Chapter 13 The Effect of Information on Payoff in Kleptoparasitic Interactions

Mark Broom, Jan Rychtář, and David G. Sykes

13.1 Introduction

Kleptoparasitism, the stealing or attempted stealing of resources (usually food), is a very common behavior practiced by a very diverse collection of species such as insects [14], fish [12], birds [16–18], and mammals [15]. For a recent review paper with complete classification and numerous examples, see [13].

The strategies associated with stealing interactions can vary; for instance, sometimes resources are promptly forfeited while in other cases the individuals defend the resources vigorously and even engage in fights.

The effect of variation in resource value on fighting behavior was investigated in detail in [11], who used a simulation model to investigate a situation where a resource owner possesses information about the (subjective) value of a resource that an individual attempting to steal it may or may not have, using a sequential assessment game. Their model predictions included that the resource owner's probability of victory would increase with increasing resource value, based partly upon the extra knowledge that the owner had (but see [5]), and that costs and contest duration will also increase with resource value.

However, in most models, see, for example, [2, 4, 6] and references therein, the individuals value the resource equally even when the resources can differ in value

M. Broom (🖂)

J. Rychtář • D.G. Sykes

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

Department of Mathematics and Statistics, The University of North Carolina at Greensboro, Greensboro, NC 27402, USA e-mail: rychtar@uncg.edu; dgsykes@uncg.edu

J. Rychtář et al. (eds.), *Topics from the 8th Annual UNCG Regional Mathematics and Statistics Conference*, Springer Proceedings in Mathematics & Statistics 64, DOI 10.1007/978-1-4614-9332-7_13, © Springer Science+Business Media New York 2013

such as in the situations investigated in [3, 5]. The variation in value can be caused by external factors such as the size of the food item; however, it can be caused by an internal state (such as hunger) of the individuals [11].

As soon as there is a difference between individuals in resource valuation, several informational situations arise. Firstly, when individuals are aware of their own as well as their opponent's valuation. Secondly, when individuals are aware only of their own valuation. Thirdly, when individuals are not aware even of their own valuation.

A common way to model kleptoparasitic interactions is the so-called producerscrounger game developed in [1]. A number of variants of this model have been developed to consider different circumstances and assumptions (see, for example, [8–10, 19]). One advantage of this type of model is that analysis is relatively straightforward, so that clear predictions can be made. Here, we consider a scenario where one individual, a producer, possesses a valuable resource when another individual, a scrounger, comes along and may attempt to steal it.

13.2 The Model

We model the situation of a scrounger discovering a producer with a resource as a sequential game in extensive form as shown in Fig. 13.1. If the scrounger makes such a stealing attempt, then the producer can either give up the resource without any conflict or defend it. The conflict cost is c and the producer wins the conflict (and can keep the resource) with probability a.

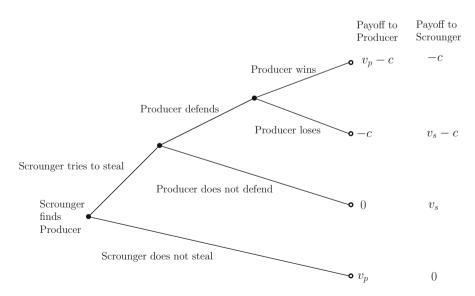


Fig. 13.1 Scheme and payoffs of the game

Let us denote the value for the scrounger as v_s , and the value for the producer as v_p . We assume that the distributions of v_s and v_p are the same. The game and the payoffs from different scenarios are shown in Fig. 13.1.

13.3 Analysis

We will analyze the game using backward induction, see, for example, [7, p. 187].

13.3.1 Full Information Case

Here we assume that individuals know the resource values for themselves as well as for their opponents. Assume that the scrounger attempts to steal. The producer has to decide whether to defend or not. If the producer does not defend, the payoff will be 0. If the producer defends, individuals will fight and the producer will lose it with probability 1 - a. Hence, the producer's expected payoff when defending is $av_p - c$. Consequently, the producer should defend only if $0 < av_p - c$ which is equivalent to

$$\frac{c}{a} < v_p. \tag{13.1}$$

Note that the producer does not need to know the value of the resource for the scrounger. All that is relevant to the producer is the fact that the scrounger attempted to steal and then the producer can evaluate the payoffs to itself.

