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Kleptoparasitic Interactions under Asymmetric Resource Valuation

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Abstract. We introduce a game theoretical model of stealing interactions. We model the situation as an extensive form game when one individual may attempt to steal a valuable item from another who may in turn defend it. The population is not homogeneous, but rather each individual has a different Resource Holding Potential (RHP). We assume that RHP not only influences the outcome of the potential aggressive contest (the individual with the larger RHP is more likely to win), but that it also influences how an individual values a particular resource. We investigate several valuation scenarios and study the prevalence of aggressive behaviour. We conclude that the relationship between RHP and resource value is crucial, where some cases lead to fights predominantly between pairs of strong individuals, and some between pairs of weak individuals. Other cases lead to no fights with one individual conceding, and the order of strategy selection is crucial, where the individual which picks its strategy first often has an advantage.

Keywords and phrases: stealing, resource holding potential, game theory, Producer-Scrounger game

Mathematics Subject Classification: 91A18, 91A40, 91A05

1. Introduction

Kleptoparasitism, the stealing or attempted stealing of resources (usually food), occurs in a variety of contexts as animals compete for resources. One often associates stealing behaviour with seabirds and their spectacular aerial contests for fish [26–28], but kleptoparasitism is a very common behaviour in nature, and is practiced by a very diverse collection of species such as insects [21], fish [17] and mammals [22]. A good review paper with nice classifications as well as numerous examples is [20]. The strategies associated with stealing interactions can vary; for instance, in some interactions resources are promptly forfeited while in others there are drawn out competitions as an individual defends its resources.

Typically when modelling kleptoparasitic interactions populations are assumed homogenous with every individual being virtually the same, see for example [4, 6–8]. However, there is variation within real populations and such a variation is usually modelled using the idea of *Resource Holding Potential* (RHP)

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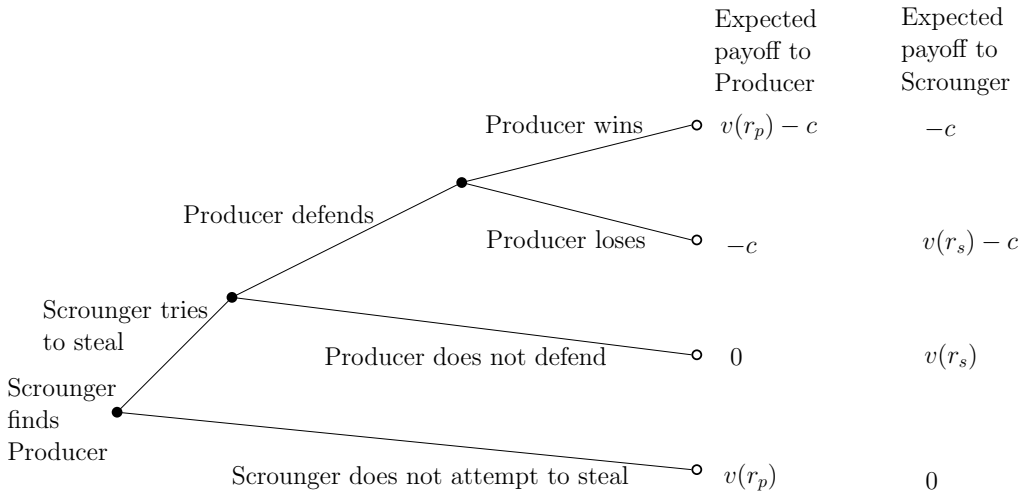


Figure 1: Scheme and payoffs of the game.

[24], which can (for example) represent the size or any other measure of strength of the individual. RHP is typically used in hierarchy formation models (see for example [3, 8, 15, 23]).

The paper [16] and references therein investigated the effect of variation in resource value on fighting behaviour. That variation is often caused by the size of the food item or the time a food owner has already spent eating the food item (see [5] for the analysis of the latter case). In this paper we investigate the situation in which the variation of the resource value is caused by differences between individuals within the population.

