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The effect of fight cost structure on fighting behaviour involving simultaneous decisions and variable investment levels

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Abstract In the "producer-scrounger" model, a producer discovers a resource and is in turn discovered by a second individual, the scrounger, who attempts to steal it. This resource can be food or a territory, and in some situations, potentially divisible. In a previous paper we considered a producer and scrounger competing for an indivisible resource, where each individual could choose the level of energy that they would invest in the contest. The higher the investment, the higher the probability of success, but also the higher the costs incurred in the contest. In that paper decisions were sequential with the scrounger choosing their strategy before the producer. In this paper we consider a version of the game where decisions are made simultaneously. For the same cost functions as before, we analyse this case in detail, and then make comparisons between the two cases. Finally we discuss some real examples with potentially variable and asymmetric energetic investments, including intraspecific contests amongst spiders and amongst parasitoid wasps. In the case of the spiders, detailed estimates of energetic expenditure are available which demonstrate the asymmetric values assumed in our models. For the wasps the value of the resource can affect the probabilities of success of the defender and attacker, and differential energetic investment can be inferred. In general for real populations energy usage varies markedly depending upon crucial param-

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eters extrinsic to the individual such as resource value and intrinsic ones such as age, and is thus an important factor to consider when modelling.

Keywords kleptoparasitism · food stealing · producer-scrounger · game theory · simultaneous decisions

1 Introduction

Animal competition takes many forms, involving a range of potential resources such as mates, territories or food. Competition can be with close relatives such as nestmates, unrelated conspecifics or members of other species, and can involve different kinds of contests such as direct fights or indirect competition, e.g. competitive begging from parents in the case of chicks within a brood. The value of different resources also varies markedly; territories can be key to mating, and if held for a long period can be of central importance in a given individual's life (Kruuk, 1972; Hamilton and Dill, 2003a; Iyengar, 2008; Kokko, 2013). Food resources may also be very valuable, or of relatively small value, but in either case tend to be relatively short-lived prizes. If an item can be eaten immediately, then once an individual takes possession of it, there may be no further possibility of another contesting it (although contest possibilities persist if this item needs to be taken to young).

Larger food items, or those with defences that need to be breached, such as shellfish, need some time to consume, and during this item there is the opportunity for others to attempt to steal the item, see for example Spear et al (1999); Steele and Hockey (1995); Triplet et al (1999). Models where this item was an indivisible one which needed to be competed for were considered in Broom and Ruxton (2003); Broom et al (2004); Broom and Rychtář (2007); Broom et al (2008); Broom and Rychtář (2011); Hadjichrysanthou and Broom (2012). Alternative models that considered the resource as a large patch of smaller items, so that the resource became divisible, were considered in the so-called "producer-scrounger" models (Barnard and Sibly, 1981; Barnard, 1984; Caraco and Giraldeau, 1991; Dubois and Giraldeau, 2005; Vickery et al, 1991); consider also Giraldeau and Livoreil (1998); Kokko (2013); Broom and Rychtář (2013) for more general reviews. We note that a key element of the former kleptoparasitism models was a time-delay element in the model which meant that contests were not simple independent ones, but the probability of a given opponent type was correlated with their strategy.

In a previous model Broom et al (2015) we considered a version of the producer-scrounger model, where the producer discovers a resource which cannot be immediately consumed, and is then subsequently found by a scrounger who challenges for possession of the resource. In earlier models of this type the competitors could only choose from a finite range of options such as fight or display, as in the classical Hawk-Dove game (Maynard Smith and Price, 1973; Maynard Smith, 1982). More realistically animals can vary the effort they make in any contest, and in Broom et al (2015) we allowed a range of investment levels; the higher the investment, the higher the chances of success, but also the higher the costs incurred. First the scrounger had to decide the level it should invest (including no investment, so it does not challenge for the resource), after which the producer chose a level of investment in response. In this paper, we consider an alternative version of the game where both individuals make the choice of investment level simultaneously.

From a modelling point of view, it is often the case (see e.g. McNamara et al, 2006)), as it is here, that the order of the players matters. But what is the most realistic ordering to model real populations? We believe that this very much depends upon the biological scenario being considered. For example, if the producer is in control of a small stationary resource, then it may make sense that the scrounger makes the first move, and the producer has to respond.

On the other hand if the resource is a large spread out territory an active defence may be best, and so there may be some complex interaction, best modelled by a simultaneous game, as in the early models of e.g. Barnard (1984) (or even on occasions a game with the producer moving first). An example of a case where large territories are defended and so simultaneous contests are plausible can be seen with the subtropical reef fish *Kyphosus cornelii* which defends sizeable gardens from kleptoparasitic rivals Hamilton and Dill (2003b). Such territories are not necessary for complex energetic contests, however. An example is the fighting behaviour of the sierra dome spider *Neriene litigiosa* where the “resource” is small but mobile (female spiders). Here the male spiders undergo fights in a series of stages, the energetic cost of which was intevstigated in deCarvalho et al (2004).

We introduce the model formally in Section 2, and go on to analyse the model in detail in Sections 3 and 4, including a comparison with the results from the sequential case. As we shall see, the results here are very different. Finally in Section 5 we discuss our results.

2 The model

A scrounger encounters a producer who has a resource item. Simultaneously both individuals decide, whether they will fight for the item or not and if they decide to fight, then how much energy they will invest into the fight. This is in contrast to our earlier paper Broom et al (2015), where decisions were sequential. As we shall see, this leads to significantly different analytical problems and predictions. This is modelled in the following way:
The scrounger chooses the amount of energy s to invest, where $s \in \{0\} \cup [S_1, S_2]$ for $0 < S_1 < S_2$. The choice $s = 0$ corresponds to the decision not to fight, otherwise the scrounger has to invest at least S_1 so that his opponent registers this as a decision to fight; S_2 is the maximal amount of energy that the scrounger can invest in the fight. Similarly, the producer chooses $p \in \{0\} \cup [P_1, P_2]$ for $0 < P_1 < P_2$.

As in Broom et al (2015), we consider the fight cost equal for both individuals and given by $(s+p)^\alpha$. One interpretation of this choice of cost function is that $s+p$ is a measure of the complexity of (or of the time taken for) the fight, and that both individuals pay more for more complex (or longer) fights. For a detailed justification of the choice of this cost function, see Broom et al (2015). If neither individual decides to fight, the producer keeps the resource. Otherwise the scrounger wins the resource with a probability of $\frac{s}{s+p}$. Accordingly, the payoff to the scrounger is

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

Similarly, the payoff to the producer is

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

We note that this is the same payoff function as used in the game Broom et al (2015), except that a constant v, representing a value of the resource, has been added to all payoffs. This has no effect on the solution of the game. It effectively considers the payoff as being the gain to the producer from the point where a new food item is discovered and neither individual is in possession, rather than from the "gain" upon the assumption that the producer possesses the item without contest.

We also note that, as written, the payoff function does not appear dimensionally consistent. The parameter alpha is intended to represent the rate at which costs increase with the total amount of effort expended by the participants. Thus we can denote e as the total amount of effort required to make the cost 1 energetic unit, and then our cost function is $((s+p)/e)^\alpha$. For convenience we select $e = 1$. We will focus on $\alpha > 0$; the case $\alpha = 0$ is investigated in Sykes and Rychtář (in press).

3 Analysis

3.1 Best responses

In this section we identify the best responses, i.e. for a given $s \geq 0$ we find the potentially multi-valued function $BR_p(s) \subset \{0\} \cup [P_1, P_2]$ such that any $p \in BR_p(s)$ maximises the function $U_p(s,p)$, and the analogous function $BR_s(p)$ for the scrounger.

If $s = 0$, then $U_p(0,p) = v - p^\alpha$ for $p \geq 0$ and so clearly $BR_p(0) = 0$. For $s > 0$ we have $\frac{\partial U_p}{\partial p}(s,p) = \frac{vs}{(s+p)^2} - \alpha(s+p)^{\alpha-1}$ for $p > -s$, in particular for all biologically meaningful values of $p \geq 0$. Consequently, for fixed s and variable p, the function $U_p(s,p)$ is increasing on $(-s, f(s)]$ and decreasing on $[f(s), +\infty)$, where

$$f(s) = \left(\frac{vs}{\alpha}\right)^{\frac{1}{\alpha+1}} - s. \tag{3}$$

Therefore

$$BR_p(s) = \begin{cases} 0 & \text{if } s=0\text{, or } s>0 \text{ and } f(s)\le 0\text{, or} \\ & \qquad 0<f(s)<P_1 \text{ and } U_p(s,0)>U_p(s,P_1), \\ \{0,P_1\} & \text{if } 0<f(s)<P_1 \text{ and } U_p(s,0)=U_p(s,P_1), \\ P_1 & \text{if } 0<f(s)\le P_1 \text{ and } U_p(s,0)<U_p(s,P_1), \\ f(s) & \text{if } P_1\le f(s)\le P_2, \\ P_2 & \text{if } f(s)\ge P_2, \end{cases} \tag{4}$$

where by $\{0, P_1\}$ we denote the fact that both 0 and P_1 are best responses to s under the given conditions.

