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Producer–Scrounger Models and Aspects of Natural Resource Use

Zoltán Barta

Abstract

Humans are currently using natural resources at unprecedented rates and it is not difficult to extrapolate how this could lead to global catastrophes of various kinds. To mitigate eventual consequences, our understanding of the processes involved must be improved. Since resource use frequently involves groups, free-riding behavior (i.e., exploiting the efforts of others) must be expected. Recent evolutionary studies indicate that exploitation of others' efforts can dramatically alter how resources are utilized. Two types of effort are exploitable: the harvesting and maintenance of resources. This chapter argues that the exploitation of harvesting efforts can be analyzed as a producer–scrounger evolutionary game. The presence of scroungers (exploiters) in a group usually decreases the overall use of resources by the group. Factors that increase the proportion of scroungers (e.g., energy reserves, existence of dominance hierarchy, or prevalence of relatedness) can further decrease resource use. By contrast, aggression and the compatibility of scrounger and producer strategies elevate resource use. In temporally unstable patches, scrounging does not affect resource use in groups that are at equilibrium. Encouraging scrounging may lower resource use, even in humans, but this raises a moral dilemma: individual scrounging is bad, reduced resource overuse by the population is good. Surprisingly, only a small portion of the literature has considered the consequences of cheating in terms of the natural resource management—a situation that demands attention in future research.

Introduction

One of the greatest problems of the Anthropocene (Lewis and Maslin 2015) is the overuse of natural resources, including fisheries, forests, clean water, air, and fertile soil. This not only inhibits humankind from developing strategies for sustainable resource use, it can easily result in ecological, economical, and

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social catastrophes on a global scale. Nevertheless, decisions are usually made on a local scale, mainly at the level of individuals. To prevent overuse, it is therefore of paramount importance to understand the processes involved in individual resource use decisions.

Most of the natural resources that are threatened by overuse can be classified as common-pool resource systems (Janssen et al. 2010). Similar to public goods, it is impossible or unfeasible to exclude anyone from using common-pool resources (Ostrom 1990). In contrast to public goods, however, resource use by one individual in a common-pool resource system decreases the amount of resources available for others (Ostrom 1990). This situation closely resembles one in which animals forage on patchily distributed food, a situation that has been widely studied in ecology and evolutionary biology. Thus, knowledge on individual decisions accumulated in these fields might potentially provide useful insights to help prevent resource overuse by humans. To facilitate this information exchange, I review the recent theoretical advancement in a special case: group foraging.

Studying group foraging is important for the following reasons: First, in many cases, both in humans and other organisms, resource use takes place in groups. In humans, for instance, local communities utilize the surrounding forests or fleets of ships exploit fish stocks. Many animals have also been frequently observed to forage in flocks (birds), schools (fish), or herds (ungulates). Second, models of group foraging consider individual decisions and, through game theory, explicitly take into account the interactions between individuals. Interacting with others can affect the dynamics of resource use by altering its costs and benefits. For instance, the benefits of investing in a local timber industry can be greatly reduced when the harvested timber is stolen. An animal analogue can be found in ground-feeding passerine birds, like sparrows, where some individuals invest in actively searching for new food patches, while others simply wait for a “neighbor” to find a patch so that they can rush in to obtain a share of the food, obviously decreasing the food intake of the patch finder (Giraldeau and Caraco 2000). At the individual level, against a backdrop of possible exploitation, the cost of investors (producers) and the benefit of exploiters (scroungers) can result in a fewer number of individuals willing to invest in the production of resources (timbers, food patches); this, in turn, may reduce the level of resource use by the group as a whole. Therefore, if the group is overusing its environment, then the spread of scroungers can mitigate the problem of overuse. The processes underlying this scenario are well captured, at least in evolutionary biology, by the theoretical framework of producer–scrounger (PS) games (Giraldeau and Caraco 2000). In this chapter I present a baseline model for producing (investing) and scrounging (exploiting) and investigate how the presence of scroungers influences a group’s intake of resources. Thereafter I review models that are extensions of the baseline model and explore how these modifications alter resource use. I conclude with a brief

investigation of how changing resource characteristics can influence the effect of scroungers on resource use by the group.

The Baseline Producer–Scrounger Game

Following Giraldeau and Caraco (2000), let us consider a group of G individuals foraging for T time units in an environment where food occurs in well-defined patches. A food patch contains F food items. We assume that the time needed to consume a patch is negligible compared to the time needed to find the patch because patches are difficult to locate. To obtain food, individuals must either invest in searching for patches or exploit the search effort of others. This is modeled by assuming that individuals can follow either a *producer* or a *scrounger* tactic. An individual playing the producer tactic actively searches for food and finds patches with rate λ . After finding a patch it consumes a portion a of the patch while alone (the finder's advantage, $a \leq F$) and shares the remaining food ($A = F - a$) with the arriving scroungers. The proportion of individuals adopting the producer tactic (producers) in the group is p . We assume that a producer never feeds from patches found by other producers, whereas scroungers only feed from patches found by producers. In other words, the tactics are incompatible (Coolen et al. 2001). Finally, we assume that scroungers are able to detect all patches found by producers and thus all scroungers can feed from each patch found.

