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A game-theoretic model of kleptoparasitic behavior in polymorphic populations

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Abstract

Kleptoparasitism, the stealing of food by one animal from another, is a widespread biological phenomenon. In this paper we build upon earlier models to investigate a population of conspecifics involved in foraging and, potentially, kleptoparasitism. We assume that the population is composed of four types of individuals, according to their strategic choices when faced with an opportunity to steal and to resist an attack. The fitness of each type of individual depends upon various natural parameters, for example food density, the handling time of a food item and the probability of mounting a successful attack against resistance, as well as the choices that they make. We find the Evolutionarily Stable Strategies (ESSs) for all parameter combinations and show that there are six possible ESSs, four pure and two mixtures of two strategies, that can occur. We show that there is always at least one ESS, and sometimes two or three. We further investigate the influence of the different parameters on when each type of solution occurs.

Key words: Kleptoparasitism, ESS, Game theory, Strategy

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1. Introduction

In this paper we shall investigate a model of kleptoparasitism, the stealing by one animal of food that has been caught by another (Rothschild and Clay 1952). The most

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common observations of kleptoparasitism have been amongst birds. An extensive review (Brockmann and Barnard 1979) gives a list of observations of kleptoparasitism by birds. It is noted there that this behavior is much more common in some orders of birds than others, and it is especially prevalent amongst sea-birds. Observations include the sighting of gulls attacking each other for food (Steele and Hockey 1995), oystercatchers feeding on cockles (Triplet et al 1999) and skuas attacking albatrosses and giant-petrels (Spear et al 1999). It should be noted that kleptoparasitism has been observed in many other types of animals as well, including insects (Jeanne 1972), fish (Grimm and Klinge 1996) and mammals (Kruuk 1972).

There is now a substantial literature of works using game theoretic models to investigate kleptoparasitic behavior in nature (eg Barnard and Sibly 1981; Stillmann et al 1997; Broom and Ruxton 1998; Ruxton and Broom 1999; Broom and Ruxton 2003). In one of the most recent papers (Broom et al 2004), the generality of the original model of Broom and Ruxton (1998) was expanded in two key ways: allowing flexibility in the likelihood that an attacker will be able to successfully steal a prey item from a handler, and allowing attacked individuals the flexibility to surrender items without a time-consuming contest. This showed that (depending on the values given to ecological variables) three different types of ESSs were possible: one where individuals both attacked others for food items and resisted attacks from others (Hawk), one where individuals attacked but did not resist (Marauder), and one where individuals did not attack, but would resist if themselves attacked (Retaliator). Further, in some circumstances, more than one of these ESS's was possible as alternates, depending on the history of the system as well as its current parameter values. The Marauder ESS is particularly interesting ecologically, giving an economic explanation for one individual to surrender a valuable food item without a fight to another individual in the absence of dominance hierarchies or intrinsic asymmetries in competitive abilities between individuals.

2. The model, behavioral stages and strategies

The basic structure of our model follows that of Broom and Ruxton (1998). Individuals forage for food, and can be in one of four behavioral stages. They are either a searcher (looking for food), a handler (preparing to consume food it has found) an attacker (trying to steal the food item from a handler it has found) or a resister (trying to resist the attack of another). We assume that individuals take an exponential time to handle a food item, and that the food is consumed in no time at the end of this period. Note that Broom and Ruxton (2003) considered handling times which were constant and different food types, where some types were consumed instantaneously at the end of the handling period as in this paper, but others were consumed continuously. One consequence of this is that the time spent handling a food item was of great importance, and this led to rather different behavior to the other models. In particular not all kleptoparasitic choices were identical; there was a threshold where opportunities were only taken if sufficiently little handling had been done (continuous consumption) or if sufficiently long handling time had elapsed (instantaneous consumption).

We consider a polymorphic population consisting of the four different bird types introduced in Broom et al (2004), (see also Broom and Rychtář, 2007; Luther at al, 2007). A bird's type is determined by its strategy, i.e. by the reaction of an individual to an encounter with another, where one of the two birds is handling food, and the other has an opportunity to try to steal it. The four strategies are:

Hawk	always attack, always resist when attacked
Dove	never attack, never resist when attacked
Retaliator	never attack, always resist when attacked
Marauder	always attack, never resist when attacked

Each bird is initially searching for food items. We assume that Doves and Retaliators find food at rate $\nu_f f$ (where f is the density of food) as opposed to Hawks and Marauders who find food at rate $\nu_g f$. When food is acquired the individual becomes a handler, the handling time of the food item following an exponential distribution with mean t_h, after which it is instantaneously consumed. Thus the food item can be thought of as an animal that has to be removed from a shell, but that the time it takes to extract the animal is unpredictable, and variable from item to item. Hawks and Marauders are searching for handlers as well (at rate ν_h). Hawks and Marauders may thus have to divide their attention between the two searches and it is possible that because of this that $\nu_g < \nu_f$. We shall in any case consider ν_g and ν_f to be potentially different, and will also consider the case where $\nu_g \geq \nu_f$. When Marauder or Hawk find a handler, they attack and try to steal its food. If they encounter Dove or Marauder, the handler surrenders the food item. If they encounter Retaliator or Hawk, the handler resists the attack and thus both the searcher and the handler engage in a fight. There are potentially many different types of costs of the fight (injury, energy loss, time loss). In our model we assume that the only cost is the time spent in the contest. The fights take a random time with exponential distribution with mean $\frac{t_a}{2}$. The attacker wins the fight with probability $\alpha \in (0, 1)$.

Let P be the total density of the population and H_d, D_d, M_d, R_d be the densities of Hawks, Doves, Marauders and Retaliators, respectively. Every individual goes through a searching and handling period, Hawks and Marauders may be involved in fights as attackers and Hawks and Retaliators may be involved in fights as resisters. Let H_s, H_h, H_a, H_r denote the densities of Hawks in searching, handling, attacking and resisting stages. The corresponding notation is used for other types, see Table 1.

We assume the total density of the population is constant and denote by P_s, P_h, P_a, P_r the densities of the population involved in searching, handling, attacking and resisting. Thus

$$P = H_d + D_d + M_d + R_d \tag{2.1}$$

$$P_s = H_s + D_s + M_s + R_s \tag{2.2}$$

$$P_h = H_h + D_h + M_h + R_h \tag{2.3}$$

$$P_a = H_a + M_a \tag{2.4}$$

$$P_r = H_r + R_r \tag{2.5}$$

We also assume that the fitness of an individual is proportional to its uptake rate, the inverse of the total consumption time (i.e. finding the food item and eating it, including all possible interruptions by others). The following equation can be found in Broom and Rychtář (2007) and determines the total consumption time T for Hawks in terms of its inverse handling ratio H_d/H_h (a similar equation holds for other strategies).

Parameter	meaning
P	density of the population
P_s, P_h, P_a, P_r	density of searchers, handlers, attackers and resisters
D_d, R_d, H_d, M_d	density of Doves, Retaliators, Hawks and Marauders
D_s, R_s, H_s, M_s	density of searching Doves, Retaliators, Hawks and Marauders
D_h, R_h, H_h, M_h	density of handling Doves, Retaliators, Hawks and Marauders
H_a, M_a	density of attacking Hawks and Marauders
R_r, H_r	density of resisting Retaliators and Hawks
h_r	handling ratio H_h/P in a population of Hawks only
f	density of food items
ν_f	area Doves and Retaliators can search for food per unit time
ν_g	area Hawks and Marauders can search for food per unit time
ν_h	area Hawks and Marauders can search for handlers per unit time
t_h	expected time to consume a food item (if undisturbed)
$\frac{t_a}{2}$	expected duration of a fight contest over food
α	probability that the attacker wins the fight

Table 1
The model parameters and notation.

$$T = t_h \cdot \frac{H_d}{H_h}. \tag{2.6}$$

The uptake rate is thus directly proportional to the proportion of time that each type of individual spends in the handling stage (see Broom and Ruxton, 1998, amongst other papers). This means that, the shorter the consumption time, the higher the fitness. We shall consider each of the strategies in turn and evaluate its uptake rate in the mixed population.

We shall investigate which mixtures are evolutionarily stable. A mixture is evolutionarily stable if

a) all birds present in the mixture have equal fitness (i.e. their inverse handling ratio is the same);
b) all birds not present in the mixture would have smaller fitness if they were only present in very small numbers (with a density approaching 0); and
c) increasing the proportion of one strategy by a small amount lowers its fitness relative to the other strategy, whereas decreasing the proportion increases its fitness relative to the other strategy.

