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Optimal aggression in kleptoparasitic interactions

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We have created and analyzed a model for kleptoparasitic interactions when individuals decide on the level of aggression in which they want to engage in the contest over a resource item. The more aggressive each individual is relative to an opponent, the higher are the chances of winning the item, but also the higher is the cost of the interaction for that individual. We consider a general class of cost functions and show that for any parameter values, i.e., for any maximal potential level of aggression of the individuals, any value of the resource and any type of the cost function, there is always a unique Nash equilibrium. We identify four possible kinds of Nash equilibria and give precise conditions for when they occur. We find that nonaggressive behavior is not a Nash equilibrium even when the cost function is such that aggressive behavior yields lower payoffs than avoiding the conflict altogether.

1. Introduction

Kleptoparasitism is the resource gathering behavior where one animal steals from another. Possible contested resources include territory, mates, and food [Iyengar 2008]. This stealing behavior is exhibited by a wide variety of species, such as seabirds [Spear et al. 1999; Steele and Hockey 1995; Triplet et al. 1999], insects [Jeanne 1972], fish [Grimm and Klinge 1996] and mammals [Kruuk 1972]. Kleptoparasitic interactions manifest in several varieties and are distinguished by the energy invested by the kleptoparasite and the resource owner. Some kleptoparasites display only minor levels of aggression and may be easily dissuaded by a highly invested adversary (e.g., catbirds steal food provisions from digger wasps, but they forgo this foraging strategy when sparrows are present because the prospect of competition with sparrows dissuades them [Benttinen and Preisser 2009]), whereas others are as aggressive as possible (e.g., male southern giant petrels will attack adult king penguins for food despite having low success rates [Hunter 1991]). Similarly, some resource owners are easily convinced to forfeit their resources (e.g., when attacked by turkey vultures, adolescent great blue herons are known to weakly resist

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the attack by pecking, but if the pecking does not dissuade the vulture then they will disgorge food [Brockmann and Barnard 1979]), whereas others engage in costly attempts to defend their resources (e.g., lapwings will undergo extensive aerial chases to avoid forfeiting food to assailing black-headed gulls [Källander 1977]).

Mathematical models of kleptoparasitism are quite common; see, for example, [Giraldeau and Livoreil 1998; Broom and Ruxton 2003; Broom et al. 2004; 2008; 2010; Broom and Rychtář 2007; 2013; Hadjichrysanthou and Broom 2012; Kokko 2013]. With mathematical modeling, we can determine the conditions under which the benefits of the various kleptoparasitic behaviors observed in nature outweigh the costs. Mathematical modeling also allows us to predict which ecological conditions make the occurrence of kleptoparasitism more likely.

Here we modify a game-theoretical "producer-scrounger" model developed in [Broom et al. 2015]. Producer-scrounger models [Barnard and Sibly 1981; Barnard 1984; Vickery et al. 1991; Caraco and Giraldea 1991; Dubois and Giraldeau 2005] describe interactions where after a kleptoparasite (i.e., the scrounger) encounters an individual with resources (i.e., the producer), the scrounger invests some amount of energy into stealing the resources while the producer attempts to defend them. Many game-theoretical models of two-individual interactions have been developed wherein the individuals have a discrete set of strategies available to them [Smith and Price 1973; Dubois and Giraldeau 2005; Broom et al. 2013], but realistically, individuals competing in kleptoparasitic interactions can invest amounts of energy from a continuous range of possibilities. This possibility is incorporated in our model, as it was in [Broom et al. 2015], where the producer-scrounger conflict is modeled as an extensive form game where the scrounger chooses its strategy first and the producer knows the scrounger's choice before making its own. Here, we present and analyze the simultaneous version of the game where both individuals have to decide without knowing the opponent's action.

The organization of our paper is as follows. In Section 2 we give a detailed mathematical description of our model. In Section 3 we analyze our model mathematically; in particular, we find best responses to opponent's actions in Section 3.1 and give conditions for Nash equilibria in Section 3.2. The results of our analysis are presented in Section 4. In Section 4.1 we show that (for the case $\alpha > 0$) Nash equilibria do not overlap and in Section 4.2 we show that the Nash equilibria exist for any parameter combination. We end our paper in Section 5 where we compare our model and its results to previous work, most notably to [Broom et al. 2015].