Under these assumptions, the food intake for a producer in a group containing $(1-p)G$ scroungers is:

$$W_p(p) = T\lambda \left(a + \frac{A}{(1-p)G+1} \right), \quad (4.1)$$

whereas a scrounger's intake is:

$$W_s(p) = pGT\lambda \frac{A}{(1-p)G+1}. \quad (4.2)$$

At evolutionary stability, $W_p(\hat{p}) = W_s(\hat{p})$ and hence the evolutionarily stable frequency of producers, \hat{p} , is:

$$\hat{p} = \frac{a}{F} + \frac{1}{G}. \quad (4.3)$$

This means that the proportion of producers increases with the proportion of food available exclusively for them (the finder's share, a/F), and decreases with group size G . Accordingly, the two strategies can coexist: $\hat{p} < 1$, if $a/F < 1 - 1/G$. The equilibrium point is stable because of the strong negative frequency dependence of the scrounger's food intake (for details, see Giraldeau and Caraco 2000).

The average per capita intake in a group of G producers foraging independently (see above) is λTF amount of resources. Thus the amount of resources used by an average individual in a group of pG producers and $(1-p)$ G scroungers is:

$$pW_p(p) + (1-p)W_s(p), \quad (4.4)$$

which simplifies to $p\lambda TF$. Accordingly, the use of resources, not surprisingly, decreases as the proportion of producers decreases, and hence the proportion of scroungers increases in the group (Vickery et al. 1991; Giraldeau and Dubois 2008).

Let us now investigate what happens in groups at evolutionary stability. To obtain the per capita intake in a group, where the proportion of producers is at the evolutionarily stable value \hat{p} , we substitute p with \hat{p} :

$$\left(\frac{a}{F} + \frac{1}{G}\right)\lambda TF. \quad (4.5)$$

From this it follows that the evolutionarily expected per capita resource use in equilibrium groups decreases when group size increases and finder's share decreases. This is not surprising because these are exactly the conditions that facilitate an increased number of scroungers at evolutionary stability (Figure 4.1).

According to the reasoning above, if a population is partitioned into multiple small foraging groups, the total rate of resource harvesting will be higher than if individuals had foraged in just a few but larger groups. Furthermore, if

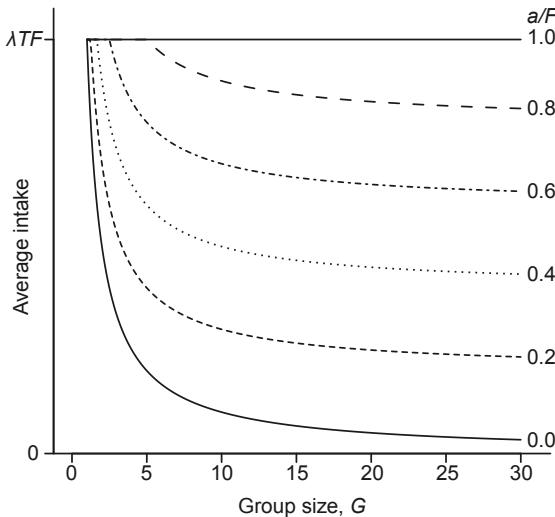


Figure 4.1 The effect of group size, G , and finder's share, a/F , on an average individual's intake in groups containing an evolutionary equilibrium proportion of scroungers. λTF marks the average intake in a group of pure producers.

the proportion of a patch available exclusively to its producer, a/F , is small, then the overall rate of resource harvesting decreases. The proportion of a/F can be small if patches are large, because relatively small amounts will be consumed by the producer before the arrival of scroungers. A high density of foragers can also result in a small a/F because high densities mean that individuals are close to each other, and hence scroungers can quickly reach a discovered food patch, leaving just a short time for its producer to consume the patch alone (Giraldeau and Caraco 2000).

By combining reasoning similar to that presented above with population dynamics, Coolen et al. (2007) pointed out that the spread of scroungers decreases the use of resources. Furthermore, they found that the coexistence of scroungers and producers among predators leads to stable population dynamics in a simple prey–predator system instead of the more usual cycling. As a consequence, they argue that prey species should be expected to evolve in such a way that facilitates scrounging in its predators. One of the possibilities they envision is that prey become more cryptic, as this increases the cost of searching and makes scrounging a more appealing option. The other possibility is that prey occur in large patches, which results in an overall smaller finder’s share; this, in turn, will increase the benefits from scrounging (Coolen et al. 2007).

Extensions of the Producer–Scrounger Game

This baseline PS model cannot, of course, address all of the complexities inherent in the social foraging process. For instance, because all individuals are treated the same, one cannot know how differences in energetic state, dominance rank, or the possibility of aggressive resource defense would influence the spread of scroungers. Taking individual differences into account, however, is important, because this makes it possible to predict the characteristics of both producers and scroungers. This knowledge, in turn, might allow the manipulation of resource users, and hence the volume of resource use.

The economic state of agents can vary widely and influence their decisions. For instance, a person close to bankruptcy values items differently than someone who is well off financially. Animals, too, can differ in their state, one of the most important differences being that of energetic state. Differences in energy levels (energetic state) can simply arise because of the inherently stochastic nature of the foraging process: individuals usually collect different amounts of energy. The energetic state can be an important determinant of behavior for two reasons (Houston and McNamara 1999):

1. It can constrain the available behavioral options for an individual: an individual with a low level of energy reserves cannot afford to rest in safety from predators, it must forage to avoid starvation.