3. Equilibrium equations for the dynamical system

In this section we will consider each strategy and evaluate its inverse handling ratio, from which its consumption time and hence uptake rate can be found. Transitions between the states follow the schematic description given in Figure 1, which then translates into the differential equations (3.1), (3.2), (3.5), (3.6), (3.7), (3.10), (3.11), (3.12), (3.15), (3.16), (3.17), (3.18) described and developed later in this section.

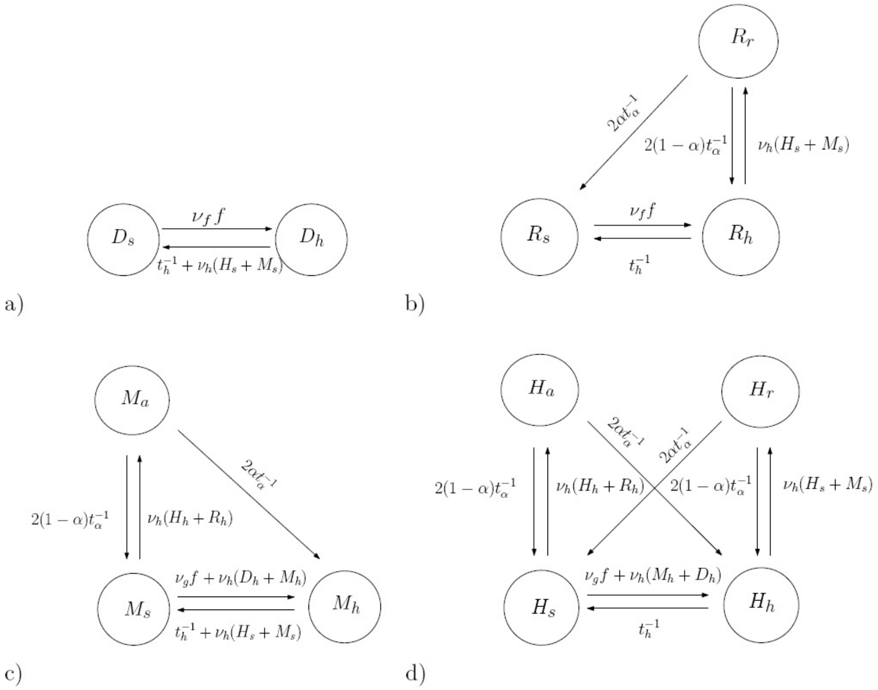

Fig. 1. Phase diagrams for a) Doves, b) Retaliators, c) Marauders, d) Hawks.

We shall assume that the populations converge to equilibrium exponentially fast, and we thus concentrate on these equilibrium values only. For the model of Broom and Ruxton (1998), this fast convergence was shown in Luther and Broom (2004). The proof of Luther and Broom (2004) also works for the special case of a single strategy population for each of the four strategies of our model. We believe that this result holds more generally for our situation with multiple strategies, and this has certainly proved the case in simulations. The parameter values that we have chosen are plausible for real populations when the time units are minutes; a sample set of simulated solutions in Figure 2 show convergence within ten minutes from a population initially composed of searchers, as is reasonable at the start of a foraging period (e.g. at the start of a new day).

3.1. *Doves*

Doves can go through searching and handling stages only. If a Dove is searching, it can become a handler if it finds a food item (with the rate $\nu_f f$). If the Dove is a handler, it can become a searcher if it finishes handling (with rate t_h^{-1}) or is found by a searching Hawk or Marauder (with the rate $\nu_h(H_s + M_s)$). This provides the following set of equations.

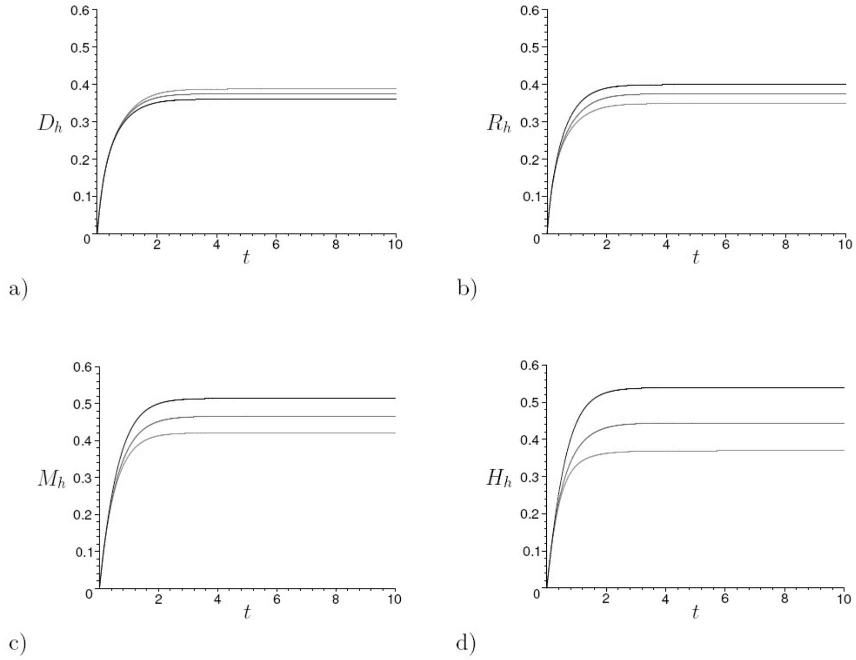

Fig. 2. Fast convergence of solutions of equations (3.1), (3.2), (3.5), (3.6), (3.7), (3.10), (3.11), (3.12), (3.15), (3.16), (3.17), (3.18). The parameter values are $t_h = 1, \nu_h = 1, \alpha = 0.5, \nu_f f = 1, \nu_g f = 0.8$. All individuals start originally as searchers with $D_s = R_s = M_s = H_s = 10$. Black lines are for $t_a = 0.3$, gray line for $t_a = 1$, light gray line for $t_a = 2$.

$$\frac{\mathrm{d}}{\mathrm{d}t} D_s = t_h^{-1} D_h + \nu_h (H_s + M_s) D_h - \nu_f f D_s \tag{3.1}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} D_h = -t_h^{-1} D_h - \nu_h (H_s + M_s) D_h + \nu_f f D_s \tag{3.2}$$

$$D_d = D_s + D_h \tag{3.3}$$

In the equilibrium, both sides of the equations (3.1) and (3.2) are equal 0 which together with (3.3) provides

$$\frac{D_d}{D_h} = 1 + \frac{1}{t_h \nu_f f} + \frac{\nu_h (H_s + M_s)}{\nu_f f} \tag{3.4}$$

3.2. *Retaliators*

Retaliators can go through searching, handling and resisting stages. If a Retaliator is searching, it can become a handler if it finds food (with rate $\nu_f f$). If the Retaliator is handling, it can become

– a searcher if it finishes handling (with rate t_h^{-1})

– a resister if it is found by a searching Hawk or Marauder (with rate $\nu_h (H_s + M_s)$).

If the Retaliator is resisting, it can become

– a handler if it wins the fight (with rate $(1-\alpha)(\frac{t_a}{2})^{-1}$),
– a searcher if it loses the fight (with rate $\alpha(\frac{t_a}{2})^{-1}$).
This provides the following set of equations (already assumed to be in the equilibrium conditions).

$$
\begin{aligned}
0 &= \frac{\mathrm{d}}{\mathrm{d}t}R_s = -\nu_f f R_s + t_h^{-1} R_h + 2\alpha t_a^{-1} R_r && (3.5)\\
0 &= \frac{\mathrm{d}}{\mathrm{d}t}R_h = -t_h^{-1} R_h - \nu_h(H_s + M_s)R_h + \nu_f f R_s \\
&\qquad + 2(1-\alpha)t_a^{-1} R_r && (3.6)\\
0 &= \frac{\mathrm{d}}{\mathrm{d}t}R_r = -2t_a^{-1} R_r + \nu_h(H_s + M_s)R_h && (3.7)\\
R_d &= R_s + R_h + R_r && (3.8)
\end{aligned}
$$

By (3.8), (3.5) and (3.7),

$$\frac{R_d}{R_h} = 1 + \frac{1}{\nu_f f} \cdot \left(t_h^{-1} + \alpha\nu_h(H_s + M_s)\right) + \nu_h(H_s + M_s)\frac{t_a}{2} \tag{3.9}$$

3.3. *Marauders*

Marauders can go through searching, handling and attacking stages. If a Marauder is searching, it can become

- a handler if it finds food (with the rate $\nu_g f$) or a handling Dove or Marauder (with the rate $\nu_h(D_h + M_h)$),
- an attacker if it finds a handling Hawk or Retaliator (with the rate $\nu_h(H_h + R_h)$).

