A Hawk-Dove game in kleptoparasitic populations

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Kleptoparasitism, the parasitism by theft, is a widespread biological phenomenon. In this paper we extend earlier models to investigate a population of conspecifics involved in foraging and, potentially, kleptoparasitism. We assume that the population is composed of two types of individuals, Hawks and Doves. The types differ according to their strategic choices when faced with an opportunity to steal and to resist a challenge. Hawks use every opportunity to steal and they resist all challenges. Doves never resist and never steal. The fitness of each type of individual depends upon various natural parameters, for example food density, the handling time of a food item, density of the population, as well as the duration of potential fights over the food. We find the Evolutionarily Stable States (ESSs) for all parameter combinations and show that there are three possible ESSs, pure Hawks, pure Doves, and a mixed population of Hawks and Doves. We show that for any set of parameter values there is exactly one ESS. We further investigate the relationship between our findings and the classical Hawk-Dove game as defined in Maynard Smith 1982. We also show how our model extends the classical one.

1 Introduction

Kleptoparasitism, is the stealing of prey that has been caught by another (Rothschild and Clay 1952). The most common observations of kleptoparasitism have been amongst birds (Brockmann and Barnard 1979). Kleptoparasitic behavior has been observed in many other types of animals as well, including insects (Jeanne 1972), fish (Grimm and Klinge 1996) and mammals (Kruuk 1972).

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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).

2 The model, behavioral states and strategies

The basic structure of our model follows that of Broom and Ruxton 1998 and Broom et al. 2007. Individuals forage for food, and can be in one of four states. They are either a searcher (looking for food, but having yet to find it), a handler (having found food, preparing to consume it) a challenger (having come across a handler, trying to steal the food item) or a defender (trying to resist the challenge of another). We assume that individuals take an exponential time, with mean t_h, to handle a food item, and that the food is consumed in no time at the end of this period.

We consider a polymorphic population consisting of the two different bird types. A bird's type is determined 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 types are:

Hawk	always attack, always resist when attacked,
Dove	never attack, never resist when attacked.

Each bird is initially searching for food items. We assume that Doves find food at rate $\nu_f f$ (where f is the density of food) as opposed to Hawks who find food at rate $\nu_g f$. Hawks are searching for handlers as well (at rate ν_h). Hawks 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 Hawk finds a handler, it challenges and tries to steal its food. If it encounters Dove, the handler surrenders the food item. If it encounters another Hawk, the handler defends its food and thus both the searcher and the handler engage in a fight. In our model we assume that the only cost of the fight is the time spent in the contest. The fights take a random time with exponential distribution with mean $\frac{t_a}{2}$. The challenger wins the fight with probability $\alpha \in (0, 1)$.

Let P be the total density of the population and H_d, D_d be the densities of Hawks and Doves, respectively. Both types go through a searching and handling period, Hawks may be involved in fights as both attackers and defenders. Let H_s, H_h, H_a, H_r denote the densities of Hawks in searching,

Parameter	meaning
P	density of the population
D_d, H_d	density of Doves and Hawks
D_s, H_s	density of searching Doves and Hawks
D_h, H_h	density of handling Doves, and Hawks
H_a	density of attacking Hawks
H_r	density of defending Hawks
h_r	handling ratio H_h/P in a population of Hawks only
f	density of food items
ν_f	area Doves can search for food per unit time
ν_g	area Hawks can search for food per unit time
ν_h	area Hawks 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 challenger wins the fight

Table 1: The model parameters and notation.

handling, attacking and defending states. Let D_s and D_h denote the densities of Doves searching and handling. See Table 1 for a summary of our notation.

We assume the total density of the population is constant.

We shall consider each of the strategies in turn and evaluate its uptake rate in the mixed population. The uptake rate is one divided by the total time needed for complete consumption (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 2006 and determines the total consumption time T for Hawks (a similar equation holds for Doves).

$$T = t_h \cdot \frac{H_d}{H_h}. \tag{2.1}$$

The uptake rate is thus directly proportional to the proportion of time that each type of individual spends in the handling state (see Broom and Ruxton 1998, amongst other papers). We assume also that the uptake rate is proportional to the fitness of individuals of that type. This means that, the shorter the consumption time, the higher the fitness.