Similarly, if $p = 0$, then

$$U_s(s,0) = \begin{cases} 0 & \text{if } s=0, \\ v-s^\alpha & \text{if } s>0, \end{cases} \tag{5}$$

and so $BR_s(0) = 0$ if $v < S_1^\alpha$, $BR_s(0) = S_1$ if $v > S_1^\alpha$, and $BR_s(0) = \{0, S_1\}$ if $v = S_1^\alpha$. For $p > 0$ we have $\frac{\partial U_s}{\partial s}(s,p) = \frac{vp}{(s+p)^2} - \alpha(s+p)^{\alpha-1}$ for $s > -p$, in particular for all biologically meaningful values of $s \ge 0$. Consequently, for a fixed p and variable s, the function $U_s(s,p)$ is increasing on $(-p, f(p)]$ and decreasing on $[f(p), +\infty)$. Therefore

$$BR_s(p) = \begin{cases} 0 & \text{if } p=0 \text{ and } v<S_1^\alpha\text{, or } p>0 \text{ and } f(p)\le 0\text{, or} \\ & \qquad 0<f(p)<S_1 \text{ and } U_s(0,p)>U_s(S_1,p), \\ \{0,S_1\} & \text{if } p=0 \text{ and } v=S_1^\alpha\text{, or} \\ & \qquad 0<f(p)<S_1 \text{ and } U_s(0,p)=U_s(S_1,p), \\ S_1 & \text{if } p=0 \text{ and } v>S_1^\alpha\text{, or} \\ & \qquad 0<f(p)\le S_1 \text{ and } U_s(0,p)<U_s(S_1,p), \\ f(p) & \text{if } S_1\le f(p)\le S_2, \\ S_2 & \text{if } f(p)\ge S_2. \end{cases} \tag{6}$$

In order to simplify conditions in (4) and (6), note the following. Firstly, $f(x) > 0$ if and only if $0 < x < \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}}$, and $f(x) = 0$ if and only if $x = 0$ or $x = \left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}}$. secondly, $f(x) < y$, $y > 0$ if and only if $x = 0$ or $v < \frac{\alpha}{x}(x+y)^{\alpha+1}$, and $f(x) = y$ if and only if $v = \frac{\alpha}{x}(x+y)^{\alpha+1}$. Finally, the inequality $U_p(s,0) > U_p(s,P_1)$ is equivalent to $v < \frac{s+P_1}{P_1}\big((s+P_1)^\alpha - s^\alpha\big)$. For this last expression we have the following inequalities:

$$\alpha s^\alpha < \frac{s+P_1}{P_1}\big((s+P_1)^\alpha - s^\alpha\big) < \frac{\alpha}{s}(s+P_1)^{\alpha+1}. \tag{7}$$

Both can be shown using the substitution $t = \frac{P_1}{s}$ and Bernoulli's inequality with the exponent $1+\alpha$, resp. $-\alpha$. Hence, the definition of $BR_p(s)$ can be simplified:

$$BR_p(s) = \begin{cases} 0 & \text{if } s = 0 \text{ or } v < \frac{s+P_1}{P_1}\big((s+P_1)^\alpha - s^\alpha\big), \\ \{0, P_1\} & \text{if } s > 0 \text{ and } v = \frac{s+P_1}{P_1}\big((s+P_1)^\alpha - s^\alpha\big), \\ P_1 & \text{if } s > 0 \text{ and } \frac{s+P_1}{P_1}\big((s+P_1)^\alpha - s^\alpha\big) < v \text{ and} \\ & \quad v \le \frac{\alpha}{s}(s+P_1)^{\alpha+1}, \\ f(s) & \text{if } \frac{\alpha}{s}(s+P_1)^{\alpha+1} \le v \le \frac{\alpha}{s}(s+P_2)^{\alpha+1}, \\ P_2 & \text{if } v \ge \frac{\alpha}{s}(s+P_2)^{\alpha+1}. \end{cases} \tag{8}$$

Similarly, for BR_s we obtain

$$BR_s(p) = \begin{cases} 0 & \text{if } p = 0 \text{ and } v < S_1^\alpha, \text{ or } v < \frac{S_1+p}{S_1}\big((S_1+p)^\alpha - p^\alpha\big), \\ \{0, S_1\} & \text{if } p = 0 \text{ and } v = S_1^\alpha, \text{ or} \\ & \quad p > 0 \text{ and } v = \frac{S_1+p}{S_1}\big((S_1+p)^\alpha - p^\alpha\big), \\ S_1 & \text{if } p = 0 \text{ and } v > S_1^\alpha, \text{ or} \\ & \quad p > 0 \text{ and } \frac{S_1+p}{S_1}\big((S_1+p)^\alpha - p^\alpha\big) < v \le \frac{\alpha}{p}(S_1+p)^{\alpha+1}, \\ f(p) & \text{if } \frac{\alpha}{p}(S_1+p)^{\alpha+1} \le v \le \frac{\alpha}{p}(S_2+p)^{\alpha+1}, \\ S_2 & \text{if } v \ge \frac{\alpha}{p}(S_2+p)^{\alpha+1}. \end{cases} \tag{9}$$

3.2 Nash equilibria, Strict Nash equilibria and Evolutionarily Stable Strategies

Since individuals can either be in the role of scrounger or producer, an individual strategy is given by a pair (s, p) in order to specify that the individual will play s as a scrounger and p as a producer.

A point (s^*, p^*) is a pure strategy Nash equilibrium if p^* is the producer's best response to s^* and s^* is the scrounger's best response to p^*. It is a strict Nash equilibrium if all alternative strategies have a strictly lower payoff. It is an Evolutionarily Stable Strategy (ESS) if in an infinite population of individuals playing (s^*, p^*), any sufficiently small (potentially) invading group playing an alternative strategy has a lower payoff than (s^*, p^*).

Since our best responses are unique, then almost all of our pure Nash equilibria are strict (the exceptions will be for non-generic cases, see Broom and Rychtář, 2013). Strict Nash equilibria are also necessarily ESSs. We note that in addition there may be mixed strategy Nash equilibria, where individuals can employ more than one pure strategy, the value used in any given contest selected according to a probability distribution. We will in general search for pure solutions only, although there are cases when these do not exist, and we discuss mixed strategy solutions then.

Since $BR_s(p^*) \subset \{0, S_1, S_2, f(p^*)\}$, we will consider these four cases separately.

3.2.1 Case $s^* = 0$

We have $BR_p(0) = 0$, which means that $p^* = 0$. Further, $0 \in BR_s(0)$ if and only if $v \le S_1^\alpha$.

Hence in this case there is only the equilibrium $(0, 0)$ and this equilibrium exists if and only if $v \le S_1^\alpha$.

3.2.2 Case $s^* = S_1$

By (9), we have either $p^* = 0$ and $v \ge S_1^\alpha$, or $p^* > 0$ and $\frac{S_1+p^*}{S_1}\big((S_1 + p^*)^\alpha - p^{*\alpha}\big) \le v \le \frac{\alpha}{p^*}(S_1 + p^*)^{\alpha+1}$. In the first case we need $0 \in BR_p(S_1)$, which holds if and only if $v \le \frac{S_1+P_1}{P_1}\big((S_1 + P_1)^\alpha - S_1^\alpha\big)$. Thus there is an equilibrium $(S_1, 0)$ if and only if $S_1^\alpha \le v \le \frac{S_1+P_1}{P_1}\big((S_1 + P_1)^\alpha - S_1^\alpha\big)$.

In the second case we have either

1. $p^* = P_1$, which holds if and only if $\frac{S_1+P_1}{P_1}\big((S_1 + P_1)^\alpha - S_1^\alpha\big) \le v \le \frac{\alpha}{S_1}(S_1 + P_1)^{\alpha+1}$; or
2. $p^* = f(S_1)$, which holds if and only if $\frac{\alpha}{S_1}(S_1 + P_1)^{\alpha+1} \le v \le \frac{\alpha}{S_1}(S_1 + P_2)^{\alpha+1}$; or
3. $p^* = P_2$, which holds if and only if $v \ge \frac{\alpha}{S_1}(S_1 + P_2)^{\alpha+1}$.