2. It can influence the value of food: a given amount of food is worth less to an animal with a high level of energy reserves than to one close to starvation.

Thus, it is expected that energy reserves affect the costs and benefits of the social foraging process, and hence the use of the producer and scrounger tactics. To investigate this effect, Barta and Giraldeau (2000) developed a state-dependent dynamic PS game. With this model, they considered a group of foragers that needed to survive several winter days and nights. They found that the use of the scrounger tactic depends on both the levels of energy reserves and the time of day. Early in the morning, individuals with a low energy level utilized the scrounger tactic whereas those with higher reserves used the producer strategy. Later in the day, however, this pattern reverses: individuals with high reserves tend to scrounge while those with low reserves produce. The reason for this pattern is rooted in the variance-sensitive properties of the tactics: the producer tactic is a variance-prone tactic so individuals using this tactic can get high amounts of food (as long as $a > 0$); however, they rarely achieve this level rarely because producers can only feed from patches they find themselves. On the other hand, use of the scrounger tactic can be a variance-averse alternative: scroungers get small amounts of food (because they have to share the patch), but frequently (as long as there is more than one producer in the group). Early in the day many individuals tend to have low energy reserves, because they have just survived the long winter night; to avoid starvation they need a small, but reliable amount of food. Later in the day animals need high reserves to survive the night. Those who are close to this limit play it safe—they use the scrounger tactic—while those who have low reserves late in the day must take risks and use the producer tactic. This policy results in a high frequency of scroungers early and late in the day, while during the middle of the day the proportion of scroungers is lower. Importantly, this state-dependent dynamic PS game model indicates that the availability of the scrounger tactic is not necessarily a cost of group foraging, as was assumed previously (Vickery et al. 1991), but may be advantageous as it can provide insurance against starvation in a stochastic world. Because of this insurance characteristic, the use of the scrounger tactic is more advantageous in this game than it is in the baseline PS game. As a result, the proportion of scroungers at evolutionary equilibrium is expected to be higher in the state-dependent game than in the baseline game, especially under medium values of finder's share. This means that average harvest rates decrease in a state-dependent world, while the survival of individuals increases when the scrounger tactic is available (Barta and Giraldeau 2000).

Dominance relationships and the dominance hierarchy that emerges are inherent parts of group life. Some individuals in a group commonly gain larger shares of limited resources (e.g., food, safety, or mates) than others do. For example, a fishing vessel fitted with a more powerful engine can pull larger fishing nets and hence get a larger share of a fish school than a vessel that is not

so well equipped. In animals, based on this asymmetry in competitive ability, individuals in a group can be ordered in a dominance hierarchy, where dominant individuals have stronger competitive abilities and hence dominate those, the subordinates, who have weaker competitive abilities. A consequence of this competitive asymmetry is that the dominance status of an individual should have a considerable effect on the individual's use of social strategy. Indeed, in Harris's sparrows (*Zonotrichia querula*), dominant individuals frequently supplant subordinates from food patches that have just been found (Rohwer and Ewald 1981). To investigate systematically how the magnitude of differences in competitive ability between individuals in a group influences social foraging decisions, Barta and Giraldeau (1998) developed a phenotype-limited model of producing and scrounging. In phenotype-limited games, individuals differ in some respect and this influences their gain from the use of different strategies. In the model by Barta and Giraldeau (2000), individuals differ in their competitive weights, which determine their share from a divided food patch. If the level of difference between the competitive weights of individuals is high, then group members vary considerably in their competitive ability; high-ranking, dominant individuals get a disproportionately large share from a divided patch. If, on the other hand, there is a low level of difference, group members are more or less the same and thus they receive about the same amount from a shared resource. Barta and Giraldeau found that when group members are more or less the same, producing and scrounging tactics are used in the same way; that is, individuals with different dominance rank do not differ in terms of the proportion of scrounging. Increasing the level of difference leads to a region of the parameter space where the relationship between dominance rank and use of scrounging is rather variable. If the level of differences in competitive ability is high, then dominant individuals use scrounging while subordinate individuals use producing exclusively (see also Hamilton 2002). When this strong correlation between dominance rank and tactic use exists, the proportion of scroungers in the group drops remarkably. In turn, this results in a higher than average food intake compared to groups where phenotypic differences do not influence tactic use (i.e., where the level of differences between individuals is low).

An issue inherently related to competition is aggression. The models considered above assume peaceful scramble competition; that is, resources are divided among individuals either equally or proportionally to their competitive weight, but without costly fights. Real animals, however, frequently defend resources aggressively. Aggression, in forms of chemical or viral warfare, is also often observed in bacteria (Brown et al. 2009a). Since aggression can significantly alter the costs and benefits of different social foraging tactics, it is important to investigate how the possibility of aggressive behavior influences the use of producing and scrounging. By embedding a hawk–dove game (a variant of the snowdrift game) into the baseline PS game, Dubois and Giraldeau (2005) presented a model where individuals can decide not just