If the Marauder is handling, it can become

- a searcher if it finishes handling (with rate t_h^{-1}) or is found by a searching Hawk or Marauder (with rate $\nu_h(H_s + M_s)$),

If the Marauder is attacking, it can become

- a handler if it wins the fight (with rate $\alpha(\frac{t_a}{2})^{-1}$),
- a searcher if it loses the fight (with rate $(1-\alpha)(\frac{t_a}{2})^{-1}$).

This provides the following set of equations.

$$
\begin{aligned}
0 &= \frac{\mathrm{d}}{\mathrm{d}t}M_s = -\nu_h P_h M_s - \nu_g f M_s + \left(t_h^{-1} + \nu_h(H_s + M_s)\right) M_h \\
&\qquad + 2(1-\alpha)t_a^{-1} M_a && (3.10)\\
0 &= \frac{\mathrm{d}}{\mathrm{d}t}M_h = -(t_h^{-1} + \nu_h(H_s + M_s))M_h + \left(\nu_g f + \nu_h(D_h + M_h)\right) M_s \\
&\qquad + 2\alpha t_a^{-1} M_a && (3.11)\\
0 &= \frac{\mathrm{d}}{\mathrm{d}t}M_a = -2t_a^{-1} M_a + \nu_h(H_h + R_h)M_s && (3.12)\\
M_d &= M_s + M_h + M_a && (3.13)
\end{aligned}
$$

By (3.12),

$$\frac{M_a}{M_h} = \frac{M_a}{M_s} \cdot \frac{M_s}{M_h} = \nu_h(H_h + R_h)\frac{t_a}{2} \cdot \frac{M_s}{M_h}$$

and by (3.10)

$$\frac{M_s}{M_h} = \frac{t_h^{-1} + \nu_h(H_s + M_s)}{\nu_h P_h + \nu_g f - (1-\alpha)\nu_h(H_h + R_h)}.$$

Thus,

$$\frac{M_d}{M_h} = 1 + \frac{t_h^{-1} + \nu_h(H_s + M_s)}{\nu_h P_h + \nu_g f - (1-\alpha)\nu_h(H_h + R_h)} \cdot \left(1 + \nu_h(H_h + R_h)\frac{t_a}{2}\right). \tag{3.14}$$

3.4. *Hawks*

Hawks can go through four different stages - searching, handling, attacking, and resisting. If a Hawk is searching, it can become
- a handler if it finds food (with rate $\nu_g f$) or a handling Dove or Marauder (with rate $\nu_h(D_h + M_h)$),
- an attacker if it finds a handling Hawk or Retaliator (with rate $\nu_h(H_h + R_h)$).

If the Hawk is handling, it can become
- a searcher if it finishes handling (with rate t_h^{-1}),
- a resister if it is found by a searching Hawk or Marauder (with rate $\nu_h(H_s + M_s)$).

If the Hawk is attacking, it can become
- a handler if it wins the fight (with rate $\alpha(\frac{t_a}{2})^{-1}$),
- a searcher if it loses the fight (with rate $(1-\alpha)(\frac{t_a}{2})^{-1}$).

If the Hawk is resisting, it can become
- a searcher if it loses the fight (with rate $\alpha(\frac{t_a}{2})^{-1}$),
- a handler if it wins the fight (with rate $(1-\alpha)(\frac{t_a}{2})^{-1}$).

It gives the following set of equations.

$$0 = \frac{\mathrm{d}}{\mathrm{d}t}H_s = -\nu_h P_h H_s - \nu_g f H_s + t_h^{-1}H_h + 2(1-\alpha)t_a^{-1}H_a + 2\alpha t_a^{-1}H_r \tag{3.15}$$

$$0 = \frac{\mathrm{d}}{\mathrm{d}t}H_h = -\nu_h(H_s + M_s)H_h - t_h^{-1}H_h + \left(\nu_g f + \nu_h(M_h + D_h)\right)H_s + 2\alpha t_a^{-1}H_a + 2(1-\alpha)t_a^{-1}H_r \tag{3.16}$$

$$0 = \frac{\mathrm{d}}{\mathrm{d}t}H_a = -2t_a^{-1}H_a + \nu_h(H_h + R_h)H_s \tag{3.17}$$

$$0 = \frac{\mathrm{d}}{\mathrm{d}t}H_r = -2t_a^{-1}H_r + \nu_h(H_s + M_s)H_h \tag{3.18}$$

$$H_d = H_s + H_h + H_a + H_r \tag{3.19}$$

By (3.18)

$$\frac{H_r}{H_h} = \nu_h(H_s + M_s)\frac{t_a}{2};$$

by (3.17)

$$\frac{H_a}{H_h} = \frac{H_a}{H_s} \cdot \frac{H_s}{H_h} = \nu_h(H_h + R_h)\frac{t_a}{2} \cdot \frac{H_s}{H_h},$$

and by (3.16)

$$\frac{H_s}{H_h} = \frac{t_h^{-1} + \alpha\nu_h M_s}{\nu_g f + \nu_h(D_h + M_h) + \alpha\nu_h R_h}. \tag{3.20}$$

Thus, by (3.19),

$$\begin{aligned}\frac{H_d}{H_h} = 1 + &\frac{t_h^{-1} + \alpha\nu_h M_s}{\nu_g f + \nu_h(D_h + M_h) + \alpha\nu_h R_h} \cdot \left(1 + \nu_h(H_h + R_h)\frac{t_a}{2}\right.\\ &\left.+\nu_h(H_s + M_s)\frac{t_a}{2}\right) \qquad (3.21)\end{aligned}$$

Note that by using equation (3.15) rather than (3.16) in the above process we get the following expression equivalent to (3.21)

$$\begin{aligned}\frac{H_d}{H_h} = 1 + &\frac{t_h^{-1} + \alpha\nu_h(H_s + M_s)}{\nu_g f + \nu_h(D_h + M_h) + \alpha\nu_h(H_h + R_h)} \cdot \left(1 + \nu_h(H_h + R_h)\frac{t_a}{2}\right.\\ &\left.+\nu_h(H_s + M_s)\frac{t_a}{2}\right) \qquad (3.22)\end{aligned}$$

4. General comparisons

We can use the inverse handling ratios from the previous sections to establish some conditions when a given strategy has (or has not) an advantage against another strategy in a general population mixture. Since all stable population mixtures require the total consumption times of all strategies involved in the mixture to be identical, this in turn will show when the mixture can be invaded by the strategy in question. We consider pairs of strategies in turn, comparing the inverse handling ratio from the previous section. In each case we give the condition for the first strategy to be better than the second one (the condition for the second strategy to be better is just the reverse of this condition).

By (3.4) and (3.9), Dove beats Retaliator if

$$1 - \alpha < \frac{t_a}{2}\nu_f f \qquad (4.1)$$

(unless $H_s + M_s = 0$ when both always do equally well).

By (3.4) and (3.14), Dove beats Marauder if

$$\frac{\nu_f f - \nu_g f}{\nu_h} > D_h + M_h + (H_h + R_h) \cdot \left(\alpha - \nu_f f\frac{t_a}{2}\right). \qquad (4.2)$$

By (3.14) and (3.22), Marauder beats Hawk if

$$\frac{t_a}{2}\nu_g f - (1 - \alpha) + \nu_h\frac{t_a}{2}\big(D_h + M_h + (H_h + R_h)(2\alpha - 1)\big) > 0 \qquad (4.3)$$

(unless $H_s + M_s = 0$ when both always do equally well).