3 Equilibrium equations

In this section we will consider each strategy and evaluate its uptake rate and its consumption time. We use the same approach as in Broom et al.

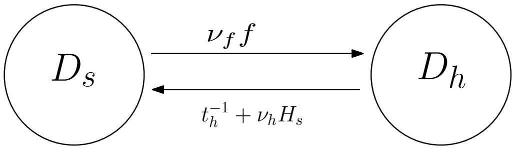

Figure 1: Phase diagram for Doves.

2007 where methods for dealing with polymorphic populations are developed in full generality.

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 (with the rate $\nu_h H_s$). This provides the following set of equations.

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} D_s &= t_h^{-1} D_h + \nu_h H_s D_h - \nu_f f D_s && (3.1) \\ \frac{\mathrm{d}}{\mathrm{d}t} D_h &= -t_h^{-1} D_h - \nu_h H_s D_h + \nu_f f D_s && (3.2) \\ D_d &= D_s + D_h && (3.3) \end{aligned}$$

These equations tend to equilibrium very fast (see Luther and Broom, 2004). In the equilibrium, both sides of the equations (3.1) and (3.2) are equal 0 which together with (3.3) provides

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

3.2 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 (with rate $\nu_h D_h$),
- an attacker if it finds a handling Hawk (with rate $\nu_h H_h$).

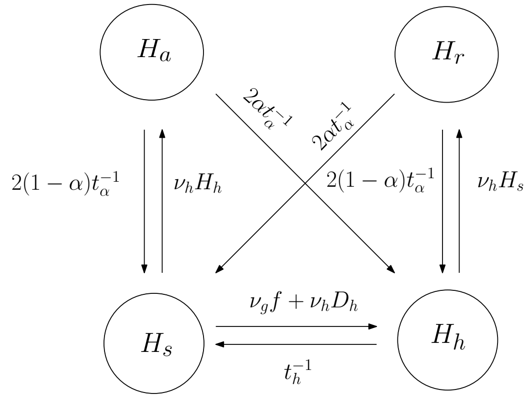

Figure 2: Phase diagram for Hawks.

If the Hawk is handling, it can become

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

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 (the left sides are set to 0 as the differential equations again tends to equilibrium very fast Luther and Broom, 2004 as seen already in the Dove case).

$$
\begin{aligned}
0 \;=\; & \frac{\mathrm{d}}{\mathrm{d}t}H_s = -(\nu_g f + \nu_h D_h + \nu_h H_h)H_s + t_h^{-1}H_h + 2(1-\alpha)t_a^{-1}H_a \\
& +2\alpha t_a^{-1}H_r
\end{aligned}
\tag{3.5}
$$

$$
\begin{aligned}
0 &= \frac{\mathrm{d}}{\mathrm{d}t} H_h = -\nu_h H_s H_h - t_h^{-1} H_h + (\nu_g f + \nu_h D_h)\, H_s \\
&\qquad +2\alpha t_a^{-1} H_a + 2(1-\alpha) t_a^{-1} H_r && (3.6) \\
0 &= \frac{\mathrm{d}}{\mathrm{d}t} H_a = -2t_a^{-1} H_a + \nu_h H_h H_s && (3.7) \\
0 &= \frac{\mathrm{d}}{\mathrm{d}t} H_r = -2t_a^{-1} H_r + \nu_h H_s H_h && (3.8) \\
H_d &= H_s + H_h + H_a + H_r && (3.9)
\end{aligned}
$$

By (3.10)

$$H_r = \nu_h H_s H_h \frac{t_a}{2}; \tag{3.10}$$

by (3.9)

$$H_a = \nu_h H_s H_h \frac{t_a}{2}. \tag{3.11}$$

Consequently,

$$H_a = H_r$$

and (3.12), (3.13) and (3.5) yield

$$(-\nu_g f - \nu_h D_h) H_s + t_h^{-1} H_h = 0 \tag{3.12}$$

which yields

$$\frac{H_s}{H_h} = \frac{1}{t_h(\nu_g f + \nu_h D_h)}. \tag{3.13}$$

Substituting (3.15), (3.12), and (3.13) into (3.11) yields

$$\frac{H_d}{H_h} \;=\; 1 + \frac{1}{t_h(\nu_g f + \nu_h D_h)} + t_a \nu_h H_s. \tag{3.14}$$

4 ESSs

We can use the inverse handling ratios from the previous section to establish conditions when a given strategy has (or has not) an advantage against another strategy in a general population mixture.