Therefore we obtain an equilibrium (S_1, P_1) if and only if

$$\frac{S_1 + P_1}{P_1}\big((S_1 + P_1)^\alpha - S_1^\alpha\big) \le v \le \frac{\alpha}{S_1}(S_1 + P_1)^{\alpha+1}, \text{ and} \tag{10}$$

$$\frac{S_1 + P_1}{S_1}\big((S_1 + P_1)^\alpha - P_1^\alpha\big) \le v \le \frac{\alpha}{P_1}(S_1 + P_1)^{\alpha+1}; \tag{11}$$

another equilibrium $(S_1, f(S_1))$ which occurs if and only if

$$\frac{\alpha}{S_1}(S_1 + P_1)^{\alpha+1} \le v \le \frac{\alpha}{S_1}(S_1 + P_2)^{\alpha+1}, \text{ and} \tag{12}$$

$$\frac{S_1 + f(S_1)}{S_1}\big((S_1 + f(S_1))^\alpha - f(S_1)^\alpha\big) \le v \le \frac{\alpha}{f(S_1)}(S_1 + f(S_1))^{\alpha+1}; \tag{13}$$

and finally an equilibrium (S_1, P_2) if and only if

$$v \ge \frac{\alpha}{S_1}(S_1 + P_2)^{\alpha+1}, \text{ and} \tag{14}$$

$$\frac{S_1 + P_2}{S_1}\big((S_1 + P_2)^\alpha - P_2{}^\alpha\big) \le v \le \frac{\alpha}{P_2}(S_1 + P_2)^{\alpha+1}. \tag{15}$$

Further, the second inequality in (13) simplifies to $v \le 2\alpha(2S_1)^\alpha$, the first inequality in (13) always holds when $\alpha \ge 1$ and simplifies to $v \ge \frac{\alpha S_1^\alpha}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}}$ for $\alpha < 1$. Finally, for $\alpha \ge 1$, (14) implies the first inequality in (15).

3.2.3 Case $s^* = S_2$

By (9), we have $v \geq \frac{\alpha}{p^*}(S_2 + p^*)^{\alpha+1}$ and either

1. $p^* = P_1$, which holds if and only if $\frac{S_2+P_1}{P_1}\big((S_2+P_1)^\alpha - S_2^\alpha\big) \leq v \leq \frac{\alpha}{S_2}(S_2 + P_1)^{\alpha+1}$; or
2. $p^* = f(S_2)$, which holds if and only if $\frac{\alpha}{S_2}(S_2 + P_1)^{\alpha+1} \leq v \leq \frac{\alpha}{S_2}(S_2 + P_2)^{\alpha+1}$; or
3. $p^* = P_2$, which holds if and only if $v \geq \frac{\alpha}{S_2}(S_2 + P_2)^{\alpha+1}$.

Therefore we obtain an equilibrium (S_2, P_1) if and only if

$$\frac{S_2 + P_1}{P_1}\big((S_2 + P_1)^\alpha - S_2^\alpha\big) \leq v \leq \frac{\alpha}{S_2}(S_2 + P_1)^{\alpha+1}, \text{ and} \tag{16}$$

$$v \geq \frac{\alpha}{P_1}(S_2 + P_1)^{\alpha+1}; \tag{17}$$

another equilibrium $(S_2, f(S_2))$ which occurs if and only if

$$\frac{\alpha}{S_2}(S_2 + P_1)^{\alpha+1} \leq v \leq \frac{\alpha}{S_2}(S_2 + P_2)^{\alpha+1}, \text{ and} \tag{18}$$

$$v \geq \frac{\alpha}{f(S_2)}(S_2 + f(S_2))^{\alpha+1}; \tag{19}$$

and finally an equilibrium (S_2, P_2) if and only if

$$v \geq \frac{\alpha}{S_2}(S_2 + P_2)^{\alpha+1}, \text{ and} \tag{20}$$

$$v \geq \frac{\alpha}{P_2}(S_2 + P_2)^{\alpha+1}. \tag{21}$$

Moreover, (19) can be simplified to $v \geq 2\alpha(2S_2)^\alpha$. Also, when $\alpha \geq 1$, (17) implies the first inequality in (16).

3.2.4 Case $s^* = f(p^*) > 0$

By (9), we have $\frac{\alpha}{p^*}(S_1 + p^*)^{\alpha+1} \leq v \leq \frac{\alpha}{p^*}(S_2 + p^*)^{\alpha+1}$ (or equivalently $S_1 \leq f(p^*) \leq S_2$) and either

1. $p^* = P_1$, which holds if and only if $\frac{f(P_1)+P_1}{P_1}\big((f(P_1) + P_1)^\alpha - f(P_1)^\alpha\big) \leq v \leq \frac{\alpha}{f(P_1)}(f(P_1) + P_1)^{\alpha+1} = \frac{vP_1}{f(P_1)}$; or
2. $p^* = f(s^*)$, which holds if and only if $P_1 \leq f(s^*) \leq P_2$; or
3. $p^* = P_2$, which holds if and only if $v \geq \frac{\alpha}{f(P_2)}(f(P_2) + P_2)^{\alpha+1} = \frac{vP_2}{f(P_2)}$.

Therefore we obtain an equilibrium $(f(P_1), P_1)$ if and only if

$$\frac{f(P_1) + P_1}{P_1}\big((f(P_1) + P_1)^\alpha - f(P_1)^\alpha\big) \leq v \leq 2\alpha(2P_1)^\alpha, \text{ and} \tag{22}$$

$$\frac{\alpha}{P_1}(S_1 + P_1)^{\alpha+1} \leq v \leq \frac{\alpha}{P_1}(S_2 + P_1)^{\alpha+1}. \tag{23}$$

Similarly as above, (22) always holds when $\alpha \geq 1$ and it simplifies to $v \geq \frac{\alpha P_1^{\alpha}}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}}$ for $\alpha < 1$.

Another equilibrium is $(f(P_2), P_2)$ which occurs if and only if

$$v \geq 2\alpha(2P_2)^{\alpha}, \text{ and} \tag{24}$$

$$\frac{\alpha}{P_2}(S_1 + P_2)^{\alpha+1} \leq v \leq \frac{\alpha}{P_2}(S_2 + P_2)^{\alpha+1}. \tag{25}$$

The last equilibrium is in the case $p^* = f(s^*) = f(f(p^*))$. We have

$$f(f(x)) = \left(\frac{vf(x)}{\alpha}\right)^{\frac{1}{\alpha+1}} - f(x) = \left(\frac{vf(x)}{\alpha}\right)^{\frac{1}{\alpha+1}} - \left(\frac{vx}{\alpha}\right)^{\frac{1}{\alpha+1}} + x. \tag{26}$$

Thus $p^* = f(f(p^*))$ if and only if $p^* = f(p^*) = s^*$ if and only if $p^* = s^* = \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}$. So the last equilibrium is $\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$ and such an equilibrium exists if and only if $S_1 \leq f(p^*) = p^* \leq S_2$ and $P_1 \leq f(s^*) = f(p^*) = p^* \leq P_2$, or equivalently

$$S_1 \leq \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}} \leq S_2, \text{ and} \tag{27}$$

$$P_1 \leq \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}} \leq P_2. \tag{28}$$

4 Results

4.1 Overview of all possible equilibria

For fixed parameters S_1, S_2, P_1, and P_2, Table 1 gives conditions on v under which the respective equilibrium is present. For low values of v neither individual will invest, leaving the producer with the reward. For larger values of v, the scrounger will jump to investing the minimum level S_1, if this level is sufficiently small in comparison to the producer's minimum level P_1, thus taking the reward. We note that there is no situation where the producer would make the equivalent jump whilst the scrounger remained at zero investment, since he gains the reward in the case where neither invest. If P_1 is small compared to S_1, this can lead to no pure equilibrium (this asymmetry of conditions between the two players is closely linked to the cases with no pure equilibrium in general, as we discuss later). As v increases the game goes through a series of stages where one or other player increases its investment. After the initial jump to the minimum level, the investment level of either (or both) increases gradually, until both individuals invest at the maximum level. For a more technical summary, including an alternative way of writing some of the key conditions, see the Appendix.

Figure 1 shows various regions of existence of equilibria when v and $S_2 = P_2$ are fixed and S_1 and P_1 vary. Figure 2 shows various regions of existence of equilibria when v and $S_2 > P_2$ are fixed and S_1 and P_1 vary. We notice that

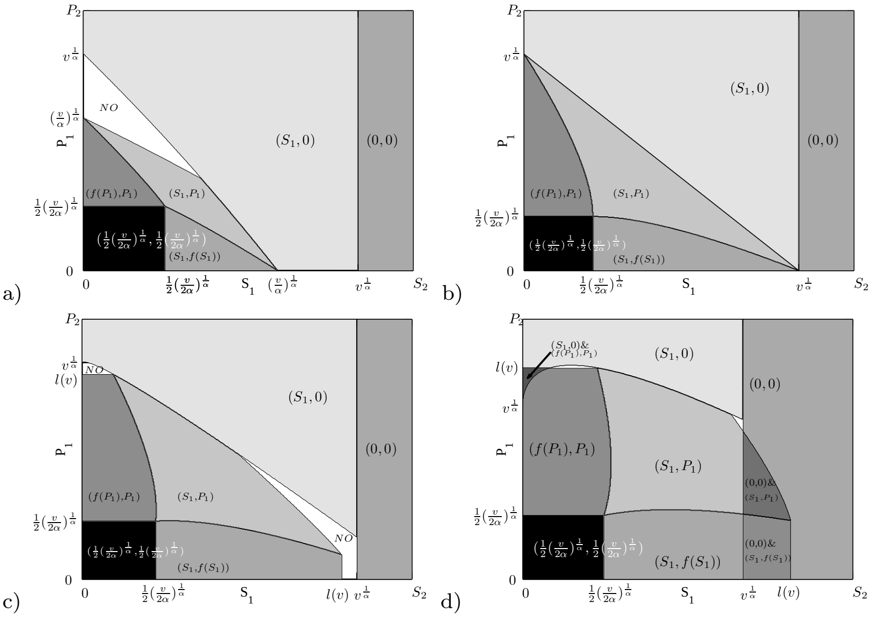


Fig. 1 Regions of existence of equilibria as $v = 1, S_2 = 1.2, P_2 = 1.2$ and S_1 and P_1 vary. a) $\alpha = 4$, b) $\alpha = 1$, c) $\alpha = 0.85$, d) $\alpha = 0.65$. White place means no pure equilibrium, the function $l(v)$ is given by $\left(\frac{v}{\alpha}\right)^{\frac{1}{\alpha}}\left(1-(1-\alpha)^{\frac{1}{\alpha}}\right)^{\frac{\alpha+1}{\alpha}}$.

