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**マレーシアのアナツバメの持つ持続可能な収穫者を利する生態学的特徴～
社会生態システムによる研究**

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【要旨】

生物多様性管理における一つの大きな課題は、持続不可能な収穫者による過剰収穫をどう制御するかである。もし、持続可能な収穫者が持続不可能な収穫者よりも、短期的にも多くの利益を得るシナリオを作成できれば、過剰収穫の問題は解決され、誰もが持続可能な収穫者となるだろう。しかし、このようなシナリオを作るのは容易ではない。特に対象とする生物の生息地に所有権が賦与されておらずオープンアクセスの状態にあるならば、このシナリオはさらに困難になる。ところが、持続可能な収穫者が持続不可能な収穫者以上の利益を得ると考えられる実例がある。それは、マレーシアのサラワク州に生息するアナツバメである。アナツバメの成鳥が作る巣は、中華料理の伝統的な高級スープの材料として使用される。ところが巣の価格が上昇したことにより、持続不可能な収穫者により、多くの巣が卵や幼鳥と一緒に採取され放棄してしまうようになった。アナツバメは洞窟の天井に巣を作るが、持続不可能な収穫者が採巣するとアナツバメはその天井から逃げてしまい、同じ場所に戻らないことが知られている。アナツバメの持つこの生態学的特徴は、持続不可能な収穫者に対するアナツバメによる処罰とみなすことができる。本論では、サラワク州のニアの洞窟でのアナツバメの保護を念頭にモデル化を行う。ニアの洞窟はルバンと呼ばれる小洞窟が多数連結し構成されている。それぞれのルバンには所有権（採取権）があり先住民に賦与され、さらにそれらを貸与された華人が巣の採取を行う。本論は、ステージ構成のある個体群動態モデルのもとで、所有権およびアナツバメによる処罰が、アナツバメの個体群動態、および持続可能な収穫者と持続不可能な収穫者の両者の経済的利益に対していかなる効果を与えるのかを検証する。本論の結果は以下のものである。アナツバメが持続不可能な収穫者から逃げた後に洞窟に戻る限り、アナツバメの処罰は、所有権システムの下で持続可能な収穫者に持続不可能な収穫者よりも高い収益を短期的にも提供する。コモンズの管理に関する既存研究は、生物種の生態学的な独特さを考慮せずに持続可能な収穫のためのルールと規制の重要性を強調してきた。本研究は、生態系の持続可能な利用の枠組みを設計するためには、社会科学的な観点からの設計だけではなく、生物種の生態学的特徴を知ることが不可欠であることを示唆している。

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Ecological feature benefiting sustainable harvesters in socio-ecological systems: A case study of swiftlets in Malaysia

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Abstract

A major challenge in biodiversity management is overharvesting by unsustainable harvesters. If a scenario could be created where sustainable harvesters benefit more than the unsustainable ones, even in the short term, the issue of overharvesting would be solved. Then, everyone would follow the lead of sustainable harvesters. However, creating such a scenario is not an easy task; the difficulty is intensified if the habitat is open-access and a property rights system is not in place. There is a special case where sustainable harvesters are believed to gain more than unsustainable harvesters: swiftlets in Sarawak, Malaysia. Edible nests built by adult swiftlets are used as ingredients for a traditional luxurious soup in Chinese cuisine. A rise in nest prices has increased the instances of unsustainable harvesters wrongfully

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collecting nests along with the eggs and fledglings, which are then abandoned. Swiftlets live in caves and build nests on cave ceilings. It is known that swiftlets escape from cave ceilings when these harvesters take the nests, and they do not return to the same place. This ecological feature appears to work as the swiftlet's punishment against unsustainable harvesters. This paper constructs a stage-structured population model and examines the effect of property rights and the punishment by swiftlets on the population dynamics of the bird and on the economic return of both sustainable and unsustainable harvesters. Our findings are as follows: the punishment by swiftlets provides sustainable harvesters a higher short-term return than unsustainable harvesters under the property rights system, as long as swiftlets return to the cave after they escape from the unsustainable harvesters. While previous studies regarding the management of a commons have stressed the importance of rules and regulations for sustainable harvesting without considering the ecological uniqueness of each species, this study suggests that ecological exploration, and the discovery of ecological features are also essential for designing a sustainable framework.

Key words: the tragedy of the commons, property rights, indirect punishment by swiftlets, difference equations

JEL classification: Q01; Q57

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Introduction

Overharvesting wildlife is a major problem in conservation biology, economic sustainability, and sustainable resource management. Specifically, overharvesting is likely to occur in an open-access shared resource or a commons (Hardin 1968; Anderies and Janssen 2013). Hardin (1968) points out two choices on how to prevent the exhaustion of the commons, or "the tragedy of the commons": (1) to provide harvesters private property rights; or (2) make the government restrict harvest yields by means of legal enforcement (Anderies and Janssen 2013; Boyd and Richerson 2018). Based on a comparative analysis of empirical data, Ostrom (1990) scrutinizes various social norms and local rules in commons, and proposed her eight famous principles illustrated by long-enduring common-pool institutions (Ostrom 1990). Moreover, Ostrom (1990) shows that resources in the commons in some areas can be sustainable without implementing either of the two options proposed by Hardin (1968) and Anderies and Janssen (2013).

Two of the eight principles in Ostrom (1990) are 'monitoring' and 'graduated sanction', which are related to one of the two choices in Hardin (1968), legal enforcement. Some theoretical studies have investigated the effect of punishment and/or monitoring on maintaining cooperation in the population, while others have attempted to explain how

graduated sanction can maintain cooperation by mathematical investigation and computer simulations (Nakamaru and Dieckmann 2009; Iwasa and Lee 2013; Shimao and Nakamaru 2013). When defectors are punished, they incur a fine, but the punishers also incur monetary and time costs. Some theoretical studies have investigated the notion that costly punishment promotes cooperation in the population (Axelrod 1986; Sethi and Somanathan 1996; Sigmund et al. 2001; Boyd et al. 2003; Nakamaru and Iwasa 2005, 2006; Nakamaru and Dieckmann 2009; Shimao and Nakamaru 2013). Other studies argue that if defectors are excluded from the group, punishment costs can be saved because exclusion serves as cost-free punishment; these studies theoretically investigate the effect of exclusion on the evolution of group cooperation (Sasaki and Uchida 2013; Nakamaru and Yokoyama 2014).

Before punishing defectors, monitoring is necessary to identify the defectors when each player cannot observe the behavior of other players directly (Chen et al. 2015). However, monitoring is also costly; it costs too much to monitor all harvesters in a vast rural area, especially when harvesters often secretly harvest or smuggle animals and plants in an unsustainable way. It is almost impossible to consistently monitor their behavior. Therefore, monitoring and punishment are not always successful in illegal cases of commons, such as

poaching, smuggling, illegal logging, and illegal dumping of industrial waste, all of which generally occur in secret and damage the natural environment (Jachmann 2003; Nakamaru et al. 2018).

Introducing private property rights is considered one possible solution to prevent overharvesting in the commons without costly punishment or costly monitoring (Hardin 1968; Anderies and Janssen 2013) because proprietors can control the way harvesting is conducted in their property, except in the case of intruders that enter and illegally exploit their land. The merit of introducing property rights is that harvesters will behave in a sustainable manner if the future return of sustainable harvesters on their own property is higher than that of unsustainable harvesters, provided the discount factor is not too low. However, private property rights are not always needed to avoid overharvesting in some socio-ecological dynamics. For example, Moritz et al. (2018) theoretically summarized eight conditions including environmental factors, the population size of harvesters, and resource-use strategies, which make open-access resources sustainable in special cases such as the swidden farmland and nomadic areas (Moritz et al. 2018). These studies suggest that the unique ecological and social factors, such as social norms and institutions in a specific area, determine whether private property rights promote the sustainable usage of resources,

such as animals and plants. According to the previous studies, sustainable usage of renewable resources is likely possible regardless of property rights. Adding future benefit to estimate the benefit of harvesters is considered another possible solution to prevent overharvesting in the commons. If harvesters estimate future return as future yield multiplied by the discount factor to then maximize the total profits over time, the total profit of sustainable harvesters is likely higher than that of unsustainable harvesters because sustainable harvesting is likely to sustain the population size rather than unsustainable harvesting. As a result, some harvesters will become sustainable harvesters. In light of this argument, many theoretical studies have calculated the optimal value of long-term profits of harvesters (e.g. Clark 1990). However, in reality, other harvesters will remain unsustainable, even though some of them are aware that future return will be higher if they behave as sustainable harvesters. Thus, unsustainable harvesters decrease the population size of targeted wildlife in the future, and the future return of all harvesters, including the sustainable ones, is reduced. In this paper, such reduction is referred to as *punishment or revenge* from wildlife to the whole community.

Why do not all harvesters regard future return as important? One answer is that they have to finance their current needs and prioritize immediate returns over future returns, especially when their economic situation is severe. This can be best exemplified by a

proverb: *Better an egg today than a hen tomorrow*. His/her discount factor is not high enough in this case. Thus, if a general framework under which the immediate return of sustainable harvesters exceeds that of unsustainable harvesters could be found, the overharvesting problem could be solved. Of course, it might be impossible to find out such a framework that can be applicable to any overharvesting problem. However, if there is a specific case where the immediate return of sustainable harvesters exceeds that of unsustainable harvesters, this might aid in the development of a more general framework for conservation biology and ecological management.

An appropriate example of the specific case is the harvest of swiftlets' nests in Sarawak, Malaysia (Lim 1999; Lim and Earl of Cranbrook 2002). The three species of edible-nest swiftlets are: white-nest swiftlet (*A. fuciphagus*), black-nest swiftlet (*A. maximus*), and glossy swiftlet (*Collocalia* spp.) (Lim and Earl of Cranbrook 2002). The swiftlets in Sarawak, Malaysia live in caves. There are three types of caves: communal caves, such as Niah Cave, personal or family-owned caves, and caves tendered to private contractors (Lim and Earl of Cranbrook, 2002: 103-104). Overharvesting happens only in communal caves, and, thus, we focus on communal caves. The cave is divided into small parts, each of which is called *lubang* (Lim and Earl of Cranbrook 2002). Local people have private property rights

over the lubangs in communal caves, which are in turn inherited from their parents. Locals have the right to access the property, withdraw products from the property, and manage the property to decide who can be excluded from accessing it, but do not have the right to sell or lease the property. Therefore, they can be categorized as "proprietors" (Schlager and Ostrom 1992). Swiftlets build their nests attached to the walls and ceilings of the caves. The nests are very small in comparison to the caves, allowing for many nests to be built on the ceiling of the caves. The swiftlets themselves have no economic value, but their nests are deemed luxury ingredients in Chinese cuisine. Chinese people believe bird's nest soup makes them healthy and beautiful; in fact, evidence suggests that it provides several health benefits (Lim and Earl of Cranbrook 2002; Marcone 2005; Guo et al. 2006; Aswir and Wan Nazaimoon 2011). Nests are made only by adult swiftlets; if the population of swiftlets decreases, the number of nests also decreases. However, smugglers or unsustainable harvesters do not care about the welfare of the swiftlets; they throw away the eggs and fledglings found in the nests in order to harvest the nests (Lim and Earl of Cranbrook 2002). As a result, the population size as well as the number of nests decrease, which has led to rising nest prices since the late 1970s.