Now, we will investigate the options for the scrounger, assuming it knows v_p . If the scrounger does not attempt to steal, the payoff will be 0. If (13.1) does not hold, then the producer will not defend against a stealing attempt and thus the scrounger should attempt to steal to get a payoff $v_s > 0$. If (13.1) holds, then the producer will defend against the stealing attempt. Hence, if the scrounger attacks, it will lose with probability a (and get a payoff -c) and win with probability 1 - a (and get a payoff $v_s - c$). The expected payoff is thus $(1 - a)v_s - c$. Hence, the scrounger should attack if

$$(1-a)v_s - c > 0 \tag{13.2}$$

which is equivalent to

$$\frac{c}{1-a} < v_s. \tag{13.3}$$

There are thus three distinct behavioral patterns as presented in Table 13.1 and Fig. 13.2.

Behavioral outcome Scrounger Producer		Condition for full information		Condition for partial information		Condition for no information	
steals	defends	v_s	v_p	Vs	v_p	E[v]	
Yes	No	any	$v_p < \frac{c}{a}$	$v_s > \frac{c\pi}{1-a\pi}$	$v_p < \frac{c}{a}$	$E[v] < \frac{c}{a}$	
No	Yes	$v_s < \frac{c}{1-a}$	$v_p > \frac{\ddot{c}}{a}$	$v_s < \frac{c\pi}{1-a\pi}$	any	$E[v] < \frac{c}{1-a}$	$E[v] > \frac{c}{a}$
Yes	Yes	$v_s > \frac{c}{1-a}$	$v_p > \frac{c}{a}$	$v_s > \frac{c\pi}{1-a\pi}$	$v_p > \frac{c}{a}$	$E[v] > \frac{c}{1-a}$	$E[v] > \frac{c}{a}$

Table 13.1 Summary of the results

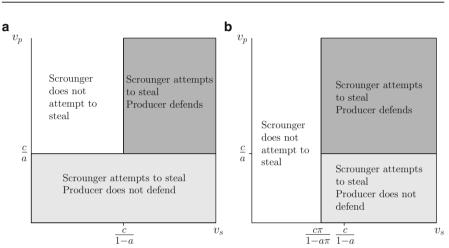


Fig. 13.2 Behavioral outcomes of the game for the same parameter values c and a but different information cases. (a) Full information case, (b) Partial information case. We note that π actually depends on c, and if c is large enough, $\pi = 0$ i.e., the white region can disappear

13.3.2 Partial Information Case

Now, assume that the scrounger knows the value v_s and the distribution of v_p (which is assumed to be the same as distribution of v_s ; in particular, it does not depend on the value of v_s), but does not know the exact value of v_p . Consequently, the scrounger does not know for sure whether the producer will defend. However, it is still true that the producer will defend if $\frac{c}{a} < v_p$. From the scrounger's perspective, the producer will thus defend with a probability $\pi = \text{Prob}(\frac{c}{a} < v_p)$. If the producer does not defend, the payoff to the scrounger will be v_s . If the producer defends, the payoff to the scrounger will be $(1 - a)v_s - c$. Hence, if the scrounger attempts to steal, his payoff will be

$$(1-\pi)v_s + \pi((1-a)v_s - c) = v_s(1-a\pi) - c\pi.$$
(13.4)

If the scrounger does not attempt to steal, its payoff will be 0. Hence, the scrounger should attempt to steal if

$$v_s > \frac{c\pi}{1 - a\pi}.\tag{13.5}$$

There are thus three behavioral patterns as presented in Table 13.1 and also in Fig. 13.2.