about whether to produce or to scrounge but whether to defend the resources aggressively or not. Escalated fights are costly in terms of energy, time, and elevated predation risk. Because producers have exclusive access to part of the discovered patch (the finder's advantage), while scroungers do not, the authors assumed a role asymmetry between producers and scroungers regarding the aggressive defense of resources. In addition to this role asymmetry, producers and scroungers were assumed to have the same fighting ability; that is, the probability to win the fight and obtain resources was the same for all foragers. Using an iterative method to solve the games, Dubois and Giraldeau (2005) found that producers always defend the discovered patch aggressively, whereas the level of aggression by scroungers depends on the circumstances (see also Dubois et al., this volume). According to Dubois and Giraldeau (2005), the level of aggressiveness differs between tactics: because producers gain more from a patch, they can afford to mount a more intense defense. This makes scrounging a less valuable option. As a consequence, the proportion of scrounging decreased and hence the use of resources increased in this game, compared to the baseline PS game. This analysis, however, did not take into account that the value of the patch might differ for producers and scroungers. One could argue that producers value the part of the patch that is going to be shared with the arriving scroungers less than the scroungers, because producers have already consumed the other part of the patch (McNamara and Houston 1989). Therefore, it might not be entirely unreasonable to assume that scroungers might behave more aggressively to obtain a share from the patch. This, of course, would change the prediction of this model. To settle this issue, a state-dependent analysis of the problem should be conducted.

A crucial assumption of the baseline PS model is the complete incompatibility of producer and scrounger tactics. In other words, a producer cannot recognize the food findings of other producers and a scrounger cannot find a patch alone. Imagine a fishing vessel that is equipped both with sonar (useful to locate schools of fish) and radar (to locate other ships) equipment. The incompatibility of producing and scrounging corresponds to the case when our imaginary fishing boat has a weak engine so it cannot power both the sonar and the radar at the same time; thus, the crew must decide to power the sonar (and hence play producer) or power the radar (and scrounge). Vickery et al. (1991) relaxed this strict assumption by introducing a third tactic, the *opportunist*, into the baseline PS game. To become an opportunist, the owner of the above fishing boat must invest in an engine that is strong enough to power both the sonar and the radar equipment at the same time; hence the boat can simultaneously look both for fish and other fishing vessels. According to Vickery et al. (1991), an opportunist can find food itself. However, its efficiency at locating patch c might be smaller than the food-finding efficiency of a pure producer: $c \leq 1$. As we have seen above, a producer can find patches with rate λ . With this formulation, the rate of patch finding by an opportunist is $c\lambda$. An opportunist is also able to detect scrounging opportunities with efficiency h , which can, again,

be smaller than the efficiency of a pure scrounger: that is, $h \leq 1$. This means that a scrounger can detect all other individuals who have found a food patch, whereas an opportunist can only detect a proportion of h of those food-finding events. According to this notation, a pure producer can be characterized as an opportunist, with $c = 1$ and $h = 0$, whereas a pure scrounger would be depicted as $c = 0$ and $h = 1$. This is the case of complete incompatibility. The case when both $c = 1$ and $h = 1$ constitutes complete compatibility; that is, a forager can freely switch between producing and scrounging without any loss of efficiency. This might work in an ideal world, but in reality some cost of switching is expected. As a consequence, c and h should correlate negatively; any increase in one of the efficiencies should result in a decrease in the other (Vickery et al. 1991). This is what Vickery et al. refer to as partial compatibility, of which they distinguish three types (see Figure 4.2a):

1. Exact compensation, when an increase in one efficiency results in the same level of decrease in the other efficiency: $c + h = 1$
2. Overcompensation, when gain in one efficiency leads to less loss in the other: $c + h > 1$
3. Undercompensation, when gains are smaller than losses: $c + h < 1$

Vickery et al. (1991) found that opportunists can only spread under the condition of overcompensation. When undercompensation occurs, just the producer-only and the producer–scrounger combination is stable, depending on the finder's share, as in the baseline PS game (Figure 4.2b). Under overcompensation, four regions of coexistence can be identified along the level of finder's share. At the lowest values of finder's share, opportunists coexist with scroungers. At immediate values of finder's share, pure opportunist is the evolutionarily stable strategy. At higher finder's share, opportunists coexist with producers. At highest finder's share values, producers dominate. With increasing level of overcompensation, the region of pure opportunists expands while the others shrink. The average intake increases with finder's share in the mixed regions but remains constant in the pure regions (Figure 4.2b, c). Increasing the level of overcompensation results in an increased average intake, but opportunists only reach the intake level of pure producers under complete compatibility ($c + h = 2$). Conditions which favor overcompensation decrease the cost of producing as well as the benefit of scrounging, and hence lead to a higher level of resource use by the whole group. Nevertheless, the above analysis does not consider the costs of making overcompensation itself possible. These costs might be substantial, as our analogy of fitting a more powerful engine (to enable the simultaneous use of sonar and radar equipment) into the fishing boat suggests. How these costs affect the equilibrium of strategies and level of resource use requires further investigation.

