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Resistance is Useless?—Extensions to the Game Theory of Kleptoparasitism

MARK BROOM AND ROGER M. LUTHER*
Department of Mathematics,
University of Sussex,
Falmer,
Brighton BN1 9QH,
UK

GRAEME D. RUXTON
Division of Environmental and Evolutionary Biology,
University of Glasgow,
Glasgow G12 8QQ,
UK

We extend the game theoretic model of kleptoparasitism introduced by Broom and Ruxton (1998, *Behav. Ecol.* **9**, 397–403) in two ways: we allow for asymmetric contests, where the probability α of the challenger winning can take any value from 0 to 1; and we allow the handler to choose not to resist the challenge, but to immediately concede and relinquish its food to the challenger. We find, in general, three possible evolutionarily stable strategies—challenge-and-resist (Hawk), challenge-but-do-not-resist (Marauder) and do-not-challenge-but-resist (Retaliator). When $\alpha = 1/2$, we find that Hawk and Marauder are the only ESS's, in contrast to the result of the original model; we also find an overlap region, in parameter space, where two different ESS's are possible, depending on initial conditions. For general α, we see that all three ESS are possible, depending on different values of the environmental parameters; however, as the average time of a contest over food becomes long, then the Marauder strategy becomes more and more prevalent. The model makes a potentially significant prediction about animal behaviour in the area of kleptoparasitism, that a searcher, when it meets a handler, will only decline to attack that handler when $\alpha < 1/2$ i.e. when the defender is more likely to win. One possible converse of this statement, that a handler whose probability of success is greater than $1/2$ should always resist a challenge, is not true.

1. INTRODUCTION

Kleptoparasitism is the stealing of food by one animal from another. It is a well-documented phenomenon, particularly amongst birds [see Brockman and Barnard (1979) and Furness (1987) for reviews], and there have been a number of

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*Author to whom correspondence should be addressed. *E-mail*: r.m.luther@sussex.ac.uk

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attempts to construct a theoretical model of the process (Beddington, 1975; Ruxton *et al*., 1992; Holmgren, 1995; Ruxton and Moody, 1997). The model of Broom and Ruxton (1998), applied the principles of game theory to this problem [following earlier efforts in this direction, such as Barnard and Sibly (1981)]. They considered, after making various assumptions, what circumstances made it beneficial for an individual animal to challenge another animal that already had some food. They found, essentially, that a challenge is worthwhile if fight times are short, or if food is scarce; in other circumstances, it is better not to challenge, but simply to search for one's own food.

In this paper, we generalise the model of Broom and Ruxton (1998) in two ways. The original model assumed that both participants in an aggressive encounter had an equal (50%) chance of winning. This may not be ecologically realistic for many systems, as there are many ecological reasons why one party or the other may be more likely than not to win an aggressive encounter over a partially handled food item. It could be that simultaneously trying to fight whilst holding on to the food item puts the handler at a disadvantage, suggesting that the aggressor will be more likely to win any contest. The converse situation where holding the food item puts the handler at an advantage because the food item can be used as a weapon is theoretically possible but we cannot think of any ecological circumstances where this has been observed. However, it may be that the handler is put at a disadvantage in terms of manoeuvrability by the weight of the part of the food item that it has already digested. Conversely, the energy obtained from the consumed part of the prey item may provide the handler with more energy than the searcher, biasing the fight in their favour. For reptiles, the greatly increased metabolic rates characteristic of food digestion may make the handler more able to expend energy on an aggressive encounter than the challenger is. Alternatively or additionally, handling may have temporarily drained the handler energetically, putting it at a disadvantage. Further, the searcher may have an element of surprise over an animal preoccupied with handling, or may have an advantage in momentum over a stationary handler; again, the converse disadvantage may apply, where the time taken by a challenger to approach the handler gives the latter a chance to escape, or else makes the challenger use more energy in catching the handler.