13.3.3 No Information Case

The analysis in the no information case is actually very similar to the full information case. The only difference is that the individuals do not know the exact value of the resource, but they do know the expected values, $E[v_p]$ and $E[v_s]$. Since we assume that the distributions of v_p and v_s are the same, we have $E[v_p] = E[v_s]$ and we will denote it just by E[v]. There are thus three distinct behavioral patterns as presented in Table 13.1.

13.4 Comparison Between Different Information Cases

The illustrative comparison is shown in Fig. 13.3 in the case where the values v_s and v_p have uniform distribution between v_{\min} , v_{\max} and are independent.

13.4.1 Comparison Between the Full and Partial Information Cases

Since the function $f(x) = \frac{cx}{1-ax}$ is increasing in x and $0 \le \pi \le 1$, we get that

$$\frac{c}{1-a} \ge \frac{c\pi}{1-a\pi} \tag{13.6}$$

with equality only if $\pi = 1$.

For now, let us consider that $\pi \in (0, 1)$. It follows from (13.3), (13.5), and (13.6) that when $v_s > \frac{c}{1-a}$, the scrounger steals regardless of v_p and thus the scrounger's expected payoff (given any distribution of v_p for the producer) is the same in the full information and partial information cases.

On the other hand, if $v_s < \frac{c\pi}{1-a\pi}$ (which is possible only if $\pi > 0$), then the scrounger does not steal in the partial information case, leaving it with the payoff 0. However, if the scrounger knew v_p , it would steal if

$$v_p < \frac{c}{a} \tag{13.7}$$

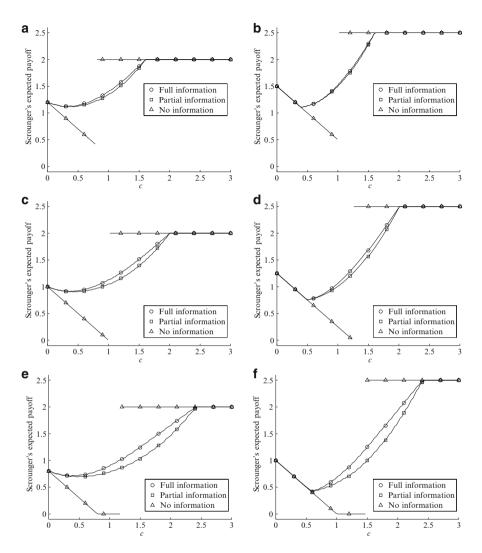


Fig. 13.3 The Scrounger's payoffs for varying cost of the fight *c*, different distribution of *v* and different values of *a* in three different information scenarios. (**a**) a = 0.4, *v* uniformly distributed in [0, 4], (**b**) a = 0.4, *v* uniformly distributed in [1, 4], (**c**) a = 0.5, *v* uniformly distributed in [0, 4], (**d**) a = 0.5, *v* uniformly distributed in [1, 4], (**e**) a = 0.6, *v* uniformly distributed in [0, 4], (**f**) a = 0.6, *v* uniformly distributed in [1, 4]

and in those cases the scrounger's payoff would be v_s . When $\pi < 1$, the distribution of v_p is such that (13.7) is satisfied with positive probability $1 - \pi$, and thus the expected payoff to the scrounger in the full information case is positive (i.e., larger than the expected payoff in the partial information case, which is 0).

It remains to investigate the values v_s such that $\frac{c\pi}{1-a\pi} < v_s < \frac{c}{1-a}$. For such v_s , if v_p is such that (13.7) holds, then the payoff to the scrounger is v_s and the payoff in the full information and partial information cases are the same. However, if v_p is such that (13.7) does not hold, then, by (13.3), the expected payoff to the stealing scrounger is negative.

Hence, overall, the expected payoff for the scrounger (given the distribution of v_p) in the full information case is larger than in the partial information case. One can also see that as *a* increases, the advantage of the full information case gets larger.

It remains to investigate the cases of $\pi = 0$ and $\pi = 1$. It turns out that in such cases, the expected payoffs for the scrounger are the same. If $\pi = 0$, then c is always larger than av_p and so the Scrounger always steals and the producer never defends. If $\pi = 1$, then c is always smaller than av_p , i.e., the producer always defends and the scrounger behaves the same way in both cases.

