Kleptoparasitic interactions modeling varying owner and intruder hunger awareness

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Abstract
We consider a game theoretical model of kleptoparasitic interaction between two individuals, the owner and the intruder. The owner is in possession of a resource and must decide whether to defend the resource against the intruder or flee. If the owner defends, the intruder must decide whether to fight with the owner or flee. The outcome of the fight depends on the hunger of the individuals, the hungrier the individual is, the more likely they are to win the fight. We consider three scenarios: (a) both individuals know their own and their opponent’s hunger, (b) individuals only know their own hunger but not that of their opponent, and (c) individuals do not know their own nor the opponent’s hunger levels. We determine Nash equilibrium strategies in each scenario. We conclude that owner is generally willing to defend more often than the intruder is willing to attack. Also, the intruder’s payoff is largest in the full information case; but the owner may benefit in the no information or partial information cases when the cost of the fight is neither too large nor too small.

1. Introduction

In nature, there are many different interactions between species, such as mutualism, commensalism, and parasitism (Dimitjian, 2000). In our paper, we will focus on kleptoparasitism, a refined form of parasitism in which the parasite fights for and steals resources (generally food) from conspecifics or other species (Iyengar, 2008). This behavior is often associated with birds (Brockmann and Barnard, 1979), but can also be observed in insects (Sivinski et al., 1999; Crowe et al., 2009, 2013), spiders (Cangiolo, 1990), reptiles (Platt et al., 2007), and mammals (Edelman et al., 2005; Focardi et al., 2017; Materassi et al., 2017). Within kleptoparasitic interactions, animals can exhibit many different types of defending, fighting, fleeing and forfeiting behavior, see for example Iyengar (2008) for a review.

Kleptoparasitism is often crucial for the dynamics of various ecosystems and should not be overlooked in trophic food web modeling (Focardi et al., 2017). Kleptoparasitic interactions can have varying levels of complexity due to a variety of factors such as age and/or size of the individuals (Broom and Ruxton, 2003) and different models try to address these factors, see for example Broom et al. (2008a), Broom and Rychtář (2009), Broom et al. (2010), Barker et al. (2012), Galanter et al. (2017) and Sykes and Rychtář (2017). Many recent models contain a high degree of detail and realism, see for example Garay et al. (2017, 2018), Varga et al. (2020a,b). The Owner–Intruder (Eshel and Sansone, 1995) and Producer–Scrounger (Barnard and Sibly, 1981) games are common ways to model kleptoparasitic interactions. The models can account for many different situations and assumptions, while yielding clear and testable predictions (Garay and Giraldeau, 1991; Dubois et al., 2003; Dubois and Giraldeau, 2005; Argasinski and Broom, 2013; Mesterton-Gibbons and Sherratt, 2014; Argasinski and Rudnicki, 2017; Cressman and Krivan, 2019; Garay et al., 2020; Argasinski and Rudnicki, 2020), see also Sherratt and Mesterton-Gibbons (2015) or Hinsch and Komdeur (2017) for recent reviews.

As noted in Hurd (2006), the game theoretical models of aggressive behavior are based on one of three distinct types of traits: (1) resource holding potential (RHP), the ability to win an all-out contest (Parker, 1974; Maynard Smith, 1982), (2) relative resource value, sometimes called motivation (Enquist, 1985; Bowler et al., 1986), and (3) aggressiveness, an individual’s tendency to escalate a contest independent of RHP and relative resource value effects (Maynard Smith and Harper, 1988).

Individual’s hunger is a substantial factor in determining the resource value (Janson and Vogel, 2006). The effect of hunger
on aggression in animals is complex (Whitehouse, 1997). There is evidence for hunger increasing overall aggressiveness even in contests for non-food items (Hazlett et al., 1975; Zack, 1975; Barnard and Brown, 1984; Erlandsson, 1988); and there is also evidence against it (da Silva Nunes and Jaeger, 1989). RHP is typically determined by body mass (Batchelor et al., 2012), body or body part size (Barlow et al., 1986), weapons (Palero and Briffa, 2017), contest experience (Mesterton-Gibbons et al., 2016), and certain behavioral (Rudin and Briffa, 2012) or physiological (Allen and Krofel, 2017) states. Hunger is often considered separately from RHP, see for example Pietraszewski and Shaw (2015). However, since hunger can determine the ability to win the contest, it makes sense to model hunger as RHP.