Notice that all these mechanisms are due to the differing activities of the two participants (handler and challenger) rather than the intrinsic physical qualities of the individuals (irrespective of their current activities). Indeed the model assumes that individuals are intrinsically identical, although at a given instant they can differ in the activity that they are performing (see below).

Our second generalisation is to allow the handler to decline to resist the challenge of an aggressive individual, surrendering the food item without a fight. Such behaviour can be seen in many social foragers, even when there is no obvious species, size or social dominance differences between the two animals. In our model this behaviour may be optimal because there is a cost (in time spent) to entering an aggressive encounter. It may be that the handler does better to save on this cost (especially if the chance of winning the encounter is low). Other costs to aggressive encounters (not modelled explicitly here) include energy, increased vulnerability to predators and enhanced risk of injury.

With these generalisations, we extend the original Broom–Ruxton (Broom and Ruxton, 1998) model, to investigate a wider pattern of evolutionarily stable strategies. We find three possibilities:

(i) to challenge a handler, and also to resist when challenged (Hawk)
(ii) to challenge a handler, but not resist when challenged (Marauder)
(iii) not to challenge, but to resist when challenged (Retaliator)

which are ESS's in varying environmental conditions, in some cases with two different ESS's possible together. We also find that when contest times are long, the Marauder strategy is the only ESS.

An implicit assumption of this modelling approach is that if one strategy produces a higher feeding rate than another, then this will translate into a fitness advantage for the genes that code for this strategy. Whilst logically reasonable for consumers in general, this assumption seems particularly likely for consumers that are highly time-stressed in their foraging. An example of this are those foragers that rely on a specific part of tidal cycles to access prey in the inter-tidal zone.

2. THE MODEL

The model is an extension of that described in Broom and Ruxton (1998), and we summarise the original model here in order to introduce our nomenclature. We have a population density of P foragers, of which at any time a density (H) are handling food, a density (S) are searching for food or for handlers that they can challenge for food, and a density (A) are involved in aggressive encounters over food. A constant density of food items f is available. The rates at which a forager finds food and handlers respectively are $\nu_f f$ and $\nu_h H$. For convenience, we assume that food items take a time to handle drawn from an exponential distribution with mean t_h, [see Broom and Ruxton (2003) for a discussion of alternative models for handling times]. At the end of the handling time, the handler returns to searching. If a forager encounters a handler, then it can choose to challenge for the food item or not. If it chooses not to challenge then nothing happens and it simply continues searching with the handler continuing handling. If the searcher decides to challenge, then the handler then decides whether to resist or not. This is different from the model of Broom and Ruxton (1998) where the handler was assumed always to resist. If the handler chooses not to resist then it returns to searching and the searcher switches to handling the food item. If the handler decides to resist, then the two participants enter an aggressive contest lasting a time drawn from an exponential distribution with mean $t_a/2$ (the factor of $1/2$ is chosen for later algebraic convenience). At the end of this time there is a winner that begins handling

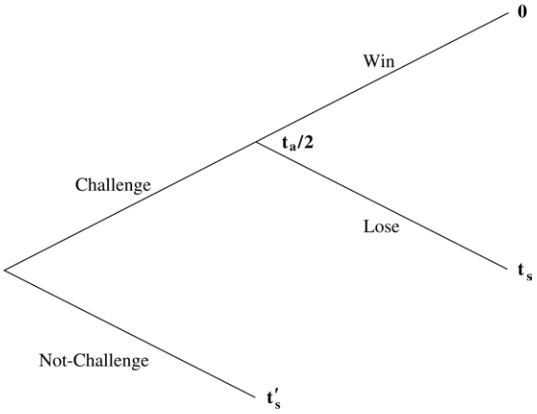

Figure 1. Tree showing possible sequences of events for a searcher encountering a handler: it may challenge, or not, and then it may win, or not. Contest time, and times to find food, are also shown.

the prey item, and a loser that begins searching. The challenging animal has a probability α of winning the fight. This is different again from Broom and Ruxton (1998) where effectively α was fixed at $1/2$.