13.4.2 Comparison Between the No Information Case and the other Cases

Let $c_0 = \inf \{c; Prob(\frac{c}{a} < v_p) = 0\}$ and $c_1 = \sup \{c; Prob(\frac{c}{a} < v_p) = 1\}$. When $c > c_0$, then $\pi = 0$ and also $\frac{c}{a} > E[v]$. Hence, in any scenario, the scrounger steals and the producer does not defend. Consequently, the expected payoff to the scrounger is the same in all information cases.

When $aE[v] < c < c_0$, the no information case is better for the scrounger than the full information case (which is better than the partial information case). Indeed, in the no information case, the scrounger attempts to steal and the producer always gives up, leaving the scrounger with the expected payoff v_s which it cannot get for any other scenario (since now $\pi > 0$ and hence there is a positive probability of having $v_p > \frac{c}{a}$).

When (1 - a)E[v] < c < aE[v], the scrounger does not attempt to steal, getting a payoff of 0. This is worse for the scrounger than in the partial information case (the scrounger attempts to steal there for some values, sometimes receiving a free resource, and still gets a positive payoff even when the producer defends) which is worse than in the full information case.

When $c_1 < c < \min\{a, (1-a)\} E[v]$, then in the no information case, the scrounger always attempts to steal and the producer always defends. This is worse for the scrounger than in the partial information case (which is worse than the full information case) since there are items that are not worth fighting for.

When $c < c_1$, then the expected payoffs in all information cases are the same, since the Scrounger always steals and the Producer always defends.

13.4.3 Summary

The amount of information available has no effect on the payoff to the scrounger when the cost of the fight is relatively small (i.e., when $c < c_1$ so that then it is beneficial to fight for any item under any informational situation) or relatively large (i.e., when $c > c_0$ so that for the producer it is not beneficial to fight for any item under any informational situation). For intermediate costs $c \in (c_1, c_0)$, having full information is better than having only partial information. Moreover, if c < aE[v], then the no information case yields even lower payoffs; and when c > aE[v], then the no information case yields the largest expected payoff.

It is clear that the variance of the resource values has a strong influence on our results. If this variance is small, then c_0 and c_1 will be close together and the intermediate region where behavior differs between the cases is small. Note that if the variance is actually zero, then there is no useful information to be had and the three cases are identical. For large variance, the intermediate region may account for all plausible cases, and the models will yield significantly different results.

13.5 Discussion

In this paper we investigated the effect of information on the payoffs of a producerscrounger game. One would be tempted to argue that having more information would yield larger payoffs and this was indeed the case for a scrounger having full information versus one with only partial information in the model described by this paper; and, for some parameter values, also the case of no information versus full or partial information case.

However, having more information is not always better. The no information case, where an individual does not know the real value of the resource, is for some parameter values the best case for the scrounger. Yet, let us point out that although this was called the no information case, the scrounger has in fact a very valuable piece of information—the scrounger knows that the producer does not know the real value either, and consequently knows whether it will fight a stealing attempt.

We note that the fact that knowing less is sometimes better has already been observed before. In [5], the authors investigate a scenario in which the value of the resource is the same for both the producer and the scrounger, but nevertheless the resource value is variable and either both the producer and the scrounger know the value, or only the producer knows it. When the scrounger knows the value of the resource, its expected payoffs are lower than when he does not know it. Also, in [7, p. 364], the authors discuss a Producer–Scrounger game that is similar to the one described here, yet again, knowing seemingly less yields larger payoffs for the scrounger.

We also note that in Fig. 13.3 we have assumed that the values of v_s and v_p are independent. The relationship between the two is particularly important in the

partial information case, where knowledge of v_s may provide the scrounger with information about v_p , and so affect π . Independence of resource valuation is actually one extreme of a spectrum, the other end of which is complete coincidence of the two. The former is more plausible when the valuation is based on hunger; then at least in the first approximation, the fact that one individual is hungry does not give any new information about its opponent, so that the assumption of independence is reasonable in this case. However, it is also true that if one individual is hungry, then it may be largely because there is not much food around and the same will be true for its opponent. Thus the correlation between the resource values may be important.In this case the latter is more plausible, and this will also be the case if food items vary in size.