Hawk is better than Dove if

$$\frac{H_d}{H_h} < \frac{D_d}{D_h}$$

which is by (3.16) and (3.4) equivalent to

$$\frac{1}{t_h(\nu_g f + \nu_h D_h)} + t_a \nu_h H_s < \frac{1}{t_h \nu_f f} + \frac{\nu_h H_s}{\nu_f f}$$

which can be further rearranged to

$$\frac{\nu_f f}{\nu_g f + \nu_h D_h} - 1 < H_s \nu_h t_h (1 - \nu_f f t_a).$$

By using (3.14), the above can be further simplified to

$$\frac{\nu_f f - \nu_g f}{\nu_h} - D_h < H_h (1 - \nu_f f t_a). \tag{4.1}$$

Doves are better than Hawks if the opposite inequality holds; and Doves and Hawks do equally well when the equality holds. The inequality will be used in the following sections in the classification of ESSs.

We explicitly state the conditions for ESSs. There are three potential ESSs - Hawks only, Doves only and a mixed population. We will investigate each one of these in turn.

4.1 Hawk as an ESS

Hawk is an ESS if a population of Hawks only cannot be invaded by a small amount of Doves. This is equivalent to the requirement that Hawks do better than Doves in a population consisting of mostly Hawks. By setting $D_h \approx 0$ in (4.1) we get that Hawk is ESS if

$$\frac{\nu_f f - \nu_g f}{\nu_h} < H_h (1 - \nu_f f t_a). \tag{4.2}$$

We can evaluate H_h in the population of Hawks only. By combining equations (3.16) and (3.15) and by using $H_d \approx P$ and $D_h \approx 0$, we arrive (as in Ruxton and Moody 1997), to $H_h = P h_r$, where h_r, the handling ratio, is the positive root of the quadratic equation

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

This yields

$$H_h = h_r P = \frac{1 + \nu_g f t_h}{2 t_a \nu_h} \cdot \left(-1 + \sqrt{1 + \frac{4 t_a \nu_h t_h P \nu_g f}{(1 + \nu_g f t_h)^2}} \right), \tag{4.3}$$

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

We can conclude that Hawk is ESS for either one of the following sets of parameter values:

- $\nu_f f \leq \min(\nu_g f, t_a^{-1})$ and P arbitrary,
- $\nu_g f < \nu_f f$, $\nu_f f t_a < 1$ and P high (satisfying (4.2)),
- $\nu_f f > \nu_g f$, $\nu_f f t_a > 1$ and P small (satisfying (4.2)).

4.2 Dove as an ESS

Dove is an ESS if a population of Doves only cannot be invaded by a small amount of Hawks. This is equivalent to the requirement that Doves do better than Hawks in a population consisting of mostly Doves. By setting $H_h \approx 0$ in (4.1) we get that Dove is ESS if

$$D_h < \frac{\nu_f f - \nu_g f}{\nu_h}. \tag{4.4}$$

Since, by (3.4), for $H_s \approx 0$,

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

we get that Dove is an ESS if

$$P < \frac{\nu_f f - \nu_g f}{\nu_h} \cdot \frac{t_h \nu_f f + 1}{t_h \nu_f f}. \tag{4.5}$$

In particular, Dove can be an ESS only if $\nu_g f < \nu_f f$, i.e. Doves find food faster than Hawks. And even then, only if $\nu_h D_h$ is smaller than $\nu_f f - \nu_g f$, i.e. the rate that Hawks find handling Doves is smaller than the Dove's advantage in finding food. Another interpretation is that this occurs only in sufficiently small populations (small populations do not give kleptoparasitic invaders a chance of finding a handler very fast).