The management system to make harvesting nests sustainable was introduced to the

Niah cave, and this system was successful. This information was discovered by one of the authors, Ayumi Onuma (AO), who has visited Kuching, Miri, and Niah in Sarawak several times since 2006. AO met Dr. Lim Chan Koon, who was a researcher on conservation biology as well as the ecology of swiftlets. He was then working for Sarawak Forest Corporation (SFC) to implement co-management plans for the sustainable harvesting of the edible nest swiftlets in the state. According to interviews that took place March 16-17, 2007, Dr. Lim informed AO of a remarkable aspect of the ecology of swiftlets that could make the management system in the Niah cave successful. Swiftlets are very sensitive birds. For example, Dr. Lim and others observed that they fly away immediately when they smell harvesters cooking a particular food, though no one can identify exactly what smell the swiftlets dislike the most. One of the most interesting ecological features of this sensitivity is that the swiftlets tend to leave the lubangs where the harvesters were trying to harvest the nests, even when the adults are caring for their chicks after hatching. According to Dr. Lim, unsustainable harvesters may lose adult swiftlets, the source of their income. This feature looks very hard to test, however, as it would require the observation of a large number of nests with chicks as well as the different ways of harvesting to judge whether a method is sustainable or not. This procedure, however, could in principle be used to make the harvesters

avoid disturbing the adults while caring for their chicks. This feature coincidentally supports the sustainable harvesting rule introduced by SFC: Harvest is prohibited during a certain breeding season of the year to allow the birds to breed and fledge at least one generation of nestling every year (Lim 2002). The local people lend their own lubangs to Chinese people harvesting nests. If the borrowers are sustainable harvesters, they obey the rules and never throw away the eggs and fledgling in the nests. If they are unsustainable harvesters, they disturb the swiftlets, and harvest as many nests as possible. More importantly, sustainable harvesters have been informed of the following ecological feature: swiftlets have a tendency to leave the habitat where unsustainable harvesters devastate and tend to settle at the location of one of sustainable harvesters (personal communication from Dr. Lim). This may be interpreted as the swiftlet's *indirect punishment* against unsustainable harvesters. The reason why this escaping behavior can be interpreted as indirect punishment is because unsustainable harvesters can no longer obtain the benefit from their lubangs once the swiftlets there have left. This can be interpreted as revenge or punishment by the swiftlets for their offspring being killed. That is, swiftlets punish the unsustainable harvesters, not in a direct way, such as attacking and injuring the harvesters, but in an indirect way that cause damage to their economic benefits. Therefore, we refer this escaping behavior as indirect punishment

in this paper. This ecological feature is a key to prevent overharvesting and to promote sustainable harvesting. This characteristic also makes people save the cost of punishing and monitoring the unsustainable harvesters, thus facilitating sustainable harvesting.

As the unique ecological feature of swiftlets works as indirect punishment against the unsustainable harvesters, the immediate harvesting yield of sustainable harvesters would exceed that of unsustainable harvesters who do not consider future return. However, as we show later on, such an ecological feature does not always benefit sustainable harvesters instead of unsustainable ones in terms of immediate profit.

What other aspect of swiftlets ensures that the sustainable harvesters are better rewarded? We focus on the effect of property rights, which, in this context, is equivalent to the right to harvest the swiftlet nests in each lubang. We hereafter call a holder of such right a "proprietor," because a "proprietor" is a proper term (Schlager and Ostrom 1992). Each proprietor can exclude other proprietor's harvest from his/her lubang, and set a monopoly of all the nests there. The proprietors lend their lubangs to any harvesters regardless of their way of harvesting. Harvesters are allowed to harvest nests attached to ceilings of their proprietors' caves. Thus, it is expected that the type of harvester—sustainable or unsustainable—will essentially determine his/her economic returns from harvesting swiftlet nests. Swiftlets whose

nests are on the lubangs lent to sustainable harvesters by proprietors are not as damaged as those in the lubangs lent to unsustainable harvesters. Therefore, introducing property rights on lubang is a good way for sustainable resource management of swiftlets. To investigate the effect of the unique ecological feature of swiftlets mentioned earlier combined with property rights on both the ecological dynamics of swiftlets and the economic benefits, we construct some mathematical models that describe the socio-ecological system of swiftlets.

There are theoretical studies dealing with the integration of social and ecological dynamics of animals and plants, or socio-ecological systems (SEs) (Iwasa et al. 2007; Fujiwara 2008; Brandt et al. 2012; Schlüter et al. 2012; Tavoni et al. 2012; Lade et al. 2013; Coutts et al. 2013). Previous theoretical work assumes very simple ecological models, such as the logistic equation, $dx/dt = rx(1 - x/K)$, in which x is the population size of one species, r is the intrinsic growth rate, and K is the carrying capacity. This simple model is often used to describe general ecological dynamics, and has contributed to the theoretical understanding of general ecosystems. However, this simple model does not always describe every ecological system properly. In the swiftlet case, the logistic equation cannot be applied. The reason, however, is not because of the swiftlets themselves, but because the nests built by adult swiftlets are the harvested objects, and the dynamics of nests cannot be described by the

logistic equation. Unsustainable harvesters harvest only the nests and throw away eggs and fledglings – the population of eggs and fledglings should be considered in the model. Then, a stage-structured model can be applied (Caswell 2001).

In this study, we show mathematically that (i) the immediate return of unsustainable harvesters is always higher than that of sustainable harvesters in an open-access shared resource; (ii) escaping from the unsustainable harvesters is not enough to make the immediate return of sustainable harvesters higher than that of unsustainable harvesters in an open-access shared resource; and (iii) the escaping of swiftlets from the unsustainable harvester's habitat makes the immediate return of sustainable harvesters higher than that of unsustainable harvesters when the property rights are introduced into the swiftlet habitats. Although this study may seem specific to swiftlets, we will propose a general conclusion that applies to the sustainable use of animals and plants.

Model

We introduce three models: the baseline model, the open-access model, and the property rights model. In the baseline model, we construct the discrete equations presenting the population dynamics of swiftlets without harvesters. In the open-access model, three types of

harvesters, who can access any habitats and harvest nests wherever they like, are introduced in the baseline model. In the property rights model, harvesters only harvest the nests in the habitat whose property right they have. In comparison with the results of three models, we will examine how the unique feature of swiftlets, different types of harvesters, and the property right influence the population dynamics and sustainable usage of swiftlets.

Model 1: The baseline model

Firstly, we will explain the baseline model. Following the ecological feature of swiftlets which we explained in Introduction, and by Lim and Earl of Cranbrook (2002), we construct the model; there is a swiftlet population in a habitat such as a cave. An adult swiftlet settles and builds a nest at an empty site on the wall or the ceiling of lubangs. Then, the adult stays in or near the nest. Each pair produces one or two eggs per breeding bout. We do not assume both males and females, but only females. We assume that an adult produces one egg. The fledged leaves the original nest, becomes an adult, settles at a new empty site, and starts nest-building. The adult generally stays in the same site, and repairs the undisturbed nest after the fledged leaves the nest. If the nest is harvested or fall spontaneously, the adult constructs a new nest in the same site.

Therefore, the existence or nonexistence of nests is a key in the population dynamics of swiftlets, and we construct the site-specific model: an empty site or an occupied site. Each occupied site has one of three states: state i ($i = 1, 2$ and 3). State 1 means a new adult settles there; in state 2, the adult settles with the nest which it has built, but it does not produce an egg; and in state 3, the adult settles with an egg, a hatching or fledgling in the nest. As a matter of convenience, we assume state 0 means an empty site. One habitat consists of infinite sites.

The reason why we assume state 1, state 2, and state 3 is because, if state 2 and state 3 are categorized as the same state, we fail to describe the difference in behaviors between sustainable and unsustainable harvesters; sustainable harvesters only collect nests which do not contain eggs and juveniles, while unsustainable harvesters collect nests with eggs and juveniles that they later throw away. Therefore, nests with and without eggs or juveniles should be assumed. If there is no site with state 1, we cannot present the situation in which an adult usually settles in the same site and restarts to construct a new nest again if the nest is harvested or fell down accidentally. We need to consider four states of swiftlets as a minimum.

Let $x_i(t)$ be the density of state i at time t in the habitat ($i = 0, 1, 2$ and 3), and

therefore, $x_0(t) + x_1(t) + x_2(t) + x_3(t) = 1$. We explain the time-transition between the four states (Figure 1) ; an adult in state 1, state 2, or state 3 dies with natural death rate (d) at time step t , and these states are changed to vacant sites (state 0) at time step $t + 1$. If the adult and the egg/hatching (state 3) survive at the rate of $(1-d)(1-d_e)$, where d_e is the egg loss rate, the hatching grow into a fledgling and the fledgling leaves the nest and becomes adult at the fledgling-adult rate (g). So, state 3 is changed into state 2 at the rate of $g(1-d)(1-d_e)$. Then, if the new adult leaving the nest finds an empty site and settles at the empty site at the settlement rate (s), state 0 is changed into state 1 at the rate of $sg(1-d)(1-d_e)x_3(t)$. This is the case because the egg and the fledgling do not settle there anymore since only an adult exists there. After an adult in state 1 survives at the rate of $(1-d)$ and builds a nest at the nest-building rate (h), state 1 is changed to state 2 at the rate of $(1-d)h$. If an adult in state 2 survives at the rate $(1-d)$ and lays an egg in the nest at the breeding success rate (b), state 2 is changed into state 3 at the rate of $(1-d)b$. After an egg in state 3 dies at the egg loss rate d_e and the adult in state 3 survives at the rate of $(1-d)$, state 3 is changed into state 2 at the rate of $(1-d)d_e$.

As mentioned later, we can obtain the egg loss rate, but not the death rate of the fledgling and the fledged. As we want to reduce the number of parameters, we simply assume

the egg loss rate includes the death of fledgling or the fledged, although it is unrealistic. We assume $0 \leq d, h, b, g, d_e, s \leq 1$. The parameter list is shown in Table 1. There are three breeding bouts per year (Lim and Earl of Cranbrook 2002): April-July, August-November, and December-March, but we assume one breeding bout. It is because introducing three breeding bouts into the model would make our model more complicated than the current model, and it would be difficult to analyze it mathematically. Figure 1 can be described by the time-discrete equations as follows:

$$x_0(t+1) = x_0(t) + dx_1(t) + dx_2(t) + dx_3(t) - (1-d)(1-d_e)sgx_0(t)x_3(t) \quad , (1a)$$

$$x_1(t+1) = x_1(t) + (1-d)(1-d_e)sgx_0(t)x_3(t) - dx_1(t) - h(1-d)x_1(t) \quad , (1b)$$

$$x_2(t+1) = x_2(t) + h(1-d)x_1(t) + (1-d)d_ex_3(t) + (1-d)(1-d_e)gx_3(t) - dx_2(t) - b(1-d)x_2(t) \quad , (1c)$$

$$x_3(t+1) = x_3(t) + b(1-d)x_2(t) - (1-d)d_ex_3(t) - dx_3(t) - (1-d)(1-d_e)gx_3(t) \quad . (1d)$$

$$\text{The population is sustainable if } h > H(d, d_e, g, s, b) \quad , (2)$$

$$\text{in which } H(d, d_e, g, s, b) = \frac{1-(1-d)(K+2)+(1-d)^2(2K+1)-(1-d)^3K}{(1-d)[-1+(1-d)(K+1)+(1-d)^2(-K+b(1-d_e)gs)]} \quad ,$$

where $K = (1-d_e)(1-g) - b$ (see Appendix A for details).

Table 1 in Lim (1999) lists the white-nest swiftlet's proportion breeding (%), hatching success (%), egg loss (%), and fledging success (%) during each of the three breeding bouts

at two places, Lubang Salai and Lubang Beruang. We assume one bout per unit of time. Therefore, we use the geometric means of proportion breeding, hatching success, egg loss, and fledging success through three bouts as the four parameters per unit of time. The geometric means of proportion breeding, hatching success, egg loss, and fledging success per breeding bout at Lubang Salai are 81.3%, 61.3%, 38.2%, and 97.4%, respectively, while at Lubang Beruang they are 83.5%, 78.0%, 21.3%, and 92.0%, respectively. The arithmetic means of two geometric means of proportion breeding, hatching success, egg loss, and fledging success are calculated as 82.4%, 69.7%, 29.8%, and 94.7%. We assume that b , d_e and g in our model correspond to the proportion breeding, the egg loss, and the hatching success multiplied by the fledging success. Then, the three parameters b , d_e , and g are estimated at 0.824, 0.298 and 0.660 ($= 0.697 \times 0.947$), respectively. The three parameters d , h , and s are unknown in Lim (1999). We then investigate the effect of these three parameters on the population dynamics.