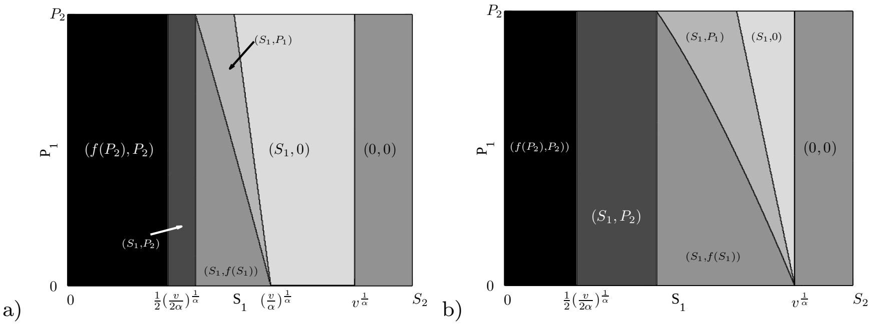


Fig. 2 Regions of existence of equilibria as S_1 and P_1 vary. a) $v = 1, S_2 = 1.2, P_2 = 0.2, \alpha = 4$. b) $v = 1, S_2 = 1.2, P_2 = 0.2, \alpha = 1$.

when S_1 and P_1 are high, then there is no real contest, the producer always investing nothing, and the scrounger sometimes making the (substantial) investment of S_1 to gain the reward. As these minimum values are decreased, we see that more complex behaviour occurs.

In Figures 3-6 we show Nash equilibria and corresponding payoffs when the opponents are fixed (i.e. S_1, S_2, P_1 and P_2 are fixed) and v varies (i.e. they play for different resources). These figures clearly show the way the investment

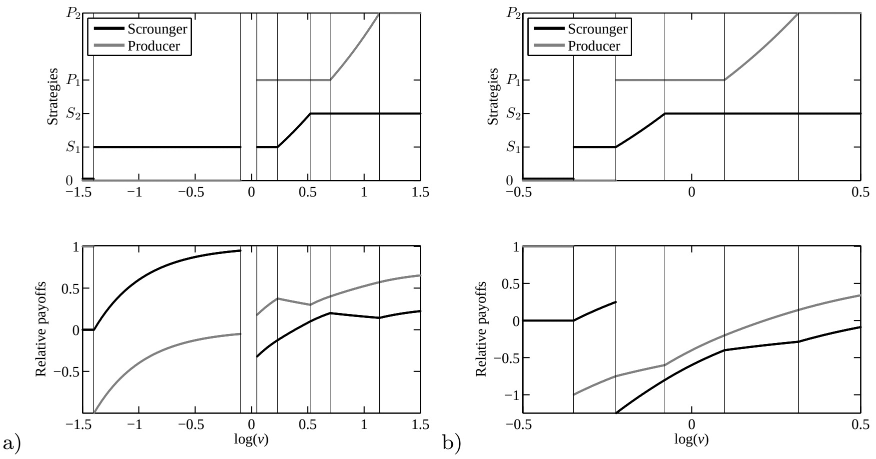


Fig. 3 Nash equilibria and payoffs relative to v (i.e. $(U_s(s^*,p^*)/v$ for the scrounger and $(U_p(s^*,p^*)/v$ for the producer) when $S_1 = 0.2, S_2 = 0.4, P_1 = 0.6, P_2 = 1$ and a) $\alpha = 2$ or b) $\alpha = 0.5$.

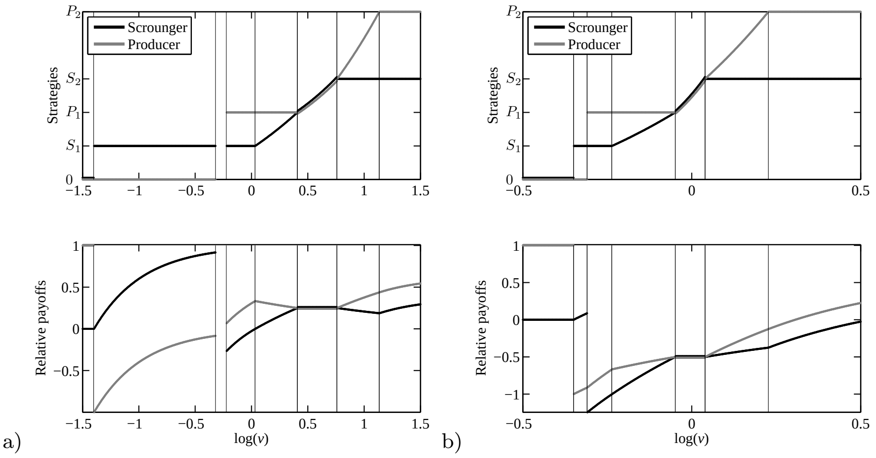
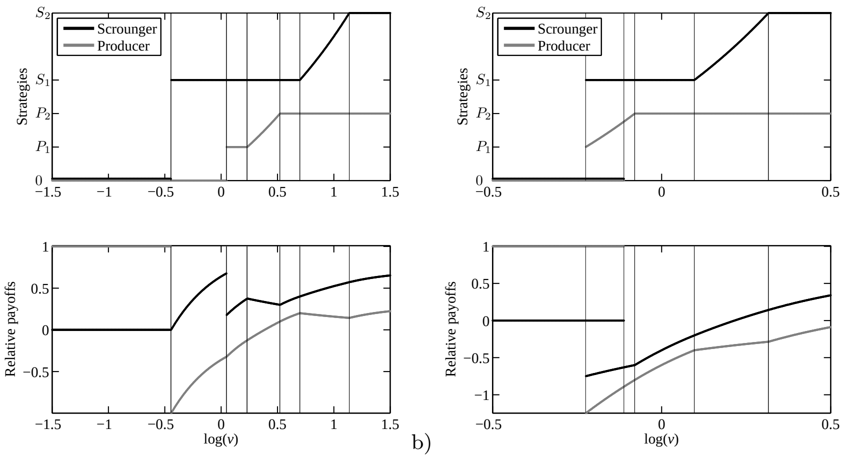


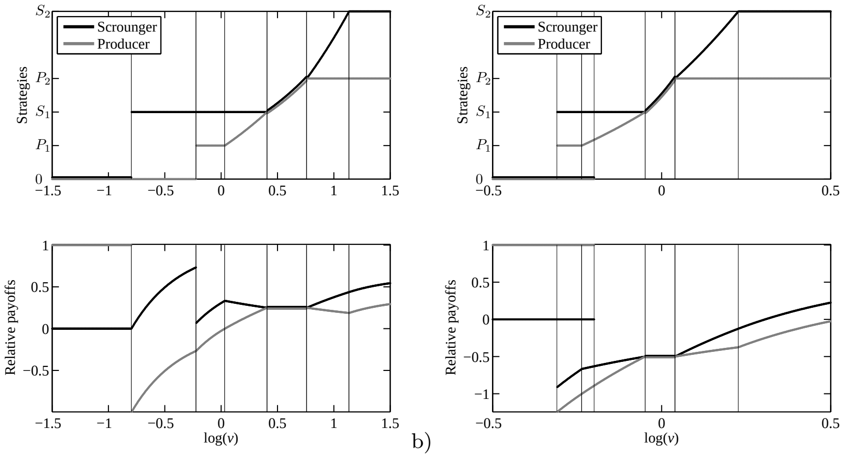
Fig. 4 Nash equilibria and payoffs relative to v (i.e. $(U_s(s^*,p^*)/v$ for the scrounger and $(U_p(s^*,p^*)/v$ for the producer) when $S_1 = 0.2, S_2 = 0.6, P_1 = 0.4, P_2 = 1$ and a) $\alpha = 2$ or b) $\alpha = 0.5$.

strategies increase, as discussed in relation to Table 1 above, with sometimes one individual, sometimes the other, being the one to increase their strategy. The payoffs are not monotone in this way, however, where the payoff of either can increase or decrease, gradually or suddenly, in response to the strategy changes of the players. In Figure 3 b), for example, we see that the scrounger receives a lower payoff for high values of v than it does for quite low values.



a) b)

Fig. 5 Nash equilibria and payoffs relative to v (i.e. $(U_s(s^*, p^*)/v$ for the scrounger and $(U_p(s^*, p^*)/v$ for the producer) when $S_1 = 0.6, S_2 = 1, P_1 = 0.2, P_2 = 0.4$ and a) $\alpha = 2$ or b) $\alpha = 0.5$.



a) b)

Fig. 6 Nash equilibria and payoffs relative to v (i.e. $(U_s(s^*, p^*)/v$ for the scrounger and $(U_p(s^*, p^*)/v$ for the producer) when $S_1 = 0.4, S_2 = 1, P_1 = 0.2, P_2 = 0.6$ and a) $\alpha = 2$ or b) $\alpha = 0.5$.