4.3 Mixed ESS

The necessary condition on a mixed ESS to exist is that both types, Dove and Hawk, do equally well in the mixture. It means

$$\frac{\nu_f f - \nu_g f}{\nu_h} - D_h = H_h(1 - \nu_f f t_a)$$

which can be further rearranged to

$$\frac{H_d}{P} = \frac{\nu_g f - \nu_f f + \nu_h D_h}{\nu_g f - \nu_f f + \nu_h D_h \nu_f f t_a} \tag{4.6}$$

Note that $\frac{H_d}{P}$ should be in $[0, 1]$. Thus, we can conclude that mixed ESS does not occur for some parameter choices - for example if $\nu_g f > \nu_f f$ and $\nu_f f t_a < 1$.

If $\nu_f f = \nu_g f$, then the equation (4.6) reduces to

$$\frac{H_d}{P} = \frac{1}{\nu_f f t_a}. \tag{4.7}$$

We will see in the next sections how this result relates to the classical Hawk-Dove game (Maynard Smith, 1982).

The mixed ESS occurs whenever Hawk is not an ESS and Dove is not an ESS. Indeed, if we regard $\frac{H_d}{H_h} - \frac{D_d}{D_h}$ as a function of a fraction of Hawks in the population, then this function is continuous and is positive in Hawks only population (Hawk is not an ESS, i.e. Doves can invade, i.e. Doves do better) whereas negative in Doves only population. Hence, there must be a root in between. It turns out that $\frac{H_d}{H_h} - \frac{D_d}{D_h}$ is a cubic function of the fraction of Hawks and thus there could theoretically be three roots. Numerical experiments, however, confirm that there is always at most one root in $(0, 1)$. This seems plausible since the function should be monotone - the fraction of Hawk handlers increases and fraction of Dove handler decreases as the fraction of Hawks increases (Hawks are more and more engaged in fights, whereas Doves have to give up the food to Hawks).

We can conclude that mixed ESS occurs if and only if neither Dove nor Hawk is ESS.

4.4 Dependence on parameters

There are 8 parameters of our model: $\nu_f, \nu_g, f, t_h, t_a, \nu_h, P$, and α. From the previous sections, it is clear that we can consider parameters $\nu_f f$ and $\nu_g f$ rather than ν_f, ν_g and f. Also, the outcomes do not depend on α at all. If we are interested in overall patterns rather than exact numbers, there is no direct dependence on t_h and ν_h. The patterns of ESS depend on $\nu_f f, \nu_g f, t_a$, and P only. As follows from (4.2) and (4.4), if we fix $\nu_g f$ and t_a, the outcomes differ based on the relative position of $\nu_f f$ with respect to $\nu_g f$ and t_a^{-1}. The table 2 summarizes the results.

Observe that Hawk and Dove are never ESS together. It follows from equations (4.4) and (4.2), since the fraction of Dove handlers in Dove only population is always greater that the fraction of Hawk handlers in Hawk only population (because Hawks are also engaged in fights).

We already noted that $\frac{H_d}{H_h} - \frac{D_d}{D_h}$ is a monotone function of a fraction of Hawks. Thus, we can conclude that there is always at most one ESS. By checking all possible cases, we see that there is always at least one ESS. Thus, there is always exactly one ESS for any parameter values.

size of $\nu_f f$	Hawk	Dove	mixed ESS
$\nu_f f \le \nu_g f < t_a^{-1}$	always	never	never
$\nu_g f < \nu_f f < t_a^{-1}$	for high P	for small P	for P in between
$\nu_g f < t_a^{-1} < \nu_f f$	never	for small P	for high P
$\nu_f f \le t_a^{-1} < \nu_g f$	always	never	never
$t_a^{-1} < \nu_f f \le \nu_g f$	for small P	never	for high P
$t_a^{-1} < \nu_g f < \nu_f f$	never	for small P	for high P

Table 2: Dependence of ESS patterns on parameter values. Condition on P in Hawk column refer to inequality (4.2), conditions on P in Dove column refer to (4.5), conditions on P in mixed ESS column are complements of the first two.