Result 1: The population dynamics of swiftlets in the habitat without harvesters

To examine if the swiftlet population does not go extinct in eq. (1) without harvesters in the habitat and using the three parameters (b , d_e and g) estimated following Lim (1999), we

calculate the effect of the natural death rate (d), the nest-building rate (h), and the settlement rate (s) on the population dynamics. $H(d, d_e, g, s, b)$ perfectly predicts the boundary between the existence and extinction of swiftlets. When h and s are higher and d is lower, the region in which the swiftlet population is locally stable is wider (eq. (2)). The population can be stable at least when the natural death rate (d) is less than approximately 0.154, which is calculated from eq. (2) with $s = 1$ and $h = 1$.

Model 2: The open-access model

To consider the effect of harvesters on the population dynamics of swiftlets, we assume the habitat is open-access and any harvester can harvest nests there. Hereafter, the model is called the open-access model. There are three types of harvesters: non-harvesters, sustainable harvesters, and unsustainable harvesters. The non-harvesters do not harvest any nests. The sustainable harvesters harvest nests in a sustainable manner, so they only harvest nests without eggs and chicks in state 2. The unsustainable harvesters harvest nests in the unsustainable manner; they not only harvest nests in state 2 but also nests with eggs and/or chicks in stage 3, and throw them away. In reality, there are smugglers who invade the proprietor's cave and harvest any nests. Here we do not assume the smugglers explicitly

because their effect on swiftlets is similar to the effect of unsustainable harvesters in the open-access model.

Let $y_n(t)$, $y_s(t)$, and $y_u(t)$ be the frequencies of non-harvesters, sustainable harvesters, and unsustainable harvesters at time t , respectively ($y_n(t) + y_s(t) + y_u(t) = 1$). For simplicity, we assume that $y_n(t)$, $y_s(t)$ and $y_u(t)$ are fixed to be y_n , y_s , and y_u . If all harvesters are non-harvesters ($y_n = 1$), the population dynamics of swiftlets follows eq. (1). For simplicity, we do not assume a closed season for harvesting.

The black arrow in Figure 2a shows the effect of sustainable harvesting on the baseline model presented in Figure 1. As sustainable harvesters only harvest nests in state 2 at the sustainable harvesting effort (p_s), state 2 is changed into state 1 at the rate of $(1 - d)p_sy_s$ during one time step (Figure 2a), where $0 \leq p_s \leq 1$. When their effort, p_s , is high, they harvest a large number of nests; when $p_s = 0$, the harvesters do not harvest nests. The rate $(1 - d)p_sy_s$ means that the sustainable harvesters harvest the nests of adults which do not die naturally at the rate of $(1 - d)$, and the effort of harvesting is proportional to the frequency of sustainable harvesters, y_s . The adult whose nest is not harvested at the rate of $(1 - p_sy_s)$ survives at the rate of $(1 - d)$ and lays an egg at the rate of b , which is hatched in state 2, so state 2 changes to state 3 at the rate of $(1 - d)(1 - p_sy_s)b$.

Although we do not model the effect of the price of a nest on the behavior of harvesters in an explicit way, we assume that high harvesting efforts are implicitly caused by high nest prices. We will prove that this assumption is appropriate from the perspective of economics in the Discussion and Conclusions section.

The black arrows labelled (X1)-(X4) and (Y1)-(Y4) in Figure 2b show the effect of unsustainable harvesting on the baseline model in Figure 1. When the unsustainable harvesters harvest nests in state 2 at the unsustainable harvesting rate (p_u), state 2 is changed into state 1 at the rate of $(1 - a_1)(1 - d)p_u y_u$ during one time step (Y1 in Figure 2b), where $0 \leq p_u \leq 1$. When their effort, p_u , is high, they harvest a large number of nests. Let a_1 be the probability that the behavior of unsustainable harvesting forces the adult in state 2 to leave the original site. As mentioned in Introduction, swiftlets have a tendency to escape from the place where the nests are harvested in the unsustainable way, and they do not go back to the place again. When the adult escaping from the original site (state 2) at the rate of $a_1 p_u y_u (1 - d)$ (Y2 in Figure 2b) is able to find a new empty site and settle there at the rate of $f x_0(t)$ (from Y2 to Y4 in Figure 2b), state 2 is changed into state 1 at the rate of $a_1 p_u y_u (1 - d) f x_0(t)$. If they fail to find a new empty site (from Y2 to Y3 in new Figure 2b), the habitat becomes empty and state 2 is changed into state 0. The parameter f is defined as the resettlement rate. For

example, if $f = 0$, adults escaping from their original sites do not settle in empty sites of the same habitat again, thus completely leaving the habitat to go elsewhere.

After some nests in state 2 are harvested and others remain there, adults whose nests are not harvested lay eggs which hatch; then, state 2 is changed into state 3 at the rate of $(1 - d)(1 - p_u y_u)$.

As the unsustainable harvesters also harvest nests in state 3 at the unsustainable harvesting effort (p_u), state 3 is changed into state 1 at the rate of $(1 - a_2)(1 - d)(1 - d_e)p_u y_u$ (X1 in Figure 2b) because the unsustainable harvesters throw away eggs and hatchlings in the nests. Let a_2 be the probability that the behavior of unsustainable harvesting forces the adult in state 3 to leave the original site. When the adult that escapes from the original site at the rate of $a_2 p_u y_u (1 - d)(1 - d_e)$ (X2 in Figure 2b), it can find a new empty site and settle there at the rate of $f x_0(t)$, and state 3 is changed into state 1 at the rate of $a_2 p_u y_u (1 - d)(1 - d_e) f x_0(t)$ (X2 to X4 in Figure 2b). If they fail to find a new empty site (from X2 to X3 in Figure 2b), the habitat becomes empty, and state 3 is changed into state 0.

The fledglings in the nests which have not been abandoned in state 3 leave the original site, and state 3 is changed into state 2 at the rate of $(1 - d)(1 - d_e)(1 - p_u y_u)g$. When a new adult leaving the original nest (state 3) can find a new empty site at the rate of s , state 0 is

changed into state 1 at the rate of $(1 - d)(1 - d_e)(1 - p_u y_u)sg$.

When incorporating the effect of sustainable and unsustainable harvesters into eq. (1), we construct the time-discrete equations for the population dynamics of swiftlets when three types of harvesters exist in the habitat:

$$x_0(t + 1) = x_0(t) + dx_1(t) + dx_2(t) + dx_3(t) - (1 - d)(1 - d_e)(1 - p_u y_u)sgx_0(t)x_3(t) \\ + a_1 p_u y_u (1 - d)x_2(t)(1 - fx_0(t)) + a_2 p_u y_u (1 - d)(1 - d_e)x_3(t)(1 - fx_0(t)) , \quad (3a)$$

$$x_1(t + 1) = x_1(t) + (1 - d)(1 - d_e)(1 - p_u y_u)sgx_0(t)x_3(t) - dx_1(t) - h(1 - d)x_1(t) \\ + (1 - d)p_s y_s x_2(t) + (1 - d)p_u y_u [(1 - a_1) + a_1 fx_0(t)]x_2(t) \\ + (1 - d)(1 - d_e)p_u y_u [(1 - a_2) + a_2 fx_0(t)]x_3(t) , \quad (3b)$$

$$x_2(t + 1) = x_2(t) + h(1 - d)x_1(t) + (1 - d)d_e x_3(t) + (1 - d)(1 - d_e)(1 - p_u y_u)gx_3(t) \\ - dx_2(t) - b(1 - d)(1 - p_s y_s - p_u y_u)x_2(t) - (1 - d)(p_s y_s + p_u y_u)x_2(t) , \quad (3c)$$

$$x_3(t + 1) = x_3(t) + b(1 - d)(1 - p_s y_s - p_u y_u)x_2(t) - (1 - d)d_e x_3(t) - dx_3(t) \\ - (1 - d)(1 - d_e)[(1 - p_u y_u)g + p_u y_u]x_3(t) . \quad (3d)$$

There are two equilibrium points of eq. (3): $(x_0^*, x_1^*, x_2^*, x_3^*) = (1, 0, 0, 0)$ and (X_0, X_1, X_2, X_3) (see Appendix B for X_0, X_1, X_2 and X_3). Appendix B suggests that the population never goes extinct for some parameters, which are discussed next.

Result 2: The results of the open-access model

What concerns harvesters the most is the immediate harvesting yield rather than the sustainability of the ecosystem. We calculate the immediate return of the sustainable and unsustainable harvesters per time step when the population reaches the equilibrium point. Let $E_s(y_s, y_u)$ and $E_u(y_s, y_u)$ be the immediate return per sustainable and unsustainable harvester per time step when the frequencies of sustainable and unsustainable harvesters in the habitat are y_s and y_u , respectively, and the population reaches an equilibrium. We assume that the only concern of the harvesters is the immediate return, and do not consider the future return. Eq. (3) shows that $E_s(y_s, y_u)$ and $E_u(y_s, y_u)$ corresponds to $(1 - d)p_s x_2^*$ and $(1 - d)p_u(x_2^* + (1 - d_e)x_3^*)$, respectively. Therefore, if the condition $p_s/p_u > 1 + (1 - d_e)x_3^*/x_2^*$ is satisfied, $E_u(y_s, y_u)$ can be less than $E_s(y_s, y_u)$. As $(1 - d_e)x_3^*/x_2^*$ is positive, p_s should be higher than p_u . The swiftlet population can be sustainable and $E_s(y_s, y_u)$ can be higher than $E_u(y_s, y_u)$ when the harvesting effort of sustainable harvesters is high and that of unsustainable harvesters is low. This result seems to show the incentive to harvest nests in a sustainable manner. However, unsustainable harvesters never stop at anything to make gains and will therefore employ substantially more effort to harvest nests than the sustainable harvesters, so the appropriate assumption is $p_u \geq p_s$ rather than $p_s > p_u$. Therefore, the condition $p_s/p_u > 1 + (1 - d_e)x_3^*/x_2^*$ is

never satisfied and $E_u(y_s, y_u)$ is always higher than $E_s(y_s, y_u)$. This result shows the incentive to harvest nests in an unsustainable manner. It is surprising that Appendix B and $p_s/p_u > 1 + (1 - d_e)x_3^*/x_2^*$ indicate that the value of a_1 and a_2 do not influence the stability of the swiftlet population when $f = 1$.

Model 3: The property rights model

In the previous section, we showed that the unsustainable harvesters generally obtain higher immediate return than sustainable harvesters; the overharvesting problem cannot be solved. In reality, different proprietors have private property rights of different sites in the habitat. We will show that private property rights cannot solve the overharvesting problem on its own in the case of swiftlets, but both the unique ecological feature of swiftlets and private property rights, taken together, can solve it. Hereafter, we call this model the property rights model.

We assume that each proprietor is one of three types of harvesters, and each proprietor can only harvest nests in the sites on his/her own section of the habitat (Figure 3). Therefore, the whole habitat is divided into three sub-types: non-harvester habitat, sustainable harvester habitat, and unsustainable harvester habitat. In reality, the smugglers harvest any nests in the

proprietor's cave sites. If we assume the smugglers in the property rights model, we need to add more assumptions, which would make our model more complicated. Therefore, we do not assume them. We will discuss it in Discussion.

Let $x_{ni}(t)$, $x_{si}(t)$, and $x_{ui}(t)$ defined as the density of state i at time step t for the non-harvesters habitat, the sustainable harvesters habitat, and the unsustainable harvesters habitat, respectively, with $\sum_i x_{ni}(t) + \sum_i x_{si}(t) + \sum_i x_{ui}(t) = 1$ ($i = 0, 1, 2$ or 3). We do not make spatial structure considerations, such as harvesters of the same type are neighbors; all harvesters are randomly distributed in the whole habitat. Basically, the states change following eq. (1) in the non-harvester habitat, eq.(3) with $y_s = 1$ in the sustainable harvester habitat, and eq. (3) with $y_u = 1$ in the unsustainable harvester habitat. We assume that the proprietor harvester type does not change in time, and therefore the total densities of non-harvesters ($\sum_i x_{ni}(t) \equiv x_n$), sustainable harvesters ($\sum_i x_{si}(t) \equiv x_s$), and unsustainable harvesters ($\sum_i x_{ui}(t) \equiv x_u$) are fixed in time.

We introduce two new assumptions (Figure 3). The first assumption is that, after the fledglings leave the nest and become adult in state 3 in the three types of habitats, they randomly settle at empty sites in the non-harvester habitat at the rate of s_n , in the sustainable harvester habitat at the rate of s_s , and in the unsustainable harvester habitat at the rate of s_u .