3. STRATEGIES FOR CHALLENGING

We are interested in the condition for challenging to be advantageous in a situation where the handler will resist. This is illustrated in Fig. 1: a searcher encounters a handler, and can choose whether or not to challenge the handler. If it does challenge, a contest ensues, lasting for a time $t_a/2$ after which there is a probability α of the challenger winning the fight and getting the food, and a complementary probability $(1-\alpha)$ that the defender will win, so that the attacker will have to resume its search; the time taken to acquire food after a failed attack is t_s. If the attacker does not challenge, then it is effectively just foraging, at a rate $v_f f$, and so its average time until it finds some food is $t_s' = (v_f f)^{-1}$.

It will be advantageous to challenge if the expected time to gain a food item by always challenging, $(t_a/2)+(1-\alpha)t_s$, is less than the expected time to gain a food item for an individual that never challenges, $(v_f f)^{-1}$.

We can evaluate t_s by writing down a recursive equation, based on Fig. 2. The expected time to find either unattended food items or handlers is given by

$$(v_f f + v_h H)^{-1} = \frac{1}{v_f f + v_h H}.$$

A food item will be found before a handler with probability $v_f f/(v_f f + v_h H)$, and similarly a handler will be found first with the complementary probability $v_h H/(v_f f + v_h H)$.

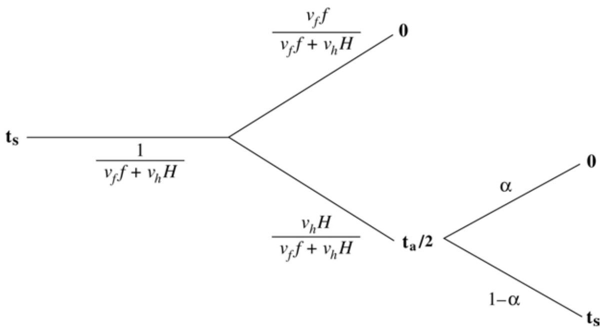

Figure 2. Probability tree for a searcher who always attacks, showing time to find food and contest time, (times in bold) together with the probabilities of finding food or a handler, and, if the latter, of winning a contest.

If a handler is found then it is challenged, and the challenge will be successful with probability α. If the challenge is unsuccessful, then the further time required to obtain a food item is simply the same t_s as is defined by the whole diagram. Hence, we find the equation

$$t_s = \frac{1}{v_f f + v_h H} + \left(\frac{v_h H}{v_f f + v_h H}\right)\left(\frac{t_a}{2} + (1-\alpha)t_s\right)$$

which can be solved to give:

$$t_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H}.$$

If we substitute this into

$$\frac{t_a}{2} + (1-\alpha)t_s < \frac{1}{v_f f}$$

then we get the condition for challenging to be advantageous:

$$v_f f < \frac{2\alpha}{t_a}. \tag{A1}$$

This has the simple interpretation that it is advantageous to challenge if the probability of winning is greater than the ratio of the mean contest time to the mean search time.

We denote by t_e [τ in Broom and Ruxton (1998)], the mean time taken for a searcher that has just encountered a handler to begin handling, assuming it attacks encountered handlers with probability p. Fig. 3 shows the possible sequences of events—if it chooses to challenge for food, then it may or may not win the fight. If it wins, there is no more time required—it has the food. If it loses, then it searches for food, either from foraging or from encountering a handler, and if the latter,

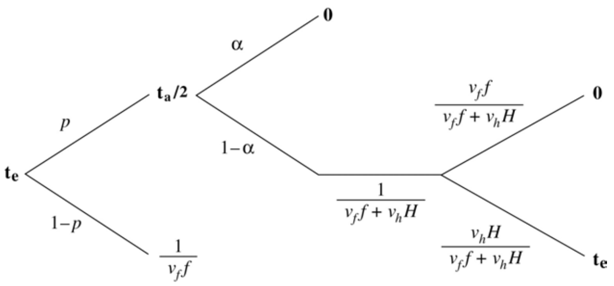

Figure 3. Probability tree for a searcher who encounters a handler, showing contest time and time to find food, (times in bold), together with the probabilities of challenging a handler, winning the contest, and finding food or a handler.