RHP can influence the probability of an individual winning a potential contest and it can also influence how an individual values a particular resource. An example of this behaviour is the case of the gardening reef fish Western Buffalo Bream, *Kyphosus cornelii* (see for example [11, 18]). The RHP for the fish is likely to be positively correlated with the size of its garden. The value of a food item for a fish whose garden is large is presumably smaller than the value of the same food item for a fish whose garden is small.

One way to model kleptoparasitic interactions is the so called producer-scrounger game developed in [2]. A number of variants of this model have been developed to consider different circumstances and assumptions (see for example [10, 13, 14, 30]). Here, we consider a scenario where one individual, a producer, possesses a valuable resource when another individual, a scrounger, comes along and may attempt to steal it.

2. The Model

We model the situation as a game in an extensive form as shown in Figure 1. One individual, a producer, is in a possession of a resource of (intrinsic) value f. Another individual, a scrounger, subsequently arrives and may attempt to steal it. If the scrounger makes such a stealing attempt, then the producer can either give up the resource without any conflict or defend it. The conflict cost is c and the producer wins the conflict (and can keep the resource) with probability a. The probability of winning depends on the RHPs r_p and r_s, respectively, of the producer and scrounger. Following [15], we consider $a = \frac{r_p}{r_p + r_s}$.

We also assume that an individual values the resource depending on its own RHP, so that the value for an individual with RHP r is given by a resource valuation function $v(r)$. The model parameters are summarized in Table 1. The payoffs from different scenarios are shown in Figure 1.

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Table 1: Used symbols and parameters.

Symbol	Meaning
$r_{\max}$	maximal RHP of an individual
$r_s \in (0, r_{\max}]$	RHP of the scrounger
$r_p \in (0, r_{\max}]$	RHP of the producer
$a = \frac{r_p}{r_p + r_s}$	Probability that the producer wins a conflict
$f \in (0, \infty)$	Intrinsic value of the resource
$c \in (0, \infty)$	Cost of a conflict
$v(r)$	Value of a resource for an individual with RHP r; we will consider functions of the form $v(r) = fr^x$.
x	Tuning parameter for the function $v(r)$.

2.1. The resource valuation function

In order to allow for different resource valuation functions but keeping the situation simple at the same time, we consider a family of functions $v(r) = fr^x$ for varying x. When $x = 0$, we have $v(r) = f$, representing the situation where all individuals value the resource equally. For $x < 0$, individuals with small RHP value the same resource more than individuals with larger RHP, an example of which is the Western Buffalo Bream mentioned in the Introduction. For $x > 0$, individuals with small RHP value the resource less than individuals with larger RHP. This might occur if the resource is a territory which helps to acquire food or mates, but needs to be defended for a long period, where stronger individuals have more chance of carrying out such a defence successfully.

3. Analysis

We will analyze the game using backward induction. Assume that the scrounger attempts to steal. The producer has to decide whether to defend or not. If it does not defend, the payoff will be 0. If it defends, it results in a fight which is lost with probability $1 - a$. Hence if the producer defends, the expected payoff when defending is $-c + av(r_p)$. Consequently, the producer should defend if

$$0 < -c + av(r_p) \tag{3.1}$$

which is equivalent to

$$c < \frac{r_p}{r_s + r_p} v(r_p). \tag{3.2}$$

Now, we will investigate the options for the scrounger. If the scrounger does not attempt to steal, the payoff will be 0. If (3.2) does not hold, then the producer will not defend against a stealing attempt and thus the scrounger should attempt to steal to get a payoff $v(r_s) > 0$. If (3.2) holds, then the producer will defend against the stealing attempt. Hence, if the scrounger attacks, it will lose with probability a (and get a payoff $-c$) and win with probability $1 - a$ (and get a payoff $v(r_s) - c$). The expected payoff is thus $(1 - a)v(r_s) - c$. Hence, the scrounger should attack if

$$(1 - a)v(r_s) - c > 0 \tag{3.3}$$

which is equivalent to

$$\frac{r_s}{r_p + r_s} v(r_s) > c. \tag{3.4}$$

There are thus three distinct behavioural patterns as presented in Table 2.