Let $M_1(t)$ be the total number of fledglings leaving their original nest and becoming adult in state 3, so $M_1(t)$ becomes:

$$M_1(t) = (1-d)(1-d_e)gx_{n3}(t) + (1-d)(1-d_e)gx_{s3}(t) + (1-d)(1-d_e)(1-p_u)gx_{u3}(t) \quad (4a)$$

Therefore, state 0 in each type of habitat is changed into state 1 at the settlement rate of $s_j M_1(t)$ ($j = n, s$ or u). We assume $s_n = s_s = s_u = 1$.

The second assumption is that, after the adults escape from the original nest in state 2 and state 3 in the unsustainable harvester habitat, they resettle at empty sites in the non-harvester habitat at the rate of f_n , in the sustainable harvester habitat at the rate of f_s , and in the unsustainable harvester habitat at the rate of f_u . Let $M_2(t)$ be the total number of adults escaping their original nest in state 2 and state 3 in the unsustainable harvester habitat. Hence, $M_2(t)$ is given by:

$$M_2(t) = a_1 p_u (1-d) x_{u2}(t) + a_2 p_u (1-d)(1-d_e) x_{u3}(t). \quad (4b)$$

Therefore, state 0 changes to state 1 in each type of habitat at the resettlement rate of $f_j M_2(t)$ ($j = n, s$ or u). If adults escaping from the unsustainable habitat never resettle at any empty sites in the unsustainable harvester's habitat, $f_u = 0$. It is natural to assume that $f_s = f_n$ because the swiftlets resettle in the same way either in the sustainable harvester's habitat or the non-harvester's habitat.

Based on these new assumptions, we construct the time-discrete equations of the population dynamics of swiftlets when property rights are introduced (Figure 3). The equations describing figure 3 are:

$$x_{n0}(t+1) = x_{n0}(t) + d(x_{n1}(t) + x_{n2}(t) + x_{n3}(t)) - M_1(t)s_n x_{n0}(t) - M_2(t)f_n x_{n0}(t) \quad (5a)$$

$$x_{n1}(t+1) = x_{n1}(t) - dx_{n1}(t) - h(1-d)x_{n1}(t) + M_1(t)s_n x_{n0}(t) + M_2(t)f_n x_{n0}(t) \quad (5b)$$

$$x_{n2}(t+1) = x_{n2}(t) + h(1-d)x_{n1}(t) + (1-d)d_e x_{n3}(t) + (1-d)(1-d_e)gx_{n3}(t) - dx_{n2}(t) - b(1-d)x_{n2}(t) \quad (5c)$$

$$x_{n3}(t+1) = x_{n3}(t) + b(1-d)x_{n2}(t) - (1-d)d_e x_{n3}(t) - dx_{n3}(t) - (1-d)(1-d_e)gx_{n3}(t) \quad (5d)$$

$$x_{s0}(t+1) = x_{s0}(t) + d(x_{s1}(t) + x_{s2}(t) + x_{s3}(t)) - M_1(t)s_s x_{s0}(t) - M_2(t)f_s x_{s0}(t) \quad (5e)$$

$$x_{s1}(t+1) = x_{s1}(t) - dx_{s1}(t) - h(1-d)x_{s1}(t) + (1-d)p_s x_{s2}(t) + M_1(t)s_s x_{s0}(t) + M_2(t)f_s x_{s0}(t) \quad (5f)$$

$$x_{s2}(t+1) = x_{s2}(t) + h(1-d)x_{s1}(t) + (1-d)d_e x_{s3}(t) + (1-d)(1-d_e)gx_{s3}(t) - dx_{s2}(t) - b(1-d)(1-p_s)x_{s2}(t) - (1-d)p_s x_{s2}(t) \quad (5g)$$

$$x_{s3}(t+1) = x_{s3}(t) + b(1-d)(1-p_s)x_{s2}(t) - (1-d)d_e x_{s3}(t) - dx_{s3}(t) - (1-d)(1-d_e)gx_{s3}(t) \quad (5h)$$

$$x_{u0}(t+1) = x_{u0}(t) + d(x_{u1}(t) + x_{u2}(t) + x_{u3}(t)) + a_1 p_u (1-d)x_{u2}(t) + a_2 p_u (1-d)(1-d_e)x_{u3}(t) - M_1(t)s_u x_{u0}(t) - M_2(t)f_u x_{u0}(t) \quad (5i)$$

$$x_{u1}(t+1) = x_{u1}(t) - dx_{u1}(t) - h(1-d)x_{u1}(t) + (1-d)(1-a_1)p_u x_{u2}(t) + (1-a_2)p_u (1-d)(1-d_e)x_{u3}(t) + M_1(t)s_u x_{u0}(t) + M_2(t)f_u x_{u0}(t) \quad (5j)$$

$$x_{u2}(t+1) = x_{u2}(t) + h(1-d)x_{u1}(t) + (1-d)d_e x_{u3}(t) + (1-d)(1-d_e)(1-p_u)gx_{u3}(t) - dx_{u2}(t) - b(1-d)(1-p_u)x_{u2}(t) - (1-d)p_u x_{u2}(t) \quad (5k)$$

$$x_{u3}(t+1) = x_{u3}(t) + b(1-d)(1-p_u)x_{u2}(t) - (1-d)d_e x_{u3}(t) - dx_{u3}(t) - (1-d)(1-d_e)(1-p_u)gx_{u3}(t) - p_u (1-d)(1-d_e)x_{u3}(t) \quad (5l)$$

If $x_n = 1$, eq. (5) is the same as eq. (1); if $x_s = 1$ (or $x_u = 1$), eq. (5) is the same as eq. (3) with $y_s = 1$ (or $y_u = 1$). Following the mathematical methods of the previous sections, we obtain the

local unstable condition of $x_{n0} + x_{s0} + x_{u0} = x_0 = 1$ numerically, and the equilibrium points by numerical calculations. Focusing on the parameters a_1 , a_2 , f_n , f_s , f_u , p_s , and p_u , we investigate the effect of the unique behavior of swiftlets on the ecological dynamics under property rights.

Result 3: Results of the property rights model

First, to see if the property rights model promotes the sustainability of swiftlets, we compare the immediate return of the sustainable and unsustainable harvesters per time step. When x_n , x_s , and x_u are fixed and the population reaches the equilibrium point, the immediate returns, $E_s(x_s, x_u)$ and $E_u(x_s, x_u)$, correspond to $(1 - d)p_s x_{s2}^*/x_s$ and $(1 - d)p_u(x_{u2}^* + (1 - d_e)x_{u3}^*)/x_u$, respectively. We numerically calculate $E_u(x_s^*, x_u^*)$ and $E_s(x_s^*, x_u^*)$ and the swiftlet population dynamics (Figure 4). Figure 4 shows the immediate return of two types of harvesters and the swiftlet population dynamics when $x_n = 0.23$, $x_s = 0.1$, and $x_u = 0.67$, which are the ratios of the different harvester types in Niah Cave, Borneo, Malaysia (Personal communication from Dr. Lim, Chan Koon). We assume that $s_n = s_s = s_u = 1$, which is reasonable because adults leave their parental habitats and settle at empty sites without being influenced by harvesters. We also assume that $f_n = f_s = 1$, because adults do not have any

preference for either non-harvester habitats or sustainable harvester habitats, and resettle at either non-harvester and sustainable harvester habitats without choosing between them. We show how the parameters a_1 , a_2 , and f_u influence the ecological dynamics and the harvester's immediate return. When $a_1 = a_2 = 0$, a situation is created in which adults do not escape from the habitat after unsustainable harvesters harvest the nests, $E_u(x_s^*, x_u^*) > E_s(x_s^*, x_u^*)$ in $p_s = p_u = 0.1$ (Figure 4(a) and (b)). When $a_1 = a_2 = 1$ and $f_u = 1$ (or $f_u = 0$), that is, adults escape from the unsustainable harvester's habitat after unsustainable harvesters harvest the nests, and those that escaped from the habitat do (or do not) resettle in the habitat of unsustainable harvesters, $E_s(x_s^*, x_u^*) > E_u(x_s^*, x_u^*)$ in $p_s = p_u = 0.2$ (or 0.1) (Figure 4c-f). Figure 4 indicates that it is critical for the sustainable harvester's immediate return to be higher than the unsustainable harvester's to benefit the adults that escape from the habitats of unsustainable harvesters.

We performed a numerical analysis using three parameter sets in Figure 4. To confirm our findings, we investigate the parameter dependence of the harvesting effort ($p_s = p_u$) and the probability of escape ($a_1 = a_2$) on the difference in the yield between the sustainable harvester and the unsustainable harvester (Figure 5). Figure 5 shows that $E_u(x_s^*, x_u^*) > E_s(x_s^*, x_u^*)$ when adults do not escape from the habitats of unsustainable harvesters ($a_1 = a_2 = 0$).

When the probability of escape is higher, $E_s(x_s^*, x_u^*) > E_u(x_s^*, x_u^*)$ holds, especially if the harvesting effort is not low. Low harvesting effort gives the unsustainable harvesters an advantage over the sustainable ones because the population of the swiftlets is abundant, and unsustainable harvesting does not deteriorate the population in the case of low harvesting effort. By comparing Figure 5(a) with Figure 5(b), we find that if the adults who escape from the unsustainable harvester's habitats do not resettle in the unsustainable harvester's habitat ($f_u = 0$), the swiftlet population goes extinct when the harvesting effort is not low (Figure 5b). This happens because resettling even at the unsustainable harvester's habitat helps sustain the population size.

In Figures 4 and 5, we assume that $p_s = p_u$. Figure 6 shows how p_s and p_u influence the outcomes. When adults do not escape from unsustainable habitats ($a_1 = a_2 = 0$), $E_u(x_s^*, x_u^*) > E_s(x_s^*, x_u^*)$ always holds (Figure 6a). The population is maintained only for low p_u . When adults escape from the unsustainable habitats ($a_1 = a_2 = 1$), higher p_u makes the difference between $E_s(x_s^*, x_u^*)$ and $E_u(x_s^*, x_u^*)$ higher (Figures 6b and c). This is because high p_u facilitates the escape of the adults from the unsustainable harvester's habitat, and this gives sustainable harvesters an advantage over unsustainable harvesters.

Now we will compare the open-access model and the property right model in terms of

the immediate return per harvester per time step. The value of a_1 and a_2 does not influence the sustainability of swiftlet population when $f=1$ in the open-access model, or when $f_n=f_s=f_u=1$ in the property rights model (Figures 5a and 6b). $E_s(x_s^*, x_u^*)$ can be higher than $E_u(x_s^*, x_u^*)$ regardless of whether p_s is higher than p_u , and $E_s(x_s^*, x_u^*)$, especially, can be much higher than $E_u(x_s^*, x_u^*)$ when p_u is high and p_s is low in the property right model (Figure 6b), but only when $p_s > p_u$ in the open-access model. The property right model promotes sustainable harvesting more than the open-access model.

In previous figures, we used Niah cave's ratio of non-harvesters, sustainable harvesters, and unsustainable harvesters ($x_n = 0.23$, $x_s = 0.1$ and $x_u = 0.67$), and examine how the ratio of harvesters influences the outcomes. Figure 7a shows the differences in the immediate return between sustainable harvesters and unsustainable harvesters when x_n , x_s and x_u are varied under the conditions $x_n + x_s + x_u = 1$, when adults escape from the unsustainable habitats ($a_1 = a_2 = 1$), and when the escaping adults resettle at the unsustainable harvester's habitats ($f_u = 1$). Figure 7a indicates that $E_s(x_s^*, x_u^*) > E_u(x_s^*, x_u^*)$ holds unless the unsustainable harvester's ratio is very high. Therefore, the case of Niah's cave is not special. Figure 7b shows the population size, which is positive in these parameter sets.