it repeats the process; if it finds food by foraging, then, again, no more time is needed. We can write a recursive equation for t_e, similar to that for t_s:

$$t_e = \frac{1-p}{v_f f} + p\left(t_a/2 + (1-\alpha)\left(\frac{1}{v_f f + v_h H} + \frac{v_h H t_e}{v_f f + v_h H}\right)\right).$$

This gives

$$t_e = \frac{(v_f f + v_h H)/v_f f + p((v_f f + v_h H)t_a/2 - \alpha - v_h H/v_f f)}{v_f f + v_h H - p(1-\alpha)v_h H}.$$

This is of the form $t_e = (a + pb)/(c + pd)$, and thus it is a monotonic function of p. Consideration of dt_e/dp shows that the sign of the gradient is the same as the sign of $t_a/2 - \alpha/v_f f$; thus, when $t_a/2 - \alpha/v_f f > 0$, t_e will have its minimum value when $p = 0$, and when $t_a/2 - \alpha/v_f f < 0$, t_e will have its minimum value when $p = 1$. This replaces the calculation of τ in Broom and Ruxton (1998), and confirms the result (A1) that kleptoparasitism is the optimal strategy whenever $t_a/2 < \alpha/v_f f$.

The last thing to notice is that if handlers do not resist challenges, so all challenges yield a prey item at no cost in time spent, then always challenging is the optimal challenging strategy.

We now turn to consider the optimal strategy for resistance.

4. STRATEGIES FOR RESISTANCE

We are now interested in a handler that has just been challenged.

As shown in Fig. 4, one option is that it could decline to resist, surrender its food, and return immediately to searching for new food. Its expected time to find another food item in this case is denoted t_s. Alternatively, it could resist, resulting in a contest lasting $0.5t_a$ on average; there is a probability α of losing the fight

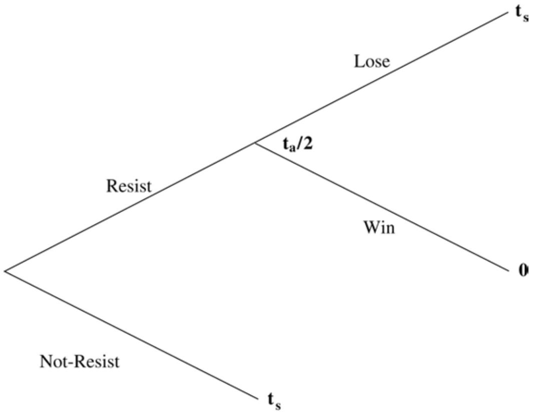

Figure 4. Tree showing possible sequences of events for a handler when challenged: it may resist, or not, and if it does, it may win the contest, or not. Contest time, and subsequent times to find food, are also shown.

to the challenger, in which case the defender would start searching again, taking time t_s, and a probability $(1-\alpha)$ that the defender retains its food, requiring no further time to begin handling. Overall, if there is a contest, the expected time to begin handling again is $0.5t_a + \alpha t_s$. Hence, the condition for resistance to be optimal is

$$0.5t_a + \alpha t_s < t_s.$$

If the rest of the population always resists, then (from our arguments of the last section),

$$t_s = \frac{1 + v_h t_a H/2}{v_f f + \alpha v_h H},$$

which when substituted, gives the condition for resisting to be optimal in a population when others are resisting as

$$v_f f < \frac{2(1-\alpha)}{t_a} + (1-2\alpha) v_h P h_r, \tag{A2}$$

where the handling ratio $h_r = H/P$, and [as derived in Broom and Ruxton (1998)], h_r is the positive solution to $v_h t_a P h_r^2 + (v_f f t_h + 1)h_r - v_f f t_h = 0$.

In the situation where the rest of the population is not resisting then $t_s = 1/(v_f f + v_h H)$ and $h_r = v_f f t_h/(v_f f t_h + 1)$ (this latter is just the Holling Type II functional response).

