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The patch distributed producer–scrounger game

Yasunori Ohtsuka *, Yukihiko Toquenaga

Division of Integrative Environmental Sciences A421, University of Tsukuba, 1-1-1, Tennodai, Tsukuba, Ibaraki 305-8572, Japan

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A B S T R A C T

Grouping in animals is ubiquitous and thought to provide group members antipredatory advantages and foraging efficiency. However, parasitic foraging strategy often emerges in a group. The optimal parasitic policy has given rise to the producer–scrounger (PS) game model, in which producers search for food patches, and scroungers parasitize the discovered patches. The *N*-persons PS game model constructed by Vickery et al. (1991. Producers, scroungers, and group foraging. American Naturalist 137, 847–863) predicts the evolutionarily stable strategy (ESS) of frequency of producers ($\hat{q}$) that depends on the advantage of producers and the number of foragers in a group. However, the model assumes that the number of discovered patches in one time unit never exceeds one. In reality, multiple patches could be found in one time unit. In the present study, we relax this assumption and assumed that the number of discovered patches depends on the producers' variable encounter rate with patches (λ). We show that $\hat{q}$ strongly depends on λ within a feasible range, although it still depends on the advantage of producer and the number of foragers in a group. The basic idea of PS game is the same as the information sharing (parasitism), because scroungers are also thought to parasitize informations of locations of food patches. Horn (1968) indicated the role of information-parasitism in animal aggregation (Horn, H.S., 1968. The adaptive significance of colonial nesting in the Brewer's blackbird (*euphagus cyanocephalus*). Ecology 49, 682–646). Our modified PS game model shows the same prediction as the Horn's graphical animal aggregation model; the proportion of scroungers will increase or animals should adopt colonial foraging when resource is spatiotemporally clumped, but scroungers will decrease or animals should adopt territorial foraging if the resource is evenly distributed.

1. Introduction

Group foraging is widely assumed to be advantageous for animals. Two of its major benefits are lower predation hazard and increased foraging efficiency (Clark and Mangel, 1986). The foraging efficiency is, for example, achieved by increasing foraging rate (Clark and Mangel, 1984; Vickery et al., 1991), reducing risk of starvation (Caraco, 1981), and increasing ability to capture elusive prey (Ward and Enders, 1985). Horn (1968) proposed a graphical model of the spatial distribution of Brewer's blackbird (*Euphagus cyanocephalus*) nests in light of foraging efficiency. The model assumes territorial and colonial nesting, and in order to minimize the average distance from nest to food, territorial nesting would be expected when the distribution pattern of the food is uniform. When the distribution pattern of the food is temporally and spatially clumped, colonial nesting would be favored. For colonial nesting, Horn (1968) suggested that there is an additional advantage: information sharing (information-parasitism) between individuals in the same colony, which makes it possible for a bird who is foraging with little success to follow a more successful bird to a better foraging area. The same argument was made in Clark and Mangel (1984). They conclude that food location is not valid information if the food is abundant. Even if food is scarce but evenly distributed, little information is derived from searching. Hence, flocking is most valuable when food is both scarce and patchily distributed (Clark and Mangel, 1984). These social foraging interactions among individuals are common in group foraging of birds, and most common is the exploitation of others' efforts to find food (Brockmann and Barnard, 1979).

Information-parasitism is beneficial for parasitic individuals but unprofitable for parasitized individuals in a group. If foragers have the option of using a parasitic strategy, they can choose group foraging with parasitism or solitary foraging without parasitism depending on the situation. The optimal parasitic policy has been analyzed by two theoretical models: the information-sharing (IS) model (Caraco, 1981; Clark and Mangel, 1984) and the producer–scrounger (PS) game model (Barnard and Sibly, 1981; Vickery et al., 1991; Caraco and Giraldeau, 1991; Giraldeau and Caraco, 2000).

Traditionally, the IS model assumes that in a group of *N* foragers all individuals search for food independently while, at the

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* Corresponding author. Tel./fax: +81 29 853 7491.
E-mail addresses: otsuka@pe.ies.life.tsukuba.ac.jp (Y. Ohtsuka), toque@ies.life.tsukuba.ac.jp (Y. Toquenaga).

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same time, monitoring the behavior of other group members, thereby allowing unsuccessful foragers to exploit food clumps discovered by others (Caraco, 1981; Clark and Mangel, 1984; Beauchamp and Giraldeau, 1996). In the IS models, therefore, if an individual can use parasitism, they always choose parasitic behavior.

The PS game model (Barnard and Sibly, 1981) is an N-person alternative—option game in which individuals use the producer strategy to find food clumps and the scrounger strategy to partake in food clumps discovered by the producers. For the PS game to apply to a group foraging situation, two assumptions must be met. First, individuals can play either producer or scrounger, but cannot simultaneously play both producer and scrounger strategy. Second, the payoffs received by a scrounger must be highly negatively frequency-dependent on the frequency of scroungers in the group (Barnard and Sibly, 1981; Vickery et al., 1991; Caraco and Giraldeau, 1991; Beauchamp and Giraldeau, 1996; Giraldeau and Beauchamp, 1999; Giraldeau and Caraco, 2000). In the PS game model, even if individuals can use scrounging, they do not always choose scrounging behavior. When those two assumptions are met, the PS game model predicts the mixed evolutionarily stable strategy (ESS) of producers and scroungers.