Our main goal is to examine the role of hunger in Owner–Intruder games. We expand on the model presented in Broom et al. (2014). We consider a scenario in which there is an Owner who is in possession of a resource that another individual, the Intruder, may want to steal. Both individuals exhibit certain levels of hunger that influence how they value the resource and how they are willing to fight for it (and consequently, how likely they will win the potentially aggressive contest). Similar to Bisen et al. (2020), we consider three different cases depending on whether the individuals are aware of the hunger level of their opponent. The full information case is the case in which both individuals are aware of their own hunger but not of the hunger of the opponent. And lastly, the no information case is when both parties are unaware of their own hunger as well as their opponent’s hunger.

The paper is organized as follows. In Section 2, we set up the basic model. In Section 3, we solve the game considering all three information cases. We discuss our findings, answer how potential scenarios would end using biological justifications, and investigate the differences between different scenarios. We conclude our paper with a discussion in Section 4.

2. Model

Similar to Broom et al. (2014) and Bisen et al. (2020), we model the conflict between the Owner and the Intruder as a sequential game in extensive form as shown in Fig. 1. The notation is summarized in Table 1.

The Owner is in possession of a resource when it spots an Intruder. The Owner has two options: (O1) it can flee the area which will result in the Intruder taking over the resource, or (O2) it can stay and defend the resource. In the latter case, the Intruder then has two options: (I1) to flee the area, or (I2) to attack the Owner. If the Intruder leaves, the Owner keeps the resource and no individual pays any cost. If the Intruder attacks, it results in a fight. The outcome of the fight depends on the hunger of the Owner, \( H_0 \), and the hunger of the Intruder, \( H_I \). The hunger determines how intensely either party will fight for the resource. Modeling hunger as RHP and following Dugatkin (1997) and Broom et al. (2014), we assume that the Owner wins the fight with probability \( \frac{H_0}{H_0 + H_I} \); the Intruder wins with probability \( \frac{H_I}{H_0 + H_I} \).

In the end, the winner will gain the resource and the loser will gain nothing. Both individuals will have to pay a cost \( c \) for the fight.

The value of the resource for an individual with hunger \( h \geq 0 \) is given by \( v(h) \). For illustrative purposes and to keep the situation similar to Broom et al. (2014), we consider functions \( v(h) = wh^x \) where \( w > 0 \) is an intrinsic value of the resource and \( x \geq 0 \) is a tuning parameter.

We will assume that both \( H_0 \) and \( H_I \) are independent identically distributed random variables. For illustrative and comparison purposes, we assume \( H_0 \) and \( H_I \) to be uniformly distributed on \([0, 6] \). We picked this support to be able to mimic the game with the dice role in the early stages of the research. Fig. 6 shows the results for log-normal distributions with varying parameters and the effect of the distribution is discussed in more details in Section 3.6.

As in Bisen et al. (2020), we will distinguish three cases: (1) the full information case when the Owner and the Intruder both know the values of \( H_0 \) and \( H_I \) (this case was essentially already considered in Broom et al. (2014)), (2) the partial information case when the Owner knows \( H_0 \), the Intruder knows \( H_I \), but neither individual knows the resource value for the opponent, and finally (3) the no information case when neither individual knows \( H_0 \) or \( H_I \). The individuals have the same choices (i.e. available actions) regardless of the information case; the Owner can either flee or defend and, if the Owner defends, the Intruder can either flee or attack. A pure strategy is the allocation of a choice for every vertex of the game. Specifically, in the no information case, a strategy for the Owner determines whether to defend or flee. A strategy for the Intruder determines whether to attack or flee in case the Owner defends. In full information case, the strategies will be functions of \( H_0 \) and \( H_I \). In the partial information case, the strategy of the Owner will be a function of \( H_0 \) (and the distribution of \( H_I \)) while the strategy of the Intruder will be a function of \( H_I \) (and the distribution of \( H_0 \)). We could consider mixed strategies, i.e. a probability distribution of all choices in a particular vertex; however, as noted in Broom and Rychtář (2013, Chapter 10) and seen below, the backward induction leads to a unique pure solution to the game in generic cases.

In this paper, the main solution concept will be a subgame perfect Nash equilibrium (Osborne, 2004; van Damme, 1991), i.e. a pair of strategies \((S_O,S_I)\) such that when \( S_O \) is adopted by the Owner and \( S_I \) by the Intruder, no individual will benefit by unilaterally changing their strategy at any vertex of the game, i.e. both individuals would behave optimally in all vertices (even those that theoretically should not be reached under the considered strategies). We will also be interested in the evolutionary stability of these equilibria. For the stability considerations, we will assume that all individuals will use \( S_O \) when in the Owner role and \( S_I \) when in the Intruder role; and we will study under which circumstances this population cannot be invaded by initially rare individuals using \((S'_O,S'_I) \neq (S_O,S_I)\), see for example Cressman (2003) and Broom and Rychtář (2013).