Substituting these values gives the condition for resistance to be optimal in a population where others are not resisting as

$$v_f f < \frac{2(1-\alpha)}{t_a} - \frac{v_h P v_f f t_h}{v_f f t_h + 1}. \tag{A3}$$

We will see that we must also consider the case where the main population is not making challenges, but where a handler may itself be challenged by a mutant aggressor. In this case $t_s = 1/(v_f f)$, and so the condition for resistance is

$$v_f f < \frac{2(1-\alpha)}{t_a}. \tag{A4}$$

Again, this may be simply interpreted as stating that it is advantageous to resist if the probability of winning is greater than the ratio of the mean contest time to the mean search time.

5. EVOLUTIONARILY STABLE STRATEGIES

There are three possible evolutionarily stable strategies (a strategy that, when played by all the population, cannot be invaded by a mutant playing another strategy):

Strategy 1: (Hawk): Challenge handlers at every opportunity and resist all challenges. This is an ESS if we satisfy both (A1) and (A2) [i.e., (A1) $\cap$ (A2)].

Strategy 2: (Marauder): Challenge handlers at every opportunity but never resist a challenge. This is an ESS if (A3) is not satisfied [i.e., (A3)$^{\mathrm{C}}$].

Strategy 3: (Retaliator): Do not challenge but resist any challenges. This is an ESS if (A1) is not satisfied but (A4) is [i.e., (A1)$^{\mathrm{C}}$ $\cap$ (A4)].

6. RESTRICTED CASE WHEN $\alpha = 1/2$

Before looking at the full model, we consider the special case when $\alpha = 1/2$, as this allows a straightforward comparison between our model and that of Broom and Ruxton (1998). The only difference is that in our model handlers have the ability to surrender food to a challenger without a fight, whereas in the earlier model they had no option but to resist any challenge.

In this case of $\alpha = 1/2$, conditions (A1), (A2) and (A4) all simplify to

$$t_a < \frac{1}{v_f f},$$

and condition (A3) simplifies to

$$t_a < \frac{1}{v_f f\left(1 + \frac{P v_h t_h}{t_h v_f f + 1}\right)}.$$

In this case, (A4) contradicts (A1)$^{\mathrm{C}}$, so that in this restricted case ($\alpha = 1/2$), Retaliator is never an ESS. If we fix all the other parameters (P, v_h, t_h and t_a), then we

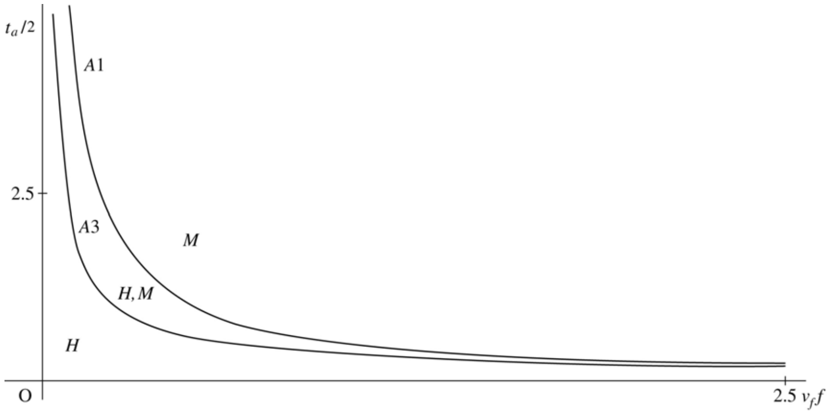

Figure 5. Graph showing how the occurrence of the Hawk and Marauder ESS's depends on the fight time, $t_a/2$ and the rate of finding food, $v_f f$, when $\alpha = 1/2$. Note that Retaliator is not an ESS when $\alpha \geq 1/2 (P = 1, v_h = 0.5, t_h = 4)$.

can see that there is a range of low values of $v_f f$ where both (A1) and (A3) hold, and so Hawk is the sole ESS, then a range of intermediate $v_f f$ values—a buffer zone—where (A1) is satisfied but not (A3), and so both Hawk and Marauder are ESS's, and finally for high $v_f f$ values neither (A1) nor (A3) hold and so Marauder is the sole ESS.