5 The classical Hawk-Dove game

The classical Hawk-Dove game is a two player matrix game with a payoff matrix

	Hawk	Dove
Hawk	$V/2 - C/2$	V
Dove	0	$V/2$

where V denotes the value of the food and C denotes the cost of the fight over the food. The entries of the matrix reflect the fact that when Hawk encounters Hawk, one of them will get a resource of value V whereas the second will will bear the cost of the fight C (or, equivalently, both will bear a cost of the fight $C/2$). When Hawk meets Dove, Hawk gets the whole resource while Dove gets nothing. Finally, when Dove meets Dove, they "split".

It can be calculated (see, e.g., Maynard Smith 1982) that if there is a mixed ESS, the fraction of Hawks in the population, $\frac{H_d}{P}$, equals to $\frac{V}{C}$.

In the setting of our model of kleptoparasitic behavior, the value of a food is the time needed to find it. If we assume that $\nu_f f = \nu_g f$, then for both, Hawk and Dove, the value is $V = (\nu_f f)^{-1}$. The cost of the fight is the time both Hawks spend fighting. Since each of them spends time $\frac{t_a}{2}$, we have $\frac{C}{2} = \frac{t_a}{2}$. In total, the mixed ESS occurs for

$$\frac{H_d}{P} = \frac{1}{\nu_f f t_a}$$

which is in an agreement with (4.7).

6 Discussion

In this paper we have developed the game-theoretic model of kleptoparasitism introduced in Broom and Ruxton (1998). Individuals are one of the two strategy types, Hawks and Doves, depending upon whether they fight for food or not. There is a difference in the foraging rates of fighters and non-fighters (perhaps because non-fighters can concentrate on searching for food rather than food and conspecifics).

We have found general expressions for the fitness of each strategy in a general population mixture, and then found conditions for which each of the pure strategies or mixed states are ESSs. Whether a strategy is an ESS or not of course depends upon the values of the population parameters (see Tables 1 and 2). Both strategies can be ESSs; a mixed ESS is also possible. There is always exactly one ESS. The existence of the mixed Hakw-Dove ESS is a new result that has not been (and in fact, could not be) captured by another model for polymorphic populations (see Broom et al. 2007).

We have also shown that our model extends the classical Hawk-Dove game. Although in a general agreement with the classical model, our model can capture a variety of parameters and distinguish between different scenarios. One of the most important advantages of our model is the explicit use of a population density. Note that the classical Hawk-Dove game model is independent of the population size, while our model can produce different (and logical) outcomes even if all other parameters are fixed and only population size varies.

The most interesting behavior occurs when $\nu_g f < \nu_f f < t_a^{-1}$, i.e. if Doves search for food faster than Hawks, and the fights do not take too long. Under these conditions, as the population size increases, the ESS shifts from pure Dove through mixed ESS to pure Hawk. Dove is ESS in small populations. Hawks cannot invade Doves in small population since they are not able to find food as fast as Doves are and yet they cannot steal too much from Doves since the density of Doves is small. As soon as the population size increases above certain threshold (described by (4.5)), Hawks can invade due to the fact that they can steal from Doves. If the population size is not too big, pure Hawk cannot be ESS. Indeed, Hawks could be invaded by Doves - they find food relatively fast, do not spend time by fighting and yet they do not have to give up the food so often as there are still not too many Hawks. However, once the population size increases above another threshold (described by (4.2) and (4.3)), Hawks become ESS - Doves cannot invade since they are almost constantly attacked by Hawks. As a matter of fact, in large populations and under these parameters, Hawks are always better than Doves regardless of the fractions of Hawks in the populations. If there are enough Hawks, they do better because Doves has to give up food too much. If there are enough Doves, Hawks do better because the can steal the food rather than having to find it by themselves.

We also note that our model can be further extended by incorporating other types of behavior, namely Retaliator (do not challenge but resist stealing) and Marauder (steal but do not resist). This is done in detail in Broom et al. 2007.

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