3. Analysis and results

We will analyze the Owner–Intruder game by using backward induction and find the subgame perfect Nash equilibrium, see for example Broom and Rychtář (2013, p. 187).

3.1. Full information case

In this section, we will assume, similar to Broom et al. (2014), that the Owner and the Intruder know \( H_0 \) and \( H_I \) and consequently the values of the items \( v(H_0) \) and \( v(H_I) \).

Assume that the Owner defends and now it is the Intruder’s turn to decide whether to flee or to attack. If the Intruder flees, it gets 0. If the Intruder attacks, it wins with probability \( H_I/(H_0 + H_I) \) and gets \( v(H_I) - c \) and it loses with probability \( H_0/(H_0 + H_I) \) and gets \(-c\). Thus, the average payoff to the Intruder (if attacking) is

\[
\frac{H_I}{H_0 + H_I}(v(H_I) - c) + \frac{H_0}{H_0 + H_I}(-c) = \left( \frac{H_I}{H_0 + H_I}v(H_I) \right) - c.
\]

(1)
The Intruder should attack only if the payoff for attacking is bigger than the payoff for fleeing, i.e. if

\[ \left( \frac{H_i}{H_0 + H_i} v(H_i) \right) - c > 0. \tag{2} \]

Now, we will investigate the options for the Owner. The Owner can either flee the area or defend the resource. If the Owner flees, it gets 0. If the Owner defends, its payoff depends on the action of the Intruder.

Case 1: Assume \( \left( \frac{H_i}{H_0 + H_i} v(H_i) \right) - c > 0 \). In this case, the Intruder attacks (if Owner defends) and thus the interaction results in a fight. The Owner wins the fight with probability \( \frac{H_0}{H_0 + H_i} \) and gets \( v(H_0) - c \). With probability \( \frac{H_i}{H_0 + H_i} \) the Owner loses and gets \(-c\). The average payoff to the Owner thus is

\[ \frac{H_0}{H_0 + H_i} (v(H_0) - c) + \frac{H_i}{H_0 + H_i} (-c) = \left( \frac{H_0}{H_0 + H_i} v(H_0) \right) - c. \tag{3} \]

The Owner should defend only if the payoff for defending is bigger than the payoff for fleeing, i.e. if

\[ \frac{H_0}{H_0 + H_i} v(H_0) - c > 0. \tag{4} \]

The Owner should flee otherwise.

Case 2: Assume \( \left( \frac{H_i}{H_0 + H_i} v(H_i) \right) - c < 0 \). In this case, the Intruder flees (if Owner defends). Thus, if the Owner defends, it gets \( v(H_0) \) which is clearly bigger than 0. Thus, the Owner should defend.

The results are summarized in Table 2.

3.1.1. Special case \( x = 0 \)

Let us now discuss the special case when \( x = 0 \). In this case, the value of the resource is \( v(h) = v_0 \), independent of the individual’s hunger. Based on the results from previous section, the Owner should defend if either

- \( \frac{H_i}{H_0 + H_i} < \frac{c}{v_0} \), in which case the Intruder will give up and the Owner will get the whole resource, or
- \( \frac{H_i}{H_0 + H_i} > \frac{c}{v_0} \) and \( \frac{H_0}{H_0 + H_i} > \frac{v_0}{v_0} \), in which case there will be a fight.

The situation is shown in Fig. 2.

Note that by adding \( \frac{H_i}{H_0 + H_i} > \frac{c}{v_0} \) and \( \frac{H_0}{H_0 + H_i} > \frac{v_0}{v_0} \), we get that there are fights only if \( 1 > \frac{2c}{v_0} \). If \( 1 < \frac{2c}{v_0} \) (or \( c > \frac{v_0}{2} \)), then there are no fights as either the Owner does not defend or the Intruder does not attack. This corresponds to a switch from the left panel of Fig. 2 (where \( c < \frac{v_0}{2} \)) to the right panel (where \( c > \frac{v_0}{2} \)).

The expected payoffs to the Owner and Intruder are shown in Fig. 5. Notice that the expected payoffs to the Owner increase sharply for \( c > \frac{v_0}{2} \) and eventually become \( v_0 \) when \( c > v_0 \). This is because for \( c \in (\frac{v_0}{2}, v_0) \), the Owner defends only when the Intruder is going to flee, i.e. only when \( \frac{H_i}{H_0 + H_i} < \frac{c}{v_0} \). Note also that the expected value of \( \frac{H_i}{H_0 + H_i} \) is \( 0.5 < \frac{v_0}{2} \). This means that the Intruder is not willing to fight as much and consequently, the Owner is willing to defend more often and get larger payoff on average.