In order to plot the patterns in the (r_s, r_p) plane, we can work with the inequalities further to obtain that the scrounger attempts to steal and the producer does not defend if

$$r_s > r_p \left(\frac{v(r_p)}{c} - 1 \right); \tag{3.5}$$

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Table 2: Summary of the results

Condition	Behaviour
$\frac{r_s}{r_p+r_s}v(r_s) < c < \frac{r_p}{r_p+r_s}v(r_p)$	The scrounger does not attempt to steal.
$\frac{r_p}{r_s+r_p}v(r_p) < c$	The scrounger attempts to steal, and the producer does not defend.
$c < \min\left\{\frac{r_p}{r_s+r_p}v(r_p), \frac{r_s}{r_p+r_s}v(r_s)\right\}$	The scrounger attempts to steal, and the producer defends.

the scrounger does not attempt to steal if

$$r_s < r_p\left(\frac{v(r_p)}{c}-1\right), \text{ and} \tag{3.6}$$

$$r_p > r_s\left(\frac{v(r_s)}{c}-1\right); \tag{3.7}$$

and finally the scrounger attempts to steal and the producer defends if

$$r_s < r_p\left(\frac{v(r_p)}{c}-1\right), \text{ and} \tag{3.8}$$

$$r_p < r_s\left(\frac{v(r_s)}{c}-1\right). \tag{3.9}$$

Note that when

$$\frac{v(r_p)}{c} \leq 1, \tag{3.10}$$

then (3.5) holds while (3.6) and (3.8) do not, i.e. the scrounger attempts to steal and the producer does not defend. This is caused by the cost of a fight being prohibitively large for the producer to fight, and so as the producer will concede, the scrounger can safely attempt to steal.

4. Optimal strategies for different resource valuations

In this section, we will consider in detail the family of resource valuation functions $v(r) = fr^x$ for different x.

4.1. The symmetric valuation; the case $x = 0$

When $x = 0$, the resource valuation function is a constant function $v(r) = f$. From equations (3.5) - (3.9) (see also Table 2) we get that there is no interaction (the scrounger does not attempt to steal) if $\frac{f}{c} > 1$ and

$$r_p > r_s\left(\frac{f}{c}-1\right), \text{ and} \tag{4.1}$$

$$r_p > r_s\left(\frac{f}{c}-1\right)^{-1}. \tag{4.2}$$

Similarly, the scrounger attempts to steal but the producer does not defend if

$$r_s > r_p\left(\frac{f}{c}-1\right). \tag{4.3}$$

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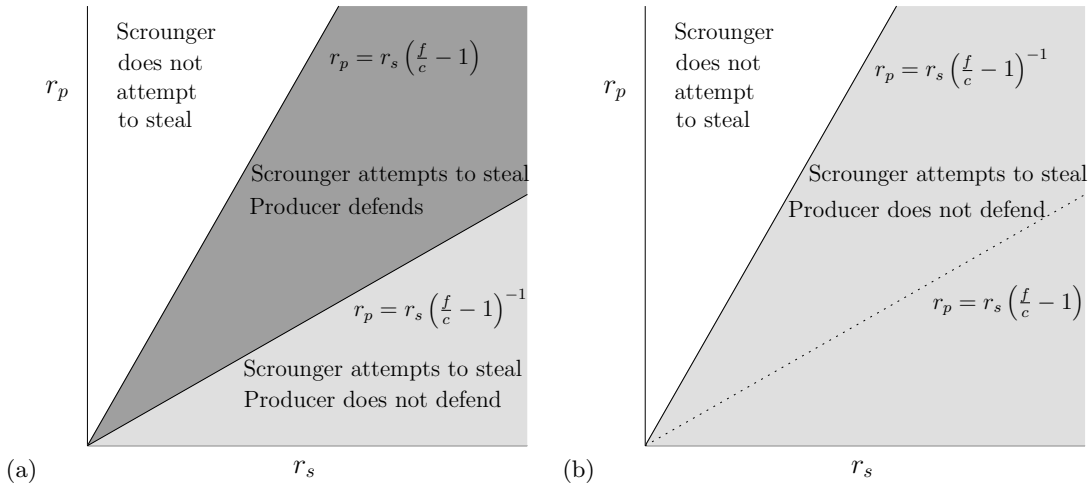