2. Model

One individual, a scrounger, is searching for resources and encounters another individual, a producer, who has a resource item of value v. Simultaneously, and

with no knowledge of the choice of the other, they both have to decide how aggressive to be in the contest for the item. The more aggressive each individual is relative to the opponent, the higher are the chances of winning the item, but also the higher is the cost of the interaction for that individual. Let $P_{\max}$ (or $S_{\max}$) be the maximum level of aggression that a producer (or scrounger, respectively) can display in a fight, and by $p \in [0, P_{\max}]$ (or $s \in [0, S_{\max}]$) we will denote the actually displayed level of aggression in a particular contest. The producer wins the fight (and the resource) with a probability of $p/(s+p)$, while the scrounger wins with probability $s/(s+p)$. If no individual fights (i.e., $p = s = 0$), then the producer is assumed to win and will keep the resource.

We will adopt the model for the fight costs from [Broom et al. 2015]. When no individual fights, the cost is 0. Otherwise, the cost to each individual is $(s+p)^\alpha$. Here, α is a tuning parameter that allows us to consider a broad range of scenarios. If $\alpha < 1$, then low aggression is costly relative to no aggression at all, but once the aggression reaches a certain level, increasing the aggression is typically not that costly in relative terms. On the contrary, when $\alpha > 1$, low aggression levels are relatively cheap, but escalating the fight (i.e., being a bit more aggressive) is relatively expensive as the function x^α is concave up. For the rest of the paper, we will assume $\alpha > 0$ except when we discuss the extreme case $\alpha = 0$ (when the cost of the fight is constant) separately in Section 4.3.

Assuming the scrounger plays $s \in [0, S_{\max}]$, the producer plays $p \in [0, P_{\max}]$, and the value of the resource is v, the payoffs to the producer and scrounger are given by

$$U_{pr}(s, p) = \begin{cases} v & \text{if } s = p = 0, \\ p/(s+p)v - (s+p)^\alpha & \text{if } s + p > 0, \end{cases} \tag{1}$$

$$U_{sc}(s, p) = \begin{cases} 0 & \text{if } s = p = 0, \\ s/(s+p)v - (s+p)^\alpha & \text{if } s + p > 0. \end{cases} \tag{2}$$

3. Analysis

3.1. ***Best responses.*** Here we will determine best responses for the scrounger and producer. A best response is a strategy that maximizes an individual's payoff given that their adversary's strategy is fixed, i.e., for a given $s \in [0, S_{\max}]$, we are looking for $p_{br}(s) \in [0, P_{\max}]$ such that

$$U_{pr}(s, p_{br}(s)) = \max_{p \in [0, P_{\max}]} \{U_{pr}(s, p)\}, \tag{3}$$

and, similarly, for a given $p \in [0, P_{\max}]$ we are looking for $s_{br}(p) \in [0, S_{\max}]$ such that

$$U_{sc}(s_{br}(p), p) = \max_{s \in [0, S_{\max}]}]\{U_{sc}(s, p)\}. \tag{4}$$

When $s = 0$, it immediately follows from (1) that $p_{br}(0) = 0$. When $s > 0$, we have

$$\frac{\partial}{\partial p} U_{pr}(s, p) = \frac{sv - \alpha(s+p)^{\alpha+1}}{(s+p)^2} \quad \text{for} \quad p > -s. \tag{5}$$

Let us define

$$f(x) = \left(\frac{xv}{\alpha}\right)^{1/(\alpha+1)} - x. \tag{6}$$

It follows from (5) that, for fixed s and variable p, the function $U_{pr}(s, p)$ is increasing on $(-s, f(s)]$ and decreasing on $[f(s), +\infty)$. Therefore,

$$p_{br}(s) = \begin{cases} 0 & \text{if } s = 0, \text{ or } s > 0 \text{ and } f(s) \le 0, \\ f(s) & \text{if } s > 0 \text{ and } 0 \le f(s) \le P_{\max}, \\ P_{\max} & \text{if } s > 0 \text{ and } f(s) \ge P_{\max}. \end{cases} \tag{7}$$

We note that the conditions in (7) are formally not mutually exclusive, but whenever two of the conditions coincide, so does the best response defined by them.