For \( c \leq \frac{v_0}{2} \), the payoffs to the Owner and the Intruder are the same, see Fig. 5. The reason behind this is as follows (see the left panel of Fig. 2). The dark gray region is symmetrical: if it contains \( (H_1, H_0) \), it also contains \((H_0, H_1)\). The Owner and Intruder will
fight in both such cases. The Owner gets \( \frac{H_0}{H_0+H_I} v(H_0) - c \) in \((H_I, H_0)\) and \( \frac{H_I}{H_0+H_I} v(H_I) - c \) in \((H_0, H_I)\). The Intruder gets \( \frac{H_I}{H_0+H_I} v(H_I) - c \) in \((H_I, H_0)\) and \( \frac{H_0}{H_0+H_I} v(H_0) - c \) in \((H_0, H_I)\). Consequently, in the dark gray region, the Owner and the Intruder get the same on average. Also, for every point \((H_I, H_0)\) in the white region where the Owner gets \(v(H_0)\) and the Intruder gets 0, there is a point \((H_0, H_I)\) in the light gray region where the Intruder will be getting \(v(H_0)\) and the Owner gets 0. Consequently, they will get the same payoff in those two regions considered together.

When we take the average of the Owner’s payoff and add it to the average of the Intruder’s payoff, we get that \(v_0 - 2cA\) where \(A\) is the area of the dark gray region. This is because one of the individuals will always get the food item, and, inside of the dark gray area, they both pay the cost \(c\). So, when \(c < \frac{v_0}{2}\), the average payoff is \(\frac{v_0}{2} - c \frac{v_0 - 2c}{v_0 - c}\).

3.2. Partial information case

In this section, we assume that the Owner knows \(H_0\) but not \(H_I\) and the Intruder knows \(H_I\) but not \(H_0\). The Intruder will also know whether or not the Owner tried to defend the resource.

The Owner’s payoff when defending is given by

\[
\begin{dcases}
\frac{H_0}{H_0 + H_I} v(H_0) - c, & \text{if the Intruder decides to attack,} \\
v(H_0), & \text{if the Intruder decides to flee.}
\end{dcases}
\]

Similarly, the payoff to the Intruder when the Owner defends and the Intruder attacks is given by

\[
\frac{H_I}{H_0 + H_I} v(H_I) - c.
\]

Table 2

<table>
<thead>
<tr>
<th>Condition(s)</th>
<th>Subgame perfect Nash equilibrium</th>
</tr>
</thead>
<tbody>
<tr>
<td>(H_I \left( \frac{v_0}{c} - 1 \right) &lt; H_0)</td>
<td>The Owner defends, the Intruder flees</td>
</tr>
<tr>
<td>(H_I \left( \frac{v_0}{c} - 1 \right) &gt; H_0) and (H_0 \left( \frac{v_0}{c} - 1 \right) &gt; H_I)</td>
<td>The Owner defends, the Intruder attacks</td>
</tr>
<tr>
<td>(H_I \left( \frac{v_0}{c} - 1 \right) &gt; H_0) and (H_0 \left( \frac{v_0}{c} - 1 \right) &lt; H_I)</td>
<td>The Owner flees, the Intruder would attack</td>
</tr>
</tbody>
</table>

Fig. 2. Behavioral outcomes in the full information case when \(x = 0\) and \(\frac{v}{c} = 3 > 2\) (left) and \(1 < \frac{v}{c} = 1.5 < 2\) (right). When \(c \approx 0\), the dark gray region takes most of the quadrant. As \(c\) increases, the dark gray region becomes thinner and thinner and eventually disappears at \(c = \frac{v}{c}\). When \(c > \frac{v}{2}\), the figure looks like the right panel. The light gray region disappears for \(c = v_0\), and, for \(c > v_0\), the Owner always defends and the Intruder always flees.

First, note that the equilibrium strategies have to be of special kind. The functions \(v(h) = v_0h^x\) and \(g(h) = \frac{h}{x+1}v(h)\) are non-decreasing in \(h\) (for every \(x \geq 0\) and every \(H_I \geq 0\)). Consequently, for all values of \(H_I\) and regardless whether the Intruder attacks or not, the Owner’s payoff is increasing in \(H_0\). Thus, if it is better for the Owner to defend when his hunger is \(H_0\), it is better for the Owner to defend when his hunger is \(H_I' > H_0\). Thus, the optimal Owner’s strategy is given by \(s_0\) such that the Owner will defend whenever \(H_0 \geq s_0\) and flees whenever \(H_0 < s_0\).