The incompatibility of tactics seems to be well supported in birds, where the different head positions required for searching for food (head down) and

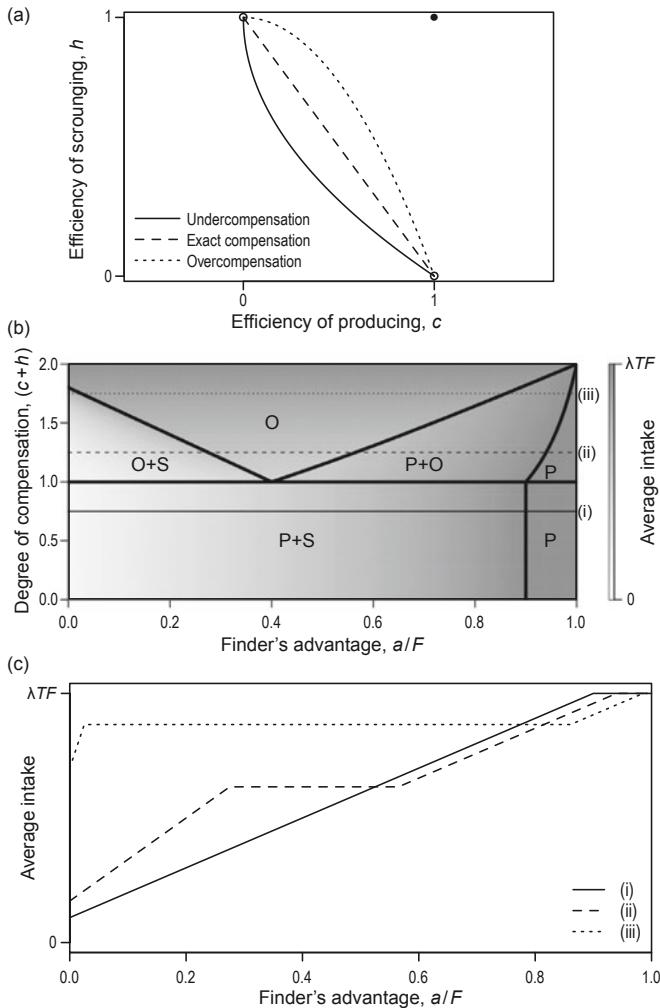


Figure 4.2 The effect of adding an opportunist tactic to the baseline producer-scrounger game on the average intake. (a) Three types of relations are depicted between the opportunist's efficiency of producing a patch, c , and scrounging a patch, h . Open circles represent the complete incompatibility of producer and scrounger tactics; the solid circle shows complete compatibility. (b) The average intake of a forager in equilibrium groups is shown as a function of a finder's share and the degree of compensation ($c + h$). Shading indicates intake: the darker the shading, the higher the intake. Undercompensation occurs if $(c + h) < 1$, exact compensation if $(c + h) = 1$, and overcompensation if $(c + h) > 1$. Black thick solid lines separate regions of different evolutionarily stable strategy composition. Letters indicate the strategic composition of the group at equilibrium: P, producer; S, scrounger; and O, opportunist. Thin black (solid and dashed) lines marked by (i), (ii), and (iii) refer to the average intake as plotted in (c). (c) The average intake is shown as the function of finder's share at different levels of compensation, marked by the thin black (solid and dashed) lines in (b).

searching for food-finders (head up) rule out the simultaneous use of such tactics (Coolen and Giraldeau 2003).

Social behavior can strongly depend on the level of within-group relatedness (Hamilton 1964), a feature that is also not incorporated into the baseline PS game. If the group consists of relatives, it is expected that the level of exploitation of efforts decreases compared to a non-kin group (Frank 2003). Others, however, argue that the effect of relatedness should depend on the costs and benefits of scrounging (Tóth et al. 2009). If scrounging imposes a high cost on producers, then high relatedness should decrease the proportion of scroungers. Alternatively, if individuals gain a substantial benefit by scrounging, then scrounging should be more common in groups of relatives than in groups of strangers. Mathot and Giraldeau (2010) modeled this proposition formally. They assumed that inclusive intake rate is a surrogate of inclusive fitness and modified the baseline PS game to include an indirect benefit for the producers and an indirect cost for the scroungers. The indirect benefit is the amount of food gained by the scroungers from the producer discounted by the within-group relatedness. The indirect cost takes into account that scroungers, by consuming part of the patches found by their relatives, decrease their relatives' intake. In the baseline PS game, producers have no options to control the level of scrounging in the group. To overcome this deficiency Mathot and Giraldeau (2010) assumed that producers can impose a cost on scroungers (e.g., through aggression). By increasing the magnitude of this cost, they were able to increase the level of control the producers exert over joining a discovered food patch by others. The authors found, not surprisingly, that increasing the cost imposed by producers on scroungers increased the equilibrium proportion of producers. For a given level of cost, increasing the level of relatedness within the group resulted in higher equilibrium proportion of producers, which, in turn, led to more intense resource use. Interestingly, if producers can discriminate between kin and non-kin scroungers by imposing higher cost on non-kin, the equilibrium proportion of producers can be lower in groups composed of kin than non-kin (Mathot and Giraldeau 2010). In other words, kin groups might contain a higher proportion of exploitative individuals than non-kin groups. The investigation of the role of social preferences (Charness and Rabin 2002) in producing-scrounging decisions might be an interesting extension of this modeling framework.

