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The effect of fight cost structure on fighting behaviour

Mark Broom · Michal Johanis · Jan Rychtář

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Abstract A common feature of animal populations is the stealing by animals of resources such as food from other animals. This has previously been the subject of a range of modelling approaches, one of which is the so called "producer-scrounger" model. In this model a producer finds a resource that takes some time to be consumed, and some time later a (generally) conspecific scrounger discovers the producer with its resource and potentially attempts to steal it. In this paper we consider a variant of this scenario where each individual can choose to invest an amount of energy into this contest, and the level of investment of each individual determines the probability of it winning the contest, but also the additional cost it has to bear. We analyse the model for a specific set of cost functions and maximum investment levels and show how the evolutionarily stable behaviour depends upon them. In particular we see that for high levels of maximum investment, the producer keeps the resource without a fight for concave cost functions, but for convex functions the scrounger obtains the resource (albeit at some cost).

Keywords kleptoparasitism · sequential game · extensive form game · food stealing · game theory

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Mark Broom
Department of Mathematics, City University London, Northampton Square, London, EC1V 0HB, UK
E-mail: mark.broom@city.ac.uk

Michal Johanis
Department of Mathematical Analysis, Charles University, Sokolovská 83, 186 75 Praha 8, Czech Republic
E-mail: johanis@karlin.mff.cuni.cz

Jan Rychtář
Department of Mathematics and Statistics, The University of North Carolina at Greensboro, Greensboro, NC 27412, USA
E-mail: rychtar@uncg.edu

1 Introduction

Animals need a variety of resources to live and reproduce, and often they have to compete with other animals for them. These resources include territories, mates and food. Their competitors can be conspecifics or member of other species, and the nature of contests vary depending upon the animals involved and the resources competed over. Territories are often of value for a significant period of time, if not indefinitely, and so provide significant opportunities for contests over ownership, with a series of intruders (Kruuk, 1972; Hamilton and Dill, 2003; Iyengar, 2008; Kokko, 2013).

Food resources however are often only available for small periods. If a food item can be consumed immediately by the individual that discovered it, then there is generally no chance for another to compete for it. Often, however, food items require a non-trivial handling time to eat them. This can be because the food item is destined for the offspring of the individual, and some must be transported to the nest or den, during which time others have the opportunity of taking it. Alternatively, it might take a while to consume because it has a tough exterior that needs to be penetrated, like a shell, or needs to be consumed in pieces which requires a bird to land to eat it (Spear et al, 1999; Steele and Hockey, 1995; Triplet et al, 1999). Such scenarios have been modelled by Broom and Ruxton (2003); Broom et al (2004); Broom and Rychtář (2007); Broom et al (2008); Broom and Rychtář (2011). Alternatively the resource might be a large food patch which just takes time to completely consume, which is the focus of producer-scrounger models (Barnard and Sibly, 1981; Barnard, 1984; Caraco and Giraldeau, 1991; Vickery et al, 1991; Dubois and Giraldeau, 2005), see also Giraldeau and Livoreil (1998); Kokko (2013); Broom and Rychtář (2013) for more general reviews.

In our model we consider a version of the producer-scrounger scenario. A producer finds a resource that takes some time to be consumed, and some time later a (generally) conspecific scrounger discovers the producer with its resource and potentially attempts to steal it. In most previous versions of the model the competitors had a choice of a discrete set of options only, for example fight or concede, or in a given contest to play aggressively or passively, as in the classical Hawk-Dove game (Maynard Smith and Price, 1973; Maynard Smith, 1982). More realistically animals can vary the amount of investment they make in a contest, which can be a small token effort (perhaps in the hope that the other will concede), an intermediate but serious effort, or a full-blown effort at the maximum level possible. We consider a scenario where a scrounger individual has discovered a producer individual with a resource, and must decide whether to fight or not. Each individual invests an amount of energy into this contest, and the level of investment of each determines the probability of it winning the contest. In addition, each individual incurs a cost for the contest, which depends upon the level of investment made. In the following sections, we carefully detail the mathematical assumptions of the model, perform a general analysis for the functional forms we have chosen, and then investigate the results for different key parameter values. Finally we discuss the implications of our results both biologically, and for future models.

2 The Model

We model the situation described above as a game in extensive form. One individual, a producer, is in possession of a resource of fixed value v. Another individual, a scrounger, comes along and may attempt to steal it. The scrounger invests $s \in [0, S]$ units of energy in the stealing attempt. When $s = 0$, nothing happens. When $s > 0$, the producer then invests $p \in [0, P]$ units of energy in defending the item. The probability that the producer successfully defends the item will be an increasing function of p, and a decreasing function of s, which for tractability of analysis we simply set as $\frac{p}{s+p}$. Such a function has been introduced in Tullock (1980), who considered the more general form $\frac{p^k}{s^k+p^k}$, which in the limit of $k \to \infty$ gives the case where the individual with the highest investment always wins, as in the classical war of attrition, e.g. see Bishop and Cannings (1978). Such functions were axiomatized by Skaperdas (1996), and our natural choice has now become widely used (see for example Congleton et al, 2008). When the individuals engage in the fight, each one incurs a cost $c(s, p)$.