Using (3.9) and (3.21), Retaliator beats Hawk under exactly the same conditions as Dove beats Marauder and in any population mixture Hawks have higher payoffs than Retaliators if and only if Marauders have a higher payoff than Doves. Expressed in formulae this is

$$\frac{H_h}{H_d} > \frac{R_h}{R_d} \Leftrightarrow \frac{M_h}{M_d} > \frac{D_h}{D_d}$$

For Hawk to be an ESS it must have a higher payoff than Retaliator, Dove or Marauder i.e.

$$\frac{H_h}{H_d} > \max\left(\frac{R_h}{R_d}, \frac{D_h}{D_d}, \frac{M_h}{M_d}\right)$$

Clearly this requires

$$\frac{H_h}{H_d} > \frac{R_h}{R_d}$$

which in turn implies

$$\frac{M_h}{M_d} > \frac{D_h}{D_d}$$

i.e.

$$\frac{H_h}{H_d} > \max\left(\frac{R_h}{R_d}, \frac{D_h}{D_d}, \frac{M_h}{M_d}\right) \Leftrightarrow \frac{H_h}{H_d} > \max\left(\frac{R_h}{R_d}, \frac{M_h}{M_d}\right)$$

Hawk is thus an ESS if and only if it cannot be invaded by Marauder or Retaliator, and consideration of invasion by Dove is superfluous. Similarly whenever Dove can be invaded by Hawk it can be invaded by one of the others. The same argument works for Marauder and Retaliator, so that whenever Retaliator is invaded by Marauder, or Marauder is invaded by Retaliator, the strategy will also be invaded by either Hawk or Dove. It is thus never necessary to consider invasion by the "opposite strategy" (where both attacking and resisting behavior differ).

5. Evolutionarily stable mixtures

We shall now consider the various possible population mixtures in turn. There are 15 possibilities to consider (each of Hawk, Marauder, Retaliator and Dove can either be included in the population or not, excluding the case where none are present).

Some of these results can be obtained by revisiting the paper Luther et al (2007). That paper considered two populations of individuals from the same species, one of which was a pure forager, and the other foraged but also indulged in kleptoparasitism (at some cost to its foraging ability). The potential kleptoparasite could attack or not (although it could not tell which type its potential victim was) and either type could choose to resist any attack or not. Under certain circumstances evolution eliminated one of the groups to leave a single population, in others a mixture of the two groups survived.

This actually incorporates our situation whenever there are exactly two different strategies in a mixture one of which is a kleptoparasite (Marauder or Hawk) and one of which is not (Dove or Retaliator), or if there is just a single strategy. Thus from the paper we can directly obtain some of the following results (for $\nu_f > \nu_g$).

5.1. *Pure ESS's*

In this section we will ask when a population consisting of a single strategy can or cannot be invaded.

5.1.1. *Dove as an ESS*

Strictly speaking, Dove is never an ESS, because it can always be invaded by Retaliator (by drift).

Once we allow a constant presence of a small amount of Hawks and/or Marauders, we get that Retaliator cannot invade Dove as long as (4.1) holds:

$$1 - \alpha < \frac{t_a}{2}\nu_f f$$

(i.e. if there is enough food or fights are too long).

By (4.2), Dove can not be invaded by Marauder if

$$D_h < \frac{\nu_f f - \nu_g f}{\nu_h}.$$

Since, by (3.4), for $D_d \approx P$,

$$D_h = \frac{t_h \nu_f f}{t_h \nu_f f + 1} P,$$

we get that Dove is an ESS if

$$1 - \alpha < \frac{t_a}{2} \nu_f f \quad \text{and} \quad P < \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{t_h \nu_f f + 1}{t_h \nu_f f}. \tag{5.1}$$

In particular, pure Dove can be an ESS only if $\nu_g f < \nu_f f$, i.e. Doves find food faster than Hawks or Marauders. And even then, only if $\nu_h P \cdot \frac{t_h \nu_f f}{t_h \nu_f f + 1}$ is smaller than $\nu_f f - \nu_g f$, i.e. the rate that Hawks and/or Marauders find handling Doves is smaller than the Dove's advantage in finding food. Another interpretation is that this only occurs in sufficiently low density populations (such populations do not give kleptoparasitic invaders a chance of finding a handler very fast).

5.1.2. *Retaliator as an ESS*

Similarly to the Dove situation, pure Retaliator can never be an ESS because it can always be invaded by Doves by drift. Nevertheless, when we allow a small presence of Hawks and/or Marauders, we get (as above) that Retaliator cannot be invaded by Doves if and only if the condition (4.1) does not hold, i.e.

$$\nu_f f \frac{t_a}{2} < 1 - \alpha.$$

When $R_d \approx P$ we get from (3.14) and (3.21) that $\frac{M_d}{M_h} = \frac{H_d}{H_h}$. As discussed in section 4, Retaliator beats Hawk if and only if Dove beats Marauder. Thus, by (4.2), one needs

$$R_h \left(\alpha - \frac{t_a}{2} \nu_f f \right) < \frac{\nu_f f - \nu_g f}{\nu_h}.$$

Since $R_h = \frac{t_h \nu_f f}{t_h \nu_f f + 1} P$, Retaliator is an ESS if

$$\nu_f f \frac{t_a}{2} < 1 - \alpha, \ \nu_f f \frac{t_a}{2} < \alpha, \ P < \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{1}{\alpha - \nu_f f \frac{t_a}{2}} \cdot \frac{t_h \nu_f f + 1}{t_h \nu_f f} \tag{5.2}$$

or

$$\nu_f f \frac{t_a}{2} < 1 - \alpha, \ \nu_f f \frac{t_a}{2} > \alpha, \ P > \frac{\nu_g f - \nu_f f}{\nu_h} \cdot \frac{1}{\nu_f f \frac{t_a}{2} - \alpha} \cdot \frac{t_h \nu_f f + 1}{t_h \nu_f f} \tag{5.3}$$

The first condition says that if fights are short or there is not enough food, then Retaliator is an ESS in a low density population only (short fights are good for Marauders or Hawks; not enough food increases the searching time, i.e. it, relatively, decreases the fight time.) Moreover, Retaliator is an ESS only if $\nu_f f > \nu_g f$, i.e. if kleptoparasitic birds have a disadvantage.

The second condition is possible only for $\alpha < 0.5$, i.e. when resisters have an advantage against their attackers. Retaliator is then an ESS in sufficiently high density populations and when the fights do not take too much time. Long fights would mean that Doves do better. A high density population is needed because kleptoparasites are forced to engage in fights and thus lose time while the substantial remainder of the Retaliator population can harvest the food undisturbed. In this sense, the denser the population, the better for the Retaliators.

5.1.3. *Marauder as an ESS*

In the population of Marauders only ($M_d = P$), there are no fights, so $M_a = 0$ and consequently the equation (3.10) reduces to

$$0 = \frac{\mathrm{d}}{\mathrm{d}t} M_s = -\nu_g f M_s + t_h^{-1} M_h.$$

Thus,

$$\frac{M_s}{M_h} = \frac{1}{t_h \nu_g f}, \quad \frac{M_d}{M_h} = 1 + \frac{1}{t_h \nu_g f}$$

and

$$M_h = P \cdot \frac{t_h \nu_g f}{1 + t_h \nu_g f}, \quad M_s = P \cdot \frac{1}{1 + t_h \nu_g f}.$$

By (4.2), Marauder cannot be invaded by Doves if

$$M_h > \frac{\nu_f f - \nu_g f}{\nu_h},$$

i.e. if

$$P > \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{1 + t_h \nu_g f}{t_h \nu_g f}. \tag{5.4}$$

Marauders cannot be invaded by Hawks if, by (4.3),

$$\nu_h \frac{t_a}{2} M_h > 1 - \alpha - \frac{t_a}{2} \nu_g f,$$

i.e. if

$$P > \frac{2}{t_a \nu_h} \left(1 - \alpha - \frac{t_a}{2} \nu_g f \right) \cdot \frac{t_h \nu_g f + 1}{t_h \nu_g f} \tag{5.5}$$

We do not need to consider the invasion by Retaliators since if Marauder is invaded by Retaliator it will also be invaded either by Dove or Hawk as discussed in Section 4. Conditions (5.4) and (5.5) together give

$$P > \left(\max \left\{ \frac{2(1-\alpha)}{t_a}, \nu_f f \right\} - \nu_g f \right) \cdot \frac{t_h \nu_g f + 1}{\nu_h t_h \nu_g f} \tag{5.6}$$

Thus, pure Marauder is an ESS if either

$$\nu_f f \frac{t_a}{2} > 1 - \alpha, \qquad \text{and} \quad P > \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{1 + t_h \nu_g f}{t_h \nu_g f} \tag{5.7}$$

or

$$\nu_f f \frac{t_a}{2} < 1 - \alpha, \quad \text{and} \quad P > \frac{2}{t_a \nu_h} \left(1 - \alpha - \frac{t_a}{2} \nu_g f \right) \cdot \frac{t_h \nu_g f + 1}{t_h \nu_g f}. \tag{5.8}$$

The distinction between the two conditions lies in the relationship between $\nu_f f \frac{t_a}{2}$ and $1 - \alpha$. If $\nu_f f \frac{t_a}{2} > 1 - \alpha$, it means a) fights are long and b) it is not beneficial to resist. Thus, Marauders cannot be invaded by Hawks nor by Retaliators. Marauders cannot be invaded by Doves if the population is dense enough (no matter how big the disadvantage of kleptoparasites) because in the population where everybody steals, Doves lose their food very fast but do not acquire it back by stealing, as Marauders do.

