2 \frac{\beta_3(X)}{\alpha_3 P} t_3^H(X) k(X) n_h(X) = 0 , \tag{C.17}$$

$$\frac{\partial L}{\partial \beta_3(x)} = -\frac{\lambda_h(x)}{f(x)} p_3 + \eta(x) \frac{\partial g_2}{\partial \beta_3(x)} + S_2 \frac{t_3^H(x) k(x) n_h(x)}{\alpha_3 P} = 0 , \tag{C.18}$$

The first order conditions with respect to Lagrangian multipliers are omitted.

Appendix D. Proof of Propositions 1, 2, and 7

Proof of Proposition 1. Combining (C.3), (C.4), and (16) yields $\eta(x) = \frac{n_h(x)}{\partial U_h / \partial C}$, and plugging this into (C.8) yields $\sigma(x) = n_h(x) \frac{\partial g / \partial M_h}{\partial U_h / \partial C}$. Substituting these equations into (C.9) and solving for S_3 yields (27). Likewise, solving (C.10) for S_2 yields (28). Solving (C.11) for S_1 with $\eta(x) = \frac{n_h(x)}{\partial U_h / \partial C}$ yields $S_1 = \int_0^{Z^H} n_h(x) \frac{\partial E / \partial N_1}{\partial U_h / \partial C} dx$. Substituting this equations into (C.12) and solving for $s_1(x)$ yields (29).||

Proof of Proposition 2. From (C.15), $t_2^A(x) = \lambda_3^O / \gamma$, where $\gamma = -S_2 \frac{N_2}{P} - S_3 \frac{N_3}{P}$. Substituting this into (4) for i = 2, $\overline{T} = \lambda_3^O (Z^A - Z^H) / \gamma$, and then solving for λ_3^O / γ yields $\lambda_3^O / \gamma = \overline{T} / (Z^A - Z^H)$. Therefore, we can obtain the optimal time density of herbivores: $t_2^A(x) = \overline{T} / (Z^A - Z^H)$.||

Proof of Proposition 7. From the proof of Proposition 1, $S_1 = \int_0^{Z^H} n_h(x) \frac{\partial E / \partial N_1}{\partial U_h / \partial C} dx > 0$. Arranging (C.13) yields

$$\begin{aligned} r(Z^H) - r_H = {} & \underbrace{S_1 n_1(Z^H)}_{\text{[13] Cost due to a decrease in plants}} \\ & \underbrace{+ S_3 \frac{t_2^A(Z^H)}{\beta_2 P} \left[\alpha_2 \rho_2 (t_2^H(Z^H)) n_1(Z^H) - \beta_2 t_3^A(Z^H) N_3 \right]}_{\text{[14] Benefit or cost of decreasing the population of carnivores}} - \underbrace{\lambda_2^O t_2^A(Z^H)}_{\substack{\text{[15] Benefit or cost of decreasing} \\ \text{the time density of herbivores}}} \\ & + S_2 \underbrace{\frac{t_3^H(Z^H)}{\alpha_3 P} \left[\alpha_3 \rho_3 (t_3^H(Z^H)) n_h(Z^H) - \beta_3(Z^H) k(Z^H) n_h(Z^H) - \alpha_3 t_2^A(Z^H) N_2 \right]}_{\text{[16] Benefit or cost of decreasing the population of herbivores}}. \end{aligned}$$

The market city boundary is determined at which $r(Z^H) = r_H$. Since S_2 and S_3 can be either positive or negative, the RHS of this equation can be either positive or negative. Hence, if the RHS of this equation is positive, then the social optimal city size is smaller than the equilibrium city size. If it is negative, then the social optimal city size is larger than the equilibrium city size.||