In full generality, the cost function $c(s, p)$ is asymmetrical and potentially different for the scrounger and producer. It consists of the true energetic cost of the investment (such as performing a complex manoeuvre in an aerial contest between birds), the potential for getting hurt by an animal's own actions (typically, the more complex the manoeuver, the more things could go wrong and the animal could end up seriously injured even if the other individual does not fight) and the potential for getting hurt by the actions of the opponent. However, in such a full generality, the mathematics would be intractable, and we thus consider a symmetrical cost function (note that it is possible to find solutions for linear asymmetric functions, as shown in Baye et al (2012)). The symmetrical cost function that we use is defined by

$$c(s, p) = (s + p)^\alpha \tag{1}$$

for $s+p > 0$ and $\alpha \geq 0$. We note that one consequence of this is that extra investment by the other player will directly affect an individual's cost, and so potentially its chosen strategy. Clearly we do not need to define the cost at $s + p = 0$, since a contested resource requires $s > 0$ and $p \geq 0$. We note that there are other symmetrical cost functions used, such as $\min(p, s)$ in the war of attrition, where effort corresponds to the time an individual is prepared to wait in a purely passive contest, so that the extra time over and above when the other individual concedes does not need to be spent.

One possible interpretation of the cost function is that $s + p$ is a measure of the total complexity of the fight and the individuals pay more for more complex fights (because the complex fights are more energetically demanding and individuals can get hurt more seriously or with higher probability as the complexity increases). Alternatively, more complex contests can take more time, and that time be a function of $s + p$. The cost paid could then be a function of the time spent; for example in lost opportunities, or predation risk through being in an exposed area. We note that Baye et al (2005, 2012) consider many possible cost functions, including conventional functions (each pays its own costs) and less conventional ones (each pays some

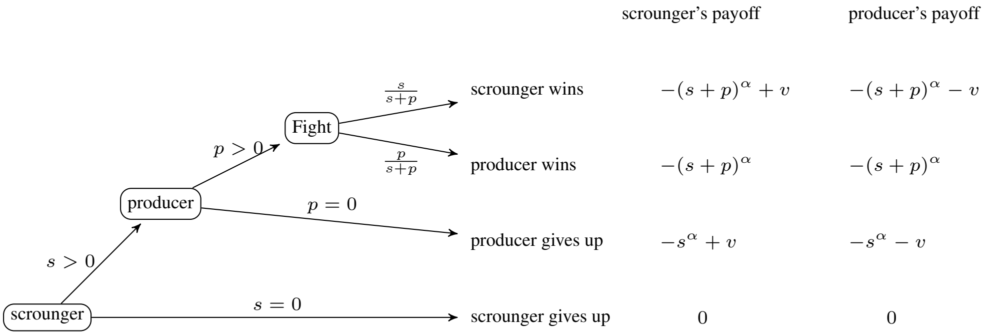


Fig. 1: Scheme of the game. First, the scrounger invests $s \in [0, S]$. If $s > 0$, the producer then invests $p \in [0, P]$. If $p > 0$, there is a fight that the scrounger wins with probability $s/(s+p)$. Both individuals pay the costs, the winner of the contest keeps the resource that was originally in the possession of the producer.

of its own and some of the other player's effort costs). Nested in their model is the case $c(s,p) = s + p$, which is also a special case considered in this paper.

Note that the cost is a function of $s + p$, which means that the producer pays the cost even if it does not engage in the fight. This is a plausible outcome under a variety of scenarios. For example, the producer may be hurt by the scrounger's attack even if the producer does not invest anything in fighting back. Similarly, if the producer does not want to fight, it may need to flee the scene and the energy expenditure of doing so may be correlated with the strength of the scrounger's attack. Finally, the cost may be interpreted as damage to the environment; for example any kind of attack on a fishing bird may scare away any potential fish and reduce its medium gain from fishing.

It is worth considering what circumstances are likely to lead to the different types of cost function, i.e. the different values of the parameter α. It seems reasonable that as the effort involved increases, the duration of the contest will increase sublinearly and the risk of injury and fitness costs due to lost energy will increase supralinearly. Thus if the major cost is due to risk of injury or lost energy, α is likely to be greater than 1, i.e. we have a convex function, whereas if time costs are the biggest problem, for example if this is due to exposure to predation risk, then we have α less than 1, i.e. a concave function.

We will study how the stealing behaviour can evolve for different values of the parameter α. When $0 < \alpha < 1$, then even a small investment in the fight is relatively costly, but enlarging an already large investment is relatively inexpensive. When $\alpha > 1$, then small investments in the fight are cheap, but enlarging an already large investment is very costly. When $\alpha = 0$, the cost of the fight is constant regardless of the investment for any contested resource (i.e. for any $s > 0$).

The individuals will always pay the cost of the fight, the producer will keep the resource item if it wins and lose it if it loses the fight; the scrounger either gains nothing if it loses or it gains the resource item if it wins the fight. The payoffs U_p and

U_s for the producer and scrounger will thus be

$$U_p(s,p) = -(s+p)^\alpha - v\frac{s}{s+p}, \tag{2}$$

$$U_s(s,p) = -(s+p)^\alpha + v\frac{s}{s+p}, \tag{3}$$

whenever $s+p>0$ and

$$U_p(0,0) = U_s(0,0) = 0. \tag{4}$$

The game is shown in Figure 1.

3 Analysis

In each case that we analyse below, the scrounger will make an initial choice of s, and then the producer will pick a value $p(s)$ which may vary depending upon the value of s actually encountered. Thus any strategy will be a choice of a single number for the scrounger, and a function of all possible encountered scrounger strategies for the producer. This will result in a realisation of the producer's strategy which is the actual value of its function for the chosen value of s, but it should be borne in mind that the producer's strategy is the response function, not just the single number (see the text at the end of Section 4.3).

3.1 Case $\alpha = 0$

Let us first examine the special case of $\alpha = 0$, i.e. a constant fight cost.

Assume the scrounger attempted to steal $(s > 0)$. The payoff to the producer will then be

$$U_p(s,p) = -1 - v\frac{s}{s+p}. \tag{5}$$

Since $\frac{\partial U_p}{\partial p} > 0$, it is optimal for the producer to fight with maximal intensity P.