When $p = 0$, we have $U_{sc}(s, 0) = v - s^{\alpha}$ which increases to $v > 0$ as s decreases to 0 while $U_{sc}(0, 0) = 0$. Thus, there is no best response for the scrounger in this case. When $p > 0$,

$$\frac{\partial}{\partial s} U_{sc}(s, p) = \frac{pv - \alpha(s+p)^{\alpha+1}}{(s+p)^2} \quad \text{for} \quad s > -p. \tag{8}$$

Consequently, for a fixed p and variable s, the function $U_{sc}(s, p)$ is increasing on $(-p, f(p)]$ and decreasing on $[f(p), +\infty)$. Hence,

$$s_{br}(p) = \begin{cases} \text{does not exist} & \text{if } p = 0, \\ 0 & \text{if } p > 0 \text{ and } f(p) \le 0, \\ f(p) & \text{if } 0 < f(p) \le S_{\max}, \\ S_{\max} & \text{if } f(p) \ge S_{\max}. \end{cases} \tag{9}$$

As with p_{br}, we note that the conditions in (9) are formally not mutually exclusive, but whenever two of the conditions coincide, so does the best response defined by them.

3.2. ***Nash equilibria.*** Here we will identify all Nash equilibria of our game. A pair of strategies (s^*, p^*) is a *Nash equilibrium* if p^* is the producer's best response to s^* and s^* is the scrounger's best response to p^*.

By (7), we only need to consider cases when $p^* = 0$, $p^* = f(s^*)$ and $p^* = P_{\max}$; and by (9), for any of those cases we only need to consider $s^* = 0$, $s^* = f(p^*)$ and $s^* = S_{\max}$.

By (9), no pair $(s^*, 0)$ is a Nash equilibrium. When $s^* = 0$, by (7), we would need $p^* = 0$ and so no pair $(0, p^*)$ is a Nash equilibrium either. We will now investigate the remaining types separately. Table 1 summarizes the results.

Nash equilibrium	conditions
$(S_{\max}, P_{\max})$	$P_{\max} \le f(S_{\max}),\ S_{\max} \le f(P_{\max})$
$(S_{\max}, f(S_{\max}))$	$0 < f(S_{\max}) < P_{\max},\ S_{\max} \le f(f(S_{\max}))$
$(f(P_{\max}), P_{\max})$	$0 < f(P_{\max}) < S_{\max},\ P_{\max} \le f(f(P_{\max}))$
$\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$	$\frac{1}{2}(v/(2\alpha))^{1/\alpha} < \min(P_{\max}, S_{\max})$

Table 1. Nash equilibria and the conditions for their existence. As $f(x) = (xv/\alpha)^{1/(\alpha+1)} - x$, the conditions are given in terms of $P_{\max}$, $S_{\max}$, v and α.

3.2.1. *Type* $(S_{\max}, P_{\max})$. By (7) and (9), $(S_{\max}, P_{\max})$ is a Nash equilibrium if and only if

$$P_{\max} \le f(S_{\max}), \tag{10a}$$

$$S_{\max} \le f(P_{\max}). \tag{10b}$$

3.2.2. *Type* $(S_{\max}, f(S_{\max}))$. By (7) and (9), $(S_{\max}, f(S_{\max}))$ is a Nash equilibrium if and only if

$$0 < f(S_{\max}) < P_{\max}, \tag{11a}$$

$$S_{\max} \le f(f(S_{\max})). \tag{11b}$$

3.2.3. *Type* $(f(P_{\max}), P_{\max})$. By (7) and (9), $(f(P_{\max}), P_{\max})$ is a Nash equilibrium if and only if

$$0 < f(P_{\max}) < S_{\max}, \tag{12a}$$

$$P_{\max} \le f(f(P_{\max})). \tag{12b}$$

3.2.4. *Type* (p^*, s^*) *where* $p^* = f(s^*)$ *and* $s^* = f(p^*)$. Solving $p^* = f(f(p^*))$ yields a unique solution $p^* = \frac{1}{2}(v/(2\alpha))^{1/\alpha}$. Indeed, we have

$$x = f(f(x)) \tag{13}$$

$$= \left(\frac{f(x)v}{\alpha}\right)^{1/(\alpha+1)} - f(x) \tag{14}$$

$$= \left(\frac{f(x)v}{\alpha}\right)^{1/(\alpha+1)} - \left(\frac{xv}{\alpha}\right)^{1/(\alpha+1)} + x, \tag{15}$$

which after simple algebra yields

$$x = f(x) = \left(\frac{xv}{\alpha}\right)^{1/(\alpha+1)} - x, \tag{16}$$

and thus

$$x = \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha}. \tag{17}$$

Consequently, the only candidate for such a type of a Nash equilibrium is

$$\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha}\right).$$

By (7) and (9) it is indeed a Nash equilibrium if $0 < f(p^*) < S_{\max}$ and $0 < f(s^*) < P_{\max}$, and since $p^* = f(s^*),\ s^* = f(p^*)$, we get that $\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$ is a Nash equilibrium if and only if

$$\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha} < \min(P_{\max}, S_{\max}). \tag{18}$$