An analytical PS game model constructed by Vickery et al. (1991) predicts the ESS frequency of producers as a function of the fraction of a producer's advantage to the total food items in a patch and the number of foragers in a group. However the model assumes the producer's encounter rate with food patches, the maximum number of discovered patches in one time unit is always one, and the ESS frequency of producers does not depend on the producer's encounter rate with food patches. In their model, it is assumed that the producer's encounter rate with food patches is nearly equal to zero; therefore, the number of discovered patches in one time unit never exceeds one. In reality, the producer's encounter rate with food patches depends on the environment of the foraging site, and multiple patches could be discovered in one time unit. In this study, therefore, we modify this assumption to the variable encounter rate, and investigate the occurrence of parasitism. If the producer's encounter rate with food patches increases, the number of patches discovered during one time unit is sure to multiply, and foragers might cease parasitism at a high encounter rate because the benefits of group foraging are reduced in such situations. Actually, some empirical studies manipulated the producer's encounter rate with food patches by altering the spatial distribution of food patches, and showed that this changes the proportional use of producers and scroungers (Giraldeau et al., 1990; Giraldeau and Livoreil, 1998; Coolen et al., 2001; Coolen, 2002).

We compare our modified PS game model to Vickery's original model (Vickery et al., 1991). In addition to this, we discuss the relationship between our modified PS game model and Horn's graphical model (Horn, 1968), because Horn's model includes the original PS game model situation as an extreme colonial strategy. A colony is a one of the animal aggregations, and some studies explained the evolutionary advantages of colonial breeding by information sharing (Ward and Zahavi, 1973). Barta and Giraldeau (2001) reappraise this hypothesis using the PS game model.

2. The PS game model

In Vickery's PS game model (Vickery et al., 1991), N individuals forage in sufficient proximity that group members playing scrounger can all detect and exploit the food uncovered by any of the group's producers. A food clump contains F items. The producer obtains a finder's advantage, a portion (a) of the patch ($0 \leq a < F$) that it can use exclusively before the scroungers arrive. The proportion of individuals playing producer is q, and the proportion playing scrounger is $1-q$. The producer's encounter rate with food patches is λ. Once a producer finds a clump, $(1-q)N$ scroungers arrive in unison and divide the remaining food items ($A = F-a$) equally among the individuals ($n = 1+(1-q)N$). The currency of fitness is energy intake, I. Patch discovery occurs sequentially, and patch exploitation time is negligible, which means that there is no handling time. Each producer's expected intake (I_P) after T time units of foraging is

$$I_P = \lambda T\left(a + \frac{A}{n}\right) \tag{1}$$

The rate of encounter with scrounging opportunities is a function only of the number of producers (qN). The scrounger's expected intake (I_S) is

$$I_S = \lambda T q N \frac{A}{n} \tag{2}$$

The ESS frequency of producers ($\hat{q}$) can be found by setting I_P equal to I_S and solving for q:

$$\hat{q} = \frac{a}{F} + \frac{1}{N} \tag{3}$$

The ESS frequency of producers ($\hat{q}$) depends on the fraction of a finder's advantage (a) to the total food items in a patch (F) and the foraging group size (N).

3. The λ-dependent PS game model

Vickery et al. (1991) supposed that patches are scarce so that the maximum number of discovered patches in one time unit is only one, and all scroungers in a foraging group rush to the discovered patch and exploit food items. This assumption is considered reasonable if the number of producers in a foraging group (qN) is a minority and if a producer's encounter rate with food patches (λ) is small enough. However, if qN is large and/or λ is not small, the number of discovered patches in one time unit might exceed one, and a number of those discovered patches might disperse scroungers in multiple exploiting groups. In such a scenario, the number of discovered patches in one time unit depends on qN and λ. We modified the PS game model, which assumes that the number of discovered patches in one time unit depends on the number of producers in the foraging group (qN) and the producer's encounter rate with food patches (λ). We call this modified PS game the λ-dependent PS game model.

All parameters in the λ-dependent PS game model are the same as in the original PS game model (Vickery et al., 1991). We assume that the number of discovered patches in one time unit is determined by binomial distribution, and scroungers are divided equally between all food patches discovered in one time unit. Assuming that when one producer finds a food patch, other i ($0 \leq i \leq qN-1$) producers find food patches during the same time unit, the producer's expected intake (I_P) after T time units is

$$I_P = T\sum_{i=0}^{qN-1}\binom{qN-1}{i}\lambda^{i}(1-\lambda)^{qN-1-i}\left(\frac{F-a}{1+\dfrac{(1-q)N}{1+i}}\right) \tag{4}$$

When j ($1 \leq j \leq qN$) producers find food patches during one time unit, the scrounger's expected intake (I_S) after T time units is

$$I_S = T\sum_{i=1}^{qN}\binom{qN}{j}\lambda^{j}(1-\lambda)^{qN-j}\left(\frac{F-a}{1+\dfrac{(1-q)N}{j}}\right) \tag{5}$$