If the scrounger does not attack ($s = 0$), its payoff will be 0. If the scrounger attacks ($s > 0$), we also get $\frac{\partial U_s}{\partial s} > 0$, so that the scrounger should invest the maximal value S in the fight. Hence, putting it together with the producer's optimal decision, the maximal scrounger's payoff for $s > 0$ is $-1 + vS/(S+P)$.

Consequently, when $v \le 1 + P/S$, the scrounger will not attack. If $v > 1 + P/S$, the scrounger will attack with maximal intensity S and the producer will fight back, also with a maximal intensity. We note that the condition for the scrounger to attack is equivalent to the value of the resource times the probability to win being bigger than the cost of the fight; this is in agreement with previous models, such as Broom et al (2004).

3.2 Case $\alpha > 0$.

For a given $s \geq 0$ we find an optimal response of the producer. Clearly, when $s = 0$, the producer's response is $p_0(0) = 0$.

For a fixed $s \in (0, +\infty)$ we have

$$\frac{\partial U_p}{\partial p}(s,p) = -\alpha(s+p)^{\alpha-1} + \frac{vs}{(s+p)^2}, \tag{6}$$

which holds for $p \in (-s, +\infty)$ (clearly $p < 0$ and $p > P$ do not correspond to real solutions as they fall outside the valid range, yet it is mathematically convenient to consider all values of p at this stage) and is continuous there. The critical points of the function $p \mapsto U_p(s,p)$, i.e. the points p where $\frac{\partial U_p}{\partial p}(s,p) = 0$, are given by

$$p = g(s) = \left(\frac{vs}{\alpha}\right)^{\frac{1}{\alpha+1}} - s. \tag{7}$$

Note that $g(s) > -s$ when $s > 0$. For convenience, we continuously extend g by setting $g(0) = 0$. Furthermore,

$$\frac{\partial^2 U_p}{\partial p^2}(s, g(s)) = -\alpha(\alpha-1)(s+p)^{\alpha-2} - \frac{2vs}{(s+p)^3}\bigg|_{(s,g(s))} \tag{8}$$

$$= -\alpha(\alpha+1)\left(\frac{vs}{\alpha}\right)^{\frac{\alpha-2}{\alpha+1}} < 0. \tag{9}$$

It follows that $\frac{\partial U_p}{\partial p}(s,p) > 0$ for $p \in (-s, g(s))$ and $\frac{\partial U_p}{\partial p}(s,p) < 0$ for $p \in (g(s), +\infty)$. Consequently, $p \mapsto U_p(s,p)$ is increasing on $(-s, g(s)]$ and decreasing on $[g(s), +\infty)$ (and attains its unique maximum on $(-s, +\infty)$ at $g(s)$). However, we have to maximise $p \mapsto U_p(s,p)$ on $[0, P]$. Thus $p \mapsto U_p(s,p)$ attains its unique maximum on $[0, P]$ at

$$p_0(s) = \begin{cases} 0 & \text{if } g(s) \leq 0, \\ P & \text{if } g(s) \geq P, \\ g(s) & \text{otherwise.} \end{cases} \tag{10}$$

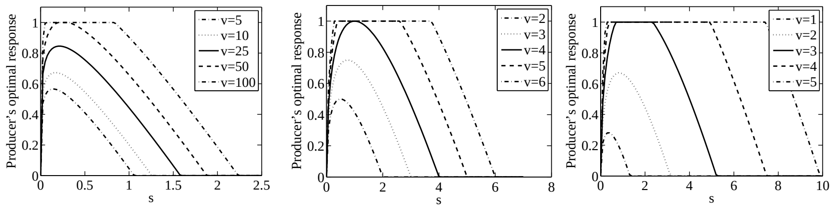
Note that $p_0(s) = \max\{0, \min\{g(s), P\}\}$ and it is a continuous function on $[0, +\infty)$. Recall that $g(0) = 0$, and, by (7), for $s > 0$ we have $g(s) \leq 0$ if and only if

$$s \geq c_4 := \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}}. \tag{11}$$

Further,

$$g'(x) = \frac{1}{\alpha+1}\left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha+1}} x^{-\frac{\alpha}{\alpha+1}} - 1, \tag{12}$$

$$g''(x) = -\frac{\alpha}{(\alpha+1)^2}\left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha+1}} x^{-\frac{2\alpha+1}{\alpha+1}} \tag{13}$$



(a) (b) (c)

Fig. 2: Producer's optimal responses to varying scrounger's investment level s and different values of v for $P = 1$. (a) $\alpha = 4$, (b) $\alpha = 1$, (c) $\alpha = 0.8$.

for $x \in (0, +\infty)$. Thus g is strictly concave on $(0, +\infty)$. Since $g'(x) = 0$ if and only if

$$x = c_1 := \frac{1}{(\alpha+1)^{\frac{\alpha+1}{\alpha}}} \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}} > 0, \tag{14}$$

the function g attains its unique maximum on $(0, +\infty)$ at c_1. It follows that the inequality $g(s) \geq P$ has a solution if and only if

$$P \leq g(c_1) = c_3 := \left(1 - \frac{1}{\alpha+1}\right) \frac{1}{(\alpha+1)^{\frac{1}{\alpha}}} \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}}; \tag{15}$$

moreover, as $g(0) = 0 < P$ and g is strictly concave on $(0, \infty)$, there exist constants $a(P), b(P)$ satisfying $0 < a(P) \leq b(P) < c_4$ and such that $g(s) \geq P$ if and only if $s \in [a(P), b(P)]$. The producer's optimal responses are shown in Figure 2.