Figure 2: Behavioural outcomes of the game for $v(r) = f$. (a) $2 < \frac{f}{c}$, (b) $1 < \frac{f}{c} < 2$. The case $\frac{f}{c} < 1$ is not shown; in that case a scrounger attempts to steal and the producer does not defend for any pair of (r_s, r_p).

When $\frac{f}{c} \leq 1$, the condition (4.3) is satisfied for any pair (r_s, r_p). When $\frac{f}{c} > 1$, the condition (4.3) is equivalent to

$$r_p < r_s \left(\frac{f}{c} - 1\right)^{-1}. \tag{4.4}$$

Finally, the scrounger attempts to steal and the producer defends if $\frac{f}{c} > 1$,

$$r_p < r_s \left(\frac{f}{c} - 1\right), \text{ and} \tag{4.5}$$

$$r_p > r_s \left(\frac{f}{c} - 1\right)^{-1}. \tag{4.6}$$

We see that we have three possible scenarios, depending on the value of $\frac{f}{c}$. When $\frac{f}{c} \leq 1$, then the scrounger attempts to steal but the producer does not defend. When $1 < \frac{f}{c} < 2$, then the scrounger attempts to steal only when r_p is not much larger than r_s and in that case, the producer gives up. If r_p is too large, the scrounger does not attempt to steal. There is never a producer defending its resource. When $\frac{f}{c} > 2$, then all three behavioural patterns are possible with the producer giving up only if r_p is relatively small compared to r_s, and the scrounger attempting to steal only if r_p is not too large (compared to r_s). For a fixed r_s, the producer gives up the resource if r_p is small, defends it if r_p is of medium size and there is no interaction if r_p is large. The scenarios are summarized in Figure 2.

4.2. The singular case $x = -1$

For $v(r) = \frac{f}{r}$, the conditions for the scrounger not attempting to steal become

$$\frac{1}{r_p + r_s} < \frac{c}{f} < \frac{1}{r_p + r_s} \tag{4.7}$$

which can never be fulfilled. Hence, the scrounger will always attempt to steal. Also, the producer will defend the resource if

$$r_p < \frac{f}{c} - r_s \tag{4.8}$$

and will not defend it otherwise. The situation is illustrated on Figure 3.

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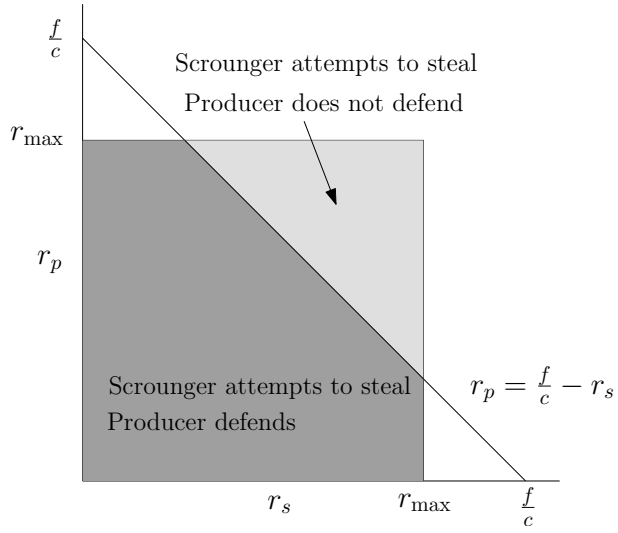


Figure 3: Behavioural outcomes of the game for $v(r) = f/r$. The scrounger always attempts to steal and if $\frac{f}{c} > 2r_{\max}$, then the producer always defends.