This is illustrated in Fig. 5. Increasing $v_f f$ means that food is easier to find, which causes a switch from a situation where aggressive interactions occur to a situation where they do not. Fig. 4 also shows the effect of varying t_a: again, as we should expect, increasing the length of aggressive interactions makes such interactions less attractive.

We may also note that, for large $v_f f$, the buffer zone is much narrower than the Hawk zone beneath it—the co-existence of the two strategies is very unlikely when there is lots of food available. This is a potentially experimentally testable prediction of our model, that if a species appeared to be showing different behaviours in different locations, in the absence of apparent differences in the ecologies of the environments, then this would suggest that this species is situated in the buffer zone. If this were true, then experimentally manipulating the situation by enhancing food supply should see all the local populations converging to the same behaviour.

We can consider the effects of the other parameters P, v_h, t_h simply by consideration of the simplified conditions (A1) and (A3). We note, however, that the (A1) line does not depend on any of these other parameters, so the occurrence of Hawk as an ESS is also independent of P, v_h, t_h. However, changing these parameters does change the (A3) line, and so affects the occurrence of Marauder as an alternative ESS to Hawk. We summarise the effects in Table 1.

It is relatively easy to compare these results with those of Broom and Ruxton (1998). The earlier model produces a condition identical to (A1). If this was

Table 1. The effect of a change in the parameters P, v_h and t_h on the occurrence of the Hawk and Marauder ESS's when $\alpha = 1/2$.

Increase Pv_h	(A3) moves towards the axes, so the buffer zone increases, and the possibility of Hawk as the only ESS becomes less
Decrease Pv_h	(A3) moves towards (A1), so the buffer zone disappears, and there is a polarisation between Hawk and Marauder
Increase t_h	(A3) moves towards a limit curve $t_a = 1/(v_f f + Pv_h)$, and there is always a region where Hawk is the only ESS
Decrease t_h	(A3) moves towards (A1), and the buffer zone disappears

satisfied then Hawk (always attack and always resist) was the sole ESS; if it was not satisfied then Retaliator (decline to attack, resist attacks) was the sole ESS. Hence, in one sense there is relatively little change, in that both models predict that if (A1) is not satisfied then no aggressive interactions occur. However, the predicted behaviour is then quite different in the two cases. In the earlier model searchers would simply ignore handlers, now searchers challenge handlers which simply give up the food item without a fight. It seems that giving handlers the opportunity to decline to resist seems to work against them. In the Broom and Ruxton model, situations where (A1) was not satisfied were advantageous to handlers, now such circumstances are advantageous to searchers.

We can explain this by realising that if we had a population all following Retaliator, (resist, but not attack), then it could be successfully invaded by a mutant 'Dove' doing no-resist, no-attack—because no attacks are occurring, resistive behaviour is unimportant. The population of no-resist, no-attack would gradually take over; but, in turn, this population would be unstable against another mutant, following Marauder (attack, no-resist), because it is always profitable to attack when there is no resistance—it's a free lunch. Thus Retaliator would be supplanted by Marauder when no-resist is an option.

One of the main conclusions of the earlier paper was that there was always a unique ESS, but this is not the case for the revised model, where between the region where one strategy is the sole ESS and the region where the other strategy is the ESS, there is a buffer zone where the two ESS's co-exist. One of the main conclusions of the Broom and Ruxton paper was that 'small changes in ecological conditions can, under some circumstances cause a dramatic change in the aggressive behaviour of individuals'. The discussion however presented ecological reasons why a sudden difference as change in ecological parameters moved a population across the (A1) line should not always be expected in real populations. This buffer zone in the new model is yet another reason why we would not expect a simple demarcation between properties of populations that show aggression and those that do not. We can still describe the properties that favour (or do not favour) aggression, but there will be no sharp dividing line between the two situations. Indeed we would predict that identical populations could be quite different