Finally, the variance of the resource value will also have a significant effect on our results. For low variance the models mainly coincide, but for high variance their predictions can be very different. It is the variability of the resource value which makes the possession or lack of information important, and the combination of variability in the value of the resource and the availability of information which makes this model an interesting one to study.

Acknowledgments The research was supported by NSF grants DMS-0850465 and DBI-0926288, Simons Foundation grant 245400 and UNCG Undergraduate Research Award in Mathematics and Statistics.

References

- 1. Barnard, C.J., Sibly, R.M.: Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim. Behav. **29**(2), 543–550 (1981)
- Broom, M., Luther, R.M., Ruxton, G.D.: Resistance is useless? Extensions to the game theory of kleptoparasitism. Bull. Math. Biol. 66(6), 1645–1658 (2004)
- Broom, M., Ruxton, G.D.: Evolutionarily stable kleptoparasitism: consequences of different prey types. Behav. Ecol. 14(1), 23 (2003)
- Broom, M., Rychtář, J.: The evolution of a kleptoparasitic system under adaptive dynamics. J. Math. Biol. 54(2), 151–177 (2007)
- Broom, M., Rychtář, J.: A game theoretical model of kleptoparasitism with incomplete information. J. Math. Biol. 59(5), 631–649 (2009)
- Broom, M., Rychtář, J.: Kleptoparasitic melees modelling food stealing featuring contests with multiple individuals. Bull. Math. Biol. 73(3), 683–699 (2011)
- 7. Broom, M., Rychtář, J.: Game-Theoretical Models in Biology. CRC, Boca Raton (2013)
- Caraco, T., Giraldeau, L.A.: Social foraging: producing and scrounging in a stochastic environment. J. Theor. Biol. 153(4), 559–583 (1991)
- Dubois, F., Giraldeau, L.A.: Fighting for resources: the economics of defense and appropriation. Ecology 86(1), 3–11 (2005)
- Dubois, F., Giraldeau, L.A., Grant, J.W.A.: Resource defense in a group-foraging context. Behav. Ecol. 14(1), 2 (2003)
- Enquist, M., Leimar, O.: Evolution of fighting behaviour: the effect of variation in resource value. J. Theor. Biol. **127**(2), 187–205 (1987)
- Grimm, M.P., Klinge, M.: Pike and some aspects of its dependence on vegetation. In: Craig, J.F. (ed.) Pike: Biology and Exploitation, pp. 125–156. Chapman & Hall, London (1996)

- Iyengar, E.V.: Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biol. J. Linn. Soc. 93(4), 745–762 (2008)
- Jeanne, R.L.: Social biology of the neotropical wasp mischocyttarus drewseni. Bull. Mus. Comp. Zool. 144, 63–150 (1972)
- Kruuk, H.: The Spotted Hyena: A Study of Predation and Social Behavior. University of Chicago Press, Chicago (1972)
- Spear, L.B., Howell, S.N.G., Oedekoven, C.S., Legay, D., Bried, J.: Kleptoparasitism by brown skuas on albatrosses and giant-petrels in the Indian ocean. Auk 116(2), 545–548 (1999)
- Steele, W.K., Hockey, P.A.R.: Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (Larus dominicanus). Auk 112(4), 847–859 (1995)
- Triplet, P., Stillman, R.A., Goss-Custard, J.D.: Prey abundance and the strength of interference in a foraging shorebird. J. Anim. Ecol. 68(2), 254–265 (1999)
- Vickery, W.L., Giraldeau, L.A., Templeton, J.J., Kramer, D.L., Chapman, C.A.: Producers, scroungers and group foraging. Am. Nat. 137(6), 847–863 (1991)