Similarly, the optimal strategy for the Intruder is given by \(s_I\) where the Intruder attacks whenever \(H_I \geq s_I\) and flee whenever \(H_I < s_I\).

Let us now calculate the expected payoffs to the Owner and Intruder when they use strategies \(s_0\) and \(s_I\), respectively. We will denote such payoffs \(P^{\text{O}}_0(s_0, s_I)\) and \(P^{\text{I}}_I(s_0, s_I)\), respectively.

We will consider several distinct cases of specific values \(H_0\) and \(H_I\) to get the formulas for the expected payoffs.

When \(H_0 < s_0\), i.e. with probability \(s_0/6\), the Owner flees and gets 0 (while the Intruder gets \(v(H_I)\)). When \(H_0 \geq s_0\), the Owner will defend. When \(H_I < s_I\), i.e. with probability \(s_I/6\), the Intruder will flee, i.e. get 0 while the Owner will get \(v(H_0)\). When \(H_I > s_I\), the Intruder will attack. In this case, the Owner gets
\[ P^I_0(s_0, s_1) = s_1 \int_0^6 v(H_0) dH_0 + \int_0^6 \int_{s_0} (\frac{H_0}{H_0 + H_1} v(H_0) - c) \times \frac{dH_1 dH_0}{6} \] 

\[ P^I_1(s_0, s_1) = s_0 \int_0^6 v(H_1) dH_1 + \int_0^6 \int_{s_0} (\frac{H_1}{H_0 + H_1} v(H_1) - c) \times \frac{dH_1 dH_0}{6} \]  

In particular, for the simplest case \( x = 0 \), i.e. \( v(h) = v_0 \), we get that

\[ P^I_1(s_0, s_1) = v_0 s_0 - (6 - s_0)(6 - s_1) c + \frac{1}{36} \int_0^6 H_1(\ln(6 + H_1) - \ln(s_0 + H_1)) dH_1. \]

While one can express the payoff in closed formulas, the expressions are too complicated. Also, it follows from (9) that given \( s_0 \), the intruder’s best strategy is to pick \( s_1 \) such that \( (6 - s_0)x = s_1(\ln(6 + s_1) - \ln(s_0 + s_1)) \). While there is such a value of \( s_1 \), it cannot be easily expressed in a closed formula. Consequently, we will focus on numerical simulations. We will fix \( v_0 \) and \( x \), i.e. consider a specific function \( v(h) = v_0 h^s \). We can then find the individual’s best response to the opponent’s strategy. Given the owner’s strategy \( s_0 \), we can find the intruder’s best strategy \( s_1 = s_1(s_0) \) that maximizes the intruder’s payoff. Also, given the intruder’s strategy \( s_1 \), we can find the owner’s best strategy \( s_0 = s_0(s_1) \) that maximizes the owner’s payoff. The best response strategies are shown in Fig. 3.

Fig. 3 illustrates that the best response for the owner is a non-increasing function of \( s_1 \) and, conversely, the best response for the intruder is a non-decreasing function of \( s_0 \). This seemingly paradoxical situation can be explained as follows. The less the intruder wants to attack (i.e. the larger the value of \( s_1 \)) is the more the owner wants to defend (i.e. the smaller the value of \( s_0 \)). If the intruder’s willingness to attack decreases, the defending owner will get the resource without fighting more frequently, making it beneficial for the owner to be more inclined to defend. At the same time, the less the owner wants to defend, the less the intruder wants to attack. As \( s_0 \) increases, the owner will defend only for higher values of hunger which makes him more likely to win the potential fight. Consequently, the intruder will want to enter the fights less often (only when sufficiently hungry itself).

We can find the subgame perfect Nash equilibrium (as a point where the graphs of the best responses cross), i.e. a pair of strategies that when adopted, no individual can improve its payoff when unilaterally deviating from its strategy. The subgame perfect Nash equilibria are shown in Fig. 4. We can see that the intruder is always willing to attack less than the owner wants to defend. Moreover, as the cost of the fights increases, the subgame perfect Nash equilibrium value of \( s_1 \) increases until it reaches the maximal value, i.e. the willingness of the intruder to attack decreases until it eventually does not attack at all. However, as \( c \) increases, the subgame perfect Nash equilibrium value of \( s_0 \) increases at first, but then decreases and eventually becomes 0, i.e. the willingness of the owner to defend decreases at first but then the owner wants to defend more and more and eventually it defends all resources.