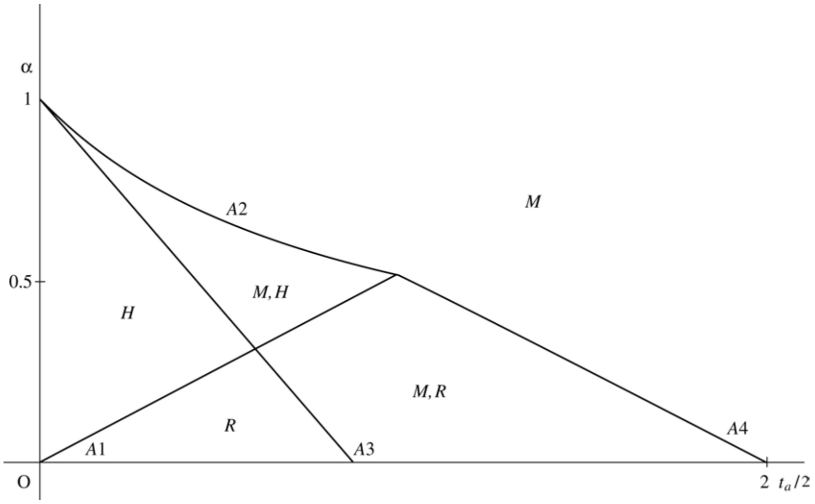

Figure 6. Graph showing how the occurrence of the three possible ESS's, Hawk, Marauder and Retaliator, depends on the fight time, $t_a/2$ and the probability α of the challenger winning the contest ($P = 1$, $v_f f = 0.5$, $v_h = 1$, $t_h = 4$).

in observed behaviour (one showing aggressive interactions and the other not) not because of differences in their current properties but because of differences in their history.

In the original model, P, v_h and t_h had no effect on the attack decision, and so did not affect the ESS strategy adopted. Now, they do effect the decision on whether or not to resist, and thus the ESS also depends on them. We see, however, that when any of them are very small, the ESS configuration approaches that in the previous model, apart from Marauder replacing Retaliator—the buffer zone, which was not present at all originally, becomes very small in the new model.

7. GENERAL CASE WHEN $\alpha \neq 1/2$

Turning now to the general case where $\alpha \neq 1/2$, the distribution of ESS's is shown in Fig. 6. Whilst the quantitative positions of the three lines are affected by the values of the parameters P, $v_f f$, v_h and t_h, and so the relative sizes of the five regions shown in Fig. 6 will vary, it is relatively easy to demonstrate that the qualitative structure shown in Fig. 6 is generic for all combinations of values for these four parameters. Hence, we can draw the following general conclusions.

For any combination of values for the other parameters, there is always a critical value of t_a, given by $t_a = 2/(v_f f)$, beyond which Marauder (attack but don't resist) is the only ESS. We also see that as α approaches 1, Marauder prevails, except when t_a is very small. Both high t_a and high α make defending a food item unattractive, whilst attacking handlers is a worthwhile strategy since such attacks will yield a food item without requiring investment in an aggressive interaction.

Table 2. The effect of a change in the parameters P, v_h and t_h on the occurrence of the Hawk, Marauder and Retaliator ESS's for general α.

Increase Pv_h	(A3) becomes steeper, so the buffer zone widens
Decrease Pv_h	(A3) approaches (A4), so Hawk and Retaliator become the sole ESS's over a wider range of t_a and α
Increase $v_f f$	(A2)–(A4) all become steeper, so Marauder becomes predominant
Decrease $v_f f$	(A2)–(A4) all become less steep, so Hawk, Retaliator—each on their own, or with Marauder—become more likely
Increase t_h	(A3) becomes steeper, but with a limit, so there are always regions where Hawk and Retaliator are sole ESS's
Decrease t_h	(A3) approaches (A4), and the buffer zone disappears

This is analogous to the explanation of the occurrence of Marauder as an ESS in the special case of $\alpha = 1/2$.