As $\frac{f}{c}$ grows, the region of pairs (r_s, r_p) for which the producer defends grows as well. Specifically, the producer defends for any $r_p \leq r_{\max}$ if $r_s \leq \frac{f}{c} - r_{\max}$. If $\frac{f}{c} > 2r_{\max}$, then the producer defends the resource in all circumstances.

4.3. The case where $-1 < x < 0$

Here we take $v(r) = fr^x$ for $-1 < x < 0$. The situation is shown in Figure 4. We see that the three behavioural outcomes are always possible, regardless of the value of $\frac{f}{c}$. Yet, the bigger $\frac{f}{c}$, the bigger the region when the scrounger attempts to steal and the producer defends. Note that unlike in the symmetric case with $x = 0$, fights occur only for relatively small values of r_s and r_p and as soon as an RHP of any (or both) of the two individuals is large enough (larger than $\left(\frac{f}{2c}\right)^{-\frac{1}{x}}$), then the scrounger either does not attempt to steal or the producer does not defend.

4.4. The case where $x < -1$

Here we take $v(r) = fr^x$ for $x < -1$. The situation is shown in Figure 5. We see that the presence or absence of the different behavioural outcomes depends on the value of $\frac{f}{c}$. The bigger $\frac{f}{c}$, the bigger the region when the scrounger attempts to steal and the producer defends. If $r_{\max} < \left(\frac{f}{2c}\right)^{-\frac{1}{x}}$, then there is always a conflict; but the conflict is present even for small values of $\frac{f}{c}$.

Also note that (unlike in the case of $-1 < x \leq 0$) here the scrounger does not steal when r_s is large and r_p is small. This is a consequence of the fact that for such parameters, the value of the resource for a scrounger is smaller than the cost of the conflict, but the value for the producer is larger than the cost of conflict. Similarly, unlike before, the producer gives up whenever r_p is large (because the value of the resource is then much smaller than the cost of the conflict). This happens even in the case of small r_s, i.e. even when the producer is almost certain to win the conflict.

Note that unlike in the symmetric case $x = 0$, fights occur only for relatively small values of r_s and r_p and as soon as an RHP of any (or both) of the two individuals is large enough, then the scrounger either does not attempt to steal or the producer does not defend.

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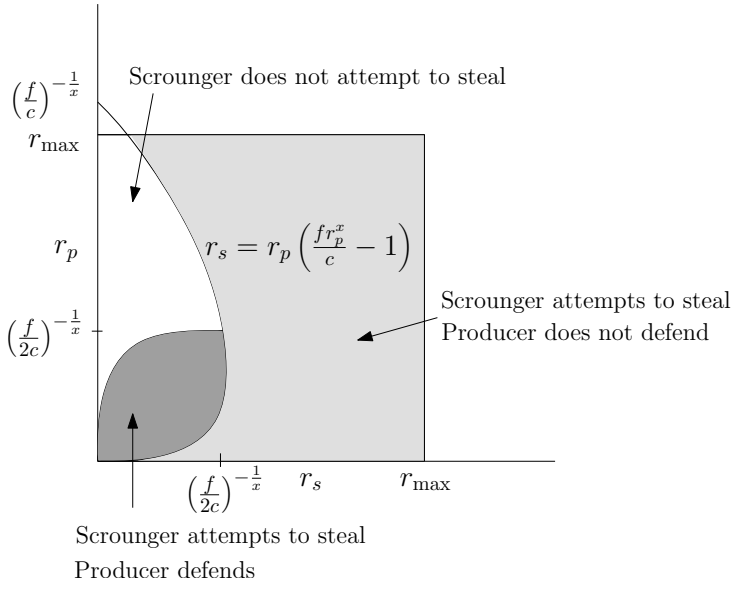


Figure 4: Behavioural outcomes of the game for $v(r) = fr^x, x \in (-1, 0)$.