To find the optimal strategy for the scrounger we have to maximise the scrounger's payoff given the producer responds optimally, i.e. the function

$$f(s) = U_s(s, p_0(s)). \tag{16}$$

We define

$$h(s) = U_s(s, P) = -(s+P)^\alpha + \frac{vs}{s+P}, \tag{17}$$

and then we have

$$f(s) = \begin{cases} 0 & \text{if } s = 0, \\ -s^\alpha + v & \text{if } s > c_4, \text{ i.e. } p_0(s) = 0, \\ h(s) & \text{if } P \leq c_3 \text{ and } s \in [a(P), b(P)], \text{ i.e. } p_0(s) = P, \\ (\alpha - 1)\left(\frac{vs}{\alpha}\right)^{\frac{\alpha}{\alpha+1}} & \text{otherwise, i.e. } p_0(s) = g(s). \end{cases} \tag{18}$$

We note that f is a continuous function on $[0, +\infty)$. We have

$$h'(x) = -\alpha(x+P)^{\alpha-1} + \frac{vP}{(x+P)^2}, \tag{19}$$

$$h''(x) = -\alpha(\alpha-1)(x+P)^{\alpha-2} - \frac{2vP}{(x+P)^3} \tag{20}$$

Notation	Meaning
S	the upper limit of the scrounger's investment in the fight
P	the upper limit of the producer's investment in the fight
α	the indicator of the concavity of the cost function
v	the value of the contested resource
$U_p(s,p)$	payoff to the producer when the scrounger plays s and the producer plays p
$U_s(s,p)$	payoff to the scrounger when the scrounger plays s and the producer plays p
$p_0(s)$	the optimal response of the producer given the scrounger played s
$f(s)$	$U_s(s,p_0(s))$, i.e. an anticipated scrounger's payoff when playing s and the producer responds optimally
$h(s)$	$U_s(s,P)$, i.e. the scrounger's payoff when scrounger plays s and producer plays P
$g(s)$	critical point of the producer's payoff function (and thus a candidate for the optimal response) if the scrounger played s
$g(P)$	critical point of the scrounger's payoff function $h(s)$ (if producer's effort is locally fixed at P
$a(P), b(P)$	solutions of $g(s)=P$; $g(s)\geq P$ if and only if $s\in[a(P),b(P)]$, $p_0(s)=P$ on $[a(P),b(P)]$
c_1	the point where $g(s)$ attains its maximum
c_2	the point where $g(g(s))=s$; $g(P)\in[a(P),b(P)]$ if and only if $P\leq c_2$
c_3	the maximal value of g, i.e. $c_3=g(c_1)$
c_4	the point where $g=0$; $g(s)<0$ if and only if $s>c_4$
c_0	the point where $h(g(p))=0$; $h(g(P))>0$ if and only if $P<c_0$
$k(P)$	a solution of $f(s)=f(g(P))$ that lies in the interval $[b(P),c_4)$
$l(S)$	a solution of $U_s(S,x)=0$

Table 1: Notations used in the manuscript. S, P, α, v are parameters of the model.

for $x\in(-P,+\infty)$. Note that $h'(x)=0$ if and only if $x=g(P)$ and that $g(P)>-P$. Since $h'(g(P))=0$ and $h''(g(P))=-\alpha(\alpha+1)\left(\frac{vP}{\alpha}\right)^{\frac{\alpha-2}{\alpha+1}}<0$, it follows that $h'>0$ and h is increasing on $(-P,g(P)]$ and $h'<0$ and h is decreasing on $[g(P),+\infty)$. The behaviour of h on $[a(P),b(P)]$ depends on whether $g(P)\in[a(P),b(P)]$, i.e. $g(g(P))\geq P$. This happens if and only if

$$P\leq c_2:=\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}. \tag{21}$$

Note that g represents a critical point of either player's payoff function if the other player's effort is effectively locally fixed. In a region where the producer's effort is locally fixed at P, such that marginal changes in the scrounger's effort do not change the producer's effort, the scrounger's payoff $f(s)$ is given by $h(s)$ and since $h'(g(P))=0$ (with $g(P)$ being the only root of h'), $g(P)$ describes a critical point of the scrounger's payoff function.

4 Results

Now we distinguish three cases.

4.1 Case $\alpha>1$

Note that in this case $c_1<c_2<c_3<c_4$. If $P>c_2$, then f is increasing on $[0,c_4]$ (this follows from the fact that h is monotone on $[a(P),b(P)]$ and $f(a(P))<f(b(P))$ by continuity) and decreasing on $[c_4,+\infty)$. Thus if $S<c_4$, then f attains its

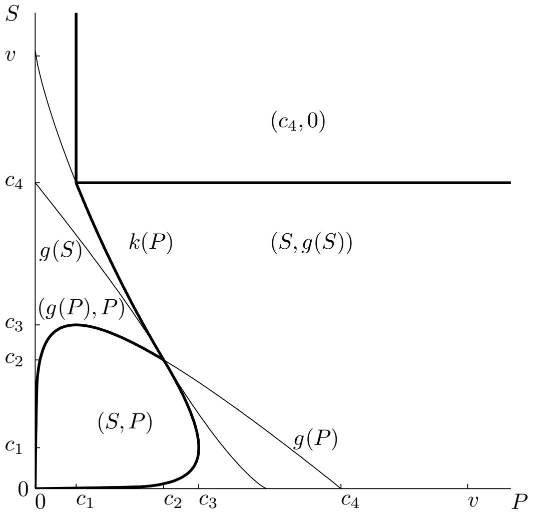


Fig. 3: Different types of equilibria for $\alpha = 4$, fixed v and varying S and P. The bold lines are the boundaries of the regions where types of the equilibrium types change. The equations for curves g and k are given in (7) and (22). The figure looks same for all values of v because the constants $c_1, \dots, c_4$ and the function $g(P) = v^{1/\alpha}\left[\left(\frac{P}{\alpha v^{1/\alpha}}\right)^{\frac{1}{\alpha+1}} - \frac{P}{v^{1/\alpha}}\right]$ and thus also a function $k(P)$ scale appropriately by a factor $v^{1/\alpha}$. The situation is analogous for any $\alpha > 1$.

unique maximum on $[0, S]$ at S, while if $S \geq c_4$, then f attains its unique maximum on $[0, S]$ at c_4.