If $\nu_f f \frac{t_a}{2} < 1 - \alpha$, resisting the attack is beneficial. Yet, when the population is dense enough, then Hawks cannot invade Marauder (they would be "doomed" to resist too much) and Retaliators cannot invade Marauders for the same reason.

5.1.4. *Hawk as an ESS*

When Hawk is the only type in the population, by (3.17) and (3.18),

$$H_a = \nu_h \frac{t_a}{2} H_s H_h = H_r$$

and, by (3.16), $H_h = \nu_g f t_h H_s$. By (3.19), we can evaluate H_h in the population of Hawks only. As done already in Ruxton and Moody (1997), $H_h = P h_r$, where h_r, the handling ratio, is the positive root of the quadratic equation

$$h_r^2 t_a \nu_h P + h_r(1 + \nu_g f t_h) - \nu_g f t_h = 0. \tag{5.9}$$

This yields

$$H_h = h_r P = \frac{1 + \nu_g f t_h}{2 t_a \nu_h} \cdot \left(-1 + \sqrt{1 + \frac{4 t_a \nu_h t_h P \nu_g f}{(1 + \nu_g f t_h)^2}} \right), \tag{5.10}$$

which can be later used for determining conditions on P from conditions on H_h.

Retaliator cannot invade Hawk only if Dove cannot invade Marauder, i.e., by (4.2) if

$$\frac{\nu_f f - \nu_g f}{\nu_h} < H_h \left(\alpha - \nu_f f \frac{t_a}{2} \right),$$

i.e. if

$$\begin{aligned} &\frac{t_a}{2} \nu_f f < \alpha \quad \text{and} \quad P h_r > \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{1}{\alpha - \frac{t_a}{2} \nu_f f}, \\ &\qquad\qquad \text{or} \\ &\frac{t_a}{2} \nu_f f > \alpha \quad \text{and} \quad P h_r < \frac{\nu_g f - \nu_f f}{\nu_h} \cdot \frac{1}{\frac{t_a}{2} \nu_f f - \alpha}. \end{aligned}$$

By (4.3), Hawk cannot be invaded by Marauder if

$$\frac{t_a}{2} \nu_g f - (1 - \alpha) < H_h \nu_h \frac{t_a}{2} (1 - 2\alpha),$$

i.e. if

$$\begin{aligned} &2\alpha < 1 \quad \text{and} \quad P h_r > \frac{\nu_g f - 2(1 - \alpha)/t_a}{\nu_h} \cdot \frac{1}{1 - 2\alpha}, \\ &\qquad \text{or} \\ &2\alpha > 1 \quad \text{and} \quad P h_r < \frac{\nu_g f - 2(1 - \alpha)/t_a}{\nu_h} \cdot \frac{1}{1 - 2\alpha}. \end{aligned}$$

By results of Section 4, if Doves invade Hawks then either Marauders or Retaliators invade Hawks so the above are the only conditions we need.

5.2. *Mixed ESS's*

We reiterate that in the current work a mixed ESS (or a mixture) refers to a population of different individuals who each play a unique pure strategy, and not to individuals who are capable of playing more than one strategy.

5.2.1. *Marauders and Doves*

A mixture of Marauders and Doves occurs if Doves can invade Marauders, Marauders can invade Doves and neither Hawks or Retaliators can invade. From the general invasion conditions, since Doves and Marauders do equally well, Retaliators and Hawks do equally well and so it is enough to consider the invasion of Doves by Retaliators only. This is equivalent to finding when it is optimal to not resist attacks in such a mixture. The inequalities (4.1) and (4.2) (the second one must hold for $M_d \approx P$ and must not hold for $D_d \approx P$) yield the conditions

$$\nu_f f \frac{t_a}{2} > 1-\alpha, \frac{(\nu_f f - \nu_g f)(\nu_f f t_h + 1)}{\nu_f f t_h \nu_h} < P < \frac{(\nu_f f - \nu_g f)(\nu_g f t_h + 1)}{\nu_g f t_h \nu_h} \tag{5.11}$$

Notice that this is possible only if $\nu_f f > \nu_g f$, i.e. if kleptoparasites have a disadvantage. A mixture of Dove and Marauder is thus only possible if kleptoparasites forage less efficiently than non-kleptoparasites, fights are sufficiently long, and the population density is at an intermediate level.

The conditions above are both sufficient and necessary for a stable mixture to occur. Indeed, when there is an equilibrium between Marauders and Doves, the condition (4.2) provides

$$D_h + M_h = \frac{\nu_f f - \nu_g f}{\nu_h}$$

and it follows that $\nu_f f > \nu_g f$. Adding equations (3.1) and (3.10) and adding $D_s + M_s$ to the result yields after rearranging

$$\frac{t_h \nu_g f}{1 + t_h \nu_g f} P < D_h + M_h < P \frac{t_h \nu_f f}{1 + t_h \nu_f f}, \tag{5.12}$$

which is exactly the condition we introduced above. Notice that the left hand side of the inequality (5.12) is P_h in a pure Marauder population, while the right hand side of (5.12) is P_h in a pure Dove population.

5.2.2. *Hawks and Retaliators*

A mixture of Hawk and Retaliator occurs if Retaliator can invade Hawk, Hawk can invade Retaliator and in such a mixture it is optimal to resist attacks, which prevents the invasion of Doves or Marauders. As in Section 4, invasion of Dove or Marauder does not occur if and only if Dove does not invade Retaliator, i.e. if, by (4.1), $1-\alpha > \nu_f f \frac{t_a}{2}$. Since Retaliator invades Hawk (and vice versa) if and only if Dove invades Marauder (and vice versa), the condition (4.2) yields

$$P \frac{\nu_f f t_h}{1 + \nu_f f t_h} \cdot \left(\alpha - \nu_f f \frac{t_a}{2}\right) > \frac{\nu_f f - \nu_g f}{\nu_h} > P h_r \left(\alpha - \nu_f f \frac{t_a}{2}\right).$$

Since $R_h = P \cdot \frac{t_h \nu_f f}{1+t_h \nu_f f}$ in a Retaliator only population, $H_h = Ph_r$ in a Hawk only population and $h_r < \frac{\nu_f f t_h}{1+\nu_f f t_h}$, the above inequalities are possible only for $\alpha > \nu_f f \frac{t_a}{2}$ and $\nu_f > \nu_g$, which yields the conditions

$$\nu_f f t_a < 2(1-\alpha),$$

$$\frac{1+\nu_f f t_h}{\nu_f f t_h} \frac{1}{\left(\alpha - \nu_f f \frac{t_a}{2}\right)} \frac{\nu_f f - \nu_g f}{\nu_h} < P < \frac{1}{h_r} \frac{1}{\left(\alpha - \nu_f f \frac{t_a}{2}\right)} \frac{\nu_f f - \nu_g f}{\nu_h}$$

A mixture of Hawk and Retaliator is thus only possible if kleptoparasites forage less efficiently than non-kleptoparasites, fights are not too long, and the population density is at an intermediate level. Note the similarity to the conditions for the Dove and Marauder mixture, the major difference being that for the Hawk-Retaliator mixture, fights must be short.

5.2.3. *Mixtures involving Dove and Retaliator*

In this section we consider all of the possible mixtures which include the strategies Dove and Retaliator, possibly with other strategies as well. These mixtures are

1) Dove and Retaliator,
2) Marauder, Dove and Retaliator,
3) Hawk, Dove and Retaliator,
4) Marauder, Hawk, Dove and Retaliator.

By (4.1), Doves and Retaliators have the same payoff only if a) $\nu_f f \frac{t_a}{2} = 1-\alpha$, or b) there are no Hawks or Marauders in the population. The condition $\nu_f f \frac{t_a}{2} = 1-\alpha$ occurs only at a precise coincidence of ecological parameters, which has zero probability for any real situation, and so is a degenerate case. Thus, there are no mixed equilibria in mixtures 2), 3) and 4).