As discussed above, the spread of scroungers decreases resource use by the group. Nevertheless, all models reviewed so far have been based on the assumption that adding more individuals to the group decreases the intake of group members. Now let us relax this assumption and investigate how the spread of scroungers affects resource use by the group under the following condition: adding a new individual to the group does not decrease the intake of group members. This situation arises when animals forage on ephemeral patches; that is, when food patches disappear before all food items are consumed by the foragers (Barta and Giraldeau 2001). Swarms of flying insects

or schools of fish are good examples of this type of food resource. The fashion industry might provide a human example for ephemeral resources (Giraldeau, pers. comm.). In the world of fashion, a design is valuable for only a limited period of time because new designs appear annually. If the producer of a new design cannot supply the market with enough goods due to constraints (e.g., insufficient production or transport capacity), the copiers (scroungers) of the new design will prosper without considerably harming the producer and each other. Resource ephemerality basically transforms the common-pool resource system into a public goods system. To investigate how scrounging influences resource use in such an environment, I present a simple model under the group-foraging scenario used above.

Since producers, by definition, arrive earlier at the patch, they can consume more food than scroungers before the patch disappears. We assume that scroungers have enough time to consume an amount A of food, while producers are able to eat $a + A$ amount. A patch contains F food items. A crucial assumption for the following argument is that patches are not depleted; that is, the food consumed by the foragers is less than F :

$$a + A + (1 - p)GA < F, \quad (4.6)$$

where p is the proportion of producers and G is the size of the group. Reading from the left, the first two terms give the consumption of the producer, who has found the patch, while the third term indicates the amount of food taken by the joining scroungers. If this condition is held, then there is no competition for food within a patch (Barta and Giraldeau 2001). To keep the model simple, we will not take into account the negative effect of overcrowding.

As producers are assumed to find food patches with rate λ , their intake during T time units is:

$$I_p(p) = \lambda T(a + A), \quad (4.7)$$

while the scroungers' intake is:

$$I_s(p) = \lambda TpGA. \quad (4.8)$$

The equilibrium proportion of producers, \hat{p} , can be calculated by setting $I_p(p) = I_s(p)$ and solving for p :

$$\hat{p} = \left(1 + \frac{a}{A}\right) \frac{1}{G}. \quad (4.9)$$

A couple of interesting observations can be made on the basis of this simple model. First, the intake of producers is independent of their proportion, and hence the scroungers' proportion. Second, as the intake of producers does not depend on their proportion, the intake of an average individual in an equilibrium group is equal to the intake of a solitary producer. Consequently, the spread

of scroungers, if their proportion reaches the equilibrium proportion, does not influence the intensity of resource use. Third, the average per capita intake changes nonlinearly with the proportion of producers. It starts from zero at $p = 0$ and increases through $\lambda T(a + A)$ at $p = \hat{p}$ to have a maximum of $\lambda TGA p_{max}^2$ at $p = p_{max} = (1 + \hat{p})/2$ and finally decreases to $\lambda T(a + A)$ at $p = 1$ (Figure 4.3). Fourth, the equilibrium number of producers, $G\hat{p} = 1 + a/A$, does not depend on group size. Therefore, the same number of producers can support scroungers in groups of widely varying size, up to a limit. This limit, G_{max} , can be estimated as follows. The maximum amount of food taken from a patch is:

$$a + A + (1 - p_{max})GA, \quad (4.10)$$

which can be simplified to GAp_{max} . G_{max} is the largest group size for which $G_{max}Ap_{max} < F$.

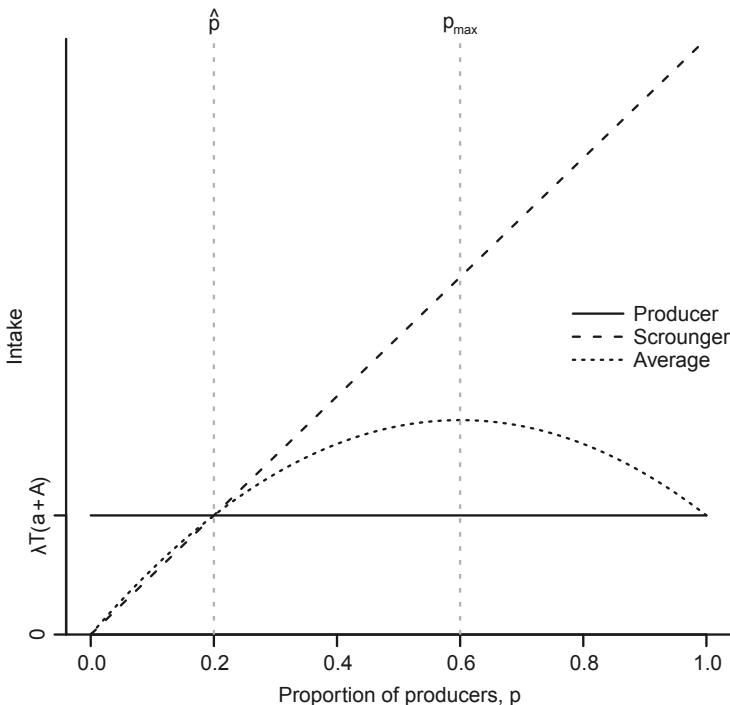


Figure 4.3 The intake of producers and scroungers is shown as the function of proportion of *producers* in a group using ephemeral resource patches (i.e., when patches disappear before the foragers can fully consume them). The intake of an average individual in the group is shown by the dotted line. The vertical dashed gray lines mark the equilibrium proportion of producers (\hat{p}) and the proportion of producers when group intake is maximized (p_{max}), respectively.