4.1.1 Equilibrium $(0, 0)$

This equilibrium is possible if (and only if) the resource is not worth enough for the scrounger to be worth fighting for. Note that when the scrounger does not fight at all, the producer simply prefers not to fight (and keeps the resource). Typically, this happens when S_1 is large compared to $v^{1/\alpha}$, i.e. when v is very small.

Table 1 All types of equilibria. For fixed parameters S_1, S_2, P_1, and P_2, we give conditions on v under which the respective equilibrium is present.

Conditions	Equilibrium	#
$v \le S_1^\alpha$	$(0, 0)$	1
$S_1^\alpha \le v \le \frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right)$	$(S_1, 0)$	2
$\frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right) \le v \le \frac{\alpha}{S_1}(S_1+P_1)^{\alpha+1}$ and $\frac{S_1+P_1}{S_1}\left((S_1+P_1)^\alpha - P_1^\alpha\right) \le v \le \frac{\alpha}{P_1}(S_1+P_1)^{\alpha+1}$	(S_1, P_1)	3
$\frac{\alpha}{S_1}(S_1+P_1)^{\alpha+1} \le v \le \frac{\alpha}{S_1}(S_1+P_2)^{\alpha+1}$ and $v \le 2\alpha(2S_1)^\alpha$ and $v \ge \frac{\alpha S_1^\alpha}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}}$ if $\alpha < 1$	$(S_1, f(S_1))$	4
$\frac{\alpha}{P_1}(S_1+P_1)^{\alpha+1} \le v \le \frac{\alpha}{P_1}(S_2+P_1)^{\alpha+1}$ and $v \le 2\alpha(2P_1)^\alpha$ and $v \ge \frac{\alpha P_1^\alpha}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}}$ if $\alpha < 1$	$(f(P_1), P_1)$	5
$\frac{\alpha}{S_1}(S_1+P_2)^{\alpha+1} \le v \le \frac{\alpha}{P_2}(S_1+P_2)^{\alpha+1}$ and $v \ge \frac{S_1+P_2}{S_1}\left((S_1+P_2)^\alpha - {P_2}^\alpha\right)$ if $\alpha < 1$	(S_1, P_2)	6
$\frac{\alpha}{P_1}(S_2+P_1)^{\alpha+1} \le v \le \frac{\alpha}{S_2}(S_2+P_1)^{\alpha+1}$ and $v \ge \frac{S_2+P_1}{P_1}\left((S_2+P_1)^\alpha - S_2^\alpha\right)$ if $\alpha < 1$	(S_2, P_1)	7
$2\alpha(2S_1)^\alpha \le v \le 2\alpha(2S_2)^\alpha$ and $2\alpha(2P_1)^\alpha \le v \le 2\alpha(2P_2)^\alpha$	$\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$	8
$\frac{\alpha}{P_2}(S_1+P_2)^{\alpha+1} \le v \le \frac{\alpha}{P_2}(S_2+P_2)^{\alpha+1}$ and $v \ge 2\alpha(2P_2)^\alpha$	$(f(P_2), P_2)$	9
$\frac{\alpha}{S_2}(S_2+P_1)^{\alpha+1} \le v \le \frac{\alpha}{S_2}(S_2+P_2)^{\alpha+1}$ and $v \ge 2\alpha(2S_2)^\alpha$	$(S_2, f(S_2))$	10
$v \ge \frac{\alpha}{P_2}(S_2+P_2)^{\alpha+1}$ and $v \ge \frac{\alpha}{S_2}(S_2+P_2)^{\alpha+1}$	(S_2, P_2)	11

4.1.2 Equilibrium $(S_1, 0)$

This equilibrium is possible if the resource is worth enough for the scrounger to fight for, but once the scrounger fights, the cost is prohibitive for the producer to fight back. This happens if either a) S_1 is relatively small and P_1 relatively large, or b) (especially for $\alpha > 1$) S_1 is large enough so that small p increases the costs for the producer without significantly improving the chances of winning the resource while large p increases the cost to make it unprofitable for the producer to fight.

4.1.3 Equilibrium (S_1, P_1)

This equilibrium happens when v is large enough for both individuals to fight for but not large enough to really engage in the fight “vigorously”. Specifically, the scrounger finds the resource attractive to “initiate” the fight and invest S_1. The producer also finds the resource attractive enough to fight back at level P_1, but the cost is prohibitive to invest more. When the producer invests P_1, the cost becomes prohibitive for the scrounger to invest more.

Moreover, in this situation, both individuals would prefer to invest even less into the fight; yet investing S_1 and P_1 is better for them than not fighting at all. Also note that when $\alpha < 1$, this equilibrium can happen simultaneously to $(0, 0)$. This phenomenon is also observed for the case $\alpha = 0$, which is analysed in detail in Sykes and Rychtář (in press).

4.1.4 Equilibria $(S_1, f(S_1))$ *and* $(f(P_1), P_1)$

These are in effect natural continuations of (S_1, P_1). As the value of the resource increases a little more, one individual finds it beneficial to fight for it with an investment above its minimal level. Note that the conditions are such that $P_1 < f(S_1) < S_1$ (for the equilibrium $(S_1, f(S_1))$) or $S_1 < f(P_1) < P_1$ (for the equilibrium $(f(P_1), P_1)$). An alternative way of thinking about this is that P_1 (or S_1) is already small enough relative to v so that the producer (or scrounger) fights at the optimal level whereas the other individual would prefer to fight less (but still prefers to fight rather than to not fight).

4.1.5 Equilibria (S_1, P_2) *and* (S_2, P_1)

Here, one individual invests at its minimum level while the other invests at its maximum. However, these equilibria occur only if $S_1 > P_2$ or if $P_1 > S_1$, i.e. the individual investing its minimum is actually stronger than the individual investing its maximum (and the stronger individual would prefer to invest less while the weaker individual would prefer to invest more).

4.1.6 Equilibrium $\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$

This is the "most natural" equilibrium. It happens for "medium" values of v and both individuals play at the optimal level and any sufficiently small change in their abilities would not change the equilibrium. This equilibrium corresponds to the fixed point $s^* = f(p^*)$ and $p^* = f(s^*)$.

4.1.7 Equilibria $(S_2, f(S_2))$ *or* $(f(P_2), P_2)$

This equilibrium happens whenever there is a strength asymmetry in the players and v is large enough. Both individuals want to fight for it but the stronger individual does not fight at full force (since the additional cost of a bigger fight does not outweigh the benefits of only a slightly higher chances of winning the fight).

4.1.8 Equilibrium (S_2, P_2)

This equilibrium happens whenever v is large enough, in which case both individuals want to fight for the reward to the maximum extent, as the value of the resource outweighs the cost of the fight.

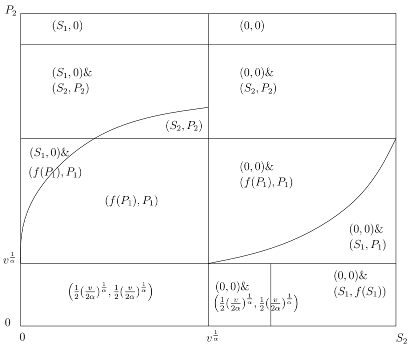


Fig. 7 Regions of existence of equilibria as $v = 0.8, S_2 = 1, P_2 = 4, \alpha = 0.36$ and S_1 and P_1 vary.

4.2 Co-existence of equilibria

Next, we consider the question of whether multiple equilibria can occur for the same parameter values. More specifically, we show that none of the equilibria when both players invest non-zero in the fights (equilibria numbered 3–11) can occur at the same time, of course unless they coincide (e.g. when $P_1 = f(S_1)$). For $\alpha \geq 1$ the only equilibria that can occur at the same time are the combinations $(0,0)$ and $(S_1,0)$ or $(S_1,0)$ and (S_1,P_1). Moreover, these two coexist only on the lines between their respective regions, which can be considered as a non-generic case (see Broom and Rychtář (2013)). Other equilibria appear to co-exist on the lines between their regions but in those cases, the equilibria coincide on those lines. For $\alpha < 1$ the equilibria $(0,0)$ and $(S_1,0)$ can occur together with any other equilibrium with the exception that $(S_1,0)$ cannot coexist with $(S_1,f(S_1))$ nor with (S_1,P_2). See for example Figure 7.