Discussion and Conclusions

It is important to make use of nature in a sustainable way to receive its benefits for a long time, and, thus, this topic has attracted the interests of many people. However, establishing a sustainable pattern of utilization might not be easy. If the habitat is open-access, for example, unsustainable harvesters always reap more benefits than sustainable harvesters, assuming unsustainable harvesters make more of an effort to harvest nests than sustainable harvesters would. As a result, the harvesters will become unsustainable in the short run, and the population of the targeted species would go extinct. Even if we remedy the drawback of open access by introducing a private property right system in the habitats, this institution cannot always solve the overuse problem. What factors besides the property right can solve this problem?

It is sometimes the case that local people who use the ecosystem to make a living know the unique features of the ecosystem, and which features would influence the decision making of harvesters and the yield of harvesting. A canonical example is the case of swiftlets in Sarawak, Malaysia. Swiftlets are said to avoid places where unsustainable harvesters are collecting their nests. As a result, some local people believe that the immediate return of unsustainable harvesters will eventually be lower than that of sustainable harvesters. This

behavior of swiftlets is interpreted as indirect punishment, though without any intentionality on their part. If this behavior benefits sustainable harvesters, their sustainable pattern of using the population may prevail. For this reason, we theoretically investigate whether the indirect punishment results in benefits to the sustainable harvesters. We hope that the ecological feature of swiftlets in addition to the introduction of property rights system may promote the sustainable use of swiftlets and other resources.

We find that, in the open-access habitat in which swiftlets leave due to the behavior of unsustainable harvesters, if sustainable harvesters make much more of an effort to harvest nests than unsustainable harvesters would, sustainable harvesters obtain more benefits than unsustainable harvesters, which can lead to sustainable usage of swiftlets. However, unsustainable harvesters generally make more of an effort to harvest nests than sustainable harvesters would, and then the unsustainable harvesters obtain more benefits than the sustainable harvesters. It is natural to suppose that this would lead to all harvesters becoming unsustainable ones though we have not considered that players can choose which type of harvesters they would be. We show that both the indirect punishment of swiftlets (high a_1 and a_2) and private property rights give sustainable harvesters an advantage over unsustainable harvesters, especially when the escaping swiftlets resettle at any harvester habitat ($f_s = f_u = f_n$

=1). However, if the escaping swiftlets do not resettle at the unsustainable harvester's habitat ($f_u = 0$), the dynamics do not work as indirect punishment on unsustainable harvesters; this counterintuitive situation occurs because as the swiftlet population reduces in size, the immediate return also becomes lower, and the parameter region where the population goes extinct increases. These findings indicate that the unique ecological features of swiftlets and property rights have a substantial combined effect on both the swiftlet population and the immediate return.

Our results, however, also show that property rights do not always give sustainable harvesters a higher immediate return than unsustainable harvesters if the unsustainable harvester's harvesting effort is too low (Figure 6b and c) even though the indirect punishment of the swiftlets is present (high a_1 and a_2). This implies that property rights are not always a panacea for implementing the sustainable usage of renewable resources, even in a world supported by the indirect punishment of nature. This may imply that it is not always easy to establish a sustainable resource use among harvesters only by introducing an institutional measure such as a property rights system without some regulation from the government. This study also suggests that not only regulations and rules established by humans but also unique ecological features may help achieve the sustainable usage of ecosystem, and we should

scrutinize the ecological features of wildlife carefully before establishing regulations and rules for sustainable usage of wildlife. We could in this way save unnecessary rules and regulations which may result in excessive costs.

In the swiftlet case, the by-products of adults have economic value but the adults themselves do not. This distinctive character is not why the immediate return of sustainable harvesters is higher than that of unsustainable harvesters. Our results suggest, more generally, that if the relationship between the life history of targeted wildlife and human harvesting behavior is similar to Figures 2 and 3, the immediate return of harvesters who harvest the targeted wildlife in a sustainable way could exceed that of unsustainable harvesters in the habitat with property rights.

It should be noted that our model does not include smugglers who intrude into the cave illegally and harvest nests in an unsustainable way because their behavior is similar to that of unsustainable harvesters. If we explicitly assume smugglers, we introduce cave guards who stand at the cave gate, monitor, and eject smugglers to the model assumption (Lim and Earl of Cranbrook 2002). The problem is that different caves have a different number of gates. If a cave has one gate, it is easy to expel smugglers from the cave. Otherwise, it is more difficult to expel them. In future work, we will consider the effect of gate guards on the exclusion of

smugglers.

We assume that high harvesting effort implies that the price of a nest is higher and harvesters have an incentive to harvest even more nests. This assumption is based on the catch-per-unit-effort production function (Clark 1990): the net profit Π can be described as $\Pi = \alpha q E S - w E^2 / 2$, in which q is the price, E is the effort, S is the harvesting stock, α is a constant, and w is a cost per effort. The harvesting cost is expressed by $C(E)$ with $dC/dE > 0$ and $d^2C/dE^2 > 0$, which is simply assumed by $w E^2 / 2$.

The profit is maximized when $E^* = \alpha q S / w$, which suggests that higher prices (higher q) make E^* higher. There are theoretical economics studies assuming that a price of renewable resource is dependent on how much each player exploits the renewable resource and then modeling the feedback between the long-term profit and the dynamics of renewable resource by using a differential game (Fujiwara 2008). Referring to the assumption of previous studies, we will extend our study by dealing with the dynamics of a nest price.

Even though both the swiftlet's indirect punishment and property rights seem to solve the overharvesting problem of swiftlets in Sarawak, the number of unsustainable harvesters is high compared with sustainable harvesters. This knowledge is a rule of thumb, but this knowledge has not been shared with all local people and harvesters (AO interviewing Dr Lim,

for example). As a result, many people still think that unsustainable harvesting makes more profit than sustainable harvesting. This paper verifies that the rule of thumb is correct. In the next step, we have to find ways to spread the knowledge over all stakeholders in order to manage the swiftlets population successfully.

There are some theoretical studies which combine ecological dynamics and human behavior, especially from the viewpoint of evolutionary game theory (Tavoni et al. 2012; Weitz et al. 2016; Chen and Szolnoki 2018). In those studies, as the evolutionary game dynamics, that is, on which the decision making or human behavior is focused, the assumption about ecological dynamics is very simple. As a result, the effect of ecological dynamics and life history of wildlife on human behavior has not been discussed adequately. In this paper, instead, we focused mainly on the outcomes of the complicated ecological dynamics while making a simple assumption about human behavior, decision making, and economic variables such as nest prices. In our future work, we will investigate the feedback between the ecological dynamics and the evolutionary game theory to show how human decision-making influences the ecological dynamics.

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Table 1 The Parameters List.

Parameter	Definition
d	The natural death rate
h	The nest-building rate
b	The breeding success rate
d_e	The egg loss rate
g	The fledging rate
s	The settlement rate
p_s	The sustainable harvesting effort
p_u	The unsustainable harvesting rate
a_1	The probability that the behavior of unsustainable harvesting forces the adult in state 2 to leave the original site
a_2	The probability that the behavior of unsustainable harvesting forces the adult in state 3 to leave the original site
f	The resettlement rate

Figure legend

Figure 1 The baseline model presenting swiftlet ecology

See the main text for the detailed explanation.

Figure 2 The flow of the open-access model

(a) shows the effect of sustainable harvesting on the baseline model. (b) shows the effect of unsustainable harvesting on the baseline model. After unsustainable harvesters harvest nests and throw away eggs and offspring, some adults in state 3 stay at the same site (X1), while others escape (X2). The site becomes empty (X3), and the adult settles at an empty site (X4). After unsustainable harvesters harvest nests, some adults in state 2 stay at the same site (Y1), while others escape (Y2). The site becomes empty (Y3), and the adult settles at an empty site (Y4). In both (a) and (b), the black line indicates the effect of each type of harvesters, and the gray line presents the baseline model or swiftlet ecology in Figure 1.

Figure 3 The flow of the property rights model

The arrow (1) means that an adult settles at an empty site chosen randomly; (2), adults escape from the unsustainable harvester's habitat; (3), grown-ups leave the parental habitats. See the detailed explanation in the main text.

Figure 4 The ecological dynamics of swiftlets and the immediate return of harvesters in the property rights model

(a), (c) and (e) show how the density of each state changes with time in the whole population.

The horizontal axis is for time and the vertical is for the density of each state. The gray line presents state 0; the dotted black, state 1; the black, state 2; the dotted gray, state 3. (b), (d)

and (f) present the immediate return per unit of time of either sustainable or unsustainable harvesters. The black line is for sustainable harvesters; the gray, the unsustainable harvesters.

The horizontal axis is for time and the vertical is for the immediate return. $a_1 = a_2 = 0$, $p_s = p_u$

$= 0.1$, and f_n, f_s , and f_u are arbitrary in (a) and (b); $f_n = f_s = f_u = 1$, $a_1 = a_2 = 1$, and $p_s = p_u = 0.2$,

in (c) and (d); $f_n = f_s = 1, f_u = 0$, $a_1 = a_2 = 1$, and $p_s = p_u = 0.1$, in (e) and (f). The other

parameters are: $d = 0.1$, $h = 1$, and $s_n = s_s = s_u = 1$. We assume that $y_n:y_s:y_u = x_n:x_s:x_u =$

0.23:0.1:0.67.

Figure 5 The difference in the immediate returns between the sustainable and unsustainable harvesters when $a_1 (= a_2)$ and $p_s (= p_u)$ are varied in the property rights model

The horizontal axis is for $a_1 (= a_2)$, which is between 0 and 1, and the vertical is for $p_s (= p_u)$, which is between 0.05 and 1. The color and the number indicate the difference in the immediate return between the sustainable and unsustainable harvesters. The gray scale bar presents the difference. If the value is positive, the immediate return of the sustainable harvesters is higher than that of the unsustainable harvesters; if it is negative, the immediate return of the unsustainable harvesters is higher than that of the sustainable harvesters. The white region means that the population is regarded as unstable. $f_n = f_s = f_u = 1$ in (a), and $f_n = f_s = 1$ and $f_u = 0$ in (b). The other parameters are: $d = 0.1$, $h = 1$, and $s_n = s_s = s_u = 1$. We assume that $y_n:y_s:y_u = x_n:x_s:x_u = 0.23:0.1:0.67$.

Figure 6 The difference in the immediate return between the sustainable and unsustainable harvesters when p_s and p_u are varied in the property rights model

The horizontal axis is for p_s , and the vertical is for p_u , and range between 0.05 and 1. The color and number indicate the difference in the yield between the sustainable and unsustainable harvesters. The gray scale bar presents the difference. If the value is positive,

the immediate return of the sustainable harvesters is higher than that of the unsustainable harvesters. The white region means that $x_0 = 1$ is interpreted as stable. $a_1 = a_2 = 0$, and f_n, f_s , and f_u are arbitrary in (a), $f_n = f_s = f_u = 1$ and $a_1 = a_2 = 1$ in (b), $f_n = f_s = 1, f_u = 0$, and $a_1 = a_2 = 1$ in (c), and. The other parameters are: $d = 0.1$, $h = 1$, and $s_n = s_s = s_u = 1$. We assume that $x_n : x_s : x_u = 0.23 : 0.1 : 0.67$.