What is quite unlike the situation at $\alpha = 1/2$ is the occurrence of a region where Retaliator (don't attack but resist mutant attacks) is the sole ESS. This occurs in a region where t_a is low (and so aggressive interactions are cheap) and α is low (so aggressive interactions heavily favour the handler successfully defending its food item). It should be no surprise that these are the circumstances where Retaliator is favoured. It is relatively easy to combine the expressions for the (A3) and (A1) lines to demonstrate that the region where Retaliator is the sole ESS never extends as high as $\alpha = 1/2$ for any combination of other parameter values. This gives a new clear and potentially testable hypothesis, that only in circumstances where handlers are more likely than 50/50 to win aggressive encounters (i.e., $\alpha < 1/2$) will searchers decline to challenge them. Of course, this does not mean that we would expect to see prolonged aggressive encounters anytime that the challenger enjoys an advantage in aggressive encounters. We see that at high α, there is no prolonged aggressive encounter (apart from at very small t_a) precisely because the handler has little expectation of winning such an encounter and so surrenders the food without a fight.

There is however an intermediate range of α values where challenging is attractive to searchers and resistance is worthwhile to handlers and so we do get aggressive interactions (and Hawk is an ESS). This only occurs when t_a is not too high. When t_a is low, then Hawk is the sole ESS for intermediate α, but, as t_a increases and so interactions become less attractive, there is then a buffer zone where either Hawk and Marauder co-exist, or Retaliator and Marauder co-exist. Finally, for high enough t_a, Marauder is the only ESS. Again this is a generalisation of the situations discussed under the special case with $\alpha = 1/2$.

Varying the other parameters $P, v_h, v_f f, t_h$ has an effect on all four boundary lines, and thus changes the prevalence of all three possible strategies. We summarise the effects in Table 2.

8. CONCLUSION

In the area of kleptoparasitism, we predict that for a given contest time, increasing change of success for the challenger always results in the same sequence of ESS's. As shown in Fig. 6, when the fight time is low, then Retaliator is followed by Hawk, then Hawk or Marauder, and finally, for highest values of α, Marauder. For longer contest times, Hawk as the only possible ESS is no longer an option—the sequence then, for increasing α, is Retaliator, then Retaliator or Marauder, followed by Hawk or Marauder, and finally, for highest values of α, Marauder. (Whilst, in principle, one could see Retaliator, Marauder, Hawk, Marauder, this is unlikely in practice.) For still higher fight times, Retaliator alone is not an ESS, and the sequence is Retaliator or Marauder, then just Marauder, and for very long contest times, only Marauder is an ESS, for any α. We can easily understand these sequences of ESS's: when α is small, then resisting is appropriate (as long as the contest time is not excessively long), but challenging against resistance is not—hence the Retaliator ESS; for values of α near $1/2$, then both resisting and challenging may be sensible, so long as the contest time is not too long, so Hawk occurs; for high values of α, resistance is likely to be a waste of time, so Marauder becomes the ESS.

We also predict the common occurrence of Marauder when fight times are long. Here we have a situation where handlers give up their food items without a fight despite the fact that they have a nonzero chance of winning the fight. This occurs because the time that must be spent in the fight can be better spent searching for another food item. Hence the decision to surrender food is made (partly) on economics grounds, and occurs in the absence of a social hierarchy or intrinsic competitive differences between individuals. This is an important and interesting concept for ecologists; when they see this behaviour it need not suggest that the individual surrendering the food is necessarily socially subdominant to the challenging individual. We can also explain the otherwise perplexing situation where individual A surrenders food to B but B also surrenders food to A; this would normally be explained by some rapid change or fuzziness in the dominance hierarchy, but we have an alternative (and perhaps more plausible) explanation. We note that similar patterns of behaviour have been predicted under a game theoretical analysis in other contexts [e.g., Mesterton-Gibbons and Adams (1998)].

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