### 3.3. No information case

In this section, we consider the case where neither the owner nor the intruder know the values of \( H_0 \) and \( H_1 \). We can thus reconsider the game and reformulate it as a normal game with two pure strategies for the owner: (1) to defend all the time (corresponding to \( s_0 = 0 \)) and (2) never defend (corresponding to \( s_0 = 6 \)). If the owner defends, the two intruder’s pure strategies are (1) to attack all the time (corresponding to \( s_1 = 0 \)) or (2) never attack (corresponding to \( s_1 = 6 \)). If the owner does not defend, the intruder will get the resource. To be able to see the game in the matrix form, we will assume that the intruder gets the resource regardless whether it attacks or not.

More specifically, when the owner does not defend, it will always get 0 while the intruder gets

\[ \frac{1}{6} \int_0^6 v(H_1) dH_1 = \frac{v_0 b^x}{x + 1}. \]

Similarly, when the owner defends but the intruder does not attack, the owner gets \( \frac{v_0 b^y}{x + 1} \) and the intruder gets 0.

In the case when \( x = 0 \), the individuals play the following matrix game

<table>
<thead>
<tr>
<th>Attack</th>
<th>Not attack</th>
</tr>
</thead>
<tbody>
<tr>
<td>Owner</td>
<td>Intruder</td>
</tr>
<tr>
<td>Defend</td>
<td>((\frac{w}{2} - c, \frac{w}{2} - c))</td>
</tr>
<tr>
<td>Not defend</td>
<td>((0, v_0))</td>
</tr>
</tbody>
</table>

It follows that when \( \frac{w}{2} < c \), the owner should defend and the intruder should not attack (if the owner defends, the intruder can get either \( \frac{w}{2} - c < 0 \) if attacking or 0 when not attacking). When \( \frac{w}{2} > c \), the owner should defend and the intruder should attack (if the owner does not defend, it gets 0; if it defends, it gets either \( \frac{w}{2} - c > 0 \) or \( v_0 > 0 \)). The precise equality \( \frac{w}{2} = c \) is unlikely and yields a non-generic game, see for example Broom and Rychtář (2013). Nevertheless, when \( \frac{w}{2} = c \), the owner may benefit from defending. Indeed, if the owner does not defend, it gets 0. However, when it defends, it can get 0 if the intruder attacks or \( v_0 \) if the intruder does not attack (and since the intruder gets 0 when attacking or when not attacking, the intruder has no strong preference for either action).

In general, the payoff matrix of the game is given in Box I.

It follows that the owner should always defend. Indeed, as in the case where \( x = 0 \), there are three options.

1. \( P^O_0(0, 0) = P^P_0(0, 0) > 0 \),
2. \( P^O_0(0, 0) = P^P_0(0, 0) < 0 \), and
3. \( P^O_0(0, 0) = P^P_0(0, 0) = 0 \).

In the first case, the owner should defend and the intruder should attack. In the second case, the owner should defend and the intruder should not attack. Finally, in the third case, the owner may benefit by defending because in that case, the intruder may choose not to attack.

### 3.4. ESS analysis and a comparison to the original Owner–Intruder game

Let us start by the no information case as this scenario most readily compares to the original Owner–Intruder game (Maynard Smith, 1982, Chapter 8) where the owner and the intruder had to make simultaneous rather than sequential choices.

The pair (Defend, Attack), i.e. be aggressive as the owner and as the intruder, corresponds to Hawk in the original game. In the simultaneous decisions, Hawk is an ESS when \( P^O_0(0, 0) \geq 0 \) (Broom and Rychtář, 2013, Chapter 8). In our sequential version,
Fig. 3. Best responses in the partial information case. In both figures, $v_0 = 1$, $c = 1$. Left $x = 0$, right $x = 1$.

Fig. 4. Subgame perfect Nash equilibria in partial information case. Left: $x = 0$, $v_0 = 1$, right $x = 1$, $v_0 = 1$.

<table>
<thead>
<tr>
<th>Owner</th>
<th>Intruder</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defend</td>
<td>Attack $P^O_0(0, 0), P^P(0, 0)$</td>
</tr>
<tr>
<td>Not defend</td>
<td>$(0, \frac{v_0 x}{x+1})$</td>
</tr>
</tbody>
</table>

with

$$P^O_0(0, 0) = P^P_t(0, 0) = \int_0^0 \int_0^0 \left( \frac{H_0}{H_0 + H_t} v(H_0) - c \right) \frac{dH_t dH_0}{6}.$$  \hspace{1cm} (12)

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Box I.

when $P^O_0(0, 0) \geq 0$, it is a subgame perfect Nash equilibrium as seen in Section 3.3. To see that it is also an ESS when $P^P_0(0, 0) > 0$, consider the following. If initially rare mutants do not defend as the Owners, the mutant Owners will get $0$ which is smaller than the payoff $P^O_0(0, 0)$ of the resident Owners. Similarly, if initially rare mutants do not attack as the Intruders, the mutant Intruders will get $0$ which is smaller than the payoff $P^P_0(0, 0)$ of the resident Intruders.