Figure 7 The difference in the immediate return between the sustainable and unsustainable harvesters and the total swiftlet population size in the whole habitats when x_n , x_s , and x_u are varied under $x_n + x_s + x_u = 1$ in the property rights model

The left vertex of the triangle graphs is for $x_n = 1$, the right one is for $x_s = 1$, and the upper one is for $x_u = 1$. The bottom side of the triangle ones presents $x_n + x_s = 1$; the left side, $x_n + x_u = 1$; the right side, $x_u + x_s = 1$. In (a), the color and the number indicate the difference in the immediate return between the sustainable and unsustainable harvesters. The gray scale bar presents the difference. If the value is positive, the immediate return of the sustainable harvesters is higher than that of the unsustainable harvesters. In (b), the triangle graph indicates the swiftlet population density in the whole habitats, which calculated until 500

times and reaches in equilibrium. The gray scale bar presents the density. The parameters are:

$$d = 0.1, h = 1, s_n = s_s = s_u = 1, f_n = f_s = f_u = 1, a_1 = a_2 = 1, \text{ and } p_s = p_u = 0.2.$$

Figure 1

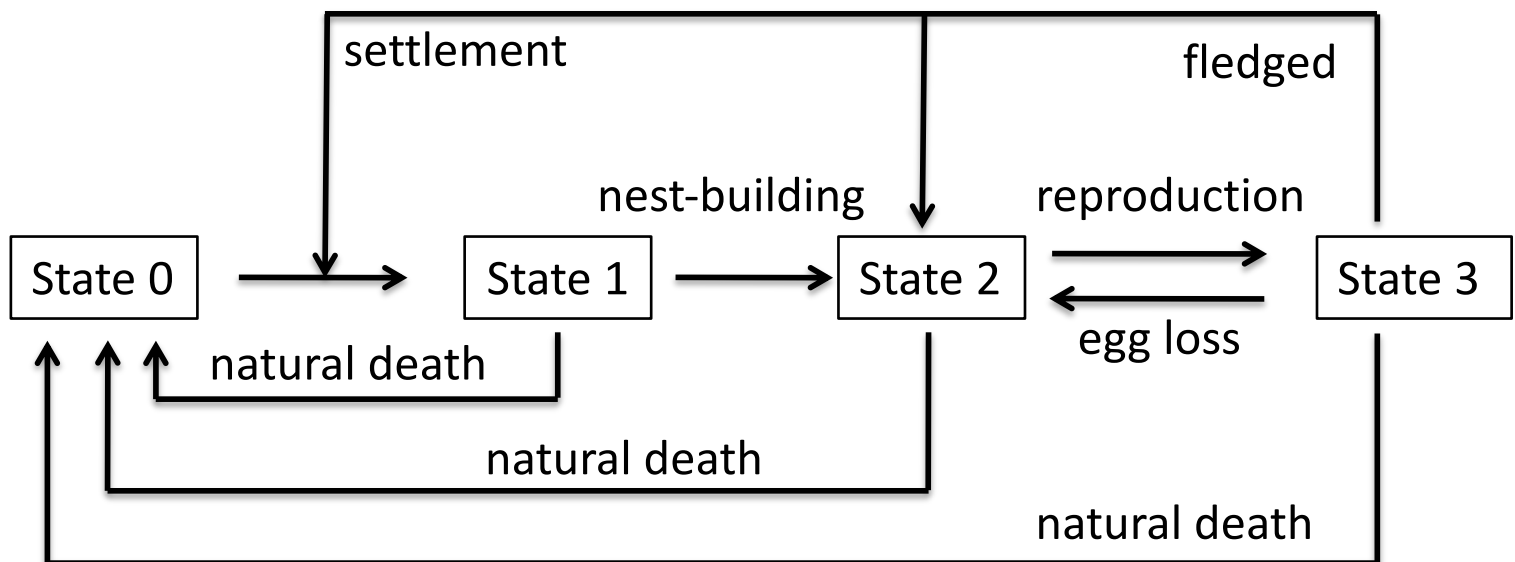
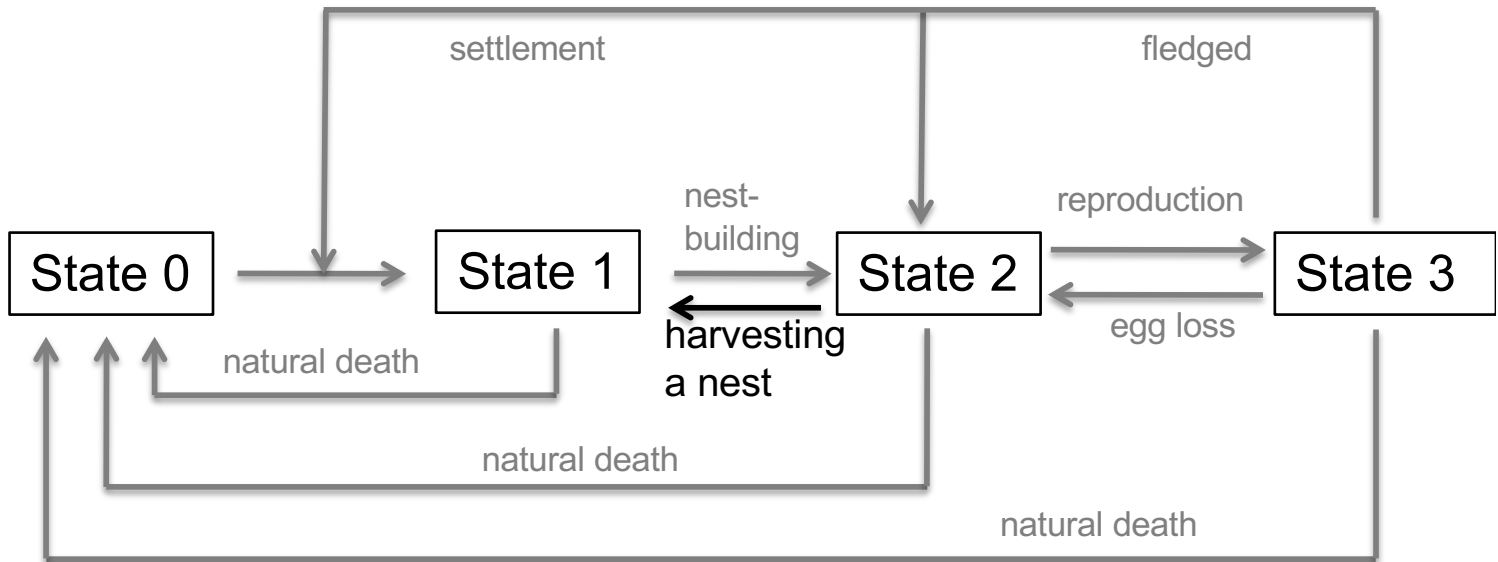


Figure 2

(a)



(b)