Discussion

Long-term use of common-pool resources usually requires two types of investment: in the actual withdrawal of resources from the resource system (“appropriation”; Ostrom 1990) as well as in the maintenance of the resource system itself (“provision”; Ostrom 1990). For instance, to obtain wood, an individual must invest in physical labor and tools to harvest timber from a forest as well as plant new seedlings to maintain the forest. Accordingly, exploiters can defect on investors by exploiting both the harvesting and maintenance efforts. Retaining the forest as our analogy, the first way to exploit could mean stealing someone’s harvested timber, whereas the second could entail not participating in the planting of new trees. Both ways of exploitation reduce, at the level of individuals, the gain of investors and increase the immediate gain of exploiters (Figure 4.4 and 4.5). As a result, both types of exploitation of others’ investment lower the proportion of investors. Nevertheless, at the level of the whole resource system, their effects differ (Figure 4.4 and 4.5).

In this chapter, by reviewing evolutionary game theoretical models of producing and scrounging, I have illustrated how decreasing the proportion of producers (investors) lowers the amount of resources that the group, as a whole, uses (e.g., in the case of exploiting harvesting efforts). If the group overuses its resources, the spread of scroungers (those who exploit the investment of others) can mitigate the environmental problem because fewer investors means that more resources will be left (Figure 4.4). Circumstances like energy reserves or dominance hierarchy facilitate the spread of exploiters whereas aggression and compatibility of producing and scrounging impede it. Kin-related benefits usually increase production, but if producers are able to discriminate between kin and non-kin scroungers, as many bacteria can (Brown, this volume), exploitation increases in kin groups, leading to a lower level of resource use. These results may indicate that there are ways to influence the spread of exploiters, even in humans, and hence alter resource use (e.g., by human groups). This creates, however, a moral dilemma. While moral value is generally not considered when we examine the exploitation of others’ efforts in animal groups, it is regarded as bad in human communities. Therefore, to combat resource overuse by humans, it does not seem to be morally acceptable to encourage such exploitation. Nevertheless, these models offer a different interpretation: resource use by the group could be lowered if some of the investors’ benefits were redistributed to those who refrain from investing. This could be accomplished, as results of social preference studies in behavioral economics show that humans are willing to sacrifice some of their own benefit if this improves the well-being of others (e.g., Charness and Rabin 2002). Implementation of a suitable (or more equitable) tax system by policy makers might offer such a solution. The effectiveness of this measure, however, needs be very carefully evaluated before any attempt is made to implement it. Finally, I note that these conclusions hold solely for common-pool resource

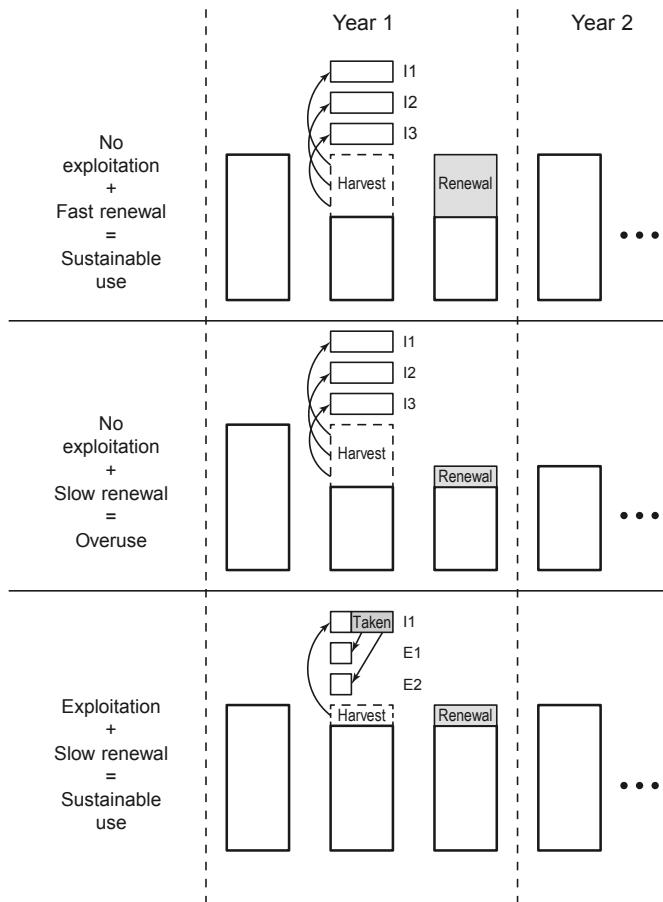


Figure 4.4 Schematic illustration of how exploitation affects harvesting efforts. Available resources are shown by boxes with thick borders. (a) Three individuals (I1, I2, I3) invest in harvesting (symbolized by the curved arrows) part of the resource (box labeled “harvest”). The renewal of the resource (gray box labeled “renewal”) is fast enough to replenish the harvested resource (cf. the first box in Year 1 with the box in Year 2). (b) Renewal is slow and cannot cover the resources used by the three investors; the resource is thus overused. (c) Two individuals (E1, E2) exploit the effort of a sole investor (I1) and take (straight arrows) part of the resource harvested by I1 (small gray box labeled “taken”). This results in an equal amount of the resource being consumed and no resource overuse.

systems. In the similar public goods resource system, where ephemerality prevents competition, the spread of exploiters does not effect the resource use by the group, as discussed above.