If there are no Hawks or Marauders in the population, Doves and Retaliators have equal payoffs here irrespective of the proportion of Doves, and so the population is subject to genetic drift, and there is not a unique equilibrium. Note that if we allowed the repeated attempted invasion by mutants of other strategies, then either Dove or Retaliator would have a fitness advantage and so a pure solution would result (this is discussed in the sections for pure Dove and pure Retaliator).

5.2.4. *Hawks and Doves*

A mixture of Hawk and Dove individuals only is not possible (because of invasion by one or other of Marauder and Retaliator). This is an extension of the result from Luther et al (2007). This result follows directly from the comparison conditions in Section 4. Indeed, if Marauder does not do better than Dove, then Hawk does no better than Retaliator. So the only possibility to have a Dove and Hawk mixture is when all types do equally well (and this situation is not possible as discussed in 5.2.3).

5.2.5. *Marauders and Retaliators*

Similarly to the Hawk - Dove mixture, a mixture of Marauder and Retaliator individuals only is not possible, due to invasion by either Dove or Hawk. This result again follows from the general comparisons from Section 4 in the same manner and is again an extension of one from Luther et al (2007).

5.2.6. *Mixtures involving Hawk and Marauder*

The remaining three mixtures are

1) Marauder and Hawk,
2) Marauder, Hawk and Dove,
3) Marauder, Hawk and Retaliator,

which all include Marauder and Hawk.

If three strategies have the same payoff, the fourth one needs to have the same payoff as follows from the general invasion conditions in Section 4. This means that neither a mixture of Hawks, Marauders and Doves, nor a mixture of Hawks, Marauders and Retaliators can be an ESS.

Finally we must consider Hawk and Marauder only.

Combining several earlier equations ((3.10)-(3.11)+(3.15)-(3.16)) gives

$$t_h \nu_g f P_s = P_h \tag{5.13}$$

Equation (3.18), combined with the facts that $P_a = P_r$, and $H_r = P_r$ gives

$$P_a + P_r = t_a \nu_h H_h P_s$$

Thus we can express $P = P_a + P_r + P_s + P_h$ in terms of P_h and H_h giving

$$\frac{P}{P_h} = \frac{t_h \nu_g f + 1 + t_a \nu_h H_h}{t_h \nu_g f} \tag{5.14}$$

We show that there is no stable mixture. To have such a mixture, we need $H_h/H_d = M_h/M_d$, which is, by (4.3), equivalent to

$$(1-\alpha) - \frac{t_a}{2}\nu_g f - \nu_h \frac{t_a}{2}(P_h - 2H_h(1-\alpha)) = 0 \tag{5.15}$$

The left hand side of (5.15) reaches its minimum value in an all Marauder population since P_h attains the maximum when there are no fights, and H_h is equal to 0. Thus if there are any roots to (5.15), pure Marauder must also be an ESS. This in turn means that as we decrease the proportion of Marauders, M_d, from P, the first root of (5.15) we reach (i.e. the largest root of (5.15)) is unstable. Thus, if there is a stable root of (5.15), there must be at least two roots. By (5.14), increasing P_h corresponds to decreasing H_h. Hence, there can only be at most one value of P_h which satisfies (5.14) and (5.15). Thus, for there to be a stable root of (5.15), there must be (at least) two population mixtures which yield the same P_h. By (5.14), H_h is the same in both mixtures as well. This determines M_h and P_s, since $M_h = P_h - H_h$ and, by (5.13), $P_s = P_h/(t_h \nu_g f)$. From (3.20) we have

$$\frac{H_s}{H_h} = \frac{t_h^{-1} + \alpha \nu_h M_s}{\nu_g f + \nu_h M_h}.$$

For two different population mixtures with the same H_h and P_h to satisfy the above, both H_s and M_s are must be larger in one of the populations than the other, which contradicts the statement that P_s is constant. Thus no such mixtures are possible, and there is not a stable Hawk-Marauder mixture.

Dove	in any pattern for relatively small P and for $\nu_f f > \max\{\nu_g f, \frac{2(1-\alpha)}{t_a}\}$
Retaliator	only if $\frac{2(1-\alpha)}{t_a} > \min\{\nu_g f, \frac{2\alpha}{t_a}\}$ $\nu_f f$ should be below $\frac{2(1-\alpha)}{t_a}$
Marauder	in any pattern, usually for high P
Hawk	in all patterns except for $\frac{2(1-\alpha)}{t_a} < \nu_g f < \frac{2\alpha}{t_a}$; $\nu_f f$ should be no more than $\frac{2(1-\alpha)}{t_a}$
mixture of Marauders and Doves	in any pattern for relatively medium P and for $\nu_f f > \max\{\nu_g f, \frac{2(1-\alpha)}{t_a}\}$
mixture of Hawks and Retaliators	only if $\nu_g f < \min\{\frac{2(1-\alpha)}{t_a}, \frac{2\alpha}{t_a}\}$ and for $\nu_f f$ between them

Table 2
Possible ESS and their occurrence.

6. Patterns of ESSs

In this section we consider the various combinations of ESS types that can occur for the same parameters. This is important, as if there is more than a single ESS at a particular combination of parameters, then identical populations in different locations can display completely different behavior due to historical conditions or chance, rather than any differences in inherent characteristics. We use the term *Patterns of ESSs* for this idea, after the work of Cannings and Vickers (1988); Vickers and Cannings (1988) (see also for example Broom, Cannings and Vickers, 1994). The *Pattern* of a game is the collection of supports (the set of pure strategies which occur with non-zero probability) of the ESSs of the game. For example the pattern (M, HR) in our game refers to the case where there is a pure Marauder ESS as well as a mixture of Hawk and Retaliator for the same parameter values (and so the same game), and no other ESSs. Note that in the study of patterns of ESSs, only the strategies involved in an ESS, rather than their frequencies, are considered.

There are six possible ESS's, four of them are the strategies Dove, Retaliator, Marauder and Hawk, two of them are mixtures of strategies: a mixture of Marauders and Doves and a mixture of Hawks and Retaliators. No matter what the parameters, there is always at least one ESS.

Table 2 shows for what parameter values the ESSs occur.

For the six ESSs, each can occur as the unique ESS, but it is also possible to have two or three ESSs for particular sets of parameter values (there cannot be four). The possible combinations of two ESSs are Hawk or Marauder, Retaliator or Marauder, and Marauder or a mixture of Hawks and Retaliators. The possible combinations of three ESSs are Hawk or Marauder or Retaliator. In total, there are ten distinct ESS combinations over the range of all parameters (six unique ESSs and four cases of multiple ESSs).

There are essentially six parameters of our model. The population density, P, the speed kleptoparasites and non-kleptoparasites search for food, $\nu_g f$ and $\nu_f f$, the duration of fights, $\frac{t_a}{2}$, attacker's chances of winning the contest, α, and the time needed for handling the food, t_h. We will fix (arbitrarily) all parameters but $\nu_f f$ and P and will investigate how the ESS outcome changes depending on them.

There are three natural breakpoints for $\nu_f f$:

Hawk or Marauder	in all orderings but $\frac{2(1-\alpha)}{t_a} < \nu_g f < \frac{2\alpha}{t_a}$
Retaliator or Marauder	in all orderings but $\frac{2(1-\alpha)}{t_a} < \min\{\nu_g f, \frac{2\alpha}{t_a}\}$
Hawk or Retaliator	only if $\frac{2\alpha}{t_a} < \nu_g f < \frac{2(1-\alpha)}{t_a}$
Marauder or a mixture of Hawks and Retaliators	only if $\nu_g f < \min\{\frac{2(1-\alpha)}{t_a}, \frac{2\alpha}{t_a}\}$
Marauder or Hawk or Retaliators	only if $\frac{2\alpha}{t_a} < \min\{\nu_g f, \frac{2(1-\alpha)}{t_a}\}$

Table 3
Multiple ESSs and their occurrence in relation to the six size orderings of $\nu_g f$, $\frac{2\alpha}{t_a}$ and $\frac{2(1-\alpha)}{t_a}$

(i) $\frac{2(1-\alpha)}{t_a}$,
(ii) $\frac{2\alpha}{t_a}$, and
(iii) $\nu_g f$

There are six possible size orderings of these breakpoints (excluding equalities), and the pattern of ESSs that we get depends to a certain extent on which ordering occurs, but the essential structure does not differ unless the ordering does. Table 3 shows for which of these size orderings the multiple ESSs occur. There is a total of eleven different patterns of ESSs. Figure 3 shows nine of these patterns for the ordering $\nu_g f < \frac{2\alpha}{t_a} < \frac{2(1-\alpha)}{t_a}$. An alternative structure which again has nine patterns, including the two patterns of multiple ESSs Hawk or Retaliator, or Hawk or Retaliator or Marauder, not in Figure 3, is shown in Figure 4 for the ordering $\frac{2\alpha}{t_a} < \nu_g f < \frac{2(1-\alpha)}{t_a}$.