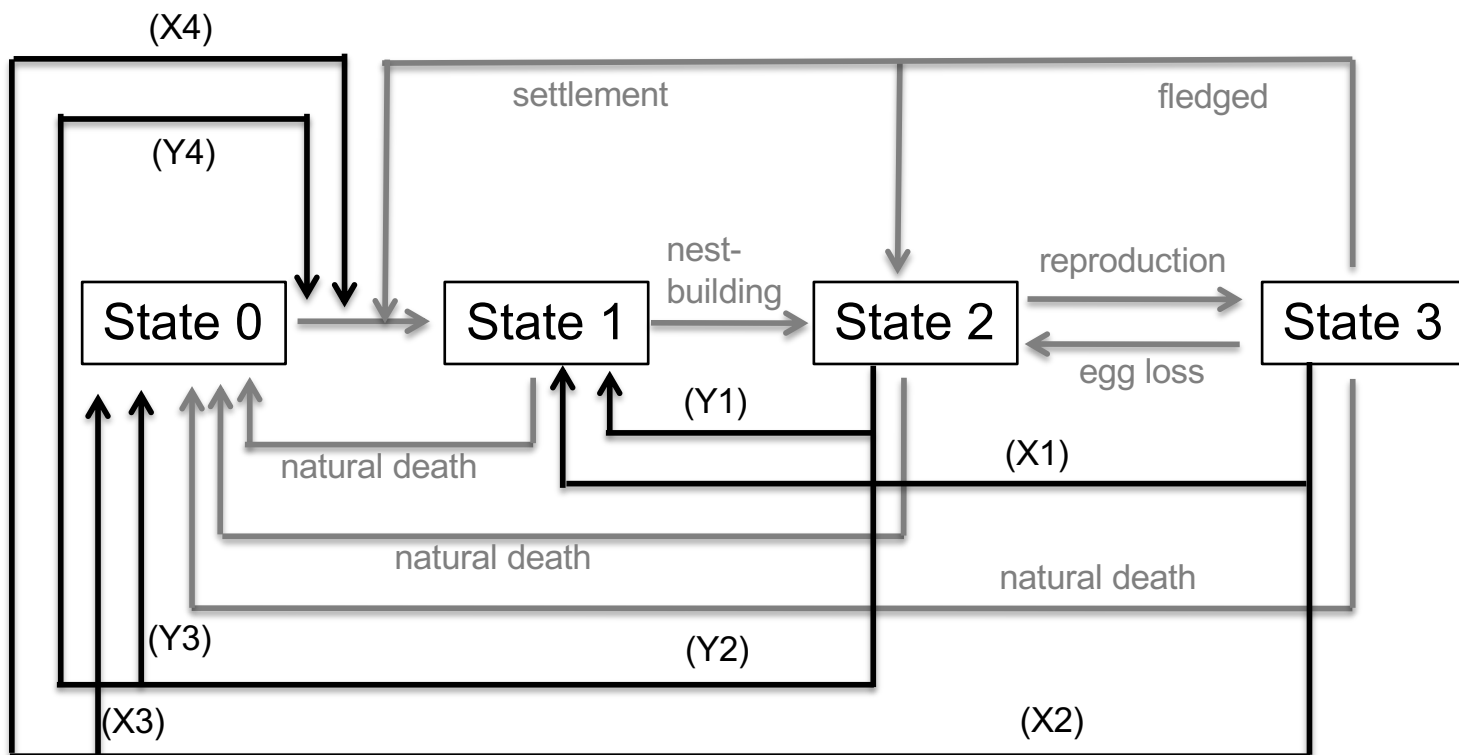


Figure 3

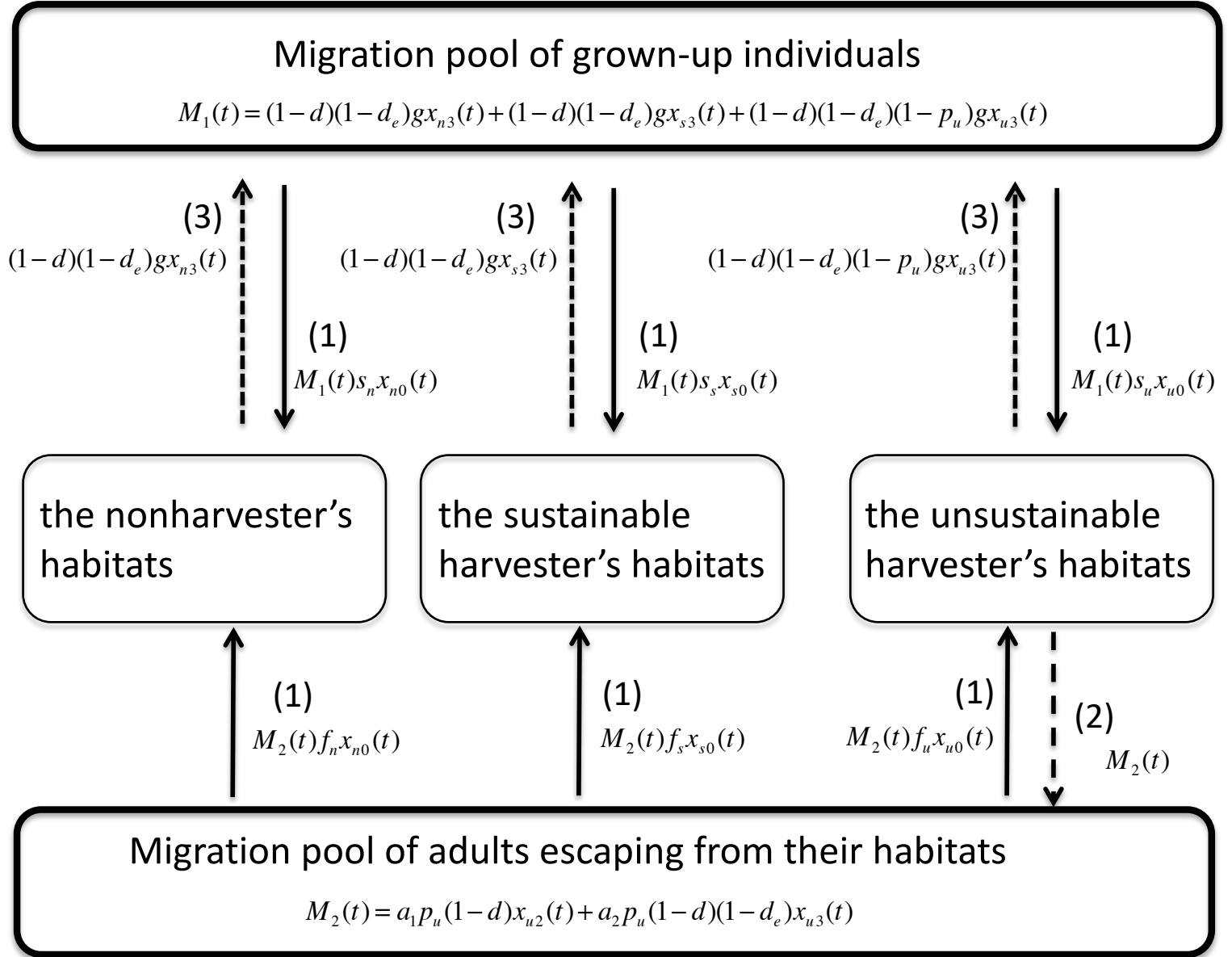


Figure 4

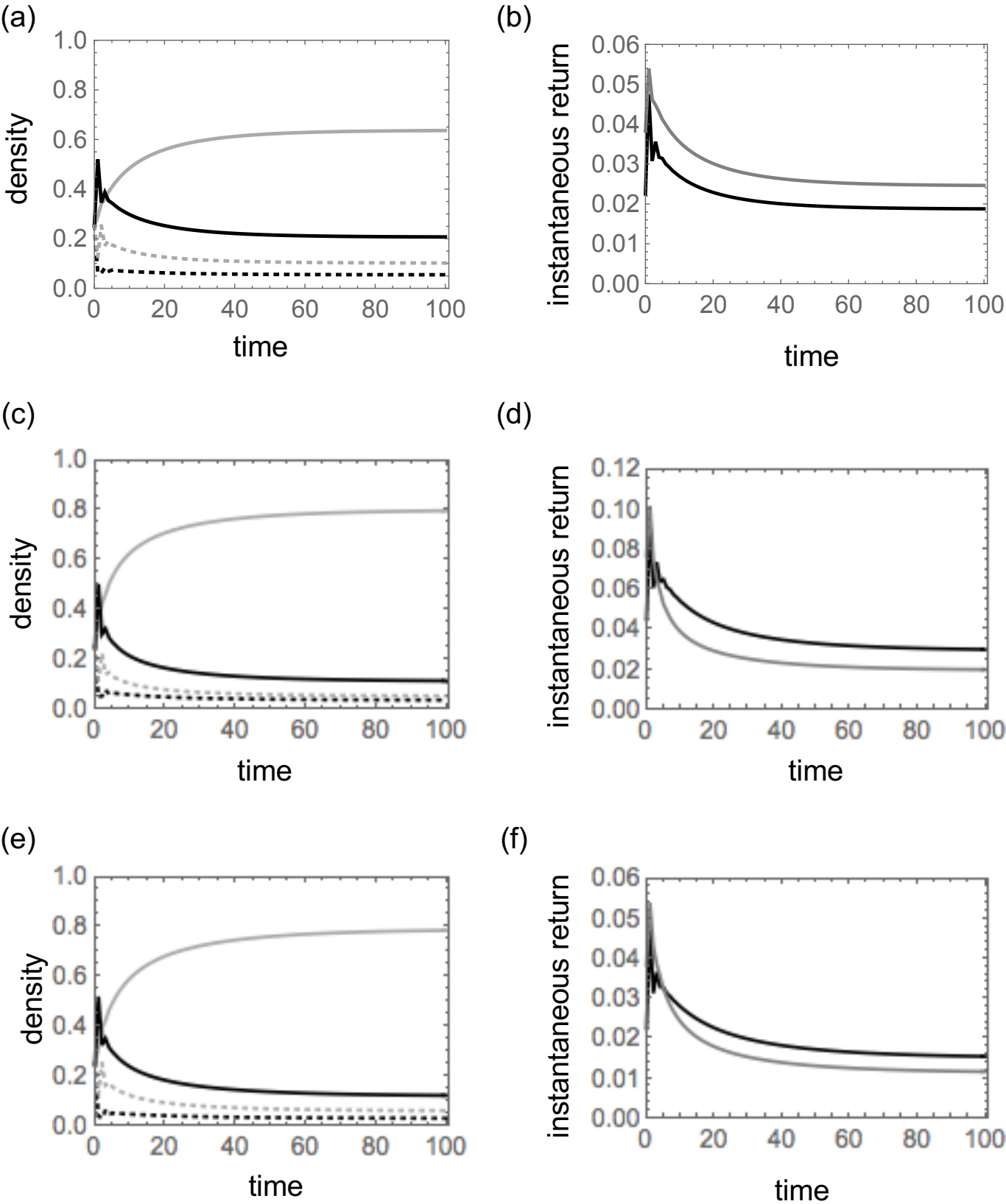
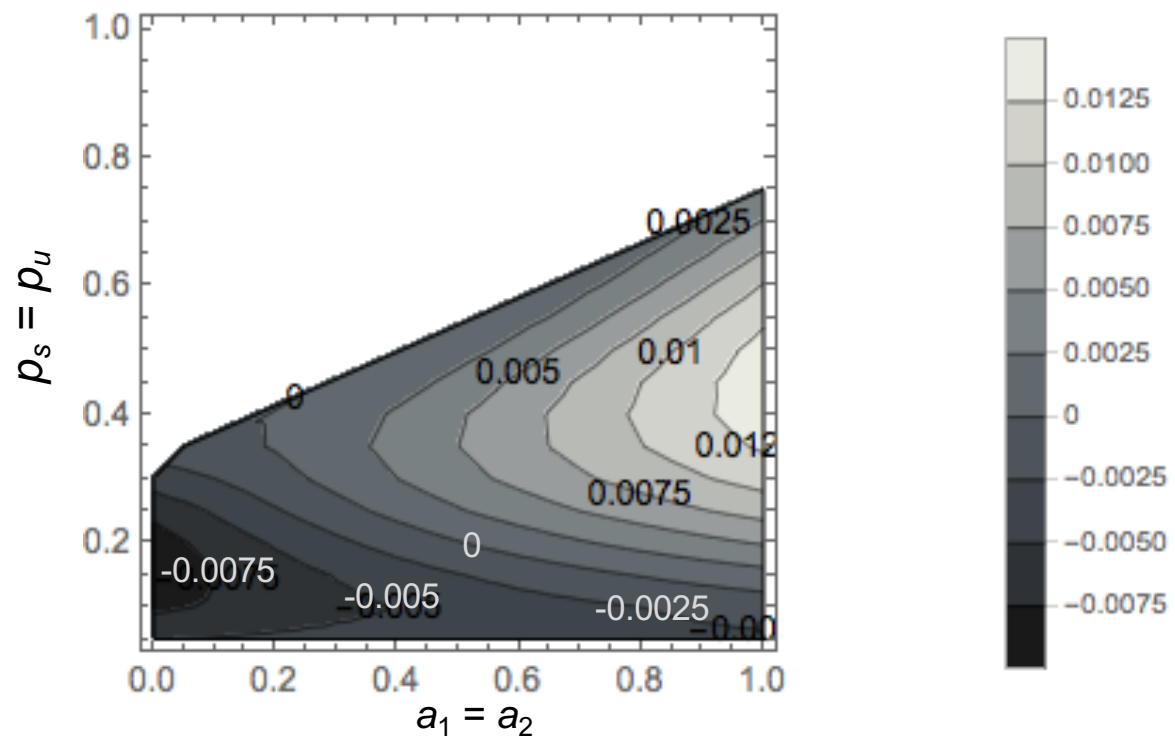


Figure 5

(a)



(b)