4. Results

We have seen that there are only four potential Nash equilibria in this game:

(1) $(S_{\max}, P_{\max})$,

(2) $(S_{\max}, f(S_{\max}))$,

(3) $(f(P_{\max}), P_{\max})$ and

(4) $\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$.

Here, we will show that under any parameter values $v > 0,\ \alpha > 0,\ S_{\max} > 0,\ P_{\max} > 0$, there exists one and only one Nash equilibrium.

The conditions (10), (11), (12) and (18) for the equilibria are given in terms of $f(x) = (xv/\alpha)^{1/(\alpha+1)} - x$. It is therefore crucial to understand the behavior of f. The following two equivalencies for $x \geq 0$ follow easily from simple algebra:

$$x \lessgtr \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha} \quad \text{if and only if} \quad x \lessgtr f(x), \tag{19}$$

and similarly,

$$x \lessgtr \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{1/\alpha} \quad \text{if and only if} \quad x \lessgtr f(f(x)), \tag{20}$$

and they will be useful when determining the existence and uniqueness of Nash equilibria.

4.1. ***Nash equilibria do not overlap.*** First, it follows from (20) that when (18) holds, one has $P_{\max} > f(f(P_{\max}))$ and $S_{\max} > f(f(S_{\max}))$, i.e., neither (12b) nor (11b) holds. Thus, $\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$ cannot occur at the same time as $(f(P_{\max}), P_{\max})$ or $(S_{\max}, f(S_{\max}))$. By (19), $f(S_{\max}) < S_{\max}$ and $f(P_{\max}) < P_{\max}$. Consequently, either $f(S_{\max}) < S_{\max} \leq P_{\max}$ or $f(P_{\max}) < P_{\max} \leq S_{\max}$, i.e., $\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$ cannot occur at the same time as $(S_{\max}, P_{\max})$.

Second, when (12) holds, then, by (20), $P_{\max} \leq \frac{1}{2}(v/(2\alpha))^{1/\alpha}$ and thus, by (19), $P_{\max} \leq f(P_{\max})$ and so $P_{\max} < S_{\max}$. By a similar argument, when (11) holds,

$S_{\max} < P_{\max}$. Consequently, $(S_{\max}, f(S_{\max}))$ and $(f(P_{\max}), P_{\max})$ are never Nash equilibria at the same time.

Finally, it is evident that neither (12) nor (11) can hold when (10) does. Consequently, there is always at most one Nash equilibria.

4.2. ***Nash equilibrium always exist.*** We show that for any $v > 0,\ \alpha > 0,\ S_{\max} > 0$, $P_{\max} > 0$, there is a Nash equilibrium. Here we will assume $P_{\max} < S_{\max}$, but when $S_{\max} \le P_{\max}$, the proofs are analogous.

If $\frac{1}{2}(v/(2\alpha))^{1/\alpha} < P_{\max} < S_{\max}$, then by (18), $\left(\frac{1}{2}(v/(2\alpha))^{1/\alpha}, \frac{1}{2}(v/(2\alpha))^{1/\alpha}\right)$ is a Nash equilibrium.

If $P_{\max} < S_{\max} < \frac{1}{2}(v/(2\alpha))^{1/\alpha}$, then by (19), $P_{\max} < S_{\max} < f(S_{\max})$, i.e., (10a) holds. Also, by (20), $P_{\max} < f(f(P_{\max}))$, i.e., (12b) holds. Consequently, if $f(P_{\max}) < S_{\max}$, then $(f(P_{\max}), P_{\max})$ is a Nash equilibrium (because we assumed $P_{\max} < \frac{1}{2}(v/(2\alpha))^{1/\alpha}$ and thus, by (19), $0 < P_{\max} < f(P_{\max})$, i.e., (12) holds); and, similarly, if $f(P_{\max}) \ge S_{\max}$, then $(S_{\max}, P_{\max})$ is a Nash equilibrium.