The most interesting ESS is pure Marauder. It can occur as a unique ESS for some parameter values, or at the same time as any of pure Hawk, pure Retaliator, a mixture of Hawk and Retaliator, or pure Hawk and pure Retaliator. It cannot occur together with Dove or the Marauder-Dove mixture. The pure Marauder ESS occurs always for high population densities. In the population of all Marauders, there are no fights and thus the total time for consumption of a food item equals $(\nu_g f)^{-1} + t_h$ (which means the sum of time needed to find a food item plus the time needed to handle the item), although in reality, the food item is often acquired by stealing from a handler. When the density of the population is high, Marauders are uninvadable because any intruder would either be spending too much time fighting (if it would resist with non zero probability) or it would be losing food items while handling but not acquiring the food by stealing efficiently enough (if not stealing with probability one).

The Dove ESS occurs for any of the ordering of parameters above as long as $\nu_f f$ is large enough and P is not too large. Having high $\nu_f f$ means that food is easy to find and thus it is not beneficial to resist. In relatively small density populations the encounters between individuals are not too frequent and therefore the opportunity to attack is not worth the associated loss of foraging efficiency ($\nu_g f < \nu_f f$), so that Marauders cannot invade.

A mixture of Marauders and Doves also occurs as an ESS for all orderings, as long as $\nu_f f$ is large and the population is of intermediate density. This mixture occurs as a transition between pure Dove and pure Marauder for large $\nu_f f$. The actual stable mixture varies from almost all Dove near the lower boundary to the region, increasing to almost all Marauder near the upper boundary.

Hawk is an ESS only for relatively small values of $\nu_f f$. Small $\nu_f f$ means that food is scarce and thus valuable. It is thus beneficial to fight for it and to resist if attacked.

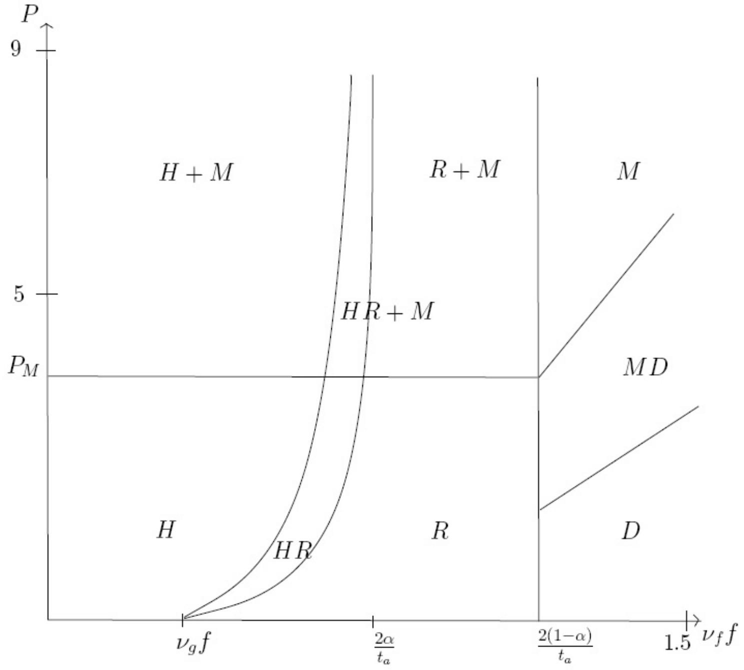

Fig. 3. Patterns of ESSs for the ordering $\nu_g f < \frac{2\alpha}{t_a} < \frac{2(1-\alpha)}{t_a}$. Legend: H = Hawk, M = Marauder, R = Retaliator, D = Dove, XY = mixed ESS of X and Y, $X + Y$ = 2 ESSs of either X or Y; $P_M = \left(\frac{2(1-\alpha)}{t_a} - \nu_g f\right) \cdot \frac{t_h \nu_h \nu_g f + 1}{t_h \nu_h \nu_g f}$. For this particular picture: $\nu_g f = 0.3, \alpha = 0.4, t_h = \nu_h = t_a = 1$, $\nu_f f$ ranges from 0 to 1.5, P ranges from 0 to 9.

Hawk can be an ESS for low density populations as well as for high density ones. The only ordering when Hawk is not an ESS is when $\frac{2(1-\alpha)}{t_a} < \nu_g f < \frac{2\alpha}{t_a}$ when Marauder is the only ESS for small $\nu_f f$. This is natural since the conditions imply a) $\alpha > 1/2$, i.e. it is beneficial to attack since the chances of success are high and b) a food item is not valuable, since $\nu_g f$ is relatively high and thus it is not beneficial to resist and lose time by fighting.

Retaliator is an ESS for medium values of $\nu_f f$. The value $\nu_f f$ should never exceed $\frac{2(1-\alpha)}{t_a}$ which is the point where resisting stops being beneficial due to the high cost of time spent fighting compared to the chances of winning the fight. On the other hand, $\nu_f f$ should be high enough in order to assure that food is not too scarce and thus it is not beneficial to look for handlers.

The mixture of Hawks and Retaliators occurs in a region between pure Hawks and pure Retaliator if $\nu_g f < \min\{\frac{2(1-\alpha)}{t_a}, \frac{2\alpha}{t_a}\}$. In this setting, when $\nu_f f$ is small, it is beneficial to fight for food and Hawk is an ESS. For larger $\nu_f f$ it is not beneficial to fight and Retaliator is an ESS. If $\nu_f f$ takes a value somewhere in between, Hawk can invade Retaliator and vice versa and the strategies coexist. For larger population densities, the same pattern occurs, but Marauder is a second ESS alternative.

If $\frac{2\alpha}{t_a} < \min\{\nu_g f, \frac{2(1-\alpha)}{t_a}\}$, then there can be three different ESS - Hawk or Marauder or Retaliator for the same set of parameter values.

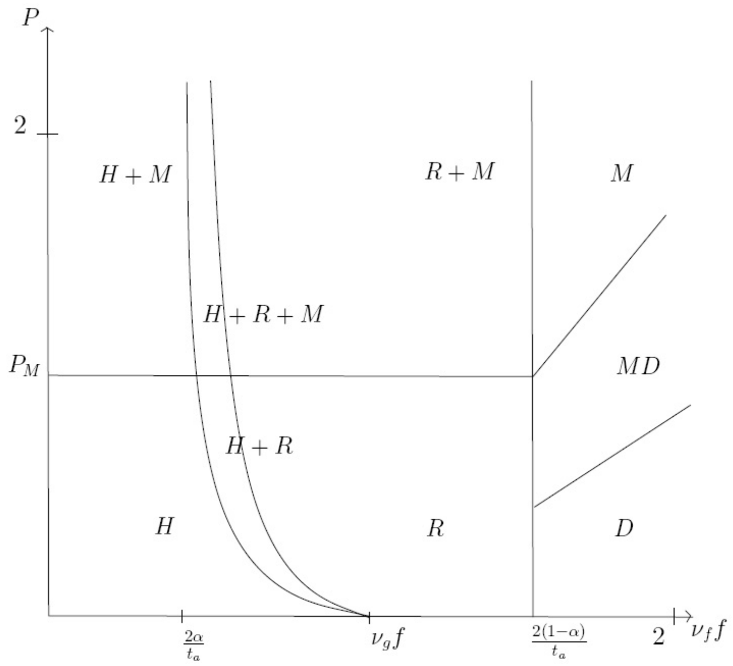

Fig. 4. Patterns of ESSs for the ordering $\frac{2\alpha}{t_a} < \nu_g f < \frac{2(1-\alpha)}{t_a}$. Legend: H = Hawk, M = Marauder, R = Retaliator, D = Dove, XY = mixed ESS of X and Y, $X+Y$ = 2 ESSs of either X or Y; $P_M = \left(\frac{2(1-\alpha)}{t_a} - \nu_g f\right) \cdot \frac{t_h \nu_h \nu_g f + 1}{t_h \nu_h \nu_g f}$. For this particular picture: $\alpha = 0.25, \nu_g f = t_h = \nu_h = t_a = 1$, $\nu_f f$ ranges from 0 to 2, P ranges from 0 to 2.