For the remaining cases we consider first the case $\alpha \geq 1$. The equilibria $(0,0)$ and $(S_1,0)$ occur at the same time when $v = S_1^\alpha$. The equilibria $(S_1,0)$ and (S_1,P_1) occur at the same time when $v = \frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right)$. The equilibria $(0,0)$ and (S_1,P_1) cannot occur at the same time due to inequality (7). Further, we easily check that $\frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right) < \frac{\alpha}{P_1}(S_1+P_1)^{\alpha+1}$ which combined with inequality (7) yields

$$S_1^\alpha < \frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right) < \frac{\alpha}{\max\{S_1,P_1\}}(S_1+P_1)^{\alpha+1} \leq 2\alpha(S_1+P_1)^\alpha.$$

Comparing this estimates against those in Table 1 (and also Table 4 from the Appendix) we obtain that neither equilibrium $(0,0)$ nor $(S_1,0)$ can occur at the same time as any of 4-11.

Finally, from (7) we obtain that $(S_1,0)$ combined with $(S_1,f(S_1))$ and $(S_1,0)$ combined with (S_1,P_2) cannot occur even in the case $\alpha < 1$. On the other hand, in this case equilibrium 1 can occur at the same time as any of the other equilibria, and the equilibrium $(S_1,0)$ can occur at the same time as any of 3,5,7–11.

4.2.1 No (pure) equilibria

As we have seen in Figure 1, there are instances of no pure strategy equilibria. These are linked to the asymmetry between the two players, and in particular the fact that $(S_1, 0)$ can be an equilibrium, but $(0, P_1)$ cannot. This leads to a break in the natural sequences of solutions; for example there is a natural progression from 1 to 2 to 3 to 4 to 6 to 9 to 11 (there are six such sequences starting 1 to 2 to 3), where regions share a boundary linked to the reversing of one condition. However, the "region" associated with $(0, P_1)$ connecting 3 to 1 does not exist, resulting in disconnected conditions between regions 1 and 3, but also between regions 1 and 5.

For region 3 the lower boundaries, must satisfy both of the following conditions: $\frac{S_1+P_1}{P_1}\left((S_1+P_1)^{\alpha}-S_1^{\alpha}\right) \leq v$, $\frac{S_1+P_1}{S_1}\left((S_1+P_1)^{\alpha}-P_1^{\alpha}\right) \leq v$.
The first of these would form a boundary with region 2, but the second has no equivalent region sharing the boundary. Thus when this is the more restrictive condition, then a gap appears which can potentially yield no pure equilibrium. This occurs if and only if

$$\frac{S_1+P_1}{P_1}\left((S_1+P_1)^{\alpha}-S_1^{\alpha}\right) < \frac{S_1+P_1}{S_1}\left((S_1+P_1)^{\alpha}-P_1^{\alpha}\right), \tag{29}$$

which rearranges to

$$\left(1+\frac{S_1}{P_1}\right)^{\alpha}\left(1-\frac{S_1}{P_1}\right)-1+\left(\frac{S_1}{P_1}\right)^{1+\alpha} > 0. \tag{30}$$

This holds for $S_1 < P_1$ when $\alpha > 1$, and for $S_1 > P_1$ when $\alpha < 1$. When $\alpha > 1$, then for any v, there is always a region of no pure equilibria when $P_1 > S_1$ as in Figure 1 a), following from the disconnect between regions 1 and 3.

For example, there is no pure equilibrium when $\alpha = 4, v = 1, S_1 = 0.1, S_2 = 1.2, P_1 = 0.8, P_2 = 1.2$. Here the players effectively decide between two discrete cases a) do not fight at all, or b) fight at the minimal level. Thus, the scrounger's payoff is

$$\begin{array}{ccc} S\backslash P & 0 & P_1 \\ 0 & 0 & -P_1^{\alpha} \\ S_1 & v-S_1^{\alpha} & \frac{S_1}{S_1+P_1}v-(S_1+P_1)^{\alpha} \end{array} \tag{31}$$

and the producer's payoff is

$$\begin{array}{ccc} S\backslash P & 0 & P_1 \\ 0 & v & v-P_1^{\alpha} \\ S_1 & -S_1^{\alpha} & \frac{P_1}{S_1+P_1}v-(S_1+P_1)^{\alpha} \end{array} \tag{32}$$

When $p = 0$, the scrounger prefers $s = S_1$ over $s = 0$. When $s = S_1$, the producer prefers $p = P_1$ over $p = 0$. When $p = P_1$, the scrounger prefers $s = 0$ over $s = S_1$. Finally, when $s = 0$, the producer prefers $p = 0$ over $p = P_1$. Note that this leads to an internal mixed equilibrium strategy.

When $\alpha = 1$, then for any v and any S_1, P_1, S_2, P_2, there is exactly one (pure) equilibrium as in Figure 1 b). When α falls below 1 there can be two regions with no equilibria, corresponding to the disconnects between the regions 1 and 3, 1 and 5. As α becomes small the disconnect boundaries discussed above do not occur, and there is always at least one equilibrium and sometimes two (although never more than two) equilibria.

4.3 Some observations for particular cases

4.3.1 The case when $\alpha < 1$

When $\alpha < 1$, we observe the following phenomenon, see any of the Figures 3-6. If the players do not engage in the conflict at all, the producer would get v and the scrounger would get 0. However, as v grows, $(0, 0)$ is no longer a Nash equilibrium (or the only Nash equilibrium) and very often (S_1, P_1) emerges as the Nash equilibrium. At the same time, the payoffs to the players at (S_1, P_1) are negative. Still, (S_1, P_1) is a Nash equilibrium. If players have to choose between 0 and S_1 (or 0 and P_1) only, then for the scrounger, $s = S_1$ will be better than $s = 0$ no matter what the producer's action (because $s = 0$ means no gain and while $s = S_1$ adds a cost, this is either compensated by the gain of the resource if $p = 0$ or is relatively small if $p = P_1$, since $\alpha < 1$, i.e. the fights are costly to start but inexpensive to continue). For similar reasons, once the scrounger invests $s = S_1$ into the fight, the producer prefers $p = P_1$ over $p = 0$ as $\alpha < 1$ and thus the fights are costly to start but inexpensive to continue. For an analysis of the case when $\alpha = 0$, i.e. when all fights are equally costly, see Sykes and Rychtář (in press). There, if an individual decides to fight, it should fight with the maximal aggression. For $v < 1$, the game is a variant of the Stag Hunt game (Skyrms, 2004) and for $v > 1$, is a Prisoner's Dilemma (see e.g. Broom and Rychtář, 2013). When $v < 1$, both (S_2, P_2) and $(0; 0)$ are Nash equilibria; and when $v > 1$, (S_2, P_2) is the only Nash equilibrium.

4.3.2 Small S_1 and P_1

When S_1 and P_1 are both small compared to v, they can effectively be treated as 0 and none of the equilibria 1-7 occur. The situation when $S_1 = P_1 = 0$ is considered in detail in Sykes (2015). The only remaining equilibria are $\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$, $(f(P_2), P_2)$, $(S_2, f(S_2))$ and (S_2, P_2). Once α and v are fixed, there is no overlap between these equilibria and always exactly one holds (see Table 1). The situation for $\alpha = 2$ and $\alpha = 0.5$ is shown in Figure 8 (the situation for other α is analogous).

4.3.3 Increasing strength

Figure 9 shows how increasing the strength of an animal affects its strategy and payoffs. Increasing the upper limit allows the affected individual to invest

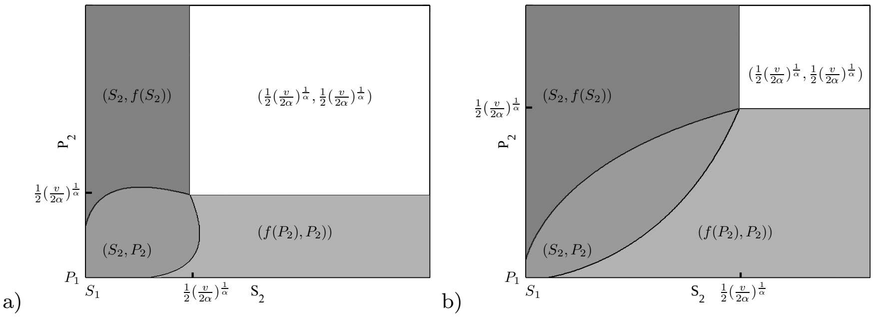


Fig. 8 Regions of existence of equilibria as $v = 1, S_1 = 0.01, P_1 = 0.01$ and S_2 and P_2 vary. The regions are similar for all α's, here a) $\alpha = 2$ and b) $\alpha = 0.5$.