If $P_{\max} < \frac{1}{2}(v/(2\alpha))^{1/\alpha} < S_{\max}$, then, by (20), $P_{\max} < f(f(P_{\max}))$, i.e., (12b) holds. Consequently,

(a) if $f(P_{\max}) < S_{\max}$, then $(f(P_{\max}), P_{\max})$ is a Nash equilibrium; and

(b) if $f(P_{\max}) \ge S_{\max}$ and $f(S_{\max}) \ge P_{\max}$, then $(S_{\max}, P_{\max})$ is a Nash equilibrium.

Since $P_{\max} < S_{\max}$, one cannot have $f(P_{\max}) \ge S_{\max}$ and also $f(S_{\max}) < P_{\max}$. Consequently, the above cases are the only two possible cases and thus there is always a Nash equilibrium.

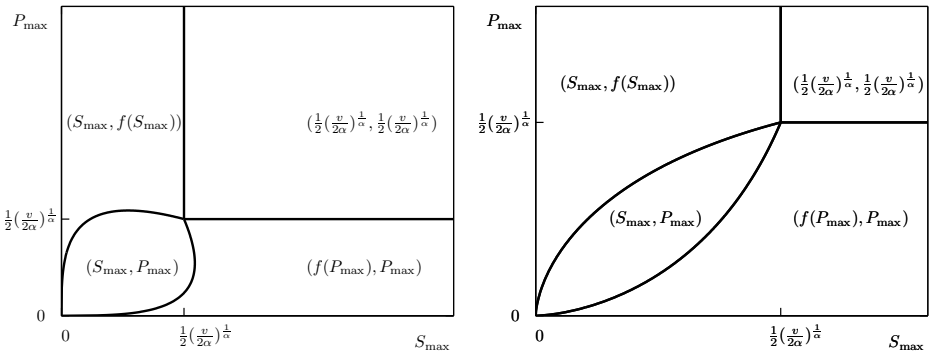

Figure 1. Regions of existence of Nash equilibria as $v = 1$, $S_{\max}$ and $P_{\max}$ varies and (left) $\alpha = 2$ and (right) $\alpha = 0.5$. Note that the regions do not overlap and the individuals are always aggressive (the level of aggression increases with increasing v (when $S_{\max}$ and $P_{\max}$ are fixed).

Figure 1 shows the Nash equilibria for fixed v and α and variable $S_{\max}$ and $P_{\max}$. Figure 2 shows Nash equilibria and payoffs for fixed $S_{\max}$, $P_{\max}$, α and variable v. We see that for small v, individuals play $\frac{1}{2}(v/(2\alpha))^{1/\alpha}$, $\frac{1}{2}(v/(2\alpha))^{1/\alpha}$. For large v, individuals play $(S_{\max}, P_{\max})$. For medium v, individuals play $(f(P_{\max}), P_{\max})$ when $S_{\max} > P_{\max}$ and $(S_{\max}, f(S_{\max}))$ when $S_{\max} < P_{\max}$. Note that as v increases, so does the optimal aggression level; yet with increasing aggression, the relative payoff may decrease, as seen in Figure 2a and c for equilibria of the form $(S_{\max}, f(S_{\max}))$ and $(f(P_{\max}), P_{\max})$. Also note that for $\alpha < 1$ and small v, the payoffs are negative for both players; see Figure 2b and d. As v grows, the payoffs eventually become positive (it happens first for a more aggressive individuals).

4.3. ***Case* $\alpha = 0$.** So far, we have considered only $\alpha > 0$. When $\alpha = 0$, the cost of a fight is the constant 1 no matter what the exact aggression levels are (as long as at least one individual is aggressive). Thus, for fixed $s > 0$, $U_{pr}(s, p)$ is increasing in p and, for fixed $p > 0$, $U_{sc}(s, p)$ is increasing in s and the individuals effectively choose between being not aggressive at all or being aggressive at their maximal level. Hence, they play the following bimatrix game where the scrounger's payoff is

$$\begin{array}{cc} S\backslash P & \begin{array}{cc} 0 & \quad P_{\max} \end{array} \\ \begin{array}{c} 0 \\ S_{\max} \end{array} & \begin{pmatrix} 0 & -1 \\ v-1 & \dfrac{S_{\max}}{S_{\max}+P_{\max}}v-1 \end{pmatrix} \end{array}, \tag{21}$$

and the producer's payoff is

$$\begin{array}{cc} S\backslash P & \begin{array}{cc} 0 & \quad P_{\max} \end{array} \\ \begin{array}{c} 0 \\ S_{\max} \end{array} & \begin{pmatrix} v & v-1 \\ -1 & \dfrac{P_{\max}}{S_{\max}+P_{\max}}v-1 \end{pmatrix} \end{array}. \tag{22}$$

It turns out that this game is a variant of the stag hunt game [Skyrms 2004] for $v < 1$ and the prisoner's dilemma game for $v > 1$.