7. Discussion

In this paper we have developed the game-theoretic model of kleptoparasitism introduced in Broom and Ruxton (1998). Individuals use one of the four different strategies first described in Broom et al (2004), depending upon whether they will attack conspecifics for food, and whether they are prepared to resist any such attack. We have also maintained the simplification that all birds are equally able fighters (so that the probability of the attacker winning is independent of the types attacking and resisting). Our model allows for a difference in the foraging rates of attackers and non-attackers (perhaps because non-attackers can concentrate on searching for food rather than food and conspecifics).

The model, in common with that of Broom and Ruxton (1998) and most subsequent models, assumes that contest times are exponentially distributed and not under the control of the participants. Note that in Ruxton and Broom (1999), however, the length of the contest was under the control of the individuals, who played a classical war of attrition to decide the winner. From this model, an exponential contest length occurs naturally from optimal play within the contest for food. The same result also occurs in the important earlier foraging models of Hines (1976, 1977) where individuals foraged and also entered contests over food, since these papers again used the war of attrition as the basis for contests, introducing it to a more complex foraging setting for the first time. As in our model, the aim was to find an evolutionarily stable foraging strategy where an individual's fitness was given by its foraging rate. There were two key differences between the Hines (1976, 1977) models and ours. Firstly there was effectively no handling time for a food item, so an individual that was successful in a contest always consumed the item, and did not have to face subsequent challenges. Secondly the proportion of food items contested was independent of the strategies played by individuals; in our model the chosen strategies directly affect the likelihood of any subsequent item being competed for, and also which type of opponent would be faced. This effect is central to this and earlier models, and is the cause of their complexity, with individual contests generally being very simple. In contrast the individual contests of Hines (1976, 1977) were more complex, and are the central feature of these papers.

We have found general expressions for the inverse handling ratio, and hence the uptake rate and the fitness, of each strategy in a general population mixture of different strategies, and then found conditions for which each of the strategies or mixtures of strategies are ESSs. Whether a strategy is an ESS or not of course depends upon the values of the population parameters (see Table 1). All four strategies can be ESSs and two of the possible mixtures of strategies can also be an ESS. There are thus six ESSs in total, each of which can be the unique ESS; indeed there is always at least one ESS. It is possible that there are two ESSs, and one case of three ESSs (but never more than three). When there are multiple ESSs, in all but one case one of these is the Marauder ESS, which can occur in conjunction with Hawk, Retaliator, a mixed ESS containing both Hawk and Retaliator, or with both pures Retaliator and Hawk. The multiple ESS case without Marauder includes pure Hawk and pure Retaliator. This gives eleven possible ESS patterns in total, which are best summarised by Figures 3 and 4.

In Section 5 we describe the conditions when each ESS occurs in more detail. In particular Hawk occurs when the food gathering ability of foragers that also attack, or general food availability, is poor and the population density is not too large (recalling that interactions happen more frequently the denser the population). Marauders generally thrive when the population density is large and food availability is also large. Retaliators do better when food levels are intermediate and the population density is not large, and Doves do better when food is plentiful and the population density is not too large. All of these results are intuitively reasonable.

In each of the situations where there is more than one ESS, which is more likely to occur? The only case where two ESSs other than Marauder occurred simultaneously was for Hawk and Retaliator (either as two pure ESSs or three pure ESSs including Marauder), which was in the case when the Hawk's foraging rate was greater than the Retaliator's. This case is perhaps unrealistic because a Hawk must split its attention between searching for food and for kleptoparasitic opportunities, whereas a Retaliator can dedicate itself to searching for food, and thus this combination is unlikely to occur. The Marauder and Retaliator case is similar to the owner intruder game of Maynard Smith and Parker (1976) where there is a symmetrical game (in the sense of payoffs for escalating or not) but with the individuals in different roles. The Marauder ESS is in some ways a paradoxical strategy, in a similar way to the anti-Bourgeois strategy X, where the owner always gives way to the intruder. The authors argued that it would be much less likely to occur in practice than Bourgeois, although they identified one case where it did occur. Thus perhaps when multiple ESSs are available, Marauder might not be observed. If strategies which involve resistance are stable, then non-resistance may never evolve. This would yield a natural single solution for realistic parameter values. This does however suppose that the individuals would naturally resist, and only not resist if this was subsequently beneficial. Even if this is true, and it might not be, if parameters change through time, they may well move to a set of values where Marauder is the unique ESS, and then move to one where two ESSs are possible, but the population starts in the still stable Marauder strategy.

The situation is in fact rather different in the case of Marauder and Retaliator being ESSs, to when Marauder and Hawk are ESSs. For the Hawk and Marauder case, Marauders do better in populations with higher food availability, Hawks do better when this availability is lower. However when all individuals play Hawk time is wasted in fighting and the consumption rate goes down, effectively mirroring lower food availability. There are thus parameter values when Marauders do better in a population of Marauders and Hawks do better in a population of Hawks.

In this paper we have considered the four most basic types of attitude to kleptoparasitic opportunity and threat; namely the four combinations of attack or not attack, with resist or not resist an attack. How do these strategies relate to the behavior of real birds? Most birds effectively play either the Dove or Retaliator strategy, and exist in a population where no food stealing takes place. If a population has the strategy Hawk there will be widespread kleptoparasitism with visible contests, and it is this strategy which yields the most obvious kleptoparasitic behavior. Our theoretical model makes predictions about when each of the basic types of behavior or mixtures of these basic types should occur, and we hope that the model will be compared to real populations to test the accuracy of its predictions.

These four different tactics all seem plausible in terms of underlying biology. A real population that played Marauder would be characterised by frequent very short contests. Behavior of this type occurs for various wading birds (see e.g. Stillman et al, 1997); often only some birds will attack, and so this example is more characteristic of our mixed populations in such cases (note that this could also be linked to dominance relationships between the birds). The Marauder tactic may also equate to the concept of stealth kelptoparasitism introduced by Giraldeau and Caraco (2000). Here kleptoaparasitic acts are not immediately detected by the victim, or the victim is not in a position to react immediately, or feature great speed by the thief. Giraldeau and Caraco discuss observations of kelp gulls (Larus domenicanus) stealing from each other reported by Hockey et al. (1989) as an example of stealth kleptoparasitism. The gulls are feeding on bivalue shellfish. They sometimes break the protective shell of their prey by dropping the bivalve from a great height onto rocks. This may give other gulls standing on the rocks the opportunity to rush in and steal the newly-exposed prey before the focal gull can swoop down from high above. In such cases, the victim does not seem generally to pursue the thief, perhaps because it would take a long time to close the height differential between them, during which time the thief will have made good their escape or even consumed the prey. Individuals play both roles, sometimes being aggressive thieves and sometimes passive victims, exactly as in the Marauder strategy. A further example of such stealth kleptoparasitism occurs in some species of birds and mammals that horde food. If one individual discovers the unguarded cache of another then it may invest significant energy in exposing and exploiting that cache, but when the victim returns they may not invest in pursuit of the thief, who may by then be a long time gone and consequently hard to find, Giraldeau and Carcaco discuss several studies that observe this behavior. The other three tactics can be seen to more easily reflect conventional aggressive contests. Again in gulls, Hesp & Barnard (1989) discuss differences between immature and mature black-headed gulls, Larus ridindus. Younger gulls tended both to avoid attacking and to show little resistance to attack (like the Dove strategy), whereas adults showed strong aggressiveness when in either position (like the Hawk strategy). Interestingly, aggressiveness seemed to develop first in terms of resistance to attack rather than in self-induced attacks, thus leading to individuals progressing through their lives from the Dove strategy, through Retaliator to the Hawk strategy. Further, generally aggressiveness can be related to high-value hard-to-find items (Morand-Ferron et al. 2007) and so asymmetry between individuals in their ability to find prey or their current need to eat can lead to asymmetry in their evaluation of the value of the contested prey item, leading to differential investment and so Marauder or Retaliator strategies. Such asymmetry may also be introduced by the spatial interaction of the two participants. It may simply be that if the thief can swoop on their victim in flight from above and use gravity to accelerate away, then pursuit is futile and we see a Marauder-like situations, whereas the same victim may defend their prize much more vigorously against the same thief if both meet on the ground (leading to a Hawk-type tactic involving the same participants).

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