If $P \leq c_2 < c_3$, then f is increasing on $[0, g(P)]$, decreasing on $[g(P), b(P)]$, increasing on $[b(P), c_4]$, and decreasing on $[c_4, +\infty)$. We have $f(g(P)) = h(g(P)) = v - (\alpha+1)\left(\frac{vP}{\alpha}\right)^{\frac{\alpha}{\alpha+1}}$ and $f(c_4) = -c_4^\alpha + v = v - \frac{v}{\alpha}$. Thus $f(g(P)) > f(c_4)$ if and only if $P < c_1$. Therefore in this case if $S < g(P)$, then f attains its unique maximum on $[0, S]$ at S, while if $S \geq g(P)$, then f attains its unique maximum on $[0, S]$ at $g(P)$. Finally, if $c_1 \leq P \leq c_2$, then there is $k(P) \in [b(P), c_4)$ such that $f(k(P)) = f(g(P))$. This is given by

$$k(P) = \frac{1}{(\alpha-1)^{\frac{\alpha+1}{\alpha}}} \frac{\alpha}{v} \left(v - (\alpha+1) \left(\frac{vP}{\alpha} \right)^{\frac{\alpha}{\alpha+1}} \right)^{\frac{\alpha+1}{\alpha}}. \tag{22}$$

The following summary is then easily deduced:

$$\begin{cases} P > c_2 & \begin{cases} S < c_4 & \text{maximum at } S, \\ S \geq c_4 & \text{maximum at } c_4, \end{cases} \\ c_1 \leq P \leq c_2 & \begin{cases} S < g(P) & \text{maximum at } S, \\ g(P) \leq S < k(P) & \text{maximum at } g(P), \\ k(P) \leq S < c_4 & \text{maximum at } S, \\ S \geq c_4 & \text{maximum at } c_4, \end{cases} \\ P < c_1 & \begin{cases} S < g(P) & \text{maximum at } S, \\ S \geq g(P) & \text{maximum at } g(P). \end{cases} \end{cases} \tag{23}$$

It means that the scrounger will play either c_4, $g(P)$ or S. The corresponding responses by the producer will be $p_0(c_4) = 0$, $p_0(g(P)) = P$ (because $P \leq c_2$) and

$$p_0(S) = \begin{cases} P, & \text{if } g(S) \geq P, \\ g(S), & \text{otherwise.} \end{cases} \tag{24}$$

The situation is summarised on Figure 3. We note that sending S and P to infinity corresponds to the situation where there is no upper bound on the investments possible, and here this leads to the solution $(c_4, 0)$, where the scrounger steals the resource with no resistance from the producer.

It should also be noted that in this and later sections, sending v to 0 has similar effects to sending S and P to infinity, since although for finite S and P there are theoretical limits on the energy that can be invested, for small v the energy that any individual would invest in practice is also small.

The equilibrium investments and resulting payoffs for fixed S and P and varying v are shown in Figure 4. Also, note the discontinuity of the strategies when $S > P$. This happens for all values of α and is caused by the switch from one solution to another, when crossing from the $(S, g(S))$ region to the $(g(P), P)$ region. We can see that only the probabilities and not the payoffs are discontinuous. Thus, here we see one example of a well known fact that the maximum of the function is continuous as the parameter changes but the maximizer may not be continuous (Berge, 1963).

To examine the phenomenon in more details, let us directly examine the connections between Figures 3 and 4. For fixed values S and P (say $S = 2$ and $P = 1$) and a temporarily fixed value v, the point with coordinates $[P, S]$ falls into a specific region in Figure 3. As v grows, the regions in Figure 3 grow as well (without essentially changing shape) while the point $[P, S]$ remains fixed. Hence the point that was originally in the $(c_4, 0)$ region (such as the one for small values of v) eventually falls into the $(S, g(S))$ region (this a continuous, but not differentiable change of optimal investment level). As v grows even further, the same point then falls into the $(g(P), P)$ region (indicating a discontinuous change or a jump of optimal investment level). As v grows even more, the point then finally falls into the (S, P) region.

From the players' perspective, as v grows but is still relatively small, the scrounger's optimal investment grows to a maximal level S, while it is not beneficial for the producer to invest anything. As v grows even further, the scrounger would like to invest