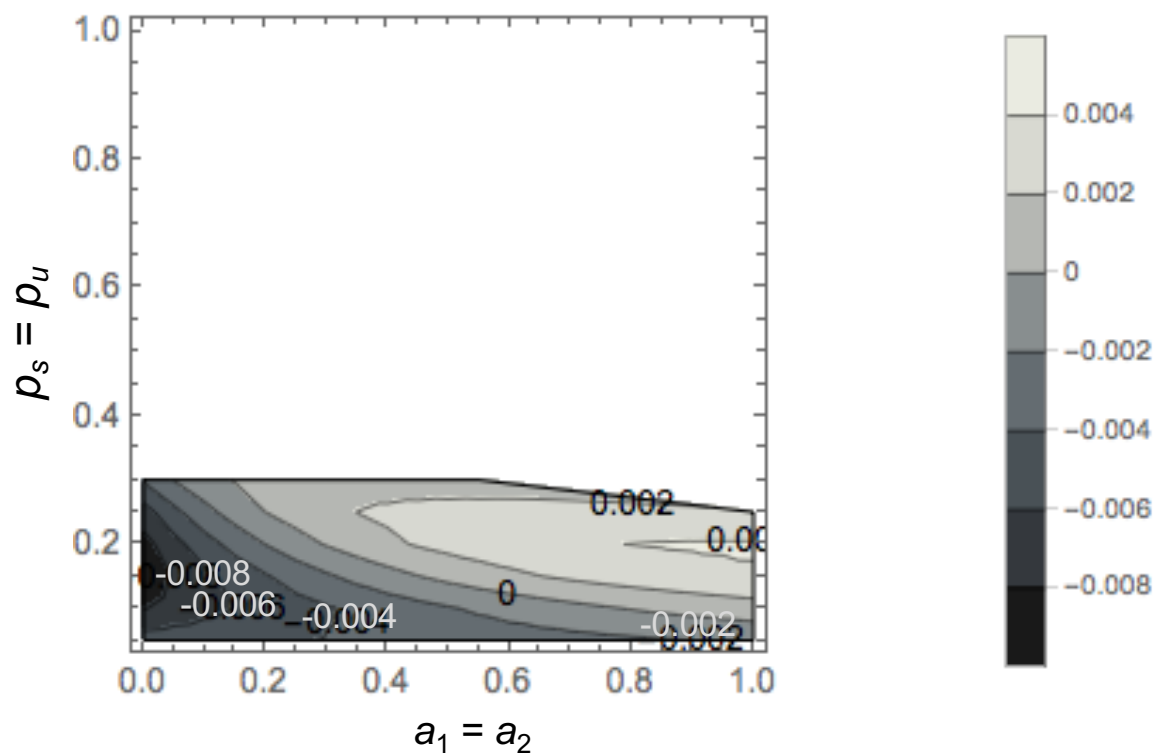


Figure 6

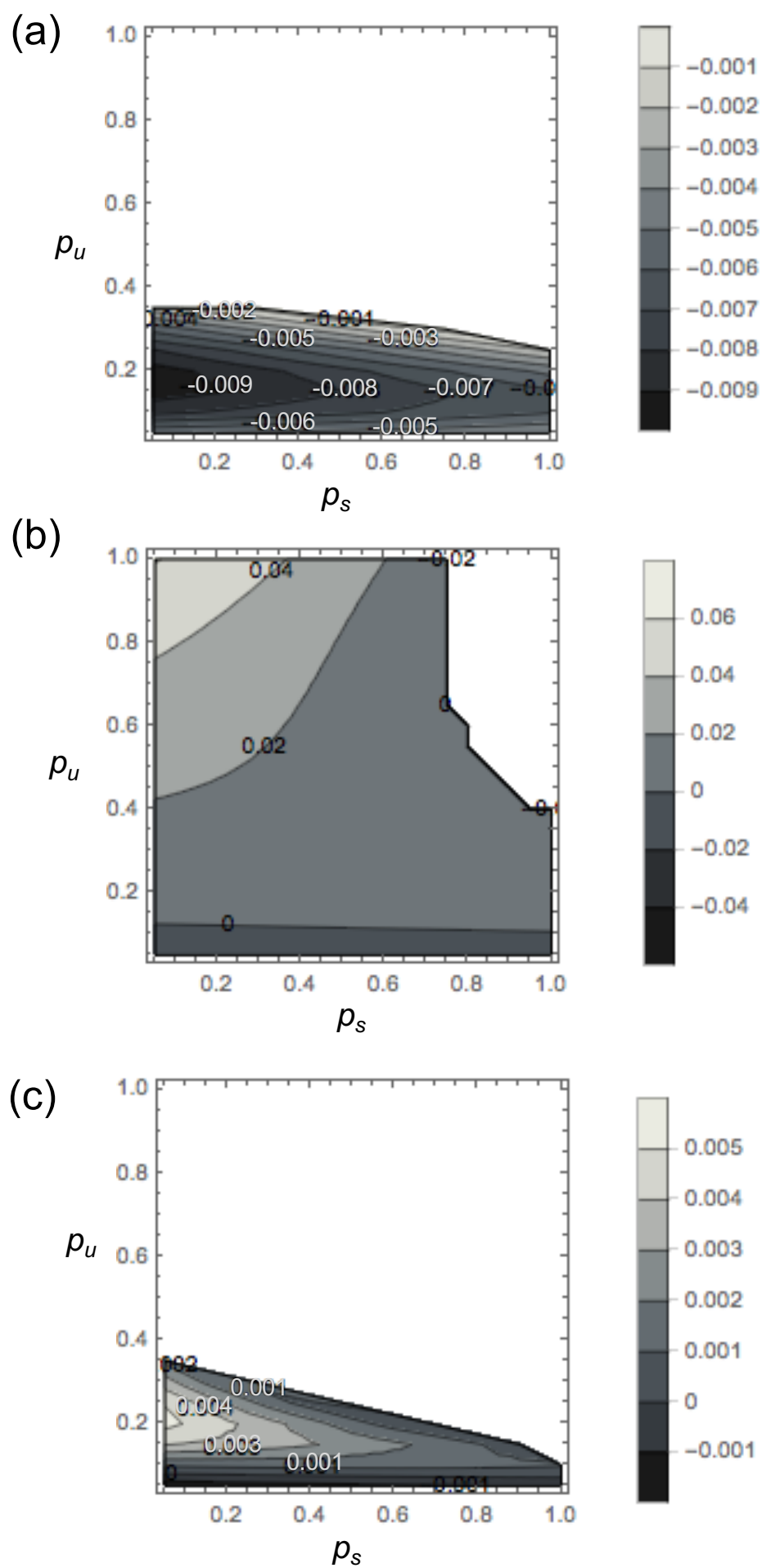
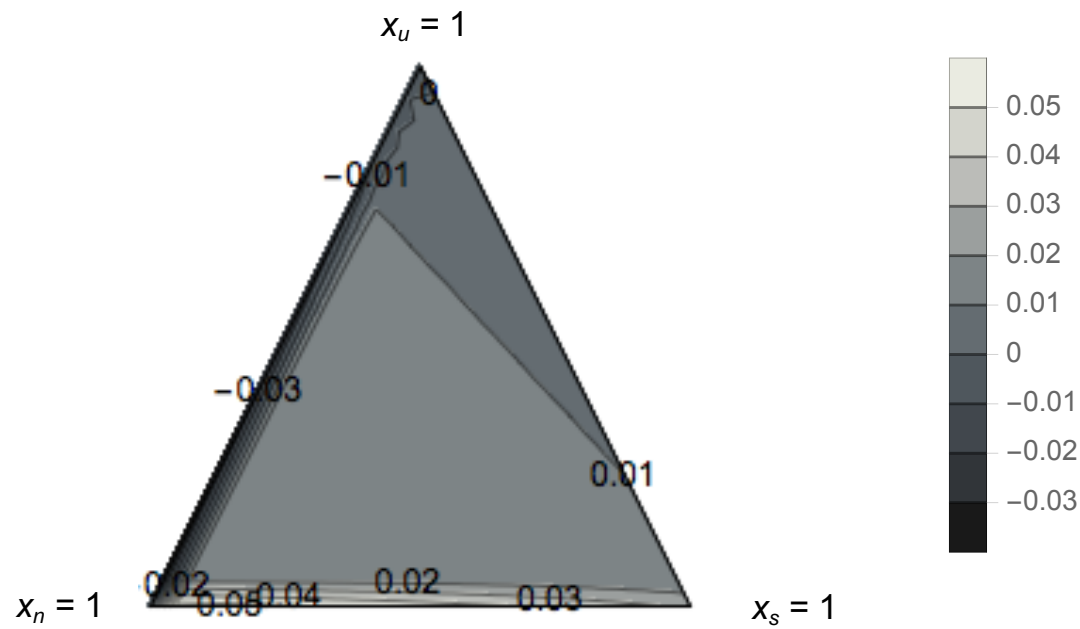
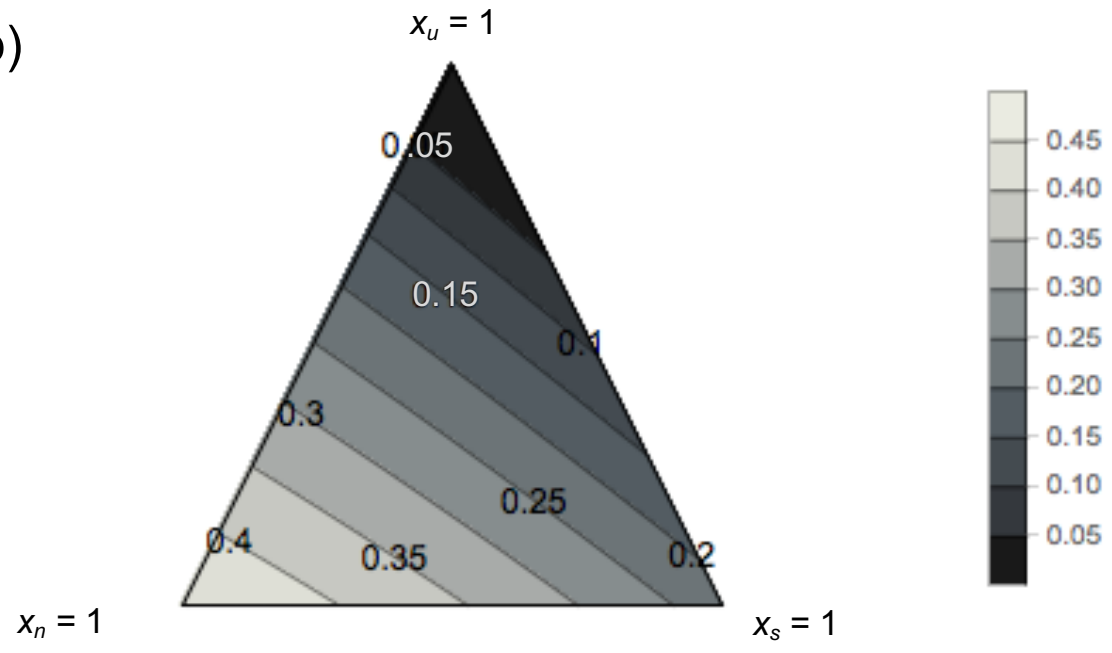


Figure 7

(a)



(b)



Appendix A

From eq. (1), we obtain two equilibrium points for $(x_0^*, x_1^*, x_2^*, x_3^*)$: one is $(1, 0, 0, 0)$ and

the other is an interior point. The interior equilibrium points of $(x_0^*, x_1^*, x_2^*, x_3^*)$ are:

$$\left(d \frac{A+B+1}{C}, B \left(\frac{1}{A+B+1} - \frac{d}{C} \right), \frac{1}{A+B+1} - \frac{d}{C}, A \left(\frac{1}{A+B+1} - \frac{d}{C} \right) \right),$$

$$\text{where } A = \frac{b(1-d)}{1-(1-d)(1-d_e)(1-g)},$$

$$B = \frac{1}{h(1-d)} \left[1 - (1-d)(1-b) - \frac{b(1-d)^2(d_e + (1-d_e)g)}{1-(1-d)(1-d_e)(1-g)} \right] \text{ and } C = (1-d)(1-d_e)gsA.$$

According to the local stability analysis of one equilibrium, $(x_0^*, x_1^*, x_2^*, x_3^*) = (1, 0, 0, 0)$, we obtain $(\lambda-1)J_1(\lambda) = 0$, in which λ is an eigenvalue and

$$\begin{aligned} J_1(\lambda) = & \lambda^3 - \lambda^2(1-d) \left[(1-b) + (1-d_e)(1-g) + (1-h) \right] \\ & + \lambda(1-d)^2 \left[\begin{aligned} & (1-b)(1-d_e)(1-g) - b(d_e + (1-d_e)g) \\ & + (1-h)(1-b) + (1-h)(1-d_e)(1-g) \end{aligned} \right] \\ & - (1-d)^3 \left\{ \begin{aligned} & (1-h) \left[(1-b)(1-d_e)(1-g) - b(d_e + (1-d_e)g) \right] \\ & + hb(1-d_e)gs \end{aligned} \right\} \end{aligned}$$

The boundary condition between the local stable and unstable region can be obtained from

$$J_1(1) = 0; h = H(d, d_e, g, s, b) \text{ in which}$$

$$H(d, d_e, g, s, b) = \frac{1-(1-d)(K+2)+(1-d)^2(2K+1)-(1-d)^3K}{(1-d)[-1+(1-d)(K+1)+(1-d)^2(-K+b(1-d_e)gs)]} \text{ where } K = (1-d_e)(1-g) - b.$$

Appendix B

In the open-access model, one of two equilibrium points, (X_0, X_1, X_2, X_3) , can be calculated

$$\text{as: } X_0 = E_1/E_2, X_1 = F_2X_3, X_2 = F_1X_3, X_3 = (1 - X_0)/(1 + F_1 + F_2) \quad ,$$

$$\text{where } E_1 = (d + h(1-d))F_2 - (1-d)(p_u y_u(1-a_1) + p_s y_s)F_1 - (1-d)(1-d_e)p_u y_u(1-a_2) \quad ,$$

$$E_2 = (1-d)(1-d_e)(1-p_u y_u)sg + (1-d)p_u y_u a_1 f F_1 + (1-d)(1-d_e)p_u y_u a_2 f \quad ,$$

$$F_1 = ((1-d)d_e + d + (1-d)(1-d_e)((1-p_u y_u)g + p_u y_u))/(b(1-d)(1-p_u y_u - p_s y_s)) \quad ,$$

$$F_2 = ((d + b(1-d)(1-p_s y_s - p_u y_u) + (1-d)(p_s y_s + p_u y_u))F_1 - (1-d)(d_e + (1-d_e)(1-p_u y_u)g))/(h(1-d)) \quad .$$

The local stability condition of $(1, 0, 0, 0)$ can be calculated as: $(\lambda - 1)J_2(\lambda) = 0$, where λ

is an eigenvalue and $J_2(\lambda) = \lambda^3 - R_1\lambda^2 + R_2\lambda - R_3$, in which

$$R_1 = (1-d)[(1-b)(1-p_u y_u - p_s y_s) + (1-d_e)(1-g)(1-p_u y_u) + (1-h)],$$

$$R_2 = (1-d)^2 \times \left\{ \begin{array}{l} (1-d_e)(1-b)(1-p_u y_u - p_s y_s)(1-g)(1-p_u y_u) \\ -b(d_e + (1-d_e)(1-p_u y_u)g)(1-p_u y_u - p_s y_s) \\ + (1-h)[(1-b)(1-p_u y_u - p_s y_s) + (1-d_e)(1-g)(1-p_u y_u)] \\ -h((1-a_1(1-f))p_u y_u + p_s y_s) \end{array} \right\},$$

$$R_3 = (1-d)^3 \times$$

$$\left\{ \begin{array}{l} (1-h)(1-p_u y_u - p_s y_s) \left\{ \begin{array}{l} (1-d_e)(1-b)(1-g)(1-p_u y_u) \\ -b(d_e + (1-d_e)(1-p_u y_u)g) \end{array} \right\} \\ + h(1-d_e) \left\{ \begin{array}{l} b(1-p_u y_u - p_s y_s)[(1-p_u y_u)sg + (1-a_2(1-f))p_u y_u] \\ -[(1-a_1(1-f))p_u y_u + p_s y_s](1-g)(1-p_u y_u) \end{array} \right\} \end{array} \right\}.$$

The local stability condition suggests that the equation $J_2(1) = 0$ indicates the boundary

between the stable and the unstable regions of $(1, 0, 0, 0)$. The condition $J_2(1) = 0$ also

indicates that neither a_1 or a_2 influences the local stability condition of $(1, 0, 0, 0)$ in $f = 1$,

and that f does not influence the local stability condition of $(1, 0, 0, 0)$ in $a_1 = a_2 = 0$.