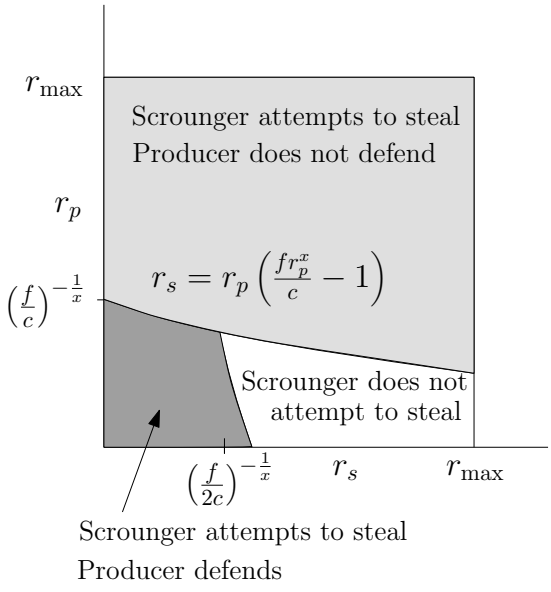


Figure 5: Behavioural outcomes of the game for $v(r) = fr^x, x < -1$.

4.5. The case where $x > 0$

Here we take $v(r) = fr^x$ for $x > 0$. The situation is shown in Figure 6. We see that the presence of the behavioural outcomes depends on the value of $\frac{f}{c}$. If $\frac{f}{c}$ is small enough (precisely, if $r_{\max} < \left(\frac{f}{c}\right)^{-\frac{1}{x}}$), then the producer never defends. If $\left(\frac{f}{c}\right)^{-\frac{1}{x}} < r_{\max} < \left(\frac{f}{2c}\right)^{-\frac{1}{x}}$, then the scrounger does not attempt to steal when r_p is large enough, but there is still no conflict here. The conflict appears only when $r_{\max} > \left(\frac{f}{2c}\right)^{-\frac{1}{x}}$ and the bigger $\frac{f}{c}$, the bigger the region when conflict happens.

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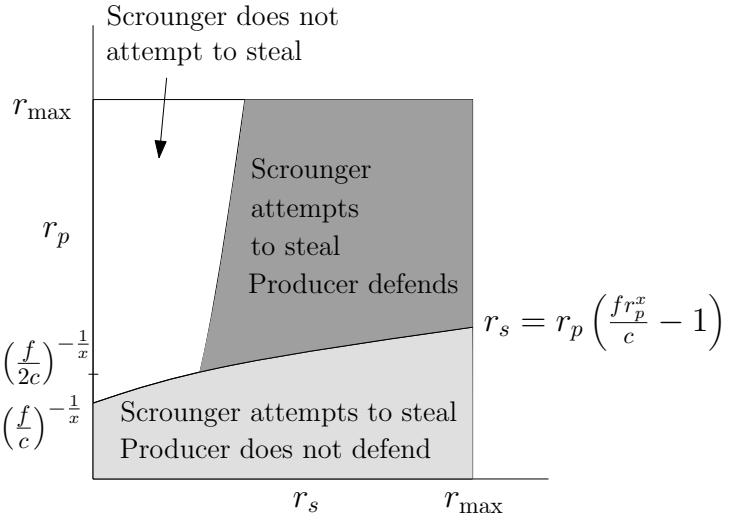


Figure 6: Behavioural outcomes of the game for $v(r) = fr^x, x > 0$.