The pair (Defend, Not Attack), i.e. be aggressive as the Owner and non-aggressive as the Intruder corresponds to Bourgeois in the original Owner–Intruder game. When $P^P_0(0, 0) < 0$, this pair is an ESS in the original game and a subgame perfect Nash equilibrium in our sequential game. To see that it is also an ESS in the sequential game, consider the following. If the initially rare mutants do not defend as Owners, the mutant Owners get $0$ which is smaller than the payoff $P^O_0(0, 0)$ of the resident Owners. Similarly, if the initially rare mutants do attack as the Intruders, the mutant Intruders get $P^P_0(0, 0) = P^O_0(0, 0)$ which is smaller than $0$, the payoff of the resident Intruders.

We note that the pair (Flee, Attack), i.e. be non-aggressive as the Owner but aggressive as in Intruder corresponds to Strategy X, later called Marauder (Broom et al., 2004) in the original Owner–Intruder game. When $P^P_0(0, 0) < 0$, Marauder is an ESS in the original version. It is also a Nash equilibrium in the sequential version. Indeed, since the Owner does not defend, the Intruder gets $v_0$ regardless their strategy, but if the Owner switched to
defending, the Owners payoff would become negative. However, this is not a subgame perfect Nash equilibrium because the Intruders do not behave optimally in the case the Owner defends. Moreover, this pair is not an ESS in the sequential version. A strategy (Flee, Flee) which corresponds to Dove in the original Owner–Intruder game is indistinguishable from the Marauder strategy — the difference would be visible only if Owners defended but they never do. Consequently, in our sequential game, Doves do equally well as the Marauders and the Marauders can thus be invaded by Doves.

Let us now consider the full information case. If the subgame perfect Nash equilibrium contains a region of \( H_0 \) and \( H_I \) where the Owners should flee (this happens for example when \( c \) is small), the equilibrium is not stable. Indeed, such a strategy could be seen as playing Marauder for some values of \( H_0 \) and \( H_I \). Similarly as discussed above, such a population could be invaded by mutants that play Doves instead of Marauder for those values but are identical to the resident population otherwise. However, if the subgame perfect Nash equilibrium strategy does not contain any Marauder-type behavior, then it is also stable as any deviation from the optimal action means a lower payoff against the resident strategy.

Finally, similarly to the above reasoning, in the partial information case, the subgame perfect Nash equilibrium with \( s_O > 0 \) (i.e. when the Owner does not defend all the time) is not stable. Again, such individuals are playing Marauder-like behavior for some values of \( H_0 \) which could be invaded by a strategy that adopts a Dove-like behavior for those values and is same otherwise. However, when \( s_O = 0 \), such an equilibrium is evolutionary stable.

### 3.5. Comparisons between different information states

The payoffs to the Owner and Intruder playing the subgame perfect Nash equilibria are illustrated in Fig. 5. We can see that the Intruder’s payoff is always maximal in the full information case and minimal in the no information case. The situation for the Owner is more complicated. When the cost of the fight is small, the full information case is best and the no information case is worst. As \( c \) grows, there is a discontinuity in the Owner’s payoff in the no information case and, for some values of \( c \), the no information yields the maximal payoff and the partial information case the minimal payoff. As \( c \) grows even more, both the no information case and the partial information case yield the maximal payoff and the full information case yields the smallest payoff.

### 3.6. The effect of an underlying distribution

The outcomes of the game for various underlying distributions of hunger levels are shown in Fig. 6. We used log-normal distributions with a shape \( a = 1 \) and varying rate \( b \in \{1/3, 1, 3\} \). We truncated the hunger levels to the interval \([0, 6]\). As \( b \) grows, the distribution of hunger levels becomes more bi-modal. These
changes have a relatively small effect on the best responses in the partial information case. With the increasing $b$, the best response to a relatively aggressive strategy is becoming slightly more aggressive (for example, as seen in Fig. 6 second row, the Owner’s best response slightly decreases with $b$ for small $s_I$). At the same time, the best response to a less aggressive strategy is to become less aggressive (for example, as seen in Fig. 6 second row, the Owner’s best response increases with $b$ for medium and large $s_I$). With increasing $b$, the subgame perfect Nash equilibrium is less aggressive for medium and large fight costs and slightly more aggressive for small fight costs.