When the producer plays $p = P_{\max}$, the scrounger always prefers $s = S_{\max}$ over $s = 0$. When the scrounger plays $s = S_{\max}$, the producer always prefers $p = P_{\max}$ over $p = 0$. Consequently, $(S_{\max}, P_{\max})$ is always a Nash equilibrium. When the scrounger plays $s = 0$, the producer prefers $p = 0$. When the producer plays $p = 0$, the scrounger prefers $s = 0$ when $v < 1$ and prefers $s = S_{\max}$ when $v > 1$. Consequently, when $v > 1$, $(S_{\max}, P_{\max})$ is the only Nash equilibrium, and when $v < 1$, both $(S_{\max}, P_{\max})$ and $(0, 0)$ are Nash equilibria.

Note the paradoxical situation in the case when

$$1 < v < \frac{S_{\max} + P_{\max}}{S_{\max}}.$$

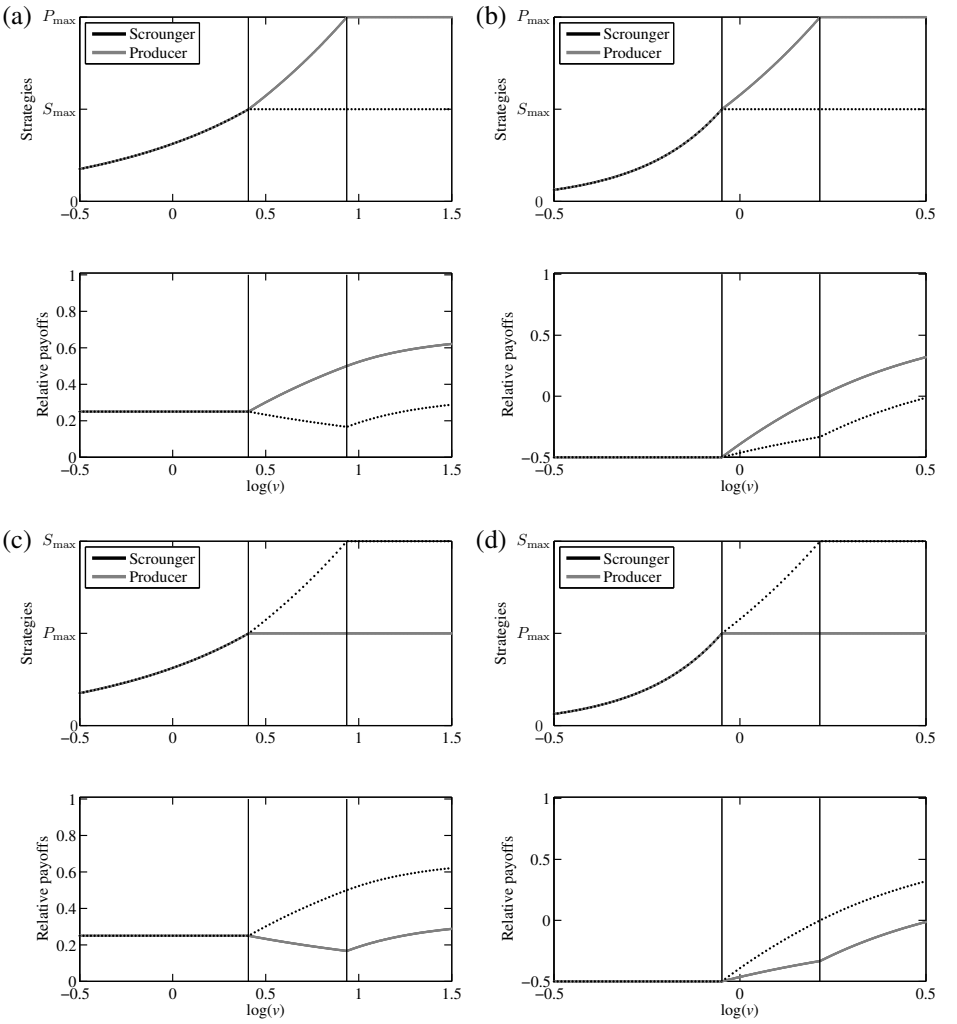

Figure 2. Nash equilibria and payoffs relative to v (i.e., $U_{sc}(s^*, p^*)/v$ for the scrounger and $U_{pr}(s^*, p^*)/v$ for the producer) when: (a) $S_{max} = 0.4$, $P_{max} = 0.8$, $\alpha = 2$, (b) $S_{max} = 0.4$, $P_{max} = 0.8$, $\alpha = 0.5$; (c) $S_{max} = 0.8$, $P_{max} = 0.4$, $\alpha = 2$; and (d) $S_{max} = 0.8$, $P_{max} = 0.4$, $\alpha = 0.5$. The vertical lines show the switch between Nash equilibria.

In this case, as in the prisoner's dilemma game, (S_{max}, P_{max}) is a Nash equilibrium but the scrounger is getting a negative payoff (and the producer is also getting strictly less than v). Hence both individuals would prefer not to engage in an aggressive conflict. Yet $(0, 0)$ is not a Nash equilibrium because once either of the individuals decides not to be aggressive, the other one will be better off by being as aggressive as possible.

5. Discussion

We have created and analyzed a model for kleptoparasitic interactions when individuals decide on the level of aggression in which they want to engage in the contest over a resource item. We show that for any parameter values, there is a unique Nash equilibrium. We have provided explicit formulas for all of four possible types of Nash equilibria and have also derived explicit conditions for their existence.

Our model extends the model of [Broom et al. 2015] where the authors considered sequential decisions whereas we consider simultaneous decisions (or equivalently, a situation when both individuals have to chose the action without knowing the opponent's action). The analysis in our model is more complicated because individuals only know that the opponent will chose the optimal level of aggression, but unlike in the setting of [Broom et al. 2015], what is optimal depends on individual's own action as well. Our results also differ from the sequential setting, as our game does not admit multiple Nash equilibria (when $\alpha > 0$) and it is also optimal to express at least some level of aggression. When v is small (relative to the maximal potential level of aggression of at least