The exploitation of maintenance efforts differs fundamentally from the exploitation of harvesting efforts (Figure 4.4 and 4.5). Exploitation of maintenance reduces the amount of available resources and can undeniably lead to an

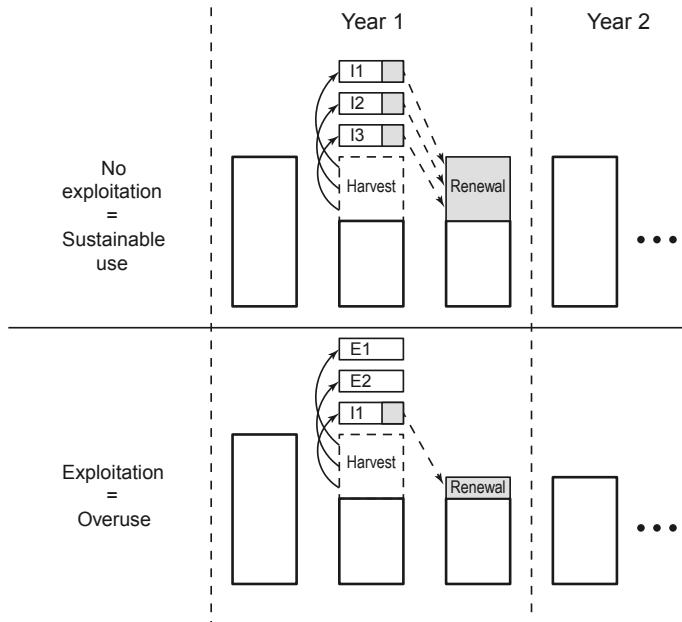


Figure 4.5 Schematic illustration of the exploitation of maintenance efforts. (a) Three investors (I1, I2, I3) invest (straight dashed arrows) part of their harvested resources (small gray boxes) into the renewal of the resource system (“renewal”), which allows the resource system to recover. (b) One investor (I1) invests into the renewal of the resource system while two exploiters do not. This results in the overuse of the resources and a larger gain for the exploiters.

overuse of resources (Figure 4.5). In addition, exploiters always exact a larger gain than investors because they achieve the same from the result of the investors’ investment but save the costs of investment (Figure 4.5). Accordingly, there is nothing to prevent the spread of exploiters. As a consequence of these differences, the exploitation of maintenance efforts resembles the prisoner’s dilemma game and can easily result in a “tragedy of the commons” outcome (for a more detailed comparison of the two scenarios, see Valone et al., this volume).

An important point neglected by the models reviewed here is density dependence. One could argue that groups which contain many scroungers use resources less efficiently than groups of producers. The remaining surplus, however, would allow more individuals to forage on the area. The increased number of individuals finally results in the same level of resource use as the groups consist of only producers. This seems reasonable, but to clarify how density dependence influences resource use in a social foraging setting we need more detailed PS game models with explicit density dependence included. The situation might be complicated by the fact that the cost and benefit of foraging tactics could change with the age of the individuals, as the state-dependent

PS game suggests. This indicates that we need an age-structured population model to investigate how density dependence affects resource use in social exploitation.

An important result of this review is that exploiters (scroungers) can significantly influence the state of the resource systems. Therefore, their existence needs to be taken into account when managing natural resources. A literature search, however, revealed that the governance of natural resources co-occurs with cheating in only 493 (3.3%) out of over 14,000 articles that presumably address the management of natural resources (Table 4.1). This 3.3%, a negligible interest, indicates that the examination of cheating and defection is largely missing from the studies of governance of natural resources. The models reviewed here as well as the findings of this literature search suggest that management of natural resources could be substantially improved by considering the effects of scroungers (or free riders).

Conclusions

The evolutionary games of producing and scrounging provide an appropriate framework to investigate the effect of exploitation of harvesting effort on resource use by humans. As resource use usually takes place in groups, this kind of exploitation is almost inevitable. A review of current PS models indicates that the spread of scroungers (exploiters) decreases resource use in the population. According to these models, several factors can facilitate as well as impede the spread of scroungers in a group. This indicates that it might be possible to lower resource use in human groups by setting conditions to promote scrounging. The moral dilemma that results from this awaits careful analysis and further investigation.

Table 4.1 Results of an online literature search on the link between governance of natural resources (Search Set #1) and cheating (Search Set #2). The column “Search Term” gives the actual search terms used on Thomson Reuters’ Web of Science web site on 02/09/2015. Search Set #3 returned those articles that presumably addressed cheating in resource management.

Search Set	Search Term	Number of Articles
#1	((ecosystem NEAR/2 service\$) OR (natural NEAR/2 capital\$) OR (natural NEAR/2 resource\$)) AND (governance OR management)	14,721
#2	((free rider\$) OR (cheating) OR ((prisoner’s OR prisoners) AND dilemma\$) OR (social NEAR/2 dilemma\$) OR (“tragedy of commons”) OR (public good\$) OR (scroung*))	74,846
#3	#1 AND #2	493

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