5. Discussion

In this paper we have developed a model of resource stealing behaviour, based upon the model developed in [2]. In our model, there are differences between individuals in Resource Holding Potential (RHP) and this affects not only their chances of winning any conflict, but also how much they value a particular resource. We have found that there is a strong effect from the relationship between RHP and the value of resources on how much and when aggressive behaviour occurs in the population. If weaker individuals value a resource more highly ($x < 0$ in our model), then fights occur mainly between these weaker individuals, and if stronger individuals value a resource more highly, then it is these individuals that fight.

The clearest example of the former case is where individuals are competing for resources to survive, where desperate individuals are prepared to fight and those that are well-fed are not. For example the competitive behaviour of some birds will change with the season, and engage in stealing only when food is rare in the winter, and not in the summer (e.g. Olrog's gull, see [12]). Foraging models where the value of the food item, and consequently the optimal choice of the forager, depend upon the state of the individual in this way are discussed in detail in [19]. This variation can take other forms in addition to how aggressive to be to conspecifics, such as the willingness to take more predation risks by being less vigilant.

The competition for longer term advantages such as a position in a dominance hierarchy where dominant individuals have most mating opportunities is an example of the latter case where resources are more valuable to stronger animals. In these situations, dominant individuals fight for the top positions in the hierarchy, as the difference between first and second can be large, but individuals lower down the order often do not compete at all, as all lower positions are of similar value, and the probability of a lowly ranked individual defeating a highly ranked one is small. The division of resources within such a group is termed reproductive skew (the more the inequality, the higher the reproductive skew, [29]) and the higher the skew, the greater the benefit in challenging ([25] consider this in ant colonies with multiple queens). We should also note that psychological reasons often back up this situation, where the strong that are used to winning are more likely to fight and win in the future (winner effects), and even more significantly the weak that are used to losing are less likely to fight and more likely to lose any future fights (loser effects, e.g. [15]).

Often in our game there is no contest, as either the second individual to arrive at the resource (the scrounger) does not challenge, or, if it challenges, the first individual (the producer) concedes. Which

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of these occurs depends strongly on the parameters. In general the case where the producer concedes is more common, and so the position of the scrounger being the first to choose its strategy yields it an advantage. This may seem surprising, as the producer can choose its strategy based upon knowledge of the scrounger strategy whereas the scrounger has no such knowledge, but in fact this has been observed before in related models, such as in [9] or in the kleptoparasitism model of [4] and in evolutionary games with sequential decisions more generally; see for example the game of brood care and desertion [19].

If the contests in the game were of different form, this could potentially lead to different results. We have chosen the simplest model where the scrounger makes the initial decision and there is some response by the producer. This is logical, for example, if the scrounger discovers the producer and can challenge before the producer knows it is there. However, if the producer sees the scrounger approaching from some distance and can take a defensive position associated with its strategy of choice, then it would be more reasonable to assume the reverse order. As we have seen in the above, the order of the players in a sequential game can make a real difference. Moreover real interactions would likely involve a sequence of choices by the players, leading to more complex play. An alternative way of modelling such situations using simple games would be to treat the contest as one involving simultaneous decisions (this was in fact often the approach from the earlier producer-scrounger models, see for example [1]).

Finally we should briefly discuss the difference between the model used here, and the alternative models of stealing behaviour, such as in [4]. These models assume a single indivisible resource, which cannot be shared. Furthermore it takes time to find and handle and fights take time to complete (lost time being the main cost of fighting, as opposed to energetic or injury costs). Thus choice of strategy directly affects the opportunities available to individuals, so that the population level behaviour is more complicated; for example an individual which always surrenders its resource will waste less time in fights, and will be more likely to find a producer than one who always fights. Producer-scrounger models, including the model in this paper, typically neglect such factors and involve instantaneous contests which result in energetic cost. In addition, producer-scrounger models usually involve divisible resources which can be shared (though this is not strictly necessary, and our sequential approach makes no use of this). In particular the population complications are removed, and such models can focus on the individual contest as an independent entity, which allows such contests to be more complicated and yet still mathematically tractable. Note that this is realistic in cases of low population density when interactions are rare, but less so in cases where interactions are very common.

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