one of the individuals), the sequential model allows individuals to avoid the actual conflict, while they still fight aggressively in our simultaneous model. The difference between the two models is largest for concave down cost functions ($\alpha < 1$) when the individuals would be better off without engaging in any fight (and this is indeed the Nash equilibrium for sequential decisions) but they still end up being aggressive when the decisions need to be made simultaneously. On the other hand, when v is large, then both the sequential and simultaneous decision models yield the same Nash equilibria.

The fight cost function plays a critical role in the determination of the equilibrium solutions. The fight cost functions that are considered in our model have the form $(s + p)^\alpha$, where $0 \leq \alpha$. It would be possible to model the fight cost function with greater complexity to increase the model's realism (see, e.g., [Baye et al. 2005; 2012]), but we have worked with the present fight cost formulation because it encompasses several possible fight cost functions without sacrificing the model's tractability. The appropriate setting for fight cost structure (i.e., for α) will of course depend on the interactions being modeled. Circumstances that lead to different settings of α are considered in [Broom et al. 2015]; in particular, $\alpha > 1$ corresponds to interactions for which the primary cost is risk of injury or lost energy whereas $\alpha < 1$ corresponds to interactions for which the primary cost is a time cost. Such a time cost can be opportunity cost (i.e., lost time that can otherwise be spent foraging) or it can be the predation risk incurred by prolonged exposure while fighting for resources.

Similarly to [Broom et al. 2015], we assume that all individuals know the values of all parameters; in particular the scrounger knows $P_{\max}$ and the producer knows

$S_{\max}$ and both individuals know the cost function and v. In [Broom and Rychtář 2009; 2016; Broom et al. 2013; 2014], the authors study the situation when v is not known to one of the individuals. However, as shown in Figure 1, different $P_{\max}$ may not only yield different behavior of producer but may also yield different behavior of the scrounger. Thus, not knowing the opponent's maximum potential level of aggression will potentially influence the choice of individual strategies. Consequently, it would be interesting to model such a scenario.

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dgsykes@tamu.edu *Department of Mathematics, Texas A&M University, College Station, TX 77843-3368, United States*

rychtar@uncg.edu *Department of Mathematics and Statistics, The University of North Carolina at Greensboro, Greensboro, NC 27412, United States*

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