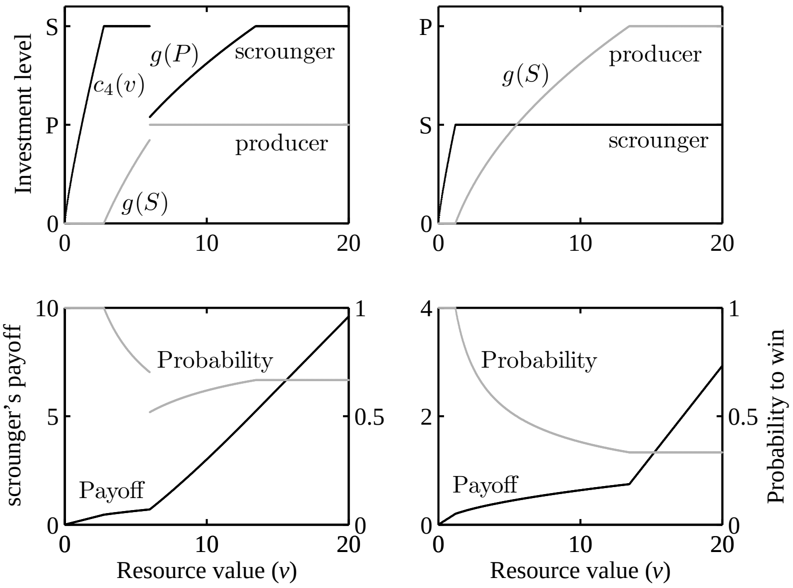


Fig. 4: Equilibrium investment levels for the scrounger and producer and the scrounger's payoffs and probability of victory when (a) $S = 2$, $P = 1$, $\alpha = 1.2$ (left column) and (b) $S = 1, P = 2, \alpha = 1.2$ (right column) are fixed. We note that g is in fact a function $g(x) = g_{\alpha,v}(x) = \left(\frac{vx}{\alpha}\right)^{\frac{1}{\alpha+1}} - x$. In this figure, $g(S)$ means a function $v \mapsto g_{\alpha,v}(S)$, and $g(P)$ is interpreted analogously.

more but it cannot because it has reached its maximum already, and thus it becomes beneficial for the producer to invest (it improves the odds of winning the fight and the increase of the reward value outweighs the cost associated with the investment). As v continues to grow, the producer invests more and more and since the scrounger cannot invest more than S, its odds of winning decrease and at one point, the odds decrease so much that the reward does not justify the cost and it becomes beneficial to invest less than maximum.

4.2 Case $\alpha = 1$

Note that in this case $c_1 = c_2 = c_3 = v/4 < c_4 = v$. If $P \geq c_1$ then f is zero on $[0, c_4]$. If $P < c_1$, then f is zero on $[0, a(P)]$ and $[b(P), c_4]$, increasing on $[a(P), g(P)]$ and decreasing on $[g(P), b(P)]$. Therefore we obtain

$$\begin{cases} P \geq c_1 & \begin{cases} S < c_4 & \text{maximum anywhere in } [0, S], \\ S \geq c_4 & \text{maximum anywhere in } [0, c_4], \end{cases} \\ P < c_1 & \begin{cases} S \leq a(P) & \text{maximum anywhere in } [0, S], \\ a(P) < S < g(P) & \text{maximum at } S, \\ S \geq g(P) & \text{maximum at } g(P). \end{cases} \end{cases} \tag{25}$$

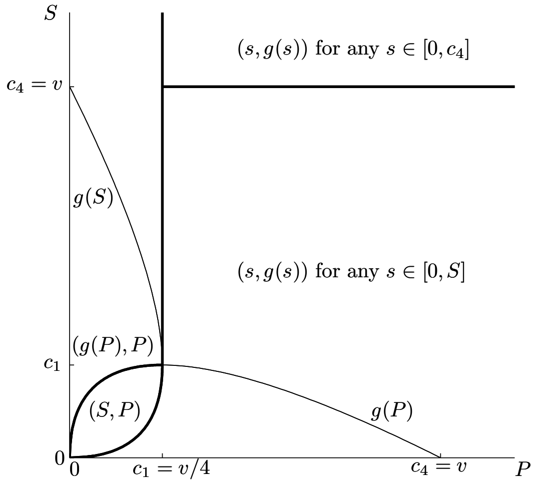


Fig. 5: Different types of equilibria for $\alpha = 1$, fixed v and varying S and P. The bold lines are the boundaries of the regions where types of the equilibrium types change. The equation for the curve g is given in (7). The scrounger can chose from multiple equilibria. Note that the graph of $a(P)$ coincides with the lower branch of the graph of $g(S)$ because $a(P)$ is the smaller solution of $P = g(s)$.

This means that the scrounger will play either $g(P)$, S, anything between 0 and c_4, or anything between 0 and S. The corresponding responses by the producer will be $p_0(g(P)) = P$ (because $P \le c_2 = c_1$), $p_0(S) = P$ (because $g(S) \ge P$) and $p_0(s) = g(s)$ in the remaining cases. The situation is summarised in Figure 5. Here sending S and P to infinity leads to a solution of the form $(s, g(s))$, where the resource is contested by both parties.

The equilibrium investments and resulting payoffs for fixed S and P and varying v are shown in Figure 6.

We note that there are large ranges of the scrounger's investment level which give the same maximum payoff of 0 to the scrounger. This can be seen directly by substituting into the formula

$$f(s) = U_s(s, p_0(s)) = -(s + p_0(s)) + v\frac{s}{s + p_0(s)} \tag{26}$$

$$= -(s + \sqrt{vs} - s) + v\frac{s}{s + \sqrt{vs} - s} = 0 \tag{27}$$

for the large range of s values where $p_0(s) = g(s)$.

4.3 Case $\alpha < 1$

Note that in this case $c_2 < c_3 < c_1 < c_4$. If $P > c_2$, then f is decreasing on $[0, +\infty)$ (this follows from the fact that if $P \le c_3$, then h is monotone on $[a(P), b(P)]$ and