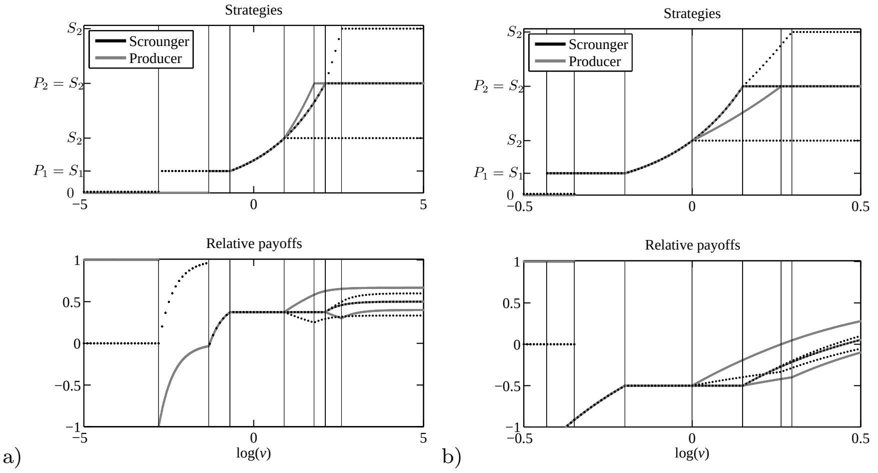


Fig. 9 Nash equilibria and payoffs relative to v (i.e. $(U_s(s^*, p^*)/v$ for the scrounger and $(U_p(s^*, p^*)/v$ for the producer) when $S_1 = 0.2, P_1 = 0.2, P_2 = 1$ $S_2 \in \{0.5, 1, 1.5\}$. a) $\alpha = 4$ or b) $\alpha = 0.5$. When $\alpha > 1$, higher value of S_2 corresponds to higher investment level and payoff to the scrounger and lower investment and payoff to the producer. When $\alpha < 1$, higher value of S_2 corresponds to higher investment level to both scrounger and producer, and higher payoff to the producer.

more in the fight and the individual also does it when v is large enough. When $\alpha > 1$ (investing a little is cheap but increasing the investment is eventually costly), investing more also yields a higher payoff. When $\alpha < 1$ (investing a little is expensive but investing more is relatively cheap compared to the initial investment), the situation is more interesting as then even the other individual invests more.

4.4 A comparison with the results of Broom et al (2015)

In Broom et al (2015) the scrounger made an initial investment, to which the producer responded. This led to very different results to that in the current paper where decisions are simultaneous.

For sufficiently high values of the bounds on available effort, one or other individual was forced to concede. For a concave function with $\alpha < 1$ the scrounger will not challenge and thus the producer obtains the reward with no investment level at all (for any non-zero level the optimal producer investment is sufficiently large). For a convex function with $\alpha > 1$ then the scrounger will make a sufficient level of investment to force the producer to concede. Only when $\alpha = 1$ could there be non-zero levels of investment.

For sufficiently low values of the upper bounds on effort (Broom et al (2015) did not consider lower bounds), the outcome depended significantly on which individual had the higher upper bound. Both individuals would invest, but at most one of these would be at an intermediate level. The individual with the higher upper bound would generally invest at a higher level, and thus win the resource with higher probability. Results in this case are similar to those in the current paper.

We note that in general the intermediate strategies available in the current paper, where both individuals invest but not at maximum or minimum level are not present in Broom et al (2015), and so the simultaneous nature of the game here has a big effect. This in fact mirrors the general contrast between simultaneous and sequential games (Maynard Smith, 1982; McNamara et al, 2006) including the most basic of all evolutionary games, matrix games. In matrix games mixed strategies occur only for simultaneously play Selten (1980), and this can be thought of as an analogous result to that regarding intermediate levels of investment here (though as noted above, for sequential games with low maximum threshold, it was possible for one of the individuals to invest at an intermediate level). Thus this type of relationship may hold for a great variety of games.

5 Discussion

In this paper we have built on our previous work Broom et al (2015) considering a producer scrounger competition over resources, where the participants decide the level of effort that they put into contesting the resource. The larger the effort the larger the chance of winning the resource, but also the larger the cost. Models of this type have also been considered in economics, see for example **?**Skaperdas (1992); Baye et al (2012). A feature of our model is the existence of limits to the available effort, which also feature in such models, such as Che and Gale (1997); Roberson (2006). In our previous work decisions were sequential, with the scrounger choosing an attacking strategy, followed by a defensive one from the producer. In the current paper, the individuals make their decisions simultaneously. We have both analysed this situation, and then compared it to the previous model to identify key areas of similarity and difference.

The game is governed by a number of model parameters. For example, there is both a minimum level of effort required (at least to have any effect in the contest) and a maximum level available, and these can differ between the players, S_1, S_2 for the scrounger and P_1, P_2 for the producer. We have assumed that all model parameters are known to both players, including the minimum and maximum levels of their opponent, i.e. we have a game with perfect information (note that we have also considered related models with imperfect information in Broom et al (2013); Broom and Rychtář (2016b)). This is of course reasonable if all individuals are identical, or an opponent has been previously encountered. Otherwise, an individual would have to gauge an opponent's ability from appearance or behaviour; this may at least imply that there should be some error involved in making the assessment of the ability of a stranger (Dugatkin, 1997; Dugatkin and Dugatkin, 2007; Kura et al, 2015). As shown in Figure 9, different S_2 not only yields different behaviour of the Scrounger, but also different behaviour of the Producer. Thus, not knowing the opponent's strength would potentially influence the strategies.

We have found the complete set of pure Nash equilibria for our model, which are summarised in Table 1. We find in particular that there are always at most two such equilibria, with sometimes there being none. When the bounds on the available effort for the two players are sufficiently wide, so that the minimum values P_1 and S_1 are low and the maximum values P_2 and S_2 are high when compared to the reward, then both individuals choose the same intermediate level of investment. When this is not the case the asymmetries between the players comes into play, meaning that different values of reward can have a surprising effect on the strategies and rewards received for the two players. For example in Figure 3 b) both chosen strategies jump (from zero to their minimum non-zero level) and hence the payoffs also jump, and an increase in reward value can actually lead to a lower payoff for one of the participants. The results here are sometimes very different from those in Broom et al (2015) when sequential decisions occurred. For example, when bounds on the available effort in that paper were wide then there was never a contest between the protagonists.

A question arises then, about whether simultaneous or sequential decisions are most realistic, and indeed if sequential, which individual should choose first. This was discussed in Broom et al (2015). In general, it is probably more realistic to consider any interaction as an extended contest where both individuals make a sequence of choices, and this would be a natural way to extend the current work. Such a situation is considered in a related scenario in Broom and Rychtář (2016a), where it is shown that provided that reward values and contest durations are fixed (except when one individual concedes) and known, the single decision approximation of simpler models like those considered here can be good.

When would our model be useful in real situations? As mentioned in the Introduction, situations of territorial defence where territories are large as in

Hamilton and Dill (2003b) for the subtropical reef fish *Kyphosus cornelii* are a natural type of situation to consider for models with simultaneous decision-making. Here taller vegetation means a more valuable territory leading to more kleptoparasitic behaviour. Another interesting possibility is that of the archerfish *Toxotes chatareus* as investigated in Davis and Dill (2012). Here fish shoot down small prey such as crickets with jets of water, but other fish can try to steal the prey item. Here the shooting fish can be regarded as the owner, and both fish have to move to acquire the target; the greater the energy they put into their attempt to take the prey, the greater the chance they have to acquire it. To properly use our model in a real situation, however, we need some way of inferring the level of energy used in an actual contest, and as observed by Hack (1998), this is hard to do and not very often attempted.

There are cases where we do have good energetic measurements however, including in the work of Hack (1998) themselves. Here house crickets *Acheta domesticus L.* compete in contests for females. In this paper, contests involved a range of different fighting strategies, and the energetic investment of the crickets was estimated using levels of their oxygen consumption. The authors observed that different fighting strategies required different levels of energy, and that energy expenditure was an important consideration in strategy choice. A similas situation involves contests between male sierra dome spiders *Neriene litigiosa* as in deCarvalho et al (2004). In this paper, spiders of varying ages (the number of days since sexual maturation) and sizes compete against other males for female spiders. These contests are long, and can be thought to comprise three main stages; display, ritualised wrestling and real fights. The level of energy used was measured using the carbon dioxide production of the spiders. This was observed to go up with the stages, with a particarly big jump between the first and second stages. This could be modelled as a complex sequential contest (containing some simultaneous choices), but as in Broom and Rychtář (2016a) might be well approximated by a single choice of energy investment, with low investment indicating concession before later stages. The authors observed that older spiders generally used less energy and larger spiders generally used more energy, so that there is likely (but not necessarily) an asymmetry of ability of asssessment of reward values amongst the spiders.