The distribution has only a minimal effect on the payoffs in the no information case. In all information cases, the Intruder’s payoff increases with increasing $b$. As the fight cost increases, there is a discontinuity in the Owner’s payoff in the no information case. This discontinuity appears for larger $b$ even in the full and the
In this paper, we developed a model to investigate kleptoparasitic interactions when hunger is a factor which influences not only how the individuals value resources, but also how likely they are to win a potential conflict. We distinguished three separate scenarios: (1) the full information case when individuals know their own hunger as well as the hunger of their opponent, (2) the partial information case when the individuals know the hunger value for themselves but not their opponents, and (3) the no information case when the individuals do not know any hunger values at all. For each information case, we determined when it is optimal for the Owner to defend their resource and for the Intruder to attack.

We saw that the Owner benefits most when the cost of the fight is relatively high. In this case, the Intruder will not risk the fight and with the Owner knowing this, they will decide to bluff and defend the resource.

When the cost of the fight is relatively low, the Owner benefits from knowing as much as possible. The Intruder prefers the full information case over the partial information case which in turn is better than the no information case. However, when the cost of the fights is neither too small nor too large, the Owner does best in the no information case.

Our model predictions seem to agree with actual experiments and previous work. Small food items are defended by semiaquatic bug Veila caprai (Erlandsson, 1988); this corresponds to Owner defending items of small value, i.e. when the cost of the fight is relatively large. Similarly, García et al. (2010) found that more valuable items triggered higher rate of Intruder’s attacks. At the same time, contests in nature are frequently won by the animal with the higher resource holding potential (Mesterton-Gibbons et al., 1996).

The distinction amongst the three scenarios is an extension of the model in Bisen et al. (2014). They considered only what we call here the full information case. Our model also extends the model presented in Bisen et al. (2020). They considered variable value of the resources and the three different information cases, but the probability to win an aggressive constant was a fixed parameter. We model hunger as RHP and consider that the hunger level influences not only the value of the resource but also the probability of winning the contest. This variable probability to win caused larger differences between the full and the partial information cases than what was observed in Bisen et al. (2020). Moreover, here we saw that the Owner’s payoff may be larger in the partial information case than in the full information case; whereas when the winning probability is constant as in Bisen et al. (2020), the Owner’s payoff in the full information case is always at least as large as in the partial information case. Also in our model the Owner always defends in the no information case, but will flee for intermediate fight costs in the Bisen et al. (2020) model.

This non-existence of Marauder behavior in the no information case also distinguishes our no information case from the original simultaneous Owner–Intruder game considered in Maynard Smith (1982). Marauder’s strategy is a common outcome of many game-theoretical models, although it is rarely observed in nature, see for example Broom and Rychtář (2007) and Broom et al. (2008a). While Marauder-like behavior is still an equilibrium in our model in the partial or full information cases, the regions of such a behavior are generally small, similarly to what was observed in Broom et al. (2008b). Perhaps more importantly, strategies with Marauder-type behavior are not stable in our model, possibly offering an insight why the Marauder strategy is not overly common in nature.

We assumed no correlation between the hunger levels. However, environmental factors may cause a positive correlation and our model can be extended by incorporating this correlation. If the hunger levels are positively correlated, the probability to win a fight would be more or less constant, i.e. the situation would be similar to a scenario investigated in Bisen et al. (2020) yet with correlated and potentially unknown resource values. Such a scenario was considered in Bukina et al. (2020) who found that (a) the correlation does not affect the Intruder and (b) the Owner would benefit from a larger correlation when their hunger is small (because in this case the Intruder would give up) and benefits from a no correlation when their hunger is large (because otherwise the Intruder would almost certainly be also hungry and thus try to fight). Even if the hunger levels are uncorrelated, it may also be plausible to assume that the distribution of the hunger values for the Owners is different than the distribution for the Intruders. If the Owners are assumed to be overall less hungry than the Intruders, a Marauder-like behavior may re-emerge from the model.

Our model can be extended further by more detailed considerations of how hunger levels influence outcomes of the fights. While the hungriest individual may be more determined to win, it is conceivable that once the hunger is above a certain threshold, the probability to win the fight decreases with increasing hunger, i.e. the hunger can have both a positive and negative influence effect on the outcome of the conflict.

4. Conclusions and discussion

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Declaration of competing interest

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