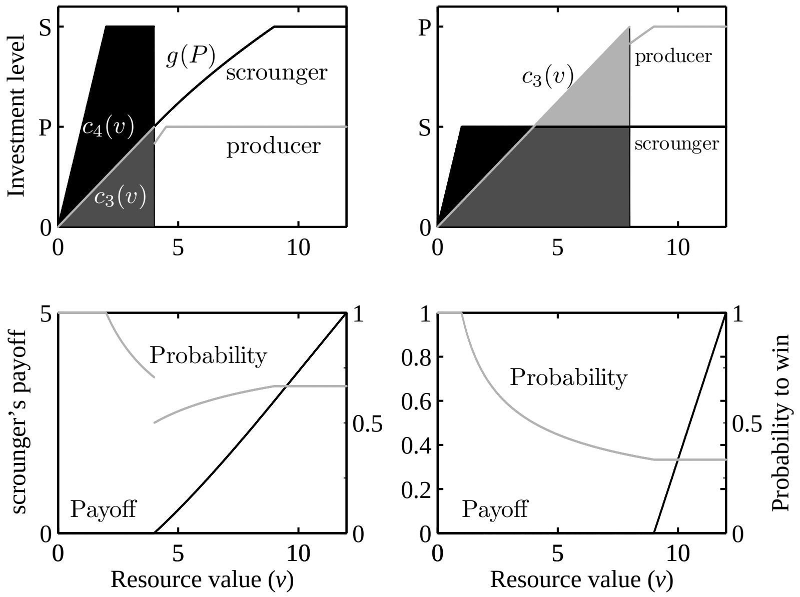


Fig. 6: Equilibrium investment levels for the scrounger and producer and the scrounger's payoffs and probability of victory when (a) $S = 2$, $P = 1$, $\alpha = 1$ (left column) and (b) $S = 1, P = 2, \alpha = 1$ (right column) are fixed. Here, the scrounger has a choice for any s in the black and darker gray region, the producer then replies by $p = g(s)$ which falls in the darker or lighter gray region. Probability of scrounger's victory depends on the scrounger's strategy, the maximal probability (corresponding to maximal optimal investment level) is shown.

$f(a(P)) > f(b(P))$ by continuity) and so it attains its unique maximum on $[0, S]$ at 0. If $P \le c_2$, then f is decreasing on $[0, a(P)]$, increasing on $[a(P), g(P)]$, and decreasing on $[g(P), +\infty)$. Thus f still attains its maximum on $[0, S]$ at 0 unless $h(g(P)) > 0$, which happens if and only if

$$P < c_0 := \left(\frac{\alpha}{\alpha+1}\right)^{\frac{\alpha+1}{\alpha}} \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}} < c_2. \tag{28}$$

In this case we need to know whether S lies in the interval where h is positive. We define

$$l(S) = (vS)^{\frac{1}{\alpha+1}} - S. \tag{29}$$

Note that $h(S) > 0$ if and only if

$$P < l(S). \tag{30}$$

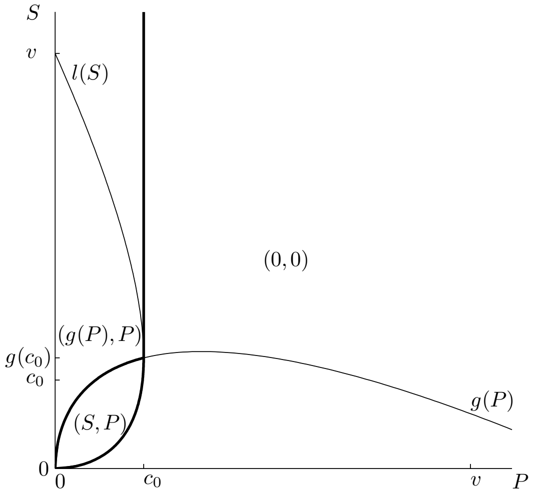


Fig. 7: Different types of equilibria for $\alpha = 0.8$, fixed v and varying S and P. The bold lines are the boundaries of the regions where types of the equilibrium types change. The equations for curves g and l are given in (7) and (30). The situation is analogous for any $\alpha < 1$.

Thus we may conclude that

$$\begin{cases} P \geq c_0 & \text{maximum at } 0, \\ P < c_0 & \begin{cases} S \leq g(P) \text{ and } P \geq l(S) & \text{maximum at } 0, \\ S \leq g(P) \text{ and } P < l(S) & \text{maximum at } S, \\ S > g(P) & \text{maximum at } g(P). \end{cases} \end{cases} \tag{31}$$

This means that the scrounger will choose to play either 0, S or $g(P)$. The corresponding responses by the producer will be $p_0(0) = 0$, $p_0(S) = P$ (because in this case $P < l(S) < g(S)$) and $p_0(g(P)) = P$ (because in this case $P < c_0 < c_2$). The situation is summarised in Figure 7. Sending S and P to infinity here yields the solution of (0,0), with the scrounger not challenging for the resource in the unbounded investment case. This may seem a counterintuitive result because it appears that the scrounger would be better off playing $s > 0$ and then gaining a reward for a little cost (after the producer gives up by playing $p = 0$). However, $p = 0$ is just the realisation of the actual producer's strategy, which is to play a specific function of $p_0(s)$ given by (10), against whichever s occurs. For $\alpha < 1$, when $s > 0$, then the producer's best reply is $g(s)$ (at least in the case when P is large), which would yield a negative payoff to the scrounger, and hence the scrounger should indeed play 0.

The equilibrium investments and resulting payoffs for fixed S and P and varying v are shown in Figure 8.