As mentioned above, energetic expenditure is not often measured in real contests, so can we apply our model in cases where it is not? In Goubault et al (2007) the parasitoid wasp *Goniozus nephantidis* female wasps lay their eggs within host (in this work the caterpillar of the rice moth *Corcyra cephalonica*). These in turn can be parasitised by other wasps, and so female wasps defend the caterpillar, and so fights between defender and attacker can occur. Here the value of the caterpillar to the defender changes with time, as the eggs are laid in the hosts and then hatch into larvae, but no other attributes are likely to change between these early and later contests. In particular before eggs are laid the host has no offspring to defend, and after hatching larvae are at relatively low risk, but eggs can be destroyed by intruders. It was observed in Goubault et al (2007) that for contests at the egg stage, the defender was more likely to win than at the other stages. Thus while an energetic measurement has not been made, a differential of investment can be inferred by the win probability. We note that in this example the attacker and defender will value the resource differently except for when no eggs have been laid by the defender, so our model with its current assumptions willl not directly be able to explain this differential assessment. It will still be applicable to the problem when no eggs have been lain, where differences in intruder and owner size, or the size of the defended caterpillar, can be considered. In general in all of the considered examples, we see that energetic investment will vary markedly depending upon a number of factors. These can be properties of the individual such as their size and age, but also extrinsic factors such as the value of the resource. Thus we argue that energetic aspects are an important factor to consider when modelling animal contests.

A potential future development would be to introduce heterogeneity within the population in the parameters. For instance, individuals may value the resource differently, depending upon information they have about the resource (differences in assessment) as considered in Broom et al (2013). Alternatively, they both may know all about the resource but still value it differently, e.g. because of hunger levels (Broom et al, 2014). Similarly individuals may know their own bounds upon investment but not those of their opponents as discussed previously, and they may then need to estimate these based upon past observations of the distribution of values within the population and/or cues from the specific opponent.

In general animals need to make trade-offs between the energy they allocate to different activities, and thus the kind of investment decisions made in this paper are likely to be important in many scenarios. We contend that, for this reason, such energetic considerations should be considered in a large range of evolutionary models.

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Appendix

Here we consider alternative ways of representing some of the results from the main body of the paper. Table 2 summarises the precise conditions on S_1, S_2, P_1, P_2 under which a given equilibrium type can occur for some values of v. Most of the conditions easily follow from the facts that the intervals described in Table 1 must be non-empty. The additional condition for the equilibrium (S_2, P_1) (and (S_1, P_2)) follows from (7). For equilibrium $(S_1, f(S_1)$ (and similarly for equilibrium $(f(P_1), P_1)$) and $\alpha < 1$ the condition $\frac{\alpha S_1^\alpha}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}} \leq 2\alpha(2S_1)^\alpha$ is always satisfied, since $(1-\alpha)^{1/\alpha} < \frac{1}{2}$; the condition $\frac{\alpha S_1^\alpha}{\left(1-(1-\alpha)^{1/\alpha}\right)^{\alpha+1}} \leq \frac{\alpha}{S_1}\left(S_1 + P_2\right)^{\alpha+1}$ simplifies to $\frac{S_1}{P_2} \leq \frac{1-(1-\alpha)^{1/\alpha}}{(1-\alpha)^{1/\alpha}}$. For equilibrium (S_1, P_1) the fact that the intervals in Table 1 are non-empty follows from (7) (and also interchanging by S_1 and P_1). Further, these intervals have non-empty interior if and only if $\frac{S_1+P_1}{S_1}\left((S_1+P_1)^\alpha - P_1^\alpha\right) \leq \frac{\alpha}{S_1}(S_1+P_1)^{\alpha+1}$ and $\frac{S_1+P_1}{P_1}\left((S_1+P_1)^\alpha - S_1^\alpha\right) \leq \frac{\alpha}{P_1}(S_1+P_1)^{\alpha+1}$, which simplifies to the condition in Table 2. Finally, for equilibrium $(S_1, 0)$ we can use (7) in case $\alpha \geq 1$. From Table 2 we immediately obtain Table 3 and the necessary conditions shown in Table 4.

Now by comparing the conditions in various tables we can see why none of the equilibria when both players invest non-zero in the fights (equilibria numbered 3–11) ever occur together. This is summarised in Table 5.

Table 2 Conditions for all types of equilibria. Here, we give conditions on parameters S_1, S_2, P_1, and P_2 under which equilibria are present for some value of v.

#.	Equilibrium	Conditions on S_1, S_2, P_1, P_2
1	$(0, 0)$	always possible
2	$(S_1, 0)$	for $\alpha \geq 1$ always possible, for $\alpha < 1$ if and only if $\frac{P_1}{S_1} \geq c > 0$, where $(1+c)^\alpha = 1 + \frac{c}{1+c}$
3	(S_1, P_1)	for $\alpha \geq 1$ always possible, for $\alpha < 1$ if and only if $\frac{(1-\alpha)^{1/\alpha}}{1-(1-\alpha)^{1/\alpha}} \leq \frac{P_1}{S_1} \leq \frac{1-(1-\alpha)^{1/\alpha}}{(1-\alpha)^{1/\alpha}}$
4	$(S_1, f(S_1))$	$P_1 \leq S_1$ and moreover $\frac{S_1}{P_2} \leq \frac{1-(1-\alpha)^{1/\alpha}}{(1-\alpha)^{1/\alpha}}$ if $\alpha < 1$
5	$(f(P_1), P_1)$	$S_1 \leq P_1$ and moreover $\frac{P_1}{S_2} \leq \frac{1-(1-\alpha)^{1/\alpha}}{(1-\alpha)^{1/\alpha}}$ if $\alpha < 1$
6	(S_1, P_2)	$P_2 \leq S_1$
7	(S_2, P_1)	$S_2 \leq P_1$
8	$\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$	$P_1 \leq S_2$ and $S_1 \leq P_2$
9	$(f(P_2), P_2)$	$P_2 \leq S_2$
10	$(S_2, f(S_2))$	$S_2 \leq P_2$
11	(S_2, P_2)	always possible

Table 3 Possible equilibria related to relative positions of S_1, S_2, P_1, P_2. '●' means that in this case the equilibrium is always possible for some value of v, '$*$' means that for $\alpha \geq 1$ the equilibrium is always possible for some value of v, while for $\alpha < 1$ there are certain additional conditions (to be found in Table 2) that need to be satisfied in order for the equilibrium to be present.

relations between	equilibrium										
S_1, S_2, P_1, P_2	1	2	3	4	5	6	7	8	9	10	11
$S_1 < S_2 < P_1 < P_2$	●	$*$	$*$		$*$		●			●	●
$S_1 < P_1 < S_2 < P_2$	●	$*$	$*$		●			●		●	●
$S_1 < P_1 < P_2 < S_2$	●	$*$	$*$		●			●	●		●
$P_1 < P_2 < S_1 < S_2$	●	$*$	$*$	$*$		●			●		●
$P_1 < S_1 < P_2 < S_2$	●	$*$	$*$	●				●	●		●
$P_1 < S_1 < S_2 < P_2$	●	$*$	$*$	●				●		●	●

Table 4 Necessary conditions

#	Equilibrium	necessary condition
3	(S_1, P_1)	$v \le \frac{\alpha}{\max\{S_1,P_1\}}(S_1 + P_1)^{\alpha+1} \le 2\alpha(S_1 + P_1)^{\alpha}$
4	$(S_1, f(S_1))$	$v \le \frac{\alpha}{S_1}\big(S_1 + \min\{S_1, P_2\}\big)^{\alpha+1} \le 2\alpha(S_1 + P_2)^{\alpha}$
5	$(f(P_1), P_1)$	$v \le \frac{\alpha}{P_1}\big(\min\{S_2, P_1\} + P_1\big)^{\alpha+1} \le 2\alpha(S_2 + P_1)^{\alpha}$
8	$\left(\frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}, \frac{1}{2}\left(\frac{v}{2\alpha}\right)^{\frac{1}{\alpha}}\right)$	$2\alpha(2\max\{S_1, P_1\})^{\alpha} \le v \le 2\alpha(2\min\{S_2, P_2\})^{\alpha}$
9	$(f(P_2), P_2)$	$v \ge \frac{\alpha}{P_2}\big(\max\{S_1, P_2\} + P_2\big)^{\alpha+1} \ge 2\alpha(S_1 + P_2)^{\alpha+1}$
10	$(S_2, f(S_2))$	$v \ge \frac{\alpha}{S_2}\big(S_2 + \max\{S_2, P_1\}\big)^{\alpha+1} \ge 2\alpha(S_2 + P_1)^{\alpha+1}$
11	(S_2, P_2)	$v \ge \frac{\alpha}{\min\{S_2,P_2\}}(S_2 + P_2)^{\alpha+1} \ge 2\alpha(S_2 + P_2)^{\alpha}$

Table 5 Reasons why intersection cannot occur

	4	5	6	7	8	9	10	11
3	Tbl. 1	Tbl. 1	Tbl. 1	Tbl. 1	Tbl. 4	Tbl. 4	Tbl. 4	Tbl. 4
4		Tbl. 2	Tbl. 1	Tbl. 2	Tbl. 1	Tbl. 4	Tbl. 1	Tbl. 4
5			Tbl. 2	Tbl. 1	Tbl. 1	Tbl. 1	Tbl. 4	Tbl. 4
6				Tbl. 2	Tbl. 2	Tbl. 1	Tbl. 2	Tbl. 1
7					Tbl. 2	Tbl. 2	Tbl. 1	Tbl. 1
8						Tbl. 1	Tbl. 1	Tbl. 4
9							Tbl. 2	Tbl. 1
10								Tbl. 1