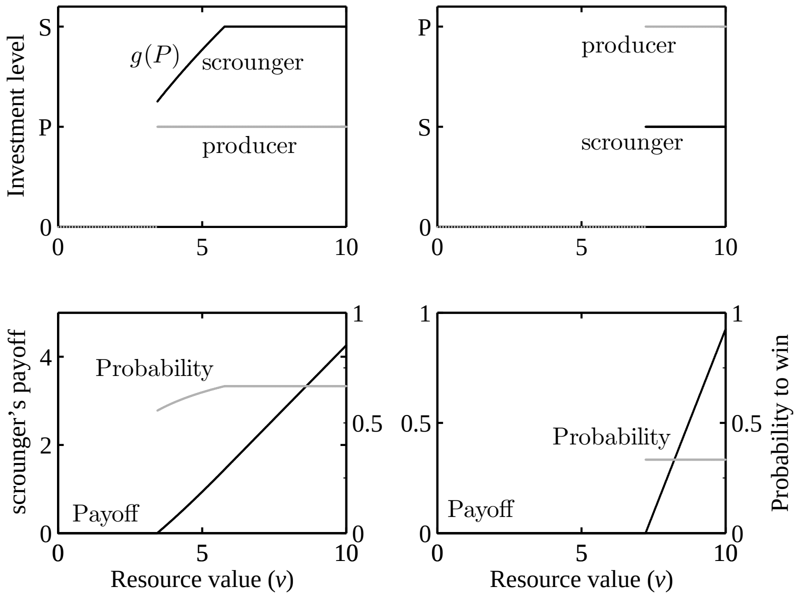


Fig. 8: Equilibrium investment levels for the scrounger and producer and the scrounger's payoffs and probability of victory when (a) $S = 2$, $P = 1$, $\alpha = 0.8$ (left column) and (b) $S = 1, P = 2, \alpha = 0.8$ (right column) are fixed.

5 Discussion

Previous game-theoretical models of food stealing behaviour Broom and Ruxton (2003); Broom et al (2004); Broom and Rychtář (2007); Broom et al (2008); Broom and Rychtář (2011) have considered a number of different scenarios for when an animal tries to gain resources by stealing, rather than by directly acquiring them itself. Typically these models only consider a small range of options for the players involved, for example to attempt to steal or not (Crowe et al, 2009; Broom et al, 2013, 2014), or play Hawk or Dove in a contest Broom et al (2009); Grundman et al (2009). Such a discrete set of options is commonly considered in wider ecological scenarios, for example patch foraging, where the choice may be to forage on a particular patch (Fretwell and Lucas, 1970; Křivan et al, 2008). In many real situations, individuals will have a greater flexibility of options, for example forage for a while and then move to a different patch (Charnov, 1976). We also note that our model can be applied beyond biological sciences, such as to quantity-setting games in economics between two firms (Varian and Repcheck, 2005, Ch. 27).

Often contests are decided not by the strongest, but by the individual with the greatest desire or need to win the resource, as they may put in a disproportionate effort as the reward is so important to them. Thus energetic investment can be thought of as a strategic investment under the control of the individual animal, and can plausibly vary from zero upwards, perhaps to some maximum value depending upon the animal's energy reserves. However, the bigger the investment in the contest, the bigger the chances of winning, but also the bigger the costs of the potential contest. This creates another trade-off situation for the individuals. This is the situation that we consider in this paper: related models from economics have been considered, for example in Tullock (1980); Baye et al (2012); Skaperdas (1992). We note that the role of budget limits has been analysed, see for example Che and Gale (1997); Bester and Konrad (2004), and plays a crucial role in Colonel Blotto games (Roberson, 2006).

We have shown that when maximum investment levels are low or equivalently when v is large compared to the maximum investment levels, generally both animals should play at the maximum level. However, when they are high or v is not too large, then the equilibria depend greatly upon the nature of the cost function. For a convex function the scrounger can find a sufficient investment level (but one not too high to be profitable) to force the producer to concede. For a concave function the scrounger will not challenge, so the producer keeps the resource with no investment. Only at the boundary linear case will there be a contest for the resource.

If the individuals do not have the same maximum level, we saw that the situation is typically more favourable to the individual with higher maximum. When $S > P$, then the scrounger always invests more than the producer and obtains a favourable payoff. When $P > S$, then the producer invests more than the scrounger for large values of v. Interestingly, as seen at Figure 4b, when the payoff is convex, $P > S$ and v is relatively small (but not too small), then a scrounger invests more than a producer (and is thus likely to win the fight). Still, regardless of the convexity of the payoff function, when $P > S$ the scrounger's payoff is small (relatively to the value of v).

As we have seen, the order of the players in such a sequential game can make a real difference. We have assumed that the scrounger is the first player and the producer is the second. This makes sense, as usually the producer will be in control of a stationary resource and the scrounger will have to make the first move. However, there may be situations where the reverse is true, for example if the resource is sufficiently large or spread out that an active defence is required to chase off an intruder. In this case, the results that we have obtained for producer and scrounger would be swapped. There may also be circumstances where the game can be assumed to be one involving simultaneous decisions (as in the earlier models, such as Barnard (1984)), which would require a different game-theoretical model. See for example McNamara et al (2006) where authors study the differences between the two approaches for a similar game.

Our model assumes the there is a homogeneous population of producers and similarly for scroungers. This means that the scrounger can predict the producer's response to its effort with perfect accuracy. In a real biological situation, individuals vary in their fighting ability and other factors, commonly known as Resource Holding Potential (RHP) Parker (1974). In Broom et al (2014) authors explicitly model a similar scenario where individuals differ in RHP (although the difference is known to both parties). A scenario where the individuals value the resource differently has been studied in Broom et al (2013). We hypothesise that in a heterogeneous population, the role of information will be crucial in determining the outcome. If individuals know the exact RHP of their opponents, then results very similar to those we have already obtained will occur, where (in the absence of energy limits) one individual will concede. However, with uncertainty, there will likely be more contests where both individuals fight.

Note that we have also used rather simplistic functions for both the probability of victory, and the cost of the contest. These were for reasons of mathematical tractability. It is possible to consider alternative forms for each of these functions. Similarly the costs, the probability of victory and the maximum energy investment of the animals may all depend upon some property of the animal, for example its Resource Holding Potential, see for example Hurd (2006). These could be considered in later versions of the model. The main rationale for this paper, however, was to introduce the concept of energetic investment into food stealing contests, as well as to show some of its effects, and as mentioned earlier there is a significant range of existing models where